ASPECTS OF OLFACTION, SOCIAL BEHAVIOUR AND ECOLOGY OF AN ISLAND POPULATION OF THE EUROPEAN RABBIT (ORYCTOLAGUS CUNICULUS)

Ian Alexander Sneddon

A Thesis Submitted for the Degree of PhD at the University of St. Andrews

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ASPECTS OF OLFACKTION, SOCIAL BEHAVIOUR AND ECOLOGY OF AN
ISLAND POPULATION OF THE EUROPEAN RABBIT
(Oryctolagus cuniculus)

Ian A. Sneddon B.Sc.

Submitted for the degree of Doctor of Philosophy
to the Psychology Department, The University of
St. Andrews.

November 1984.
(a) I hereby certify that this thesis which is approximately 75,000 words in length has been written by me, that it is the record of work carried out by me, and that it has not been submitted in any previous application for a higher degree.

Date 9/12/84  Signature of candidate

(b) I hereby certify that the candidate has fulfilled the conditions of the Resolution and Regulations appropriate to the degree of Ph.D. of the University of St Andrews and that he/she is qualified to submit this thesis in application for that degree.

Date 7/12/84  Signature of supervisor

(c) I was admitted as a research student under Ordinance No. 12 on 6/1/74 and as a candidate for the degree of Ph.D. on 6/1/75; the higher study for which this is a record was carried out in the University of St Andrews between 9/74 (year) and 12/77 (year).

Date 9/12/84  Signature of candidate
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ABSTRACT

Olfactory behaviour in the European rabbit (Oryctolagus cuniculus) has been studied extensively under laboratory and semi-natural conditions. Results of observations on aspects of the olfactory behaviour of a free-living population of rabbits are presented. To facilitate interpretation of these results, considerable preliminary information about the population was collected. The study was conducted over a three year period on the Isle of May off the east coast of Scotland. A total of 326 rabbits were trapped and marked to permit identification in the field, and data on sex, age and social status of these individuals was collated.

Data on the overall structure and fluctuations in the population are presented. The social organisation and home ranges of rabbits at four study sites throughout the three years are described. Observations indicate that the social organisation of free-living populations is more complex and variable than previous descriptions of semi-natural populations would have led us to expect.

The reproductive performance of the population was investigated and intra and interwarren variations are analysed with respect to warren and group size. Results indicate an inverse relationship between warren size and reproductive success. The most frequently observed group composition (2 males, 2 females) was also the most reproductively successful.

Daily and seasonal activity patterns of different age, sex and social status classes of rabbits are described.

Olfactory communication was investigated by analysis of the
frequency, daily and seasonal variation, and behavioural context of odour related activities performed by members of different age, sex and social status classes. The importance of using appropriate methods for the sampling of behaviour in field studies of olfaction is stressed. The present study concentrates on behaviour related to latrines; chin marking of the substrate and of conspecifics; enurination and urine squirting; and pawsraping. The results suggest that different scent products may carry similar information but analysis of variations in the frequency and context of odour deposition suggests that the deposition of scent fulfills a variety of functions.
CHAPTER 1

INTRODUCTION
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INTRODUCTION

(I) Field Study of Mammal Behaviour

In the century since the publication of Darwin's last book, 'Expression of the emotions in man and animals' (1872), the study of animal behaviour has undergone a remarkable transformation. It cannot be said, however, to have followed a single upward path. The twentieth century has witnessed many approaches to the subject, and these can be seen, with hindsight, to have had varying degrees of influence on the development of contemporary animal behaviour research. It is probably true to say that the classical European ethology tradition, which inherited many of its basic principles from ideas of Darwin, has had a substantial part to play in the growth of the modern discipline. It may seem curious, therefore, that the study of mammalian behaviour was slow to develop within the ethological tradition, particularly as Darwin had relied frequently on examples of the behaviour of mammals to support his arguments.

There would appear to be several possible reasons for this phenomenon. In general the early European ethologists were naturalists, and their emphasis on the study of behaviour in natural conditions became one of the major features of their approach. In the British Isles, where the amateur naturalist tradition has been particularly strong during the twentieth century, the emphasis has been largely on bird study rather than on the study of mammals. There are only some 50 species of land mammal in the British Isles and, although they are relatively easy to identify, a large number are nocturnal or secretive in nature and are rather difficult to observe under natural conditions. In
addition to the emphasis on natural observation, the early ethologists focussed their attention on relatively stereotyped, species-characteristic behaviour, seeing this as a logical starting point upon which to build the study of animal behaviour. The animals chosen for such investigations were primarily birds, fish and insects, for while the complexity and variability of mammalian behaviour are the features which attract the interest of many researchers, they undoubtedly made the mammals appear to be inappropriate subjects upon which to begin the study of behaviour.

This was in sharp contrast to the approach of the American comparative psychology tradition, which was based on laboratory observation and concentrated on learning in mammals. One way of viewing the differences in these two traditions is to regard comparative psychology as being a 'top-down' approach, using man as the model against which the 'intelligence' of animals might be compared, whereas classical ethology was a 'bottom-up' approach, attempting to investigate the causation, function, ontogeny and evolution of behaviour by beginning with the study of simple, stereotyped actions. Thus the study of mammalian behaviour under natural conditions did not quickly fit into the classical ethological tradition. Tinbergen's 'Social behaviour in animals' (1953) was subtitled 'With special reference to vertebrates' but makes only the occasional passing reference to mammals.

By the early 1950s, however, field work on mammal behaviour was being pursued by researchers working within the frameworks of different disciplines. Controversy over the existence of population cycles in small mammals captured the interest of many ecologists during the 1930s after the early work by Elton and others (see Finerty, 1980 for review). This work laid a firm
foundation for the developing study of population dynamics and has had an important influence on modern animal behaviour.

Field work on primate behaviour was pioneered by Carpenter, also in the 1930s (eg. Carpenter, 1934) and has continued uninterrupted and at an every increasing rate. That the primates have always held a particular fascination for man is amply illustrated by the enormous volume of research published since these early studies. The contribution of primatologists, however, extends further than providing us with a wealth of information about primate behaviour. They have been in the forefront of the development of observational methodology and have made major theoretical contributions to the general study of animal behaviour.

Research on the behaviour of the European rabbit also commenced before the middle of the century. Although rabbits had commonly been used in laboratory research, chiefly for physiological investigations, field studies of their behaviour were prompted largely by financial considerations. The rabbit is the most serious agricultural pest mammal in the British Isles. Annual crop damage estimates vary, but are counted in tens of millions of pounds sterling. In Australia, where they were introduced in the nineteenth century to provide sport for hunters, they proved to be an even more serious problem and the extent of their depletion of sheep grazing has never accurately been assessed.

While clearly throughout the middle decades of this century, field work on mammal behaviour was being carried out, albeit with a variety of aims and in rather piecemeal fashion, it was not
until the 1960s that mammal research blossomed. This expansion coincided with an increasing interest in social behaviour, parental care and olfactory communication, areas in which the study of mammals proved to be particularly fruitful.

(ii) The Present Study - (a) Identity, social organisation and activity.

The initial impetus for the present project was a desire to investigate olfactory communication in a free living population of rabbits. Olfaction has probably been studied more intensively in the rabbit than in any other mammal, but at the time of the instigation of the study in 1974, olfactory communication in the rabbit had not been studied under natural conditions by observation of a free living population. Indeed, the only published research on any aspect of the behaviour of a population of free living rabbits studied in situ was the result of 6 months of 'almost daily' observation of a small population of unmarked rabbits (Myers and Schreider, 1964). Thus, a large body of literature had built up describing the behaviour of rabbits in artificial enclosures, in laboratories, or after having been introduced to experimental paddocks. The results of these studies have become accepted as a realistic reflection of the behaviour, social organisation and population dynamics of the wild rabbit. Such generalisation, given the shortage of evidence from field observations, seems premature. Additionally, almost all of this research has been carried out in Australia where the climate and vegetation may have quite different effects on the breeding season and behaviour from that in the British Isles.

While the project's initial aim was the study of olfaction it quickly acquired wider objectives and in the process, perhaps
inevitably, became more 'species based' than 'problem based' in the sense that while the project concentrated entirely on rabbits, only a minority of the research is directly concerned with olfaction.

Clearly, any understanding of the causation and function of chemical communication, depends upon having considerable information about the lives and behaviour of the individuals concerned. The animals must be identifiable which, in the case of the rabbit, because of a lack of discriminating physical features, involves trapping and marking. During this process individuals were sexed and weighed and an index of growth rate obtained from retrapping data which, in turn, permitted the approximate age of individuals to be calculated from body weight. The social status of the marked rabbits was assessed by scoring the outcomes of agonistic interactions. Thus for a considerable number of rabbits in the study population, information on sex, age and social status was available.

The results of the early major studies on the social organisation of the rabbit appear to show considerable variation in the populations observed (Southern, 1940; Lockley, 1961; Mykytowycz, 1958, 1959; Myers and Poole, 1959, 1961). However, later works which have briefly summarized this early research (eg. Myers et. al., 1971; Mykytowycz and Fullagar, 1973) have presented a much simplified version of its findings, omitting to mention the observed variations. It became clear during observations that the social organisation of this free living population was more complicated and varied than might have been anticipated from the accounts in many recent publications. Therefore, a further section of the project was taken up in investigation of this problem and
with the analysis of the relationship between differences in social organisation and reproductive success.

The climate in the area of Australia where most of the previous rabbit research has been conducted is somewhat Mediterranean in its seasonal pattern of temperature and rainfall. This pattern is quite different from that in the British Isles and it was not clear if many of the Australian observations on temporal and seasonal distribution of behaviours could be directly applied to rabbits living in a Northern temperate climate. In an attempt to clarify this point, variations in the activities of rabbits at different times of the day and different times of the year were recorded.

It is evident that, while the collection and analysis of this information was initially seen as a necessary prerequisite to understanding olfactory communication, it occupied a large proportion of the research time in the field and forms a major part of this thesis. It is hoped, therefore, that it may aid future researchers in assessing the generalizability of many of the results of the studies carried out on artificially enclosed populations of rabbits.

(iii) The Present Study – (b) Olfactory Communication

Considerable laboratory research has been carried out to ascertain if rabbits can discriminate between the scent products of males and females, young and adults, dominant and subordinate animals etc. Evidence of an ability to discriminate between such odours is obviously of considerable importance and implies that such discrimination has some biological significance in the normal behaviour of the rabbit. However, just what this significance is
has not yet been determined.

The final sections of the present thesis, therefore, describe the results of an investigation into possible differences in the timing, frequency and behavioural context of deposition and investigation of various odour products by different age, sex and social classes of rabbits. There are obvious difficulties in studying odour in the field, where there is no knowledge or control over previously deposited scents, and where the deposition of some odour products cannot be reliably observed. There is, thus, an inevitable concentration on certain aspects of chemical communication at the expense of others. However such limitations were felt to be acceptable given that the primary aim of the study was to gain some field evidence to permit assessment of the general applicability of the previous research carried out under more controlled conditions.
CHAPTER 2

STUDY SITE
(1) The Rabbit on the Isle of May

Although some writers have suggested that the rabbit was introduced to the British Isles by the Romans (e.g. Lever, 1977) there is no evidence to suggest that the present population is descended from Roman stock. It seems more likely that rabbits were introduced in considerable numbers subsequent to the Norman invasion of 1066. While there is no mention of rabbits in the Domesday Book of 1086, they appear to have been well established in the Scilly Isles by 1176 (Sheail, 1971), on the Isle of Lundy by 1183 and on the Isle of Wight by 1255 (Perry, 1978). During the middle of the thirteenth century the number of accounts of established rabbit warrens increased considerably (Lever, 1977) and in the reign of Alexander II of Scotland (1214-1249) rabbits are known to have been protected from poachers by royal statute.

In the reign of Alexander III (1249-1286) the keeper of the king's warren at Crail in Fife (the closest mainland settlement to the Isle of May) is recorded as having received an annual salary of 16/8d for his services. However, rabbits are not positively mentioned in the records of the Isle of May until 1329 (the first year of the reign of David II) (Lever, 1977). In that year, the King's Chamberlain paid 8s. to 4 men for catching rabbits on the island. Perry (1978) suggests that the stock for most Scottish warrens at this time may have been provided by the Isle of May. Small offshore islands seem to have been particularly favoured as sites for rabbit warrens at this time, partly because they did away with the need for protection against predators and poachers, and partly because the rabbit was hardly enough to withstand the
rigours of the climate and made efficient use of the sparse island vegetation. Certainly, records do suggest that rabbits were established on the Isle of May and on the neighbouring Fife coast relatively early but there is, as far as can be ascertained, no documentary evidence to support the suggestion that these warrens acted as a source of stock for the rest of Scotland.

The history of the Isle of May is described in some detail by Eggeling (1960). It seems probable that rabbits were introduced to the island towards the end of the 13th century when the tenancy of the priory, which had been established on the island around the middle of the 12th century, was in dispute. During the years 1288-1313 the priory changed hands several times between the monks of Reading in Berkshire and the monks of St. Andrews in Fife. However, the earliest firm documentary evidence of rabbits on the island dates from 1329 by which time the monks were no longer living on the island but were continuing to manage it and to harvest its produce. This situation continued until 1549 when the island passed to lay ownership. The reasons for the sale of the island were probably those which made physical residence on the island impractical: its insular situation; the small revenue it yielded; and its susceptibility to raids by the English and by pirates. An attack by the English before 1549 had left the island at the time of sale in a devastated condition. The prior described the island as 'now waste and spoiled of its rabbits'. The fact that one report states that "the warrens were ........ completely destroyed" suggests that, as was common on the mainland, special earthwork warrens may have been constructed for the rabbits (Sheail, 1971).

The continued presence of rabbits, however, is illustrated
by the record that in 1803 the right of pasturage (£26 per year) included the use of the rabbit warren. Although, in 1884 when there were 6 milking cows, a horse and 3 donkeys on the island and 'abundant sweet pasturage for 60 sheep', the rabbits must have been present in only limited numbers as they are described as being confined to hollows in the rocks and near the cliff edge. By 1936 the situation had changed considerably. The domestic animals had long gone and the island was no longer cultivated to any great extent. This removal of competition for grazing and for space may have been an important factor in allowing the rabbits to spread over the island: 'of mammals living on the island there are only two and by far the more important is the rabbit which swarms all over it' (Southern, 1938). By the early 1950's "Rabbits were swarming everywhere and grazing the turf so short that it was difficult to find a single grass in flower' (Eggeling, 1960).

Whether the rabbits were subject to periodic population crashes similar to those reported on Skokholm by Lockley (1961) is not recorded, but in March 1955 myxomatosis broke out and by October 1955 the population had been decimated. It is recorded in the bird observatory diary that by the autumn of 1955 only a handful of rabbits had survived. However, obviously a viable number survived the winter because by 1959 the population was almost restored to its pre-1955 level. During the spring of 1975, at the start of the present study, the population was again suffering an epidemic of myxomatosis and it was reported by regular visitors to the island that noticeable outbreaks of infection seemed to occur 'every few years'. The 1975 epidemic is discussed more fully in Chapter 3.

Although the bulk of the population consisted of rabbits of
the wild-type common on the mainland, there were considerable numbers of albinos and dark coated animals. These are undoubtedly descendents of domestic rabbits released on the island. A very few were genuinely black in colour, but more common by far were what seemed phenotypically to be crosses between the black type and the wild type. The suggestion that these rabbits are indeed the results of such crosses is supported by the observation that they tended to occur more frequently in and around the warrens containing black rabbits. Offspring of crosses between albino and wild-type rabbits appeared to be albino although it is possible that wild-type offspring were also produced from such a cross. Certainly no rabbits of 'mixed-type' were observed. There appeared to be no rabbits with white facial markings reported on some other offshore islands and on the island. The survival of feral populations of domestic rabbits on islands has been reported by several authors (eg. Watson, 1961; Shipp et. al., 1963; Asahi, 1962). On some predator free islands, domestic rabbits have continued to thrive for over 100 years. Stodart and Myers (1964) conducted a series of experiments to compare the behaviour of wild and domestic white rabbits in 3/8 acre enclosures in S.E. Australia. Although they report many basic similarities in behaviour, the results show that domestic rabbits exhibit a more diurnal activity cycle than wild rabbits. However the data on activity patterns were collected on a group of domestic rabbits in isolation and not when mixed with wild rabbits. Strangely, they report that more wild-type offspring were killed by aerial predators than white domestic offspring but it is suggested that where mammalian predators are present the white coat colour is a severe disadvantage, particularly given the more diurnal activity pattern of the domestic rabbits. Unfortunately domestic-type
rabbits were not present in sufficient numbers on the island to permit a meaningful comparison of daily activity patterns to be conducted.

Apart from the periodic trapping by man, mentioned above, the Isle of May is completely free of mammalian predators. Birds were never seen to take live rabbits, but Cranham (1972) reports that herring gulls and lesser black backed gulls frequently prey on young rabbits on the Farne Islands. Both species are present on the Isle of May in considerable numbers during the breeding season.

(ii) The Island

The Isle of May is a mile-long exposure of a sill of analcite-dolerite rock with columnar structure lying at 2 33 W, 56 11 N in the mouth of the Firth of Forth (see fig. 2.1). The long axis points from NW to SE and the island has a maximum breadth of a third of a mile. The total area is 143 acres (58ha.) of which at least one tenth consists of rocky foreshore. The highest point of the island is almost 60m above sea level and is dominated by the 19th century lighthouse. In general terms, the island slopes gradually from the centre down to the north and south ends and from the 50m high west cliffs down to the rocky eastern foreshore. The common names used occasionally in this thesis to refer to important features of the island's geography are shown in fig. 2.2. The island was designated a National Nature Reserve in 1956 with the agreement of the Commissioners of Northern Lighthouses who own the island. Management is undertaken by the Nature Conservancy Council in co-operation with a committee representing the Scottish Universities, the Mid Lothian ornithological Club and the Commissioners of Northern Lighthouses.
MAY Island lies at 2°33'W, 56°11'N in the mouth of the Firth of Forth. Nearest landfall is the Fife fishing village of Crail at some 6 miles distance.
May Island: Location of some of the features of the island's geography and common place names used in the thesis.
(iii) **Soil**

The soil cover is generally shallow, the only exceptions being the bottoms of some of the small valleys or depressions. Over much of the island there is only a thin capping of turf over the underlying rock, such soil as there is being a dry, crumbly peat composed of the partly broken down remains of sea pink, grasses and other plants. Only in a very few places is there anything approaching a loam. Cinder deposits from the 17th century beacon blanket fairly extensive areas on the highest part of the island particularly around the watchtower, and many of the gullies and the Tennis Court area contain significant deposits. Certain areas were at one time enclosed by stone walls to serve as lighthouse keeper's gardens, and large quantities of topsoil were imported to improve the quality of the soil. These gardens have largely fallen into disuse although, during the course of the study, small plots were occasionally cultivated and attempts made to protect the resulting crops from rabbits. The quantity and composition of the soil cover therefore varies considerably across the island. This variation can be seen as one factor influencing both the distribution of vegetation and the distribution of rabbits throughout the island.

(iv) **Vegetation**

Although occasional references to the island's vegetation can be found in many of the historical accounts of the island, the first modern record of the general distribution of vegetation was compiled by Southern in 1938. Southern divided the vegetation into 6 basic categories:

1. The majority of the island was classed as grassy heath with
rock outcrops (dominant species - Agrostis, Holcus, Galium)

(ii) The shoreline was classed as bare rock with occasional Armeria maritima

(iii) Some areas at the south end and on Rona were designated Thrift Heath (Armeria maritima, some Silene maritima and Glaux)

(iv) The area around the watchtower was classed as waste ground (Urtica, Carduus, Arctium etc.

(v) Certain depressions on the North Plateau and along the Low Road were classified as damp ground. It should be noted here, however, that there is no true bog on the island, the very few permanently wet places are simply badly drained depressions were occasionally rushes and sedges have been recorded.

(vi) The south wall of the valley containing the loch and Burnett's Leap were classed as cliff face.

These categories were used by Bell (1958) as a basis for his study of the island's vegetation in relation to exposure features. By 1957, however, when the study was conducted there has been considerable changes in the abundance and distribution of the various species comprising the islands vegetation. Nardus stricta was noted as being the dominant grass in the areas designated "grassy heath" and both Silene maritima and Armeria maritima had become much more abundant. Eggeling (1960) remarks "sea-pink is co-dominant with sea-campion in a belt of ground encircling almost the whole island and is an important constituent of the vegetation almost everywhere". The island is almost totally lacking in shrubs and trees. There have been numerous attempts made in recent years
by ornithologists to plant various species of trees and bushes to provide cover in the large heligoland bird traps, but these efforts have been largely unsuccessful. The island is very exposed to wind and spray and this has a seriously limiting effect on vegetation. There are, therefore, no areas of woody cover: the island is devoid of even those plants, such as whin and bracken, which are common on many other offshore islands. It is evident that the vegetation is also affected a great deal by the selective grazing pressure of the rabbit. Gillham (1955) reports on the influence of rabbit grazing on the vegetation of two islands off the Pembrokeshire coast. The vegetation of Grassholm, which is rabbit free, is dominated by red fescue (Festuca rubra), whereas the vegetation of Skokholm, which is heavily grazed by rabbits, is dominated by Holcus lanatus, Armeria maritima, bracken and ling. Experiments revealed that if rabbits were excluded from areas of Skokholm the vegetation changed to the Grassholm type.

Conversely, the vegetation seems to be an important factor in determining the distribution of the rabbit. Thompson and Worden (1956) suggest that the cover afforded by vegetation is the main determining factor in establishing a new focus for a rabbit warren. In particular, the shelter given by tree roots or by ragwort or nettles (both rabbit resisting species which grow on disturbed ground) seems to attract rabbits. Southern (1940) reports that the hedgerows surrounding pasture land tend to be occupied first by rabbits with subsequent colonization of the open fields occurring only when these warrens are well established. Southern also notes the frequent occurrence of nettles on the disturbed ground of rabbit warrens.

During the summer of 1975 as part of this project the
island's vegetation was recorded and although it is classified on the basis of the amount of cover which it afforded the rabbit population rather than on more strictly botanical criteria, there is considerable overlap between these categories and those formulated by Southern.

(i) Bare rock foreshore.

(ii) Grassy heath. The majority of the island is covered by short cropped grass (dominant species Nardus stricta and clumps of thrift (Armeria maritima)) frequently interspersed with outcrops of bare rock.

(iii) Common orache (Atriplex patula) and common sorrel (Rumex acetosa) occurring often in thick patches in clefts near the shoreline.

(iv) Sea Campion (Silene maritima). Dense beds of campion are particularly prevalent on the south-western corner of the island and give a certain amount of cover to the rabbits.

(v) Tall vegetation giving sparse cover. Areas thinly covered in Yorkshire Fog (Holcus lanatus), while bent (Agrostis stolonifera) and curled dock stems (Rumex crispus) are placed in this category.

(vi) Tall grasses giving good cover. Dense clumps of yorkshire fog and white bent occurred throughout the island and provided good cover.

(vii) Other tall vegetation giving good cover. Nettles (Urtica dioica), thistles (Carduus spp.) and curled dock (Rumex crispus) occurred in areas of disturbed ground, principally in those areas covered in cinder deposits from the old beacon. These plants provided dense cover for rabbit warrens.
The distribution of vegetation in these categories is displayed in fig. 2.3. Obviously the vegetation changed considerably across the seasons, the most noticeable changes occurring in the areas of waste or disturbed ground. In the winter months such ground was a bare mixture of ash, cinders and soil and by mid summer was covered by a dense tangle of nettles and thistles. This was particularly evident in the area around the watchtower at the highest point of the island, in the untended gardens and in Thistle Field, Tennis Court and Cross Park. The other major changes in the summer months were in the increase in cover afforded by long grasses over large areas of the island and the appearance of extensive beds of campion on the southern plateau and in the Tennis Court area.

The relationship between the amount of cover afforded by vegetation and the distribution of rabbit warrens can be seen by comparing fig. 2.3 with fig. 2.4. Fig. 2.4 shows the location of rabbit burrows on the Southern half of the Island during the late summer of 1975. Discrete warrens are well established collections of burrows located principally in small valleys or depressions, in areas covered by cinder deposits or in low lying areas of the island. Small single burrows excavated in the vicinity of large warrens were found to be occupied mainly by young rabbits. Southern (1940) suggests that this is the common pattern of warren expansion. However, the varying depth of soil found on the island imposes severe restrictions on the extent to which such expansion can take place. The outbreak of myxomatosis in 1975 resulted in a large number of unoccupied burrows being recorded. These were easily identifiable by the absence of the normal patch of bare earth and the growth of vegetation in the mouths of the burrows.
Vegetation - Summer 1975

- Bare rock foreshore and grassy heath (Nardus stricta, Armeria maritima)
- Common orache (Atriplex patula) and common sorrel (Rumex acetosa)
- Sea campion (Silene maritima)
- Thin coverings of tall vegetation e.g. Yorkshire fog (Holcus lanatus) and white bent (Agrostis stolonifera)
- Tall grasses in dense clumps e.g. Yorkshire fog and white bent
- Other tall, dense vegetation e.g. nettles (Urtica dioica), thistles (Carduus spp.) and curled dock (Rumex crispus)
Shaded areas represent dense vegetation. Note the spatial correlation between this and the main warrens in study areas.

- Unoccupied warrens or burrows
- Small, freshly dug burrow systems, usually occupied by juveniles
- Re-occupation of previously abandoned burrow systems
Overlay

Shaded areas represent dense vegetation. Note the spatial correlation between this and the main warrens in study areas.
Population distribution - late August, early September 1975

- **Warrens** - discrete collections of >6 burrows, inhabited by adult rabbits
- **Unoccupied warrens or burrows**
- **Small, freshly dug burrow systems**, usually occupied by juveniles
- **Re-occupation of previously abandoned burrow systems**
It is interesting to note the frequency with which young rabbits excavated fresh burrows rather than occupying disused burrows, although this did occur on occasions as can be seen from the diagram.

The suggestion that dense vegetation acts as a focus for warren development is supported. It is readily apparent from examination of figs. 2.3 and 2.4 that most areas of dense vegetation coincide with the location of well-established warrens although it is also true that some large warrens occur in areas lacking such cover. There seem to be four possible alternative explanations for this spatial correlation.

(i) Rabbits are attracted to areas covered in dense vegetation.

(ii) The correlation is coincidental. The underlying soil depth and composition has an important effect on the vegetation and also varies in its suitability as a medium for burrowing. Ash deposits support abundant growths of nettles and thistles which thrive on such disturbed ground: they also provide an excellent medium for burrowing. Deep soil allows the growth of taller vegetation, especially as, on the island, such deposits commonly occur in sheltered valleys and depressions. The depth and position of such soil deposits also makes them ideal locations for the construction of large warrens. On the other hand, the exposed grassy heath which covers most of the island has a very thin overlay of soil and is only suitable for the digging of shallow burrows or scrapes.

(iii) The disturbance of the soil by the rabbits and the deposition of their faeces and urine differentially favours the growth of certain plants. For instance it is known that
Distribution of visits to the island: figures refer to number of days in each calendar month when author was at the study site.
Urtica dioica favours nitrogen rich disturbed soil. (iv) The rabbits' feeding behaviour has a selective influence on the distribution of plant species in the immediate vicinity of warrens.

It seems probable that a combination of factors (i), (iii) and (iv) are involved in the relationship. There is certainly evidence that rabbits are attracted to areas of dense vegetation (Thompson & Worden, 1956; Southern, 1940) and it is probable that they, in turn, influence the quantity and composition of the vegetation, maintaining or increasing the attractiveness of the warren site.

The climate of the island is discussed in Chapter 8.

Time on Island

In the period between February 1975 and September 1977 the author was present on the island on 208 days. Distribution of days on the island across calendar months is shown in fig. 2.5. Travel to and from the island was by small lobster boat from Crail or Anstruther and landing at either of the two jetties on the island was frequently rendered impossible by even a moderate swell. The timing and length of visits were therefore determined, at least to some extent, by the tides and weather conditions, and took place in all calendar months except December and January. A total of 21 visits were made, varying in length from 2 to 19 days. Distribution of observation time during these visits is discussed in the relevant sections below.
CHAPTER 3

DEMOGRAPHY

Throughout the study general demographic information on the island's population of rabbits was collected, partly to permit comparison with past and future studies, and partly to secure essential background information to aid interpretation of the behavioural observations made during the present study.

An index of the variation in the overall size of the island's population over the three years of the study was obtained by means of line transect sight counts. While obviously this is an inaccurate indication of absolute numbers in the population, it is a useful method for obtaining a rough guide to population fluctuations. At the start of the study a considerable number of rabbits were suffering from the effects of myxomatosis and fluctuations in the numbers of infected animals were also monitored during sight counts.

In the quest to obtain meaningful results from behavioural observations in the field it is clearly advantageous if individual animals can be identified with confidence at a distance. It was therefore decided to trap and mark as many of the rabbits in the study areas as was possible. During the processing of trapped animals, their sex and body weight was also recorded. Since 28.8% of the animals trapped were retrapped at least once, an index of growth rate could be obtained. From this information it was possible to compute the approximate age of an animal based on its body weight. Thus, information on sex and age was available for every marked rabbit.
Because demographic information on populations of rabbits, which has been published in previous studies, appears to vary according to the methods employed in its collection, the data on population variation, myxomatosis, trapping, body weights and growth rates presented in this chapter are preceded in each case by details of the methods used in the present study for their collection.

(i) Variation in Population Size

(a) Methods

Throughout the study, variation in overall population size was monitored by means of line transect sight counts. The method was first developed by botanists but has been widely used in modified form for sampling populations of both birds and mammals (e.g. Webb, 1942; Yapp, 1956). Normally the observer is required to walk along a transect at a slow, even pace counting the number of animals observed. Myers (1954) has used a combination of counts of rabbits on warrens where this was possible, and more orthodox line transect sight counts in woodland, while sampling population variations to gain an impression of the effectiveness of the myxoma virus in controlling rabbit numbers. Sight counts are used most effectively when the animals being sampled are flushed from cover and are clearly observed, and when the animals in the transect are present in low enough numbers or are sufficiently slow moving to permit an accurate record to be obtained. However, several modifications of the basic method are necessary when sampling an animal such as the rabbit which is a colonial burrow dweller. The problems are quite different from those encountered when dealing with, for example, woodland birds. The rabbit shows a characteristic escape response when disturbed.
It will bolt for the safety of its burrow and, if the disturbance is at a reasonable distance, will almost invariably stop and sit alert at the mouth of the burrow waiting to ascertain if the danger necessitates going to ground. An observer advancing at a steady pace will readily elicit such escape behaviour and, if he continues to advance, the rabbit will go to the ground. As the island is largely composed of roughly undulating terrain and over most of its surface there is very little ground cover to hamper observation, it was found that the most successful method of dealing with these problems was for the observer to advance steadily, while hidden, to a vantage point and then stop and count the visible rabbits through 10 x 40 binoculars. He would then advance slowly watching the rabbits go to ground, noting those which he may have missed in the initial scan, as far as the next vantage point and repeat the process. While the rabbits beyond the next vantage point could not see the approaching observer, it is probable that to some extent a "knock on" effect occurred. Rabbits escaping from the observer occasionally ran beyond the next vantage point and may, in turn, have disturbed the rabbits there.

The island was divided longitudinally into four transects and the observer was required to cover the distance along one transect (the length of the main island) from South to North in approximately one hour. The four transects were walked simultaneously at various times during the duration of the study and, due to the varying width of the island, strict conventions were followed by observers at the narrower sections to avoid more than one observer counting the same animal. Most of the data, however, comes from transect number four (the easternmost transect) which was always covered by the author and was walked
regularly throughout the study. It was initially hoped that these counts would provide an indication of total population numbers. However, clearly, the accuracy of this method for estimating the total number of members of a particular species in a given area varies greatly from species to species and the estimates for one species vary in different habitats and under different conditions. No claim is made, therefore, that any idea of total population numbers can be gained from the data. Rather, the results are a useful index of variation in population size over the period of the study.

A total of 60 counts were carried out between 0700 and 0800 hours in the morning and approximately one hour before sunset in the evening. Durret (1957) points out that the daily activity pattern of rabbits is of great importance in determining the accuracy of such counts and, although it was attempted to carry out the evening counts at the time of greatest above-ground activity, seasonal variation in the daily activity pattern undoubtedly introduces a source of error into any comparison made across months. The data, therefore, give a rough index of population fluctuation and the most valid comparisons are those drawn between the same months in different years.

(b) Results

Figs. 3.1 and 3.2 are compiled from data from transect 4. Data from the other transects were collected intermittently, and while they augment the data from transect 4, counts were not carried out frequently enough to be included in this analysis. It is clear from the data that the population, in all three years, rises throughout the breeding season from the low number of animals surviving the winter. In the spring of 1975, however, when
the study commenced, the population was suffering from the effects of an epidemic of myxomatosis. Although the incidence of infection was at its highest in March and diminished thereafter, it is clear that the effect on numbers lasted throughout 1975 when transect counts are considerably lower than in the two succeeding years. The winter of 1975/76 was unusually severe and this, in conjunction with the low numbers present at the start of the winter means that by March 1976 the population appeared to be very small indeed. Nevertheless, it can be seen from figs. 3.1 and 3.2 that the rate of increase is very high during the breeding season and that by August the population is restored to a high level. It is interesting to note that the number of rabbits observed in the morning in 1976 exceed those observed in the morning in 1977 whereas the reverse is true for the evening counts. It seems probable that this is due to the high proportion of young animals in the population in 1976. It was observed that young animals have a more erratic daily activity pattern than adults and a higher proportion of young remain above ground throughout the morning. This phenomenon is discussed in more detail in chapter 8. The number of juveniles observed in each sight count was recorded but this becomes increasingly inaccurate as the season progresses and visual discrimination between adults and the growing juveniles becomes more difficult. However analysis of the data reveals that in the four counts carried out in April 1976 (when visual discrimination was relatively easy) the mean proportion of young rabbits was 62.5% whereas in the four counts carried out in April 1977 the mean proportion of young was 51.2%.

(2) **MYXOMATOSIS**

As already mentioned, during the spring of 1975 there was a
Fig. 3.1

Evening sight counts. Mean number of rabbits observed during line transect sight counts carried out on transect 4 approximately 1 hour before sunset.

Fig. 3.2

Morning sight counts. Mean number of rabbits observed during line transect sight counts carried out on transect 4 between 0700-0800 hrs. G.M.T.
widespread outbreak of myxomatosis which diminished thereafter. As the myxoma virus is transmitted by the rabbit flea, the most probable explanation for the occurrence of the virus on the island is that an infected flea was carried to the island by a gull and somehow transferred to a rabbit. The virus appeared first in 1955 (Eggeling 1960) but it is not known if there were further introductions of infection in the intervening period. The strain of virus was not identified as, at the start of the study, no marked animals were available to permit the accurate assessment of recovery rates. The epizootic did not seem to follow the "normal" pattern reported in other populations. Ross (1972) suggests that rabbits which have survived the infection form the bulk of the winter population and in spring the females give birth to young which are protected by the mothers' antibodies for a period of 2-3 months. As the summer progresses, the number of susceptible animals rises and in late summer an epizootic occurs, leaving only the immune animals to last through the winter and repeat the process. In the island population the incidence of infection was at its highest during the early part of the breeding season. It then fell sharply and rose again only slightly in mid summer. The normal epizootic in late summer did not occur. Reasons for this are not clear.

(a) Methods

During 1975 an index of the number of infected animals was obtained by recording the number of animals showing signs of the virus in the course of the sight counts. Each observed rabbit was placed in one of five categories. If the observer was close enough to observe the physical condition of the rabbit, it was recorded as being either "morphologically healthy" or "morphologically
sick", depending on whether or not it showed the very obvious symptoms of the virus. In the absence of clear physical evidence the observer could make a decision about the health of the animal on behavioural criteria. The normal escape response of a healthy rabbit has already been described. However, rabbits suffering from myxomatosis show signs of impaired vision and are generally less alert. This results, in most cases, in infected animals reacting more slowly to an approaching observer and in showing an abnormal escape response. On the basis of these differences, rabbits were recorded as "behaviourally healthy" or "behaviourally sick". Animals for which no such evidence was observed were recorded but were included in neither the "healthy" nor the "sick" categories. Such detailed recording was only possible in 1975 when the number of rabbits observed in each count was low but no instance of infection was noted in either 1976 or 1977.

(b) Results

Fig. 3.3 shows the course of the infection in the spring and summer of 1975. Rabbits not clearly identified as healthy or infected are excluded from the data. At the start of the study it seemed probable that the effect of myxomatosis would be an important factor in any analysis of the behaviour of the rabbits on the island. In fact this did not turn out to be the case, but some preliminary observations revealed interesting differences in the activity patterns of healthy and infected animals. It was noticed that there seemed to be a higher proportion of infected rabbits above ground in the morning than in the evening and further observations revealed that the number of infected rabbits above ground remains fairly constant throughout the day while healthy rabbits follow a regular daily activity pattern (discussed...
Rabbits showing signs of myxoma infection during 1975 expressed as a percentage of total observed rabbits (rabbits not clearly identified as healthy or infected are not included in the data). No observations were made in June.

**Fig. 3.4**

<table>
<thead>
<tr>
<th></th>
<th>March 1st Evening</th>
<th>March 2nd Evening</th>
<th>mean evening score</th>
<th>March 2nd Morning</th>
<th>March 3rd Morning</th>
<th>mean morning score</th>
</tr>
</thead>
<tbody>
<tr>
<td>Healthy</td>
<td>24 (53.3%)</td>
<td>30 (46.15%)</td>
<td>27 (49%)</td>
<td>12 (37.5%)</td>
<td>23 (41.8%)</td>
<td>17.5 (40.23%)</td>
</tr>
<tr>
<td>Infected</td>
<td>21 (46.7%)</td>
<td>35 (53.85%)</td>
<td>28 (51%)</td>
<td>20 (62.5%)</td>
<td>32 (58.2%)</td>
<td>26 (59.77%)</td>
</tr>
</tbody>
</table>

Numbers of healthy rabbits and rabbits showing obvious signs of myxoma infection above ground at the height of the epidemic on 3 days in March 1975. Data in each column are from sight counts on all 4 transects walked simultaneously either between 0700-0800 hours G.M.T., or 1 hour before sunset.
in Chapter 8). This means that a greater number of healthy rabbits are above ground during the evening, reducing the proportion of infected rabbits observed. Data for two days in March, at the height of the epidemic, are presented in fig. 3.4. Data from later months show a similar pattern but considerable variation is introduced by the increasing presence of both healthy and infected young rabbits in the sample. As mentioned above, young rabbits show a more erratic daily activity pattern than adults. In addition, it was observed that infected rabbits were frequently involved in aggressive encounters, being chased or displaced by healthy animals of both sexes but it was not possible to collect detailed quantitative data as the epidemic had declined by the time sufficient animals were marked to make such observations meaningful.

(3) TRAPPING

(a) Methods

A summary of the various possible methods for trapping rabbits is provided by Thompson and Worden (1956), but many of these methods were found to be simply not practical on the Isle of May. For example, the terrain on the island did not lend itself to long-netting, and the use of dogs or ferrets was regarded as undesirable for a variety of reasons (eg. the island is a National Nature Reserve and the possibility of interference with ground nesting or burrow nesting birds was regarded as an unjustifiable risk). The ideal method of trapping rabbits for the present study would have been one which resulted in as many rabbits as possible being caught from a warren while at the same time causing a minimum of disturbance to their environment and to their behaviour. Such a method, unfortunately has yet to be found. Each
method used suffers from a number of drawbacks and these are discussed in more detail below. The first method used was snaring. The snares used were fashioned from brass wire and were fitted with an extra metal "eye" to prevent the snare from closing fully. If the snares are kept in good condition and are checked frequently when set, this is a safer method than the standard snare, and only one rabbit died as a result of trapping. However, there are many practical difficulties with this method if one hopes to trap a particular group of rabbits. It is at its most useful if the aim is simply to trap large numbers of rabbits and the identity of the rabbits is unimportant e.g. in large scale demographic studies (or for food). Snares can only be set in a limited number of locations, on rabbit "runs". The snares do not seem to have to be particularly well concealed as those set on open runs were often as productive as those set in runs through tall vegetation, although snares set without the cover of undergrowth were seldom productive on flat ground. However, trapping by this method, like most open trapping methods is a fairly "hit and miss" affair. Despite extensive snaring over a long period, many of the rabbits in the study warrens were never trapped, while others would appear on several consecutive nights in the same snare.

As several of the study warrens occurred in locations unsuitable for snaring, an alternative method was implemented. Fencing was erected around three warrens on open, flat ground (Cross Park 1, Tennis Court 1 and Tennis Court 2). In all three cases the warren was bounded on one side by a stone wall (see Appendix 1) and the fencing on the open sides was dug into the ground to a depth of 9-12 inches. Box traps were set in the
fencing at regular intervals to provide a way in and out for the rabbits. The box traps were constructed from wood, reinforced with aluminium corner pieces (see Appendix 1) and measured 25 cm x 25 cm x 50 cm. A small transparent perspex flap (12 cm x 12 cm) was set into one end of the trap and could be prevented from swinging outwards by pushing home a small bolt. At the other end of the tunnel a sheet of transparent perspex could be inserted into grooves in the walls when it was wished to trap rabbits, to block their escape. Rabbits were acclimatised to the traps by pinning up the swing door to permit a permanent clear passage through the tunnel for a period of 3-4 weeks. The doors were then allowed to hang free so that the rabbits had to push through the perspex door in order to enter or leave the warren. When it was wished to trap the rabbits, the bolt on the swing door was engaged and, at the other end of the tunnel, the sheet of transparent perspex was inserted. The design of the traps and the methods used for acclimatising the rabbits to their use are similar in principle to those described by Southern (1940). Southern set his fencing as close to the burrows as possible to ensure that the rabbits would have to leave the enclosure to feed, and the rabbits became accustomed to using the swing door tunnels very quickly. In the present study it was found that, although the rabbits would freely use the tunnels with the doors pinned open, they were reluctant to use the tunnels when it was necessary to push open the swing doors. Thompson and Worden (1956) report that similar difficulties were encountered in several studies using this trapping method. The boxtraps, therefore, met with limited success. In the Tennis Court 1 warren, which is a very small collection of burrows with virtually no food inside the enclosure, they were used reasonably productively throughout 1976 and 1977 but, particularly at the
Cross Park 1 warren the rabbits seldom used the traps and went to
great lengths to dig under the fencing. In fact many of the traps
at Cross Park were destroyed during winter gales in the severe
winter of 1975/76, leaving the rabbits free access to and from the
warren but by the spring of 1976 the population of the warren had
diminished drastically. Although this may have been wholly due to
the privations of the winter, the surrounding unfenced warrens
expanded more rapidly during the following breeding season. From
spring 1976 the boxtraps in Cross Park 1 and Tennis Court 2 were
removed and snares were occasionally set near the gaps in the
fencing. Rabbits usually left the warren slowly throughout the
afternoon to feed on the grazing areas outside the fencing and
appeared to find no difficulty in avoiding the snares. The best
method of trapping the members of these two warrens was found to
be to allow the rabbits to emerge to feed outside the fencing and
then to startle them into dashing back to the warren. This
procedure often resulted in several rabbits being trapped in the
fence snares and they could then be quickly removed and marked.
The use of boxtraps at Tennis Court 1 and fence snares at Cross
Park 1 and Tennis Court 2, therefore, permitted more controlled
trapping of the rabbits from these warrens then would have been
possible with open snares. At the other study sites (Cross Park 2,
Thistle Field and Nettle Hollow) open snaring was possible because
of the presence of tall vegetation and, particularly at Thistle
field, this method resulted in a good capture rate. At numerous
other locations on the island, snaring was carried out
periodically to yield data on weight, age, sex ratios etc. It was
found that the snares were more productive if they were frequently
moved and reset in fresh areas and therefore the recapture ratio
of rabbits outside the main study areas was low. Throughout the
course of the study a few young rabbits were simply captured by hand as and when the opportunity arose.

(b) Results

Phillips (1955) reports that the sex ratio of captured rabbits varies considerably with the trapping method used. During rabbit clearance schemes in Wales it was found that snaring yielded 62% males and 38% females whereas ferreting and hole-trapping both yielded more females than males. In the present study a total of 326 animals were trapped. Fig. 3.5 shows the number and sex ratio of animals trapped by each method. It is clear that snaring yields a higher proportion of males than the other methods, although the sample size for the other methods is small. The sex ratio in rabbits is equal pre-natally and in the first weeks of life, and it is believed that the proportion of females present in a population increases with age (Southern, 1964). The predominance of females in the adult population is not reflected in the data obtained from any of the trapping methods employed in the present study. It is suggested by Thompson and Worden (1956) that this discrepancy may be due to the location of the traps. Snaring selectively traps those animals which venture out into open runs, whereas the other methods concentrate on the warren itself. It is generally accepted that females are more sedentary than males and are thus less likely to venture into the areas where open snares can be set. It seems probable that use of a method such as ferreting which gives access to animals within burrows would be resulted in a more accurate capture sex ratio.

(4) Adult Bodyweights

Myers (1964) reports adult bodyweights throughout the spring
Fig. 3.5

<table>
<thead>
<tr>
<th>Capture Method</th>
<th>Captures</th>
<th>Chi square test of significance of difference from equal sex ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Males</td>
<td>Females</td>
</tr>
<tr>
<td>Open snare</td>
<td>143</td>
<td>98</td>
</tr>
<tr>
<td>Fence snare</td>
<td>24</td>
<td>19</td>
</tr>
<tr>
<td>Box trap</td>
<td>17</td>
<td>17</td>
</tr>
<tr>
<td>Hand</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>Total</td>
<td>188</td>
<td>138</td>
</tr>
</tbody>
</table>

Numbers and sex ratios of rabbit trapped using the four different capture methods.
and summer of a single year in two enclosed populations of rabbits. Mean bodyweights ranged from 1408g - 1520g in males and from 1393g - 1660g in females. Mean weight increased gradually throughout the period of recording but it is important to note that the rabbits were provided with excess food and water. Data from a Welsh rabbit clearance scheme (Stephens, 1952) show that the mean weight of adult males ranged from 1416g - 1465g while females varied from 1409g - 1458g. Unfortunately the methodology for the collection of data in these two studies differs in two important respects. The Australian results, based on data gathered during the breeding season, show that at each time of recording, the mean weight of adult females is higher than that of adult males. That this finding is not supported by Stephens' results is probably due to the fact that the data for the Welsh study were collected between September and January, largely outside the breeding season. The other methodological difference concerns the animals contained in the samples. As his data was collected during the breeding season, Myers' definition of "adult" is based presumably on the breeding status of the animals in the study populations. Those animals included in the sample are therefore probably at least approximately one year old. Stephens classifies all animals over 16 weeks old as "fully grown" and the weights of all such animals are included in the data. Lockley (1964), however, suggests, on the basis of records collected from a sample of 100 enclosed wild rabbits, that rabbits continue to increase in weight until the age of twenty months when the mean body weight is just over 1500g. If this is indeed the case there is surprisingly little difference between the mean weights of rabbits in the two studies given the inherent differences in age structure. There is considerable circularity in the procedure used by Stephens. Age is
computed from bodyweight using a regression equation obtained from data from another population (Southern, 1940). Age, based on this computation, is then used to categorise the animals in the sample in order to arrive at results showing the mean weight of animals in each age group.

(a) Method

In the present study analysis of bodyweights is carried out only on those rabbits which had survived from the breeding season in the previous year i.e. animals born in the same calendar year as trapping are not included in the data. Only animals trapped in 1976 and 1977 are included in the sample and, as the breeding seasons in 1975 and 1976 ended in May of each year and trapping in subsequent years did not commence until February, all of the animals included in this analysis are at least 9 months old. All rabbits which were trapped were placed in a transporter box and transferred to one of several holding pens adjacent to the field station. They were then sexed and weight was recorded to the nearest 0.01 kg. After marking they were released near the point of capture. It is generally easy to distinguish those rabbits born within the year from older animals. The apophyseal line of the tibia-fibula normally fuses at approximately 9 months of age (Watson and Tyndale-Biscoe, 1953) and this can be detected by rubbing the thumbnail down the anterior edge of the tibia of the hind limb. This was regarded as a valid independent measure of age.

(b) Results

Fig. 3.6 summarises the data on adult bodyweight of males and females for both 1976 and 1977. A total of 92 weight records of 70 rabbits make up the sample. No rabbits are included in the
### Table 3.6

<table>
<thead>
<tr>
<th>Year</th>
<th>N (obs)</th>
<th>Mean (g) Body Weight</th>
<th>S.D.</th>
<th>Coefficient of Variation (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>1976</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Males</td>
<td>38</td>
<td>1477.9</td>
<td>117</td>
<td>7.92</td>
</tr>
<tr>
<td>Females</td>
<td>14</td>
<td>1443.6</td>
<td>105.8</td>
<td>7.33</td>
</tr>
<tr>
<td>All Rabbits</td>
<td>52</td>
<td>1468.7</td>
<td>114.1</td>
<td>7.77</td>
</tr>
<tr>
<td><strong>1977</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Males</td>
<td>20</td>
<td>1491.5</td>
<td>120.8</td>
<td>8.1</td>
</tr>
<tr>
<td>Females</td>
<td>20</td>
<td>1505.5</td>
<td>163.7</td>
<td>10.87</td>
</tr>
<tr>
<td>All Rabbits</td>
<td>40</td>
<td>1498.5</td>
<td>142.2</td>
<td>9.49</td>
</tr>
</tbody>
</table>

Mean bodyweight of adult males and females in 1976 and 1977.
data for more than one year. The slight difference in mean bodyweights between 1976 and 1977 may be due to the severe winter of 1975/76 having affected the quantity and quality of food available early in 1976. Only the mean bodyweights of females in 1976 fall within the range reported by Stephens (1952). The age composition of the sample probably accounts for the finding that females in 1977 and males in both years show mean bodyweights greater than those reported by Stephens. Mean bodyweights for both sexes in both years fall within the range reported by Myers (1964) for a sample composed of rabbits of similar ages to those in the present study. Lockley's suggestion that rabbits continue to increase in weight until the age of 20 months appears to be supported by data presented in fig. 3.7. Most of the rabbits in the sample are between 10 months and 18 months old and it can be seen that, throughout both years, the mean bodyweight of the adults in the sample increased. The monthly figures show considerable variation, probably due to the relatively small sample size, but the trend seems to be quite clear.

(5) **Growth Rates**

Southern (1940), using capture/recapture data from a population of rabbits at Sheepstead in Berkshire, calculated a regression equation for estimating the ages of rabbits weighing between 200g and 950g.

\[ X = 0.188 + 104.06W \]  where \( X \)=age in days and \( W \)=bodyweight in Kg

Slight differences between the rates of males and females were noted but these were not statistically significant. However, there is no indication as to the generality of these findings. From Southern's equation one would expect a rabbit at the age of 50 days to weigh approximately 478g and at 100 days to weigh


<table>
<thead>
<tr>
<th></th>
<th>Feb</th>
<th>March</th>
<th>April</th>
<th>May</th>
<th>June</th>
<th>July</th>
<th>August</th>
<th>Sep</th>
<th>Oct</th>
<th>Nov</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>1976</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Males</td>
<td>-</td>
<td>1462.5</td>
<td>1434</td>
<td>1449</td>
<td>1385</td>
<td>1506</td>
<td>1492.5</td>
<td>1517</td>
<td>-</td>
<td>1600</td>
</tr>
<tr>
<td>Females</td>
<td>-</td>
<td>1385</td>
<td>1395</td>
<td>1427</td>
<td>1490</td>
<td>1427</td>
<td>1480</td>
<td>-</td>
<td>-</td>
<td>1640</td>
</tr>
<tr>
<td>All</td>
<td>-</td>
<td>1437</td>
<td>1423</td>
<td>1442</td>
<td>1420</td>
<td>1482</td>
<td>1490</td>
<td>1517</td>
<td>-</td>
<td>1613</td>
</tr>
<tr>
<td>Rabbits</td>
<td>-</td>
<td>1446</td>
<td>-</td>
<td>1476</td>
<td>1475</td>
<td>1522</td>
<td>1535</td>
<td>1492</td>
<td>1595</td>
<td>-</td>
</tr>
</tbody>
</table>

**Monthly variation in mean bodyweight of adult males and females in 1976 and 1977.**

---

44
approximately 959g. Myers (1964) reports the growth rates of young rabbits in his two enclosed populations which were kept at different density levels. From this data one would expect a rabbit at 50 days old to weigh between 490g and 510g and at 100 days to weigh between 1015g and 1070g. Dunnet (1956) also reports growth rates of young rabbits. It appears therefore, that although there is very little data available, there is considerable variation in growth rates between populations, and that use of a formula computed from data collected on one population may be inapplicable if applied to another population. As the exact date of birth of most young born in the study warrens was unknown, it was necessary to use some form of computation based on bodyweight to estimate age. As equations based on data from previous studies may have limited applicability it was felt necessary to gain some measure of growth rates within the island population. This is possible using capture/recapture data from young rabbits. Data showing recapture ratios are presented in fig. 3.8. Southern (1940) reports that his data indicate a basically linear growth rate for rabbits weighing 200 - 950g which can be computed to be in the region of 9.58g/day. Myers (1964) gives no information on the linearity of the growth rate, but reports the mean growth rate of nestlings to be 8.8g/day and the rate of post nestlings to vary between 10.5 - 11.2g/day.

Growth rates were calculated from the weights of recaptured animals.

(a) Method

Data from the present study suggest that growth follows a roughly linear pattern in rabbits weighing up to 1100g and therefore only animals below this weight are included in the sample. At weights greater than 1100g the growth rate was slower and became more variable between individuals and more erratic.
Table 3.8

<table>
<thead>
<tr>
<th>Times Captured</th>
<th>Males</th>
<th>Females</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>131</td>
<td>101</td>
<td>238</td>
</tr>
<tr>
<td>2</td>
<td>41</td>
<td>27</td>
<td>68</td>
</tr>
<tr>
<td>3</td>
<td>11</td>
<td>7</td>
<td>18</td>
</tr>
<tr>
<td>4</td>
<td>5</td>
<td>3</td>
<td>8</td>
</tr>
<tr>
<td>TOTAL</td>
<td>188</td>
<td>138</td>
<td>326</td>
</tr>
</tbody>
</table>

Frequency of retrapping of males and females. Total for all capture methods.

Table 3.9

<table>
<thead>
<tr>
<th>Year</th>
<th>Mean growth rate</th>
<th>S.D.</th>
<th>Coefficient of variation(%)</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>1976</td>
<td>9.24 g/day</td>
<td>0.49</td>
<td>5.33</td>
<td>12</td>
</tr>
<tr>
<td>1977</td>
<td>8.8 g/day</td>
<td>0.62</td>
<td>7.01</td>
<td>14</td>
</tr>
</tbody>
</table>

Mean growth rates of rabbits weighing 200-1100 g in 1976 and 1977.
within individuals. It was also found that animals retrapped within ten days showed lower growth rates than would be expected. It seems probable that the snaring and the handling necessary during marking adversely affect the rabbits, and therefore only rabbits retrapped after a period of 10 days had elapsed from previous capture are included in the sample. In addition, it was suspected that young rabbits, living in well established warrens such as those in the study areas, had higher growth rates than those living among the rocky outcrops which constituted a large part of the terrain where open snaring was possible. As it was most important to estimate the age of the young in the study warrens, it was decided to include only retrap data from those animals living in established warrens in the analysis of growth rates. These restrictions severely limit the number of animals useful in such an analysis but they were seen as essential if a realistic index of growth rate for animals in the study areas was to be arrived at.

(b) Results

The mean growth rates for rabbits weighing 200-1100g in the two years of the study are shown in fig. 3.9. More accurately, the equations for calculating age based on bodyweight (derived from regression line equations calculated by the Method of Least Squares) are

for 1976 X = 101.9W + 2.188

for 1977 X = 120.5W - 2.1212

where X = age in days and W = weight in kg.

These equations were used in conjunction with observation records to establish an approximate date of birth for animals trapped in the study area. Although the sample size is small, the
coefficient of variation in growth rates in both years is very low. In addition, where the time of emergence of a litter was observed within one or two days and one or more members of the litter were subsequently trapped, the date of birth estimated from bodyweight closely matched the date of birth estimated from observations. However, it is accepted that the sample size is so small, that considerable error in such estimates is probable, and therefore dates of birth are estimated only to the nearest ten day block in 1976 and 1977. In 1975 the sample size was too small for even such a crude analysis to be undertaken.

(6) Influence of Habitat on Growth Rates

During 1977 young rabbits were trapped frequently in the area of rocky outcrops, to the east of Tennis Court, called Ardcarran. The area appeared subjectively to be a poorer quality habitat than the area containing the main study warrens. The soil cover is thin and patchy, permitting only short burrows to be dug in the hollows between the rocks. The terrain did not permit the clustering of burrows and therefore nothing resembling a warren was in evidence in this area. In addition, the food supply appeared to be of poorer quality and in lower quantity than, for instance, in the areas around the Cross Park and Tennis Court warrens. In previous years it had been noted that many of the young from the Tennis Court and Cross Park areas emigrated to Ardcarran during the summer. It was also found that a few of these rabbits had moved into other warrens in the surrounding area by the following spring, but most of these young rabbits disappeared during the winter. Some of the young of each year, however, simply remained in the warren within which they had been born and it was hypothesised that growth rates of these animals would be higher.
than those of young rabbits trapped in the Ardcarran area. The constraints on elapsed time to recapture and on maximum weight, again apply to the data.

The mean growth rate of young rabbits trapped in the Ardcarran area in 1977 is 5.92g/day (S.D. = 1.37; N = 14; C.Var. = 23%). The derived equation for finding age from bodyweight is

\[ X = 159.47W + 2.33 \]

The results of a Man-Whitney U test on the two samples reveal that there is a significant difference between the growth rates of young rabbits trapped in Ardcarran and those trapped in the Tennis Court and Cross Park areas.

\[(n = 14; n = 14; U = 8.5 \ p < 0.001)\]

There appear to be two avenues of explanation for this finding. The first is that the habitats differ in some important way and that the factor(s) giving rise to this difference affect the growth rate of young rabbits. The second is that the subsection of the young rabbits which emigrate from the parental warren have an inherently lower growth rate than those rabbits remaining in the warren. Certainly, only a subsection of young rabbits do leave the warren and it is possible that there are inherent differences between those rabbits which stay and those which emigrate. It has been suggested, for instance, (Lockley 1964) that the offspring of dominant individuals are more likely to remain in the parental warren than the offspring of subordinate individuals, and it is possible that offspring of dominant individuals also have higher growth rates. However, those rabbits trapped in one of the study warrens and then trapped later in Ardcarran (N=3) showed higher growth rates while living in the study warren areas. This is admittedly a tiny sample, but it does
suggest that the quality of the environment affects growth rate, although this by no means rules out the possibility that there were also genetic influences on growth rates.
CHAPTER 4

SOCIAL ORGANISATION - PREVIOUS STUDIES
(i) Methods

Despite the wide distribution of the European rabbit throughout the world and its obvious economic importance, systematic observation and recording of its behaviour was not attempted until 1940. Niethammer (1937) had previously carried out a small scale programme of marking rabbits on a farm in Germany but made few observations on behaviour. The difficulties inherent in studying the behaviour of a primarily nocturnal, burrow dwelling species are readily apparent and have led to a situation in which almost all of our current knowledge of rabbit behaviour is based on observations made on controlled, semi-natural populations living in artificial enclosures.

(a) The Sheepstead Study

Southern (1940) points out that the distribution of a population of rabbits is not random and that the main unit of a population is the colony or warren. He uses the analogy of a contour map to describe the distribution in which each peak represents a focal point of high density and the slopes around the peak indicate the gradually diminishing influence of the members of that colony. This means that normal grid capture/recapture methods will yield little useful information on the numbers and movements of rabbits. Southern, therefore, chose to study a single isolated warren covering an area of approximately 0.5 acres. A fence was erected around the warren and seven "smeuses" and box traps (smaller than the traps used in the present study, but similar in method of operation) were set into this fence to
provide both passage for the rabbits and a convenient periodic capture method for the experimenter. There was insufficient food available for the population within the enclosure and many were therefore compelled to use the traps. It was estimated that the "sphere of influence" of the warren extended over approximately 2 acres. Individuals caught in the traps were marked with celluloid eartags to allow easy field identification. The estimated proportion of marked animals in the population during the first year rose from 28 percent in March to 56 percent in September. During the remainder of the three year study period, the proportion of marked animals was maintained at 40-50 percent. The total time spent in observation over the three years was 162 hours (Southern 1948). The observational sampling methods are not described in detail. The only information supplied is that "the main object was to make as many ear-tag identifications as possible, so that only part of the time could be spent on following out sequences of behaviour". For the first time a description of the main characteristic behaviour patterns of the rabbit was compiled and the population dynamics of the warren were discussed in some detail. However, little information on territorial behaviour or on the ranges of individual animals was collected.

(b) The Orielton Study

Study of the rabbit continued in the U.K. throughout the following decade but the emphasis shifted to reproduction and mortality in large populations (e.g. Brambell, 1944; Stephens, 1952; Phillips et.al., 1952). Further observational study of rabbit behaviour did not occur in the U.K. until 1955 when Lockley (1961) constructed two one-acre enclosures in order to study the
social behaviour of rabbits under conditions of differing population density. Lockley had spent the previous three years completing a survey of the spread and the vectors of myxomatosis and had first hand experience of the difficulties inherent in the study of wild rabbits. The study site was situated in S.W. Wales and the enclosures were stocked with a combination of locally trapped wild rabbits and rabbits transported from the small island of Skokholm off the Welsh coast.

In the "high density" enclosure the population was permitted to grow unchecked and in the "low density" enclosure the young were removed at weaning age. Thus, not only the population density, but also that entire age and social structure differed between the two enclosures. A combination of natural and artificial warrens was provided for the rabbits and they were permitted to dig burrows and extend the warrens as needed.

Only a small proportion of the inhabitants were trapped and marked during the breeding season, but after the breeding season each year the warrens were opened up and the rabbits netted. Lockley tried to reproduce Southern's method of surrounding each warren with fencing containing smeuses but found that it caused "considerable disruption to their normal territorial behaviour" (Lockley, 1961) and he quickly abandoned the procedure. No indication is given of the sampling methods used in gathering data and it seems probable that no formal method was adhered to. The behaviour, territories and social organisation of the various groups of rabbits were recorded in addition to detailed comparative demographic information on the two populations.

By 1950 the rabbit had become a major economic problem in
Australia and the search for effective means of control was assuming increasing importance. Several workers had confined populations within enclosures to enable experimental work on the transmission and epidemiology of myxomatosis and detailed experiments on other control methods to be carried out (Myers, 1958). In some cases, as with Southern's study population, the rabbits were confined in situ but an increasingly popular practice was to construct enclosures around suitable habitat and to introduce rabbits from outside.

(c) The Canberra Study

In 1957 it was decided to utilise one of these enclosures of approximately 1.75 acres, at the CSIRO wildlife survey section in Canberra, for the study of rabbit social behaviour (Mykytowycz, 1958). It was felt that, by stocking the enclosure with marked rabbits of known sex and age, more detailed information on the behaviour of the animals could be obtained. For this reason, adult laboratory rabbits bred from wild stock were introduced as the nucleus population. Two artificial warrens were provided, in addition to hollow log shelters placed around the enclosure periphery. Observations commenced in February, 1957 and continued until August, 1961 during which time, disturbance of the expanding population in the form of systematic handling, removal and replacement of individuals was common (Mykytowycz, 1958, 1959, 1960, 1961).

Little information is provided on the sampling methods used during observation. The enclosure was entered and searched each morning and the resting position of each rabbit was noted. Behavioural observations were made in the late afternoon and at night from an elevated hide situated outside the enclosure. A grid
system was used to plot the movements of individuals. Data on many aspects of behaviour and social organisation were obtained in addition to a detailed record of the dynamics of the population.

(d) The Albury Study

Shortly after the start of the Canberra study, a further enclosure system was constructed at the CSIRO field station in Albury, N.S.W. in order to study the effects of different population densities on the behaviour and physiology of the rabbit. For this purpose three enclosures of 2 acres each were constructed and stocked with different numbers of locally captured adult wild rabbits. Log shelters were provided above ground and no warrens were allowed to develop (Myers and Poole, 1959). The enclosures were entered and searched each day, the location or "lie-up position" of each individual being noted. In addition, the populations were netted and handled once a month when a census was taken. Observations commenced in October, 1957 and continued until March, 1959 at which time the remaining rabbits in the two lower density enclosures were added to those in the high density enclosure for a further year. The observational techniques were similar to those employed in the Canberra study and, again, no information is supplied on the behavioural sampling methods used. During the first two years of the study, observations on behaviour and social organisation were recorded and comparisons drawn between the three populations at different densities. However, as the study progressed, the emphasis shifted to the detailed study of population dynamics under conditions of high density.

Several other studies were conducted in Australia and New Zealand during the 1950's and 1960's (e.g. Bull, 1956, 1961; Dunnet, 1957; Gibb, 1977) on both wild and enclosed populations,
but they were either concerned with specific aspects of behaviour or with the effects of population density on aspects of breeding and are discussed in the relevant chapters below. The four large scale studies already mentioned provide almost all of the data upon which the current picture of rabbit social organisation is based.

(2) Results
(a) The Sheepstead Study

Over the three year study period Southern (1940, 1948) succeeded in maintaining the proportion of marked rabbits in the study population at around 40-50 percent. It was estimated that 30 percent of the total population was above ground during a normal evening activity period. During August and September 1939 the position of each marked rabbit was regularly recorded and a picture of their "territorial conservatism" was constructed. Adult females were found to be more conservative than adult males in that their movements were restricted to a smaller area of the warren. The young were, in general, less conservative than adults, juvenile females being least conservative. Southern states that the adult females are the most stable element in rabbit organisation and they aggressively repel other rabbits, especially females and young, from their "territory".

The adult males are reported as having "spheres of influence" - a term which is not defined beyond stating that each male spent most of its time in a particular area. Three or four males were particularly active in each year and were responsible for most of the sexual chasing observed in their areas of the warren. The criterion used by Southern to assess dominance was the number of observed approaches to females. By this criterion, his
The most dominant male was one which was observed to make seven approaches to females and he includes in the "dominant males" category, a rabbit which made only one recorded approach to a female. No data on inter-male aggression is given. No comparative conclusions about the movements of dominant and subordinate individuals can be drawn, as data on movements were collected in 1939 and data on dominance relationships were collected in subsequent years.

During the course of this study it was noted that colonization occurred as a result of females using breeding stops outside the main warren area. Some of the young born in such stops simply remain there, extending the burrows as the year progresses. Occasionally the young in several such small burrow systems extend them in such a way that they join up forming one large system, but more frequently, as the main warren system itself expands, it engulfs these small burrow complexes. Expansion in this manner is largely dependent on the distribution of vegetation cover above the ground.

Young rabbits up to the age of approximately four months play together and mix freely with other members of the warren, but by late July when the young females are approaching sexual maturity, the adult males begin to monopolise them and the young males are increasingly harrassed and may eventually be driven out of the warren altogether. By the second half of August the young females are definitely sought by adult males and are attacked furiously by adult females if they cross into their "territories".

A steady trickle of young rabbits left the warren in the spring and summer of 1939. Migration was mostly to nearby warrens,
cover and fresh burrows. Of the 21 marked rabbits leaving the warren, none travelled further than 280 yds and most covered much shorter distances.

(b) The Orielton Study

By studying a small population, consisting entirely of marked individuals, Lockley (1961) was able to make detailed observations of each rabbit's behaviour and thus build up a more accurate picture of social structure. During the first phase of the study no movement was permitted between the two 0.5 acre enclosures. Two quite distinct populations, therefore, were under observation. Small mixed sex groups formed in both enclosures, each consisting of one male and between one and three females. All females belonged to such a group. Among the males in each group there was soon established an order of dominance. Initially one male was dominant over each 0.5 acre enclosure and monopolised the majority of the females. The remaining males ranged over small sub-sections of each enclosure. Dominance was assessed by Lockley on the outcome of aggressive interactions. It was observed that the dominance hierarchy among the males was quickly established by fighting, and that thereafter secondary individuals retired on the approach of a recognised superior. In this way, serious aggressive encounters were generally avoided. Dominance was largely correlated with age and males, it was observed, did not generally become dominant before the age of eighteen months. Even after the stabilization of the dominance hierarchy, the dominant male spent a great deal of time challenging and thus displacing other rabbits. Subordinate males invariably retreated but the response of females was more variable.

Adult females were observed to be largely sedentary,
supporting Southern's statement that adult females are territorially conservative. The dominant female was found to be the mate of the dominant male, and her progeny were born within the main warren. The offspring of subordinate females, however, were normally born in breeding stops dug in the open away from the central warren and were often attacked subsequently by the dominant couple if they attempted to enter the warren. This, suggests Lockley, confers a distinct advantage of the offspring of dominant rabbits, and they are more likely to become dominant in their turn.

In October 1955, once observations had been made on the stabilised social systems, the dominant male in enclosure A was removed and placed in enclosure B. He was at once attacked by the dominant male and assumed a solitary and subordinate role. During this period another male in enclosure A quickly assumed the dominant position, moving into the vacated warren and monopolising the females there. As further evidence for the sedentary nature of adult females, his own mate remained in her small warren alone. After a three week period the previous dominant male was returned to enclosure A. Serious fighting resulted and the exiled male failed to regain his dominant position. Their positions in the hierarchy were then reversed; the exiled male inhabiting the warren and mating with the female deserted by the new dominant male. The important result of this experiment, however, is that the new dominant male did not continue to exert his authority over the defeated male and two exclusive territories ensued. By the third breeding season, there were three mixed sex groups in enclosure A, each with its own distinct, defended territory. No single male now had free access to the entire enclosure. This
situation is similar to that observed in the Australian studies discussed below. The social organisation in enclosure B, however, which was not subjected to such manipulations remained, as first described, with several mixed sex groups but with only one overall dominant male having access to the entire enclosure.

Results from the Orielton study support those of Southern in suggesting that physical growth of the warren takes place primarily by the extension and subsequently assimilation of nursery burrows. Lockley further suggests that the female is responsible for the major work involved in establishing and extending the warren.

(c) The Canberra Study

In the first phase of the study the stock animals were confined to a single artificial warren within the enclosure for a period of five weeks. Food and water were provided. Smeuses set in the fence around the warren were then opened and the rabbits gradually spread throughout the enclosure. The findings in this initial period closely parallel those in the Orielton study. A period of fierce fighting was accompanied by the gradual emergence of a linear dominance hierarchy. Once this hierarchy had developed, the population entered a relatively stable phase with few serious aggressive interactions. Mykytowycz used aggressive chasing as the criterion for dominance. In the first instance, one male emerged as being dominant over the entire population and he moved freely throughout the enclosure. It was observed that, unlike the dominant male, subordinate animals do not assert a claim over a particular territory. It is suggested that their presence in primarily a small sub-section of the enclosure is due entirely to an avoidance of animals higher in the hierarchy. As in Lockley's
study, this situation continued until the dominant male was removed as part of a series of experimental manipulations.

Mykytowycz suggests that rabbits have a "compulsion" to form dominance hierarchies and that individuals of equal status do not exist. Any dispute, it is reported, resulting in a physical fight is concluded with the winner taking top rank and the loser falling far down the hierarchy. This is precisely what occurred on the re-introduction of the previous dominant male. A fierce struggle with the new dominant male ensued, resulting in the newly reintroduced male losing and dropping to the bottom of the hierarchy. However, unlike the situation in the Orielton study, this did not immediately result in the splitting of the population into groups within separate territories. This occurred quite spontaneously later in the breeding season as the number of rabbits within the enclosure increased. Group A remained within the established warren and was socially stable. Group B was composed primarily of surface dwelling animals and had a very loose social organisation.

At the onset of the second breeding season, fierce fighting broke out in the loosely-knit group B, between both males and females and seven quite distinct mixed sex groups emerged. The composition of these groups varied considerably. The number of females within each group appears to have been directly related to the quality and number of burrows within the group territory. The number of males in each group appears to have been unrelated to the number of females and may have been dependant on the pugnacity of the dominant male. Female numbers varied between 1 and 7. Male numbers varied between 1 and 5. There were only a small number of high quality established burrows within the enclosure and the
object of much of the fighting as undoubtedly to secure access to one or more of these. There was no such fighting in the socially stable group A.

During the initial exploration phase of the study, the females were more mobile than the males but soon settled into the pattern of territorial conservatism described by Southern and Lockley. During the breeding season, females became very aggressive towards strange rabbits, particularly other adult females and young, whereas adult males were observed to be lacking in overt aggression towards young. However, at around the age of 3 months, young rabbits, particularly young males, were frequently chased by the dominant male, and many were forced to live outside the warren. At the start of the second breeding season only two of the thirteen surviving males born in warren A remained in residence. In contrast, nine of the twelve surviving females remained in residence.

(d) The Albury Study

This study was carried out as a series of experiments; the prime independent variable being the density of the population in the three enclosures. The results show that as density increases, home range and territory size diminish and the number of mixed sex groups increases. Male home ranges remain larger than female ranges and dominant male home ranges remain larger than those of their subordinates. Myers and Poole (1959) report that the size of mixed sex groups is limited to two or three males and three or four females. It is also suggested that group formation is primarily a function of female behaviour, as observations indicated that, at the onset of a breeding season, females have a strong tendency to congregate in small groups. There seems to be
no such mutual attraction among the males which simply distribute themselves among the available female groups and, through fighting, establish a linear dominance hierarchy in each group. The protection of each group of females by the males effectively amounts to territorial defence, as strange males are excluded from the area used by the females. The suggestion is made that the limit to the number of females in a group is not determined by the inability of the males to protect more than a certain number, but rather by the inability of females to recognise and tolerate more than three or four others. The number of males within a group is limited by the aggression of the dominant male. Only the top two ranking males in each group had access to females and any remaining male which did not adopt an entirely subordinate role was frequently harried and usually forced to leave. New groups may form when a female leaves an established group and becomes a separate source of attraction for males. Initially Myers and Poole discuss male and female groups as quite separate entities stating that in the medium and high density enclosures "each female group was overlapped completely by a male group" (Myers & Poole 1959). However, they confidently report the paternity of litters produced by the females of certain groups without giving details of how this was ascertained. One must assume that it was based on Observed Matings. They subsequently applied the term "breeding group" to these small groups of males and females with overlapping home ranges. In the low density enclosure the two males and four females formed a single group in which one male was completely dominant over the other. In the medium density enclosure two groups formed, each consisting of two males and three females. In each group one male dominated the other and the two groups possessed quite distinct territories. In the high density
enclosure, the situation was more complex. A total of three mixed sex groups emerged; two of which were composed of two males and three females as in the medium density enclosure; the third comprised three males and four females and a further two males were unattached to any particular group. The dominant male of one group had access to two of the females in a second group, but it is interesting to note that the two female groups remained distinct. One of the unattached males was dominant over the other and also over the subordinate males in two of the established groups. It is suggested that the occurrence of strong, sexually active "satellite" males may be common in natural populations.

Whereas Mykytowycz describes male and female dominance hierarchies in similar terms, the results of the Albury study indicate that the relationship between males is very different from that between females. Myers and Poole observed no complete female dominance hierarchy and, although in general, aggression between females increased with the size of the population, they conclude that "some females were by nature aggressive, others very quiet, a difference probably genetically determined". (Myers & Poole 1961). The results of the Canberra and Albury studies also disagree over the inheritance of dominance. While Mykytowycz concludes that dominant individuals are usually the offspring of dominant parents, no such trend is discernable in the Albury results. Such discrepancies are possibly due to the different experimental conditions under which the studies were conducted. Myers and Poole (1959), referring to the results of their first paper, admit that "the close contact of breeding groups at warrens, together with the presence of other are classes, points to a more complex pattern of social behaviour in natural
populations than that described here for confined, adult rabbits".

Almost all of the current knowledge about the social organisation of the European rabbit, therefore, is based on the findings of these four major studies. Southern laid a firm foundation by describing the basic principles of rabbit social behaviour but Lockley suggests that the methods employed may have interfered with the natural territorial behaviour and ranges of the observed rabbits. Lockley himself expanded on this early work but the enclosure sizes may again have interfered with the behaviour of the study populations. In his own words "The territory of the dominant buck was artificially determined or curtailed in these experiments by the limits of the enclosures ... how much ground can a dominant buck control". Lockley's results, therefore, can be applied to the behaviour of naturally occurring populations only with certain caveats. The two Australian studies, while allowing the enclosed populations considerably more freedom of movement, involved periodic major disruptions of the study populations. In both studies the rabbits were introduced into novel environments and, in the interests of gathering precise demographic data, were frequently captured and handled. Furthermore, in the Albury enclosures, the rabbits were not permitted to dig burrows or construct warrens and in the Canberra enclosure artificial warrens were initially provided.

While the reported results of the four studies on enclosed populations reflect considerable variation and complexity in the social organisation of rabbit populations, more recent papers by the authors of the Australian studies accept, without qualification, that the "breeding group" is the fundamental unit of rabbit social organisation.
"The social unit of rabbit populations is the breeding group, a small assemblage of one to three males and one to five females which, together, protects an area of land in which feeding, resting and breeding takes place, and which fulfills all requirements of territory" (Myers et al., 1971).

"Rabbits live in small breeding groups. Within the group, a linear order of dominance develops separately for each sex. Each group occupies a territory which is defended by all its members and respected by strangers.... A few breeding groups together form a social entity and occupy a common grazing and sheltering ground. All individuals within the social entity are known to one another. (Mykytowycz and Fullagar, 1973).

The only purely observational study of a naturally occurring population of wild rabbits published before the start of the present study was carried out in S. E. Australia in 1961 (Myers and Schneider, 1964). Between June and November 1961 "Almost daily observations between 3 p.m. and dusk" were carried out on a population of 26 adults and (by the conclusion of the study) 69 young. Five separate small warrens were observed and no interwarren interactions were recorded. No animals were marked during the course of the six month study. Individuals "became recognisable by virtue of differences in size, shape of head, and colour". No information is given on the sampling methods used for observing behaviour. The aim of the study appears to have been the validation of the previous CSIRO enclosure studies and the authors conclude "The observations suggest that there is no major difference between the basic pattern of social behaviour of confined rabbit populations and of free-living wild rabbits, and emphasize the value of intelligent use of confined populations for the further study of rabbit ecology. An enclosure of less than 1 acre would have represented more than the average area over which each warren colony moved".
While such a statement goes some way to answering criticisms of the enclosure studies the Myers and Schneider study lasted only six months and was based on observations of small warrens. The length of the study is important as it covers only one breeding season and leaves the important question of immigration and emigration unanswered. The inability of rabbits to come and go freely from the study area must surely be one of the major flaws of the enclosure studies, and the fact that this study of a natural population did not cover the time of year when the restructuring of the social system occurs must cause some concern. The size of the warrens is important as they each consisted of only one small mixed sex group (varying from one to two adult males and one to three adult females). Thus the social organisation of the observed free-living population closely resembled that of the Albury enclosed population (i.e. small mixed sex "breeding groups" inhabiting exclusive defended territories). A further study conducted by Mykytowycz and Gambale (1965), designed to investigate inter-warren activity in a 45 acre enclosure, was also set up with this basic social organisation. However, while small warrens of this type are common, it is by no means clear if the large colonies frequently observed in natural populations possess a similar social organisation.

The behaviour of free-living populations of rabbits began to attract the interest of British researchers during the 1970's. Little of this work has yet been published, but a study conducted by Bell (1977 Ph.D. thesis, 1980) was also concerned with an island population. Bell visited the island of Skomer off the Welsh coast four times during 1974 and 1975 and spent 110 hours observing a small group of unmarked rabbits. As in the Myers and
Schneider (1964) study, individuals were recognised "on the basis of natural distinguishing features". Although the study concentrated largely on olfaction and the findings are discussed more fully in later chapters, Bell reports that the social organisation of the rabbits under study was similar to that reported by Myers and Poole (1959, 1961). However, in reporting her first visit to the island, she mentions that there were two warren groups of eight and six adults in the study area and that a single dominant male (resident in the smaller group) moved freely between the two groups.

Thus, despite the concentration of research over the past 30 years on small warrens, composed largely of single mixed sex groups, there is considerable variation in the reported details of social organisation in the rabbit. In addition, the procedures involved in stocking and setting up the Australian enclosure studies, the subsequent interference in the normal development of warrens and the absence of normal immigration and emigration from the populations mean that, despite the assurances of the researchers involved, the general applicability of their findings to natural populations must remain in doubt.
CHAPTER 5

BEHAVIOURAL OBSERVATIONS: METHODS
CHAPTER 5

BEHAVIOURAL OBSERVATIONS: METHODS

In this chapter the general methods employed in the remainder of the project are outlined. In some cases, where the techniques used are particularly applicable to only specific sections of the project, they are briefly outlined in this chapter but discussed in more detail in the chapter to which they apply.

(a) Study Areas

During the three year period covered by the present study, observations were carried out in several areas of the island. The initial rationale for such duplication was based on observations made on early visits to the island, which indicated that myxomatosis was a major mortality factor. It was feared that if myxomatosis continued to inflict high mortality throughout the study period, then major fluctuations in local sections of the population were probable. Although interesting in its own right, the study of the effects of the myxoma virus was not the primary aim of this project and it was hoped that, if some warrens were decimated by the virus, others would remain unaffected. This fear proved unfounded and, following the spring of 1975, myxomatosis ceased to be an important cause of death. However, preliminary observations of the warrens in the three areas revealed interesting variations in social organisation and it was decided to continue recording behaviour at all three sites. A further site on flat, level ground was added to the areas under study during the spring of 1976 principally to permit the accurate observation and recording of behaviour related to olfactory communications.

To some extent the study areas were chosen for ease of
observation, either because a particularly suitable vantage point was available, or because the geography of the warren area made it possible to observe the member rabbits over their entire normal daily geographical ranges. The presence of a suitable vantage point, which can be approached without disturbing the animals under observation, is very important in the case of the rabbit. Although such disturbance is undesirable at any time of the day, it is most troublesome in the early morning. Throughout the afternoon and evening rabbits, when disturbed, will go to ground and normally will reemerge after a short time. In the early morning, however, it was found that they would go to ground if disturbed and would frequently fail to reemerge until the afternoon. If left undisturbed they would often remain above ground for a considerable time. Obviously data on activity patterns is rendered worthless if the observer is instrumental in altering that pattern. Many areas of the island proved unsuitable, usually because undulating ground rock outcrops or high vegetation made observation difficult, or occasionally because areas were being used at certain times of the year by other researchers.

Six warrens in three areas (Nettle Hollow, Cross Park and Thistle Field) were observed throughout the three years of the project, and observations on two warrens in Tennis Court commenced in April 1976. In these areas, further warrens may either have been present at the start of the study and become unoccupied during the study, or were formed during the study. These are discussed fully below.

Observations on the Thistle Field warrens were made from the field station. The Nettle Hollow study site was overlooked by an abandoned W.W.II observation station. Most of the windows remained
intact and it served as an excellent vantage point as the observer
was some 5m. above ground level with a clear view of the warren
below. At Cross Park a canvas hide was erected on high ground
either to the southeast or to the northwest of the study area and
at Tennis Court a similar system was employed until 1977 when an
elevated wooden hide was constructed on high ground at the
northern end of the study site. In August 1976 one of the Cross
Park warrens and two of the Tennis Court warrens were surrounded
by fencing containing box traps (as described in Chapter 3). At
the warrens in Thistle Field and Nettle Hollow no such artificial
restrictions on movement were imposed and the only disruption at
these study areas was caused by the periodic snaring of
individuals.

Observation and identification of individuals was aided by
10 x 40 binoculars and a 15X-60X telescope.

(b) **Marking**

The marking of animals for field studies can fulfill two
quite distinct functions. Firstly, to collect information on
weight, growth, age and movements etc. If marking is to fulfill
this function it is necessary simply to be able to identify an
animal when it is retrapped. The second function is to permit
collection of information on behaviour, social organisation etc.
by direct observation. In this case it is necessary to mark an
animal in such a way that it can be identified at a distance in
the field. In rabbits, this latter function has been fulfilled in
previous studies either by the use of numbered ear tags of various
types (eg. Southern, 1940; Myers and Poole, 1959; Tyndale-Biscoe,
1953; Lockley, 1961) or, alternatively, by dying the fur in a
distinctive pattern (eg. Rowley, 1956; Mykytowycz, 1958). Both
methods suffer from certain drawbacks. Ear tags tend to get torn out and lost and fur dye has a limited useful lifetime. A sample of chicken wing tags, as used by Lockley (1961), was tested on a small number of rabbits, but these were found to be insufficiently distinguishable over the observation distances required. Suitable plastic ear tags could not be obtained at the start of the study and therefore it was decided to use fur dye.

Each rabbit was dyed in a distinctive pattern with "durafur Black R" supplied by ICI Dyestuffs Division. This pattern was still clearly distinguishable after 6 months and, although it faded slowly thereafter, identification was possible in most cases up to 9 months after initial marking. Because of the limited effective life of the dye, all rabbits were also tattooed with an identification number inside one ear to permit remarking if retrapped. Within the main study warrens, rabbits were retrapped more extensively than in other areas to permit such remarking.

(c) Observational Sampling Methods

Data on various aspects of behaviour and social organisation were collected using different sampling methods. The first method employed is described rather grandly by Altmann (1974) and Lehner (1979) as ad libitum sampling and involves the recording of data in a relatively unstructured way. Indeed, it might reasonably be claimed that, in terms of recording behaviour, to refer to the procedure as a sampling method is misleading. Undoubtedly only a sample of behaviour is recorded, but often no conscious decision on the part of the observer is made to bring this about. Rather, the sample of an animal's behaviour which is actually observed and recorded tends to be that behaviour which is most "eye-catching". However, because of the lack of constraints on the observer, it is
a useful method for building up a general picture of the structure, social organisation and movements of group of animals.

Over the three years of the project approximately 600 hours were spent in ad lib sampling of the study warrens. The observer simply noted the numbers and if possible the identity of the rabbits present, the location of the burrows from which they emerged or to which they returned, the geographical ranges of individuals and social interactions. The aim of these observations was to build up a general background picture of the behaviour and social organisation of the rabbits in the study areas.

In the absence of any information to the contrary, one must assume that data published in previous studies were gathered in this way. Unfortunately however, the method does not yield valid quantitative data on many aspects of behaviour. To gain accurate, quantitative data on activity patterns, interactions and sequences of behaviour, for instance, one must adopt a more formal sampling method.

In the present study, therefore, a further 450 hours of observations during 1976 and 1977 were carried out using 3 more formal sampling procedures. The first of these is referred to as "scan sampling" by Lehner (1979) and was employed specifically to collect data on activity patterns. At predetermined intervals the identity, location and behaviour of all visible animals in a study warren were recorded. Details of the method used and the temporal distribution of samples are given in Chapter 8, but information on the location of animals was also used to supplement data from ad lib observations in the plotting of home ranges.

The next sampling method employed is referred to by Altmann
(1974) as "focal-animal sampling". In the present study it was used to collect data on aspects of olfactory communication, particularly on behavioural sequences and the relative frequency of behavioural events across the various age/sex/social classes. These results are discussed in later chapters, but details of movements and interactions etc. have also been used to help in compiling the general picture of social organisation.

Focal animal sampling involves recording as near to a complete description of an animal's movements and behaviour as possible within a set sample period. Temporal distribution of samples is described in Chapter 10. The sample period used in the present study was 50 minutes and data was recorded using a cassette tape recorder and transcribed as soon as possible after the sample period.

Only animals above ground at the start of the sample period were considered as subjects. This may seem a ludicrously obvious remark, but much of the development of observational methodology in the field and the subsequent discussion of the validity of procedures in the animal behaviour literature has been based on studies of primates. Thus, in focal animal sampling, it is recommended (Altmann, 1974) that an animal is selected for observation on a random basis or, depending on the particular aims of the study, according to some prearranged schedule. Rabbits, however, are only above ground for a certain proportion of the day and it would obviously be fruitless to initiate a sampling period while waiting for the predesignated individual to emerge. It is evident that modifications to the basic methods are essential in order to adapt them to the study of animals in widely differing circumstances.
In addition, most observations were carried out on animals which had been marked or which had identifying characteristics. If an unmarked or unidentifiable subject left the observer's field of view for whatever reason, it was not always possible to positively identify it, if and when it reappeared. Such animals were occasionally selected as subjects, however, and in these cases observations were curtailed if the rabbit in question disappeared from view. Unless positive identification was possible, observation was not continued on the reappearance of what seemed to be the same rabbit. However, in the majority of cases where clear identification was possible, if the rabbit went below ground or disappeared from view in some other way, observation continued during the period of absence until either the rabbit reappeared or the sample period ended. Distribution of focal animal samples and further details of procedure are presented in chapter 10.

The final sampling method employed has been variously described as "event-sampling" (Hutt and Hutt, 1974), "complete record" (Slater, 1978) and "all occurrences" Lehner (1979). This method involves an attempt to record all the occurrences of one or a few behaviours in a group of animals in a given sample period. In contrast to focal-animal sampling described above, the focus here is on the behaviour and not on the individual. In the early summer of 1976 and 1977 observations were carried out with the specific intention of recording agonistic interactions and determining the social status of individuals. In each of the two years, each warren in the study areas was observed for 2 hours on 2 separate days. Observations in 1976 were conducted in May and those in 1977 in May and June. All observations were made in dry weather between 1300 and 1900 hrs G.M.T. - the time of most
daylight surface activity. The observer attempted to record every intrawarren agonistic interaction between adults and, where possible, to identify the participants and assess the outcome.

In addition, therefore, to the information from ad lib observations of warrens, the results of more formal samples of behaviour have also been used to help compile a general descriptive picture of the home ranges and social organisation of the members of the study warrens.

(d) Assessment of Dominance

The concept of dominance has been widely applied in studies of animal behaviour, occasionally in a descriptive fashion, but largely as an explanatory concept. The problems of definition and assessment have been discussed frequently over the past decade (e.g. Richards, 1974; Bernstein, 1981). In general, researchers have tended to assess dominance either on the basis of priority of access to resources or on the outcome of agonistic interactions. In the rabbit, previous researchers have tended to assess dominance on the outcome of agonistic interactions (e.g. Mykytowycz, 1958; Myers and Poole, 1959; Lockley, 1961) but several additional characteristics have been attributed to dominant males (e.g. Bell, 1977). These include;

(i) large range
(ii) large number of displacements or chases of other rabbits
(iii) participation in extensive scent marking "tours"
(iv) responsibility for a large proportion of observed scent marking
(v) relatively high percentage of time spent above ground
(vi) relatively large amount of involvement in defence of warren.
One of the common methods of assessing the social status of individuals in a group of animals is to draw up a dominance matrix based on the outcome of conflicts between pairs of animals. A complete matrix of this type can only be compiled if all of the individuals comprising the group can be identified.

In the present study only a subsection of the rabbits living in each warren at any given time were marked and, although some of the remaining individuals could be recognised by physical features (eg. size, fur colouring, scars, tears in the ear, etc.), this meant that in only three cases was it possible to compile a complete dominance matrix for a warren. In the other warrens in the study areas there were at least two rabbits which could not be identified with confidence. In these cases the numbers of intrawarren interactions involving marked or otherwise recognisable individuals was noted, along with a record of the sex of their opponent, where possible, and an assessment of the outcome. In addition, the total number of intrawarren conflicts between adults was noted, even where these did not involve recognisable individuals. Thus it was possible to calculate the relative level of involvement of recognisable individuals in agonistic encounters and to assess the proportion of these encounters which they won or lost.

A total of 9 warrens were observed during the two years; 7 were observed in both years while Thistle Field 3 was observed only in 1976 and Nettle Hollow 2 only in 1977. During 4 hours of observation on each warren in each year all occurrences of intrawarren agonistic interactions between adults were recorded. Results are presented in appendix 2.
In 13 of the 16 social aggregates observed, the individual which was involved in the greatest number of agonistic encounters and which won most of these conflicts was marked. In the remaining 3 cases such individuals were recognisable. It seems probable that the large geographical ranges covered by such individuals and the generally higher level of activity (see Chapters 6 & 8) make them more susceptible than other members of the population to trapping by snares set on open runs.

It is possible that a more complete picture of the social organisation of the study warrens could have been obtained if all of the rabbits present had been identifiable. However, it is difficult to see how this could have been accomplished other than by digging out the warrens each year. The disruption to the warrens which would inevitably have arisen from such a procedure would undoubtedly have affected the social organisation and behaviour of the member rabbits and was felt to be unjustifiable given that the main aim of the project was the study of social behaviour in as natural a setting as possible.
CHAPTER 6

SOCIAL ORGANISATION AND HOME RANGES
In this chapter, general outlines of the social organisation of the warrens in the 4 study areas are given. These outlines are broadly descriptive and are intended to act as a backdrop against which the later more specific and quantitative behavioural data may be viewed. They trace the development of the warrens throughout the duration of the project and are based largely on data from ad lib observations in all three years, although in 1976 and 1977 supplementary information from observations using other, more structured, sampling procedures was also used. The number and identity of rabbits present in each warren, the location of inhabited burrows, the movements and home ranges of individuals and the location of intrawarren social interactions were recorded throughout the year.

Before presenting the results of these observations, certain terms used in the text merit some explanation.

(i) **Group**: Small mixed sex groups, varying in composition between one and three males and one and five females and occupying a territory which is defended by all of its members against intruders, are viewed by many researchers (eg. Mykytowycz, 1964; Myers et.al., 1971; Bell, 1977) as the fundamental units of rabbit social organisation. They are widely referred to as "breeding groups". A few breeding groups together form a "social entity" or a "colony" (Mykytowycz, 1974). These authors, however, present little direct evidence that members of breeding groups breed exclusively with other members of the same group. It might be argued that such a conclusion follows implicitly from the
suggestion that all intruders are excluded from the group territory, but certainly Mykytowycz and Myers mention the existence of "shared grazing areas" in many warrens.

In the present study small mixed sex groups of similar composition were observed in every warren within the study areas. Members of such groups shared a small collection of burrows and a geographical range. However, it was observed that, in warrens containing more than one group, such ranges were not necessarily defended against members of other groups. Thus, in these cases, such ranges were not necessarily exclusive to members of one group. In the present study, therefore, small mixed sex groups were differentiated on the basis of the geographical location of their shared group of burrows and shared home ranges, and not on criteria such as shared defended territory or breeding partners. Since the criterion of exclusive defended territory did not appear to be met in many cases, describing these small groups of adults as "breeding groups" seems difficult to justify, and the term "groups" is used instead.

(ii) Warren: Here, the term "warren" is used both to refer to a geographically distinct collection of rabbit burrows and to the rabbits inhabiting them. The rabbits inhabiting a warren are referred to by Mykytowycz (1974) as a "colony" or a "social entity". Each warren contains one or more groups and may be of considerable size. The warren at Sheepstead, studied by Southern (1940), covered approximately 0.5 acres and contained up to 70 adults. No warrens on the island appeared to be as large as this and in the study areas the largest observed warren contained 19 adults. Observations showed that an area around the warren is defended by member rabbits. While most defence involves adults,
they do not all participate in intrawarren conflicts with equal frequency.

(iii) **Home Range**: The commonly accepted and often quoted definition of home range, as the area covered by an animal in its normal daily activity (eg. Burt, 1949; Blair, 1953), is adhered to in the present study.

Clearly, the greater the number of observations of location or "fixes" of an individual, then the greater the confidence with which the observer can describe the home range of an individual. In practice such observations will be subject to the law of diminishing returns and a compromise between complete accuracy and time available for observation must be reached. The variability of ranging behaviour varies across species and the number of observations and the distribution of such observations across time required to permit an accurate description of ranging behaviour must also vary across species. The number of observations required to compile a realistic description of ranging behaviour in rabbits has not yet been determined.

Descriptions of home ranges were compiled from ad lib samples throughout all three years of the project and from focal animal and scan samples throughout 1976 and 1977. It is not possible to give data on the number of fixes for each individual as focal animal and ad lib samples are continuous records.

In the rabbit, the normal ranging behaviour of adults follows a remarkably similar pattern from day to day. Typically, in the early to mid afternoon, an adult emerges from its burrow and spends some time on the surface near the burrow before moving off to the grazing area. The grazing area, or area where the
rabbits of a warren spend most time feeding is normally located at some distance from the burrows, and the time taken reaching it appears to be dependent on the amount of good grazing along the way. At Nettle Hollow, for instance, where the warren was situated on a cinder deposit and there was very little grass near the burrows, the rabbits moved relatively rapidly to the grazing area. At Tennis Court 1, on the other hand, the rabbits made their way to the grazing area relatively slowly, stopping frequently to feed along the way. This pattern might be interrupted by social encounters, investigation of scent deposits or by scent marking bouts. Furthermore, scares would send rabbits bolting for burrows, to re-emerge some time later to follow a similar course all over again.

Variations in ranging behaviour do occur, however. Occasionally the normal pattern was affected by a combination of strong wind and rain. Alterations in ranges under such conditions were observed in area where some shelters could be gained in the lee of stone walls or buildings. Where these variations in ranging behaviour were observed they are described in the relevant section below. Sporadic major excursions from ranges occurred during chases when rabbits may cover considerable distances. Such excursions were not recorded as part of the normal ranges and after chases rabbits would usually quickly return to their home range.

It is felt that the observations of individuals were numerous enough to result in the described ranges being a realistic reflection of the limits of the normal daily ranging behaviour of the individuals concerned, at least during daylight hours. The absence of observations after darkness had fallen
clearly leaves open the possibility that nocturnal ranges vary from those observed during the day.

The home ranges shown in the maps in this chapter are a guide, therefore, to the limits of normal daylight movements by adult males. The ranges of adult females belonging to the same group were observed to be normally a subsection of the male ranges. Where exceptions occurred, these are noted in the text. Ranges of dominant males were usually considerably larger than those of other residents of a warren and again, are described in the text.

(iv) Dominant male: The method of assessment of social status is described in detail in chapter 5 but is essentially based on scored outcomes of adult intrawarren agonistic interactions. Data on the conflicts is presented in Appendix 2.

Descriptions of the changing social structure of the warrens in the four study areas are presented below. Each study area is described separately, with the position in the spring of each year documented in detail followed by a description of any subsequent changes throughout that year. Maps showing home ranges reflect the position in the spring of each year with subsequent changes described in the text.

(1) Cross Park

The Cross Park area is so named because of the configuration of stone walls which at one time had enclosed an area of pasture for livestock. The walls, except for those defining the eastern arm of the "cross", remain largely intact and enclose an area of rough pasture which slopes upward gently towards the south end.
In April 1975, when observations commenced, three warrens existed within the study area and rabbits from a fourth warren, located on raised rocky ground to the south west of Cross Park, occasionally grazed in the area (see fig. 6.1).

Warren 1, located in a cinder deposit along the northern wall of the area, was the largest in the study area in terms of the number of adult inhabitants. A total of 13 adults (6 males and 7 females) constituted 3 groups. Group 1A, consisting of 3 males and 4 females possessed a home range to the west of the warren. One pair of rabbits spent most of the time observed in each others company and occupied a burrow some 3 metres from the burrows occupied by other members of the group. One could therefore suggest that this pair constituted a separate group but it was felt that as the ranges overlapped almost completely there was no advantage to be gained by treating them as separate groups. The range of this group did not border on the ranges of groups from other warrens and therefore involvement in inter warren disputes was virtually non-existent. Occasionally, during aggressive chases the participants travelled well beyond the limits of the normal daily range. On three occasions when such chasing extended into the territory of warren 4 this elicited an aggressive response from the inhabitants of that warren (once from the female; twice from the dominant male). The dominant male of the warren was resident in group 1A but was the only member of the warren to regularly cover the combined area of the three group ranges in his normal daily activity.

Group 1B consisted of one male and one female and possessed a surprisingly large home range, overlapping largely with the group 1A range. The female was observed to spend almost all of
Cross Park study area, 1975. Aggregate subordinate adult male home ranges for each group are shown.

* Location of group burrows.

Cross Park study area, 1976. Aggregate subordinate adult male home ranges for each group are shown.

* Location of group burrows.

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their time in the section of the range to the south of the warren but the male spent a large part of the evening activity period within the group 1A range. At this time, during the breeding season, the male was evidently attracted by the females in group 1A and was involved in aggressive chases (11 obs.) as a result of approaching too close to a female. On 2 occasions he was chased by the dominant male, on 5 occasions by the other males and on 4 occasions by the female concerned. Although the group 1B range bordered on the warren 4 range the two rabbits from group 1B were never observed crossing into it. On only 7 occasions did the dominant male from warren 4 cross into the group 1B range. He was either repelled by the female (4 obs.), by the male (2 obs.) or by the dominant male (1 obs.).

Group 1C consisted of two males and two females and its range extended to the east of the warren. This group was more involved in interwarren conflict than any other as its range overlapped that of group A from warren 2 and covered a particularly attractive grazing area. Disputes at the grazing area were normally initiated when one individual approached too close to another and defence of females by males seemed common. If a rabbit from one warren strayed more than a few metres into the range of rabbits from the other they were invariably chased back.

In April 1975, warren 2 (situated in a jumble of stones and disturbed ground in the Eastern arm of the "cross") consisted of two groups and one "satellite" male. Group 2A consisted of one male and two females. The male was the dominant male of the warren and as in warren 1 regularly patrolled the combined area of the group ranges. The solitary male was frequently displaced by the dominant male but these extended into full aggressive chases on
only three occasions. This solitary male was also chased by the two females on the occasions when he approached close enough for olfactory inspection. While this male may have been a low ranking member of group 2A, his daily range included part of the group 2B range and he was therefore not regarded as an integral part of the group. The male range shown for group A of warren 2 in fig. 6.1 is the area in which the dominant male spent the bulk of his time each day in the absence of another adult male.

Group 2B consisted of a single pair. The female was observed to spend most of her time in an area to the south of the warren but the male occasionally ventured into the group 2A range, attracted by the females. Group 2B shared a territorial boundary with the members of warren 4 but aggressive interactions were rare.

As already mentioned, warren 3 was situated on raised ground to the south west of Cross Park and the main interest in this warren lay in the effect of its members on the overall social organisation of the rabbits in the Cross Park area. In April 1975 this effect was minimal. During that month rabbits from warren 3 were observed encroaching into Cross Park on only 5 occasions. On each occasion only one adult was involved (all possibly the same animal). On all occasions the encroaching rabbit grazed within 5 metres of a gap in the wall at C/D 7.5 (fig. 6.1) through which it had passed. On three of these occasions, it retired after 10-20 minutes quite spontaneously and on the remaining two occasions it retreated when the male from group 1C approached.

Warren 4 was located against the southwest wall of the southern arm at the "cross" and consisted of a single group of 2 males and 1 female. One male was dominant over the other and
frequently displaced it. All observed interwarren interactions involved either the dominant male or the female. The subordinate male was not observed to be involved in territorial defence.

Throughout the year the composition of these warrens changed considerably. In warren 1, one of the males from group 1A as found dead in July and by the same month one female from group 1A and one from group 1C were also missing. The group 1A male found dead was from the pair of rabbits living slightly apart from the rest of group 1A and the female remained in this burrow despite the loss of her mate. In August, fencing containing box traps was erected around warren 1 and by November the number of adults present had fallen considerably although none were found dead. Only 2 adult males and adult female remained in group 1A; the adult male from group 1B had disappeared and only 1 adult male from group 1C remained within the enclosed area although there were several juveniles present in each group. In addition, a group consisting of 1 adult male and 3 juveniles had established a new burrow system outside the fencing at F8 (fig. 6.1) and a group of 3 juveniles had established a new focus outside the fencing at D/E 8.5. From the population of 13 adults present in April, therefore, only 5 remained in November. Only 5 juveniles were present within the fencing in November and 2 new groups had been established outside the fencing consisting of a total of 7 rabbits.

In warren 2 the solitary male had disappeared by July and by September one of the females from group 2A was missing. By November there were no further changes in adult numbers therefore from the 6 adults present in April, 4 remained in November. During September several groups of young rabbits established themselves around the periphery of warren 2. By November one pair of dark
coloured juveniles, resident in a burrow at F7 were grazing in a section of the group 2B range and two groups of 3 and 2 juveniles established in the rocks at H/I8 were grazing near the track in the group 2A range. Including this influx therefore, in November there were 13 juveniles in and around warren 2.

During the summer of 1975 an increasing number of young from warren 3 encroached into Cross Park to graze around D9. The maximum number observed at any one time was 7 and as a result of warren 1 being enclosed by fencing in August and the reluctance of the rabbits to use the box traps, the warren 3 rabbits gradually ranged over a wider area to the west of warren 1. In October it was observed that 2 of the warren 3 young had established a burrow on the East side of the wall at D6.5.

In August the female from warren 4 was found dead and the two males had disappeared leaving 2 juveniles as the sole residents. By September these juveniles had also disappeared leaving the warren deserted.

1976

During 1976, systematic trapping and marking of the rabbits resulted in 11 of the 23 adults (48%) resident in the Cross Park area being marked. By early March when observations resumed, the social organisation of the rabbits in the area had altered considerably. The winter had been unusually severe with snow lying on the island on several occasions for up to a week. The population of rabbits had dropped noticeably and few of the adult rabbits of the previous season were in evidence. The territory defended by members of warren 1 had diminished in size on both the east and west sides of the warren. This had permitted a
corresponding expansion of the ranges of the groups comprising warrens 2 and 3. Warren 4 was not reinhabited and group 2B had expanded its range into part of the area previously occupied by warren 4 rabbits.

The greatest change had occurred in warren 1. Several of the box traps had been destroyed by winter gales and the fencing was in need of some repair. This meant that during the winter months the rabbits had free access to end from the warren without the need to use the smeuse tunnels. Despite this, none of the previous seasons adults remained and both of the groups established by juveniles outside the fencing had disappeared. The much smaller ranges of the remaining adults are shown in fig. 6.2. In March there were 2 groups comprising warren 1. Group 1A contained 2 males and 2 females. One of the females (F21) had been born in the warren during the previous season and had been marked in November 1975. Group 1B was composed was of 2 males and 1 female. The ranges of these two groups did not overlap and the dominant male (M47) which was resident in group 1A was the only rabbit to regularly traverse the combined ranges. Interwarren aggression was most frequently observed around C10-D9 with members of warren 3. At this time the members of warren 1 did not use the smeuses to the east of the warren and therefore their ranges did not bring them into contact with members of warren 2.

The groups comprising warren 2 had expanded their ranges (see fig. 6.2). The dominant male of the previous season had disappeared and the adult male of group 2B had assumed dominance. This male remained in the burrows at F6.3 even though his mate of the previous season was no longer in evidence. This is unusual in the light of previous findings (eg. Lockley, 1961) which suggest
that the removal of the dominant male is normally followed by another male both assuming dominance and taking over the burrows and often the females left by the previous dominant male. In the present case the new dominant male remained in a relatively small group while younger, subordinate males lived in a group in a larger complex of burrows. The only other adult of the previous season remaining in the warren was a female in group 2A. In March 1976, then, warren 2 contained 4 groups. Group 2A consisted of 3 males and 4 females and the range of these rabbits now extended over a large area to the west of the track. Group 2B consisted of 3 males and 2 females and again their range had expanded to the west of the track. Group 2C consisted of 2 males and 2 females and group 2D contained a single pair of adults. Ranges are shown in fig. 6.2. A solitary female was also resident in a burrow to the east of the group 2D burrows. This female was harassed by females in neighbouring groups and by April she had disappeared. The ranges of the males in groups 2A, 2C and 2D overlapped considerably and all grazed on the area of attractive pasture around F8-9 to G7-9. This area was the focus of much of the social behaviour observed during the evening activity periods and the dominant male spent a large proportion of his time there.

Warren 3 had also expanded although, as in 1975, detailed information on group composition etc. was not collected. A considerable number of warren 3 rabbits were trapped during 1976 and several of those regularly grazing in Cross Park were marked. Three adults (2 males, 1 female) grazed daily in Cross Park. One of the males and the female (F46) spent the majority of each evening activity period in the area whereas the remaining male (M79) entered the area only once or twice each evening, remaining
between 7 and 48 minutes at each visit. It is possible that M79 was the dominant male of warren 3 and was passing through Cross Park as part of his evening patrols of the territory and certainly his interactions with the two other adults supported this suggestion. All three adults were observed in interactions with members of warren 1.

Throughout 1976 the structure of the warrens in the area remained remarkably consistent. In warren 1 the unmarked adult female was found dead in September but apart from this the remaining 6 adults were still in evidence in November. In addition 7 juveniles were present; 5 belonging to groups 1A and 1B and a single pair which had established a burrow at the east side of the warren. In warren 2 the dominant male from group B had disappeared by April along with an adult female, leaving group 2B containing 2 males and 1 female. Thereafter M74, resident in group A, took over the dominant role in the warren. In August one of the adult females from group 2A was found dead and by November one of the adult males from group 2A and one of the adult males from group 2C were missing. From the 16 adults present in March, therefore, 11 remained in November. In addition 11 young were present in the warren; 3 in group 2B; 5 in group 2A and 3 in group 2C. The influx of young rabbits to the periphery of the warren observed in 1975 did not take place in 1976 possibly due to the increased number of rabbits already resident in the warren.

1977

During 1977 trapping and marking resulted in 15 of the 25 adults (62.5%) in the area being marked. In February 1977 when observations recommenced the major noticeable change was the re-expansion of the area covered by the ranges of warren 1 rabbits.
Cross Park study area, spring 1977. Aggregate subordinate adult male home ranges for each group are shown. * Location of group burrows.
Both groups 1A and 1B, consisting of 2 males and 3 females and 2 males and 2 females respectively, now covered larger ranges to the west and south west of the group burrows. In addition, a third group consisting of 2 males and 2 females was established on the east side of the warren, straddling the enclosing fence. This group's range overlapped slightly at the grazing area near the track with that of group 2A and this was a focus for a large number of aggressive interactions. The only adult rabbit remaining from the previous season was F21, now in her second adult season and still in residence in group 1A. The new dominant male (M129) had not been trapped before this season and may either have been one of the males born in the warren during the previous season or a newcomer. One of the adult females in each of groups 1A and 1B had been born in the same group during 1976 and one of the males in group 1C had been born in group 1B. It is interesting that the marked female in group 1C had been born in group C of warren 2 during the previous season and now defended territory against group 2C members. Again the dominant male (M129) was the only warren member to regularly move over the entire warren territory. Interwarren aggression occurred principally in the area to the east of the warren with rabbits from warren 2 and to the south west of the warren with members of warren 3.

Warren 2 again consisted of 4 groups situated in the same locations as the previous season (see fig. 6.3). The dominant male was still M74 residing in group 2A with 1 male and 3 females. The only other adult still in evidence from the previous season was F24, the female in group 2C. One of the adult males in group 2B had been born in group 2A in 1976. Although fig. 6.3 shows that the group ranges are similar to those reported for 1976 they did
<table>
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<th>ADULT MALES</th>
<th>ADULT FEMALES</th>
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<td>2C</td>
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<td>2D</td>
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Group composition: Number (and identity, where known) of adult males and females in warrens at the Cross Park study area.
not extend as far to the west. Only members of group 2A now ventured to the west of the track on a regular basis. Group 2B retained a very similar range and contained 2 males and two females and groups 2C and 2D contained single pairs of adults.

One group from warren 3 continued to graze in the Cross Park area and 4 adults (2 males, 2 females) regularly spent a large proportion of the evening activity period in this area. The situation observed in 1976 in which one male spent brief periods in this range was not repeated. It is possible that this group, which possessed a range quite separate from that of other warren 3 rabbits, may have become an autonomous unit.

The group structures and ranges within the warrens in the study area remained fairly stable throughout 1977 although as in previous years there was some mortality among the adults. In warren 1, F99 from group 1B and the unmarked male from group 1C had disappeared by June. In warren 2 one of the unmarked females in group 2A was found dead in June and by September both adults of group 2D had disappeared.

**Tennis Court**

Tennis Court is the description applied to the walled area of level pasture to the immediate north of Cross Park. The area was selected for observation because the unusually flat terrain permitted easy and accurate distance measurements to be taken and the relatively short, uniform turf meant that latrines and pawscrapes were easily identified. Such features made the area particularly suitable for the study of aspects of scent marking and the results of this work are reported in later sections.

In March 1976 when observations in this area commenced 3
warrens were present (fig. 6.5). Warrens 1 and 2 were enclosed by fencing set with box traps in August 1975 but trapping did not begin until March 1976. Warren 1 was a small, compact warren running along the west side of the eastern wall of Tennis Court. The enclosing fence formed a rough semicircle around the burrows with the two ends attached to the wall. The boxtraps were very successful in this warren and the capture rate was high (80% of adults and 62.5% of young). During the winter months the rabbits had decimated the vegetation within the fencing and were forced to use the box traps to leave the enclosure to obtain adequate food. The warren contained only a single group composed of 3 males and 2 females. The dominant male (M50) moved throughout the entire group range almost every day. The ranging behaviour of the remaining adults was more variable but normally on emerging in the afternoon they worked their way south from the warren feeding around C7 for an hour or so before moving farther south and turning east through the gap in the wall at C/B9 to graze around B8. The time taken over this sequence and the number of rabbits participating varied with the conditions. In a strong east wind they would spend almost the entire evening activity period in the lee of the wall around C/B 6-9. F23 grazed primarily within the Tennis Court and was only occasionally observed in the portion of the group range to the east of the wall. The unmarked female spend more time to the east of the wall than any other adult and was the only rabbit to use the gap in the wall to the north of the warren as a passage to the east side (the other members of the group would use this route only to escape back to the warren if startled). To some extent therefore the home range of this female differed from that of the other adults in the warren. It is also interesting to note that during March this female dropped a litter outside the warren to
Fig 6.5

Tennis Court study area, spring 1976. Aggregate subordinate adult male home ranges for each group are shown.
☆ Location of group burrows.

Fig 6.6

Tennis Court study area, spring 1977. Aggregate subordinate adult male home ranges for each group are shown.
☆ Location of group burrows.
the east of the wall at B5.5 consisting of 2 albino type young (M46 and F25). The only albino type adult observed in the area in the spring of 1976 was a solitary male living in the rough ground to the east of A6. This male was observed in the warren 1 range on 11 occasions and was chased off by the dominant male on 4 of these occasions. The young were only observed venturing west of the wall into the Tennis Court to graze around C5 on 5 occasions and it is possible that their presence on the eastern side of the wall influenced the range of their mother. Interwarren aggression centred around C/D 5-8 with members of warren 3.

Warren 2 was located along the southern wall of Tennis Court and in the spring was composed of 2 groups. (see fig. 6.7). Group 2A, consisting of 3 males and 2 females occupied a small set of burrows at the eastern end of the wall while group 2B, consisting of 2 males and 2 females occupied burrows to the west of this. The ranges of the members of these 2 groups were largely separate (see fig. 6.5) and both groups utilized quite distinct grazing areas. As in the case of warren 1 enclosing fencing was erected in August 1975 and trapping started in March 1976. The smeuse box traps were much less successful in this warren and were replaced in the spring of 1976 with catch-snares set in gaps in the fencing. Five of the 9 adults were trapped and marked during the year. The dominant male (M38), resident in group 2A, regularly used the area covered by both group ranges and a smaller male from group 2A (M48) also moved freely throughout both ranges although less frequently than the dominant male. The range of adult members of group A covered an area to the eastern side of the paddock and as in warren 1 the range included an area to the east of the enclosing wall. Access to this area was gained either through the
gateway at B/C 9 or through a tunnel dug beneath the wall at B/C 12.5. The range bordered on that of warren 1 and aggressive interactions were common around B/D 9. M38, M48 and the unmarked female were the individuals most commonly involved in such disputes. Members of group B were seldom involved in interwarren aggression although their range overlapped slightly with that of members of warren 3. Very little time was spent in the area to the north of the track (see fig. 6.5) although some members of the group would cross into this area at some time during most days. In fact most interactions with warren 3 rabbits involved M38 on his regular patrols of the territorial boundaries. In this case, M38 defended an area slightly larger than that covered by the ranges of the other members of the two groups.

Warren 3 was located on the side of a steep artificial bank at the northern end of tennis court. The location of the burrows did not lend itself to enclosure by fencing and the terrain did not facilitate open snaring therefore no attempt was made to trap members of this warren. In addition, several of the rabbits were very similar in appearance with no distinguishing characteristics. Therefore, beyond recording the fact that it appeared to consist of a single group of 3 males and 3 females and beyond mapping the range covered by its members (see fig. 6.5) little further detailed information was collected.

During the remainder of 1976 the ranges of the members of the three warrens altered very little but several of the adults died or disappeared. In warren 1 the unmarked female disappeared in July and M39 had disappeared by November. In warren 2, M48 disappeared from group 2A in September, M44 had disappeared from group B by November and F53 was found dead in November. Nine of
the 14 adults present in the two warrens in March remained when observations ended in November. At this time 5 juveniles, all of which had been born in the warren, were present in warren 1 and 8 juveniles, of which 4 had definitely been born in the warren, were present in warren 2.

In February 1977 warren 1 continued to consist of a single group composed of 3 males and 3 females. The dominant male (M50) was the only surviving adult from the previous season, but one male (M97) and 2 females (F56 and F63) had been born in the warren during the previous season. All 6 adults were trapped and marked. The daily range of the group members remained almost identical to that described for the 1976 season (see fig. 6.6). Warren 2 now consisted of 3 groups. Groups 2A and 2B continued to occupy the burrow systems used in 1976 but a single pair of rabbits had established a new burrow between these groups. None of the adults from the previous year had survived the winter, but M66, the new dominant male in group 2A, F67 of group 2B and M89 of group 2C were known to have been born in the warren during 1976. It is possible that some of the other individuals making up the 3 groups had also been born in the warren but they had not been trapped and marked and therefore positive identification was not possible. Group 2A consisted of 2 males and 2 females, group 2B consisted of 2 males and 3 females and group 2C, as mentioned above, consisted of a single pair. Of the 11 adults present 7 were trapped and marked. Groups 2A and 2B maintained similar ranges to those of the previous season although there was now virtually no overlap and the 2 rabbits of group 2C ranged over a surprisingly large area. However this pair generally grazed in an area shared with members of group 2B (E-F, 9-10) (see fig. 6.6) M66, the dominant male, was
### Fig. 6.7

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<th>Adult Males</th>
<th>Adult Females</th>
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### February 1977

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<td>(F, F)</td>
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Group composition: Number (and identity, where known) of adult males and females in groups in the warrens at the Tennis Court study area.
the only rabbit to regularly move throughout the entire area consisting of these group ranges. Interwarren aggression took place between members of both groups 2A and 2B and members of warren 1 as the ranges of both groups overlapped slightly at B9 and D-E 7.5 respectively.

Warren 3 again consisted of a single group composed of 2 males and 2 females. The dominant male was a large albino-type individual (M46) which had been born in warren 1 in 1976. This rabbit was particularly active in aggressive interactions with members of warrens 1 and 2 and frequently strayed into the territories of these warrens seemingly attracted by females. On one occasion this male was observed as far south as C11. The remaining members of the group, however, moved throughout a range similar to that described for 1976 (see fig. 6.6).

Throughout the year these ranges remained stable but the composition of some groups changed due to the death or disappearance of members. In warren 1 the dominant male (M50) was found dead and F97 disappeared in August. M97, the male born in the warren during 1976 assumed the dominant role. The unmarked female from group A in warren 2 disappeared in July. From the 17 adults present in these 2 warrens in February therefore, 14 remained in September at the conclusion of the study.

In warren 1, fifteen young survived until first observation and of these, 6 were trapped and marked. In warren 2, fourteen young were observed in group 2A, 9 in group 2B and 5 in group 2C. Of these 28 young a total of 11 were trapped and marked.
Nettle Hollow

Nettle Hollow is situated on a gentle east facing slope at one of the highest points in the centre of the island. The study site was overlooked by an abandoned WW II observation station. Most of the windows in this building remained intact and it offered an excellent vantage point as the observer was some 5m above ground level with a clear view of the warren system below. The warren system was located on a bed of cinders and ash from the 17th century coal burning beacon and was covered in the summer by a dense tangle of nettles and thistles, the roots of which provided some support for the burrows (see fig. 6.8). While the loosely packed cinders provided an easy medium in which to dig, the resulting burrows were prone to collapse. The rabbits were never observed feeding on either nettles or thistles and as there was little turf on the surface of the warren itself the rabbits were forced to feed on one of the grassy areas nearby.

In April 1975, a single large warren consisting of 5 groups was present in the study area. Several of the rabbits were suffering from, or showed signs of having recently suffered from, myxomatosis and the group compositions and ranges may have been affected by the death of members and by the rather abnormal behaviour shown by rabbits which had contracted the disease. Group 1A, consisting of two males and three females, inhabited a collection of burrows at G5 (see fig. 6.9) and contained the dominant male which regularly moved across most of the warren area. The remaining male was mottled in colour and slightly smaller than the dominant male and ranged over the northern portion of the warren, grazing primarily on the grassy area around C-D,2-3. The 3 females were more sedentary than the males and
Fig 6.8

Nettle Hollow study site. Summer vegetation, the shaded area shows the extent of the tall, thick vegetation around the warren (Urtica, Arctium etc.).

+ Location of observation site.

Fig 6.9

Nettle Hollow study site, spring 1975. Aggregate subordinate adult male home ranges for each group are shown.

+ Location of group burrows.
spent considerable time near the burrows and grazing around H4-6. However, during most evenings 2 of the females would at some time move to the larger grazing area around D2. The remaining female was suffering from myxomatosis and had a very limited range.

Group 1B, consisting of a single pair of rabbits inhabited burrows at G7 and the range covered an area of grazing from B7 to D11 and the routes to and from this area. The male was invariably the first to emerge from the burrow in the afternoon and covered a slightly larger range than the female. Group 1C, again consisting of a single pair of rabbits, possessed a range which overlapped considerably with that of group 1B, although on certain occasions this pair were observed grazing to the west of the burrows around H9. Again the female was generally more sedentary than the male. Group 1D, composed of three males and two females inhabited a collection of burrows on the eastern perimeter of the warren at C5. Members of this group grazed on both of the main grazing areas to the north east and south east of the warren and in the late evening occasionally moved down the slope to the east of the warren. One of the males was exhibiting signs of myxomatosis but interacted freely with other members of the warren and moved across a range similar to that of the healthy members of the group. Group 1E, consisting of one male and one female occupied burrows at E4 and moved throughout a small range which included the grassy area from B1 to D3. This pair also occasionally moved down the slope to the east of the warren to graze. The male showed the scarring around the eyes typical of a rabbit recovering from myxomatosis, but did not exhibit abnormal behaviour. Finally, a solitary individual occupied a burrow at E8. This individual was in the advanced stages of myxomatosis and appeared to be almost
completely blind. As it interacted very little with other members of the warren it was impossible to deduce its sex. Its range was severely limited, normally moving only a few feet from the burrow in order to graze.

The number of unoccupied burrows present in the warren and the existence of several groups composed of single pairs of rabbits suggest that myxomatosis had reduced the population in this area considerably. During the following months several of the rabbits which had been showing signs of the disease disappeared, although the males in groups 1D and 1E recovered. By July group 1B had disappeared and in August the male from group 1D which had recovered from myxomatosis was found dead. It is possible that the female from group 1B died and the male moved on. By November, when observations ceased, only 9 of the 17 adults present in April remained. However, throughout the breeding season a large number of young were born in the warren and there were 13 juveniles present in the warren in November.

In March 1976, when observations resumed, 4 groups were present within the warren and one group was present to the south of the warren within the range of groups 1C and 1B during the previous season (see fig. 6.10). Group 1A, occupying the same burrows as in 1975 consisted of 3 males and 3 females. One of the males (M25) and one of the females (F07) had been trapped in the warren during 1975 and although the dominant male (M51) was not trapped and marked until May 1976 it is probable that this rabbit had been the dominant male during the previous season. The range of this group had altered little from that described for 1975 but, as the total area covered by the combined group ranges had diminished, the dominant male moved over a reduced area. During
Nettle Hollow study area, spring 1976. Aggregate subordinate adult male home ranges for each group are shown.

Location of group burrows.

Nettle Hollow study area, spring 1977. Aggregate subordinate adult male home ranges for each group are shown.

Location of group burrows.
1976 the ranges of the 4 constituent groups covered an area around the periphery of the main cinder deposits of Nettle Hollow and the central area was unoccupied. However the dominant male was the only rabbit to regularly cross this area, travelling between the ranges of groups 1B and 1C. Therefore although the range of the dominant male was smaller than that recorded in 1975 it exceeded the combined ranges of the adult members of the constituent groups.

Group 1B consisted of one male and one female. This pair had inhabited these burrows during the autumn of 1975 and ranged over the rather poor grazing area to the west of the warren. They were frequently harassed by F07 and F35 from group 1A in the area where the ranges overlapped around H4-6. Group 1C, consisting of 2 males and 2 females inhabited burrows around D6 and ranged over an area at the south eastern periphery of Nettle Hollow. One of the males in this group (M22) had been born in the warren during the previous season and this male ranged more widely throughout the group range than the other members. Members of this group (particularly M22) were frequently involved in aggressive encounters with members of a warren located immediately south of B12 as the ranges of these 2 groups met at the grazing area around C10. Group 1D, consisting of 2 males and 3 females occupied the same burrows as group 1D in 1975. The range covered by these rabbits was also similar to that reported for the previous season although it was slightly reduced on the southern side. Again, rabbits from these two eastern groups occasionally ranged down the steep slope to the east of the warren, particularly during the evening activity period.

Of the 17 adults present in the warren in March, 8 (47%) were
trapped and marked during the year.

A single pair of rabbits (group 2X) had occupied a burrow at F9 during the autumn of 1975 and were still in residence in March 1976. The range of this group was not part of the range of the dominant male and they were not regarded as belonging to the main warren. In fact the daily range of this pair was very small and did not border directly on the ranges of any other rabbits. Thus they were seldom involved in social interactions with other rabbits and on only 3 occasions were they observed to be involved in aggressive encounters (always with M22 of group 1C).

Throughout the remainder of 1976 there was a high death or disappearance rate among the adults. The reason for this are not clear — certainly there was no evidence of myxomatosis in this warren in 1976. One unmarked female from group 1D disappeared in May and in July F49 disappeared and M22 was found dead in group 1C. In August the unmarked male in group 1A disappeared and by November both the dominant male (M51) and the unmarked female from group 1A had gone. Finally, the remaining pair of unmarked rabbits from group 1C had disappeared by November, leaving the group 1C burrows occupied by 3 juveniles. At the conclusion of observations in November, therefore, only 9 adults remained in the warren of the 17 present in March. As in the previous season, however, a large number of juveniles were present in and around the warren from the breeding season onwards. One interesting feature of this study area was the number of young living in and around the buildings adjacent to the warren in the late summer and autumn. In all three years up to 10 juvenile rabbits could be found in the spaces beneath a raised storage hut at H-Ill and many more occupied short scrapes dug in the ash deposits around the
Fig. 6.12

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<th>Warren</th>
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Group composition: Number (and identity, where known) of adult males and females in groups in the warrens at the Nettle Hollow study area.
periphery of the warren. A number of these young rabbits were trapped and marked and almost all had disappeared from the study area by the following spring. In November 1976 a total of 12 juveniles occupied burrows within the warren itself.

In February 1977 the process of division of the warren into two separate warrens had progressed. In 1976 group 2X was the only group not under the influence of the dominant male from group 1A but in 1977 two groups, constituting warren 2, had sole control of the grazing area to the south east of the warren. Warren 1 now consisted of only 3 groups with ranges along the northern side of the original warren territory. There was virtually no interaction between the adults of these two warrens. Of the total of 19 adults present in February, 8 were trapped and marked.

In warren 1 the only adult surviving from the previous season was F35 which continued to belong to the group occupying the burrow at G5. This set of burrows was the only site in the study area to be occupied throughout the 3 years of observations. In addition, throughout the 3 years, the dominant male of the warren was a member of the group occupying this burrow system. In February 1977, then, group 1A consisted of the dominant male (M121) and 2 females (F35, F93). The range of this group remained similar to that described for the group in previous years. All 3 members grazed at some time in the day, usually during the evening activity period, on the patch of short cropped grass to the north east of the warren. Additionally the females, in particular, spent much time in the morning and the afternoon on the patch of grass to the west of the burrows. This area was shared with members of group 1B which contained 2 males and 2 females. This group occupied a set of newly excavated burrows some 15 metres north
west of the group lA burrows and grazed solely on the area immediately to the west of the burrows. Group lC occupied burrows and possessed a range in virtually the same location as group lE in 1975. This group contained 2 males and 3 females and one of the males (M73) had been born in group lD during 1976. The range encompassed the grazing area from B2-D3 and, as the area immediately to the north was the grazing area for members of a neighbouring warren, members of both groups lA and lC were frequently involved in aggression with these rabbits.

Warren 2 contained 2 groups with largely overlapping ranges which both included the area of grazing around B7-D11 (see fig. 6.11). Group 2A was composed of 2 males and 2 females and contained both the dominant male, which was not marked, and M96, which had been born in a neighbouring warren during 1976. Neither the single male nor the 2 females constituting group 2B were trapped during 1977. This small group occupied burrows to the north east of the group 2A burrows and the range of its members was similarly extended in this direction (see fig. 6.11). Interwarren aggression was common between members of warren 2 and rabbits located in a warren to the south east at the area of shared grazing around B-C,9-10.

The adult death or disappearance rate was much lower in 1977 than in the preceding years of observation although it must be pointed out that observations ceased in September rather than in November. In September 8 of the 11 adults remained in warren 1 and 5 of the 7 adults remained in warren 2.

**Thistle Field**

The Thistle Field is an irregularly shaped, walled area of
rough pasture lying north of the ruined chapel on the southern half of the island. Large sections of the area are covered with a tangle of thistles during the summer months and, in addition, patches of nettles occur around the main warren sites. The walled pasture contains the field station, a large heligoland-type bird trap and a small bird trap in addition to the crumbling foundations of several wartime buildings. The area was selected for study because of the large number of rabbits present, the flat terrain and because of the convenience of the field station as an observation point. However, at some times during the summers, the area was subject to considerable disturbance due to the presence of both bird ringers using the traps and other workers in the field station.

In April 1975 when observations commenced there were 3 warrens in Thistle Field, Warren 1, situated in the large heligoland bird trap was the largest and consisted of 3 groups and a solitary male. Group 1A contained the dominant male, 2 further males and 3 females and occupied burrows along the base of the eastern boundary wall at A/B 5.5. Group 1B, consisting of a single pair of adults, occupied burrows a few metres from group 1A at A/B6. The ranges of these 2 groups overlapped considerably although the males from group 1A ventured farther afield in their grazing. On most days during the late afternoon members of both groups would emerge from the burrows and move slowly out while grazing to around D6.5. Throughout the evening the adults continued to move further afield while grazing, following a wide arc to the grassy area in front of the field station. The females of both groups seldom ventured farther than the limits of the range shown for the group 1B male (see fig. 6.13). Group 1C,
Thistle Field study area, spring 1975. Aggregate subordinate adult male home ranges for each group are shown.
★ Location of group burrows.

Thistle Field study area, spring 1976. Aggregate subordinate adult male home ranges for each group are shown.
★ Location of group burrows.
composed of one male and 2 females possessed a quite separate range. The group 1C burrows were situated along the inside of the bird trap fencing at B/C 5.2 and the females invariably left the burrows through a tunnel burrowed under the fencing adjacent to the burrows and moved west to a grazing area at C4-D3. The male, however, on emerging in the afternoon, sometimes travelled south within the trap, travelling to the grazing area via D6 and E5. The dominant male, from group 1A, was the only other adult to regularly use the tunnel under the trap fencing in normal activity. Other rabbits were observed using the tunnel during aggressive chases or as a means of escape when disturbed. The dominant male regularly patrolled the area covered by all three group ranges and, although it would frequently displace other males in groups 1A and 1B, the greatest number of aggressive interactions took place with the large male from group 1C. This male showed a great deal of interest in the group A females during the breeding season and during amatory chases occasionally roamed fairly deeply into the group 1A range before being chased off by the dominant male. The group 1C male also displaced other males in the warren and was observed chasing the solitary male, which occupied a burrow a few metres south of the group 1C burrows, more than any other male. The solitary male had a relatively small daily range, restricted to a long strip some 3-4 metres on either side of the outer fence of the trap. It was displaced or chased by other adults in the warren if it approached within roughly 3 metres of their position. On two occasions this male was observed following females during the breeding season but was chased off by a male each time.

Warren 2 was situated in the centre of the field, the burrows
being dug under two tangles of scrap metal netting. There were 2 groups present in April 1975 and the ranges of the males overlapped almost completely. Group 2A, consisting of 3 males and 3 females contained the dominant male and group 2B was composed of one male and 2 females. There was little intrawarren aggression between the members of these 2 groups and most aggressive interactions involved members of warren 1 in the grazing area where the ranges were adjacent (see fig. 6.13). Aggressive chases between both male and female members of the two warrens were often continued over unusually large distances (e.g. on one occasion the dominant male of warren 1 chased a warren 2 male into the "garden" area to the west of F/G1.

Warren 3 also consisted of 2 groups and was located at the southern end of the field. Group 3A, consisting of the dominant male, one other male and 2 females occupied burrows about 10 metres to the east of group 3B which contained a single pair of adults. Serious aggressive chases were rarely observed between the members of this warren and, as the ranges were not immediately adjacent to those of the other warrens in the study area there was little interwarren aggression. The ranges of the males of both groups overlapped to a large extent and all warren members grazed regularly in the area around E10-F11.

Throughout the year the most important changes in group and warren structure occurred in warren 2. In May 1975 it was observed that one adult from warren 2 had contracted myxomatosis and by July the dominant male, one other male and 4 of the females had disappeared, leaving only 2 males and one female in the warren, all living in the group 2A burrows. Members of warren 3 now grazed along the western wall, in what had been warren 2 territory, as
far as G7 and this expansion continued throughout the summer. By September, the remaining adults from warren 2 had disappeared leaving 3 young rabbits occupying the group 2A burrows. In warren 1 the solitary male had disappeared by July in addition to one of the adult males and an adult female from group 1A. In September, the female from group B in warren 3 was found dead and the adult male had disappeared. By November, when observations ceased, warren 1 consisted of; the dominant male (M05), another adult male and F14 in group 1A; the pair of adults in group 1B; and the male and F06 in group 1C. No adult members of warren 2 remained and warren 3 contained a single pair of adults in the group 3A burrows. Therefore, of the 27 adults resident in the study area in April, only 9 remained in November. There were, however, 8 young in warren 1, 2 young in warren 2 and 6 young in warren 3. In addition, new collections of burrows had been excavated at C9 and C3 and these contained 5 and 3 young rabbits respectively.

In March 1976, when observations resumed, there were again 3 warrens in the study area but, while warrens 1 and 3 remained in approximately the same locations as in the previous year, the warren 2 burrows were no longer occupied and the newly designated warren 2 was located along the eastern wall of the field at C9 in a collection of burrows which had been established by young rabbits during the autumn of 1975. While none of the adults which had been marked during the previous season remained in the study area it is possible that some unmarked adults were still present. Certainly some of the young rabbits which had been trapped and marked in 1975 were still present in the 3 warrens. Of the 31 adults present in the study area in March 1976, 11 (35.5%) were trapped and marked during 1976.
Warren 1 contained 4 groups and the burrows were again located within the heligoland bird trap. Group 1A, consisting of M28 and F05 (both of which had been recorded as being born in the warren during the previous season), the dominant male (M45) and 2 further females, occupied the same set of burrows on the eastern wall as group 1A in the previous year. Group 1B, consisting of 1 male and 1 female also occupied the same set of burrows as in 1975. On the fence side of the trap 2 groups were now present - group 1C, consisting of M37, F22 and another pair of adults; and group 1D, containing M58 and an adult female. Groups 1A and 1B occupied similar ranges to those described in 1975 although the range had increased around F/G6 to cover part of the area vacated by the central warren 2 rabbits. Members of group 1C were also grazed in the area around E6-7 but normally worked their way around to C4.5 later in the evening. F22 of group 1C, who was trapped in March when pregnant dropped a litter at the generator shed at F/G4. The reasons for dropping a litter well outside the normal daily range of any group member is not known. F22 continued to visit the young occasionally. Group 1D members were the only rabbits in 1976 to regularly use the tunnel under the fencing at B5 and although their range overlapped slightly with that of group 1C, it was largely exclusive. The dominant male (M45) again patrolled most of the warren territory on a daily basis but was not seen to use the tunnel to move from within the trap to the group 1D range or vice versa. Interwarren aggression was now frequently observed with members of both warrens 2 and 3 along the extensive boundaries between the respective territories.
Warren 2 consisted of a single group occupying a small collection of burrows against the eastern wall of the field at C9. The group contained the dominant male (M40), M61 and 3 females. Two of the females frequently passed to the east of the boundary wall through a small hole at B6.7 and it was observed that at least one litter was dropped by one of the females there. The remaining female and the two males spent all of their time within the field area, grazing primarily around D-E 8 and C-D 10. The members of warren 2 were effectively excluded from the prime grazing area around D-E, 6-7 by rabbits from warren 1 and M40 and the female most often present were frequently involved in aggressive interactions with both males and females from warren 1. While at this location the members of warren 2 were principally the recipients of aggression, at the alternative grazing patch around C-D 10 they were primarily the aggressors against intruding members of warren 3.

Warren 3 now consisted of 3 groups and continued to occupy burrows at the southern end of the field. Group 3A, the central of the three groups and located at E11.7, contained the dominant male (M15) and F01, both of which had been trapped in the warren during 1975, in addition to 2 further males and 2 further females. Group 3B occupied burrows several metres to the west and contained 2 males and 3 females of which M30 was known to have been born in warren 2 during 1975. Group 3C contained a single pair of adults and occupied a range to the east of the other two groups. Groups 3A and 3B had extended ranges along the western boundary wall into what had been the territory of the central warren 2 and the group 3B range was now adjacent to the territory of warren 1 around F-G,6-7 (see fig. 6.14). However warren 3
territory was now compressed slightly on the eastern side due to the expansion of the new warren 2.

During the year the adult population changed as follows. In warren 1 one of the females from group 1A had disappeared by the start of June and by July the male from group 1B had gone. The female in this group, however, remained resident in the group burrows until observations ceased in November. In warren 3 one of the males from group 3A and one of the females from group 3B were also missing in July. In warren 1, M37 from group 1C was found dead in mid August and it was observed that the unmarked female from the same group had also disappeared from the study area. In addition, one of the females from warren 2 had disappeared in August. M28 from group 1A was found dead in September and in warren 3 it was observed that one of the unmarked females from group 3A and unmarked male from group 3B had disappeared. By November M40 (the dominant male) and one of the two remaining females had disappeared from warren 2. In warren 3 the dominant male (M15) was found dead, one of the two remaining females in group 3B was missing, and the pair of adults constituting group 3C had disappeared. When observations ceased, near the end of November, only 15 adults remained from the initial complement of 31 noted in the spring.

A large number of young were born in the study area during 1976 and a total of 18 were marked during the year. In warren 1 33.3% of those young surviving to first observation were marked and in warren 2 37.5% of those born within the study area and surviving until first observation were marked. In November 28 young were present in the study area of which 8 had been trapped and marked.
In February 1977, when observation recommenced, the basic locations of the 3 warrens in the study area remained as they had been in 1976 and, although the size and composition of each warren had altered, the defended territories and daily ranges of the member rabbits remained similar (see fig. 6.15). Of the 29 adults present in the study area in February 1977, 15 (52%) were trapped and marked during the spring and summer of that year. Warren 1 now consisted of only 3 groups and the previous group 1B burrows were unoccupied. Group 1A contained 3 males and 3 females including the dominant male M45 which was the only rabbit remaining in warren 1 which had been marked as an adult in 1976. Group 1C contained 1 male and 2 females, one of which (F69) had been recorded as being born in group 1C in May 1976 and group 1D was composed of 2 males and 2 females. The ranges of all three groups were very similar to those reported in 1976, the only major difference being the compression of the group 1A range around E-G,5-7 which was now part of the warren 3 group B range. A great deal of interwarren aggression occurred between the members of both groups 1A and 1C and the members of warren 2 along the area of range overlap at B-E7 and to a lesser extent between the members of group 1A (particularly M45 and F90) and the members of group 3B at E6-G5. The dominant male (M45), while making daily tours throughout the warren territory followed a regular route which passed through the group 1D range but did not spend much time in the area and did not graze there.

Warren 2 now contained two groups. The only rabbit in the warren which had been marked as an adult during 1976 was M61 which had assumed the dominant position after the disappearance of M40 in November. Group 2A, therefore, contained 2 males (including
**Fig 6.1**

Thistle Field study area, spring 1977. Aggregate subordinate adult male home ranges for each group are shown.

* Location of group burrows.
M61) and 2 females, one of which (F73) had been recorded as being born in the warren in 1976. Group 2B was composed of a single male and 2 females. The ranges of the two groups overlapped to a large extent and all of the adults spend the bulk of the evening activity period grazing around D-E, 7-8. Occasionally however, particularly on days when a strong east wind was blowing, the members of the two groups grazed in separate areas in the lee of the eastern boundary wall. Due to the central position of this warren, the members were under considerable pressure from members of warrens 1 and 3 and spent more time involved in interwarren interactions than any other rabbits in the study area.

Warren 3, at the southern end of the field, was composed of 2 groups. Group 3A, occupying the eastern set of burrows at D/E 12.4 contained 2 males including the dominant male and 3 females, one of which (F37) had been born in the warren in 1976. Group 3B contained 2 males and 2 females. As mentioned above, the warren members had extended their territory farther to the north west along the western boundary wall (see fig. 6.15). This extended area was part of the daily range of group 3B and was vigorously defended by group members and by the dominant male against incursions by members of group 1A.

In April, one of the 2 females from group B in warren 2 disappeared and in June, the dominant male (M45) from warren 1 was found dead but did not seem to have suffered any wounding. The unmarked male from group 1A assumed dominance thereafter, and this change corresponded with an increase in aggressive chasing between the males in the warren, particularly between the new dominant male and M98 of group 1D. In July one of the unmarked females in group A of warren 3 disappeared and by late August the unmarked
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Group composition: Number (and identity, where known) of adult males and females in groups in the warrens at the Thistle Field study area.
female in group 1C was missing. By early September several adults had disappeared. Filll from group 1A and the unmarked male from group 1D were missing in addition to a male and female from group B in warren 3. By mid September, therefore, 21 of the 29 adults present in February remained in the Thistle Field study area.

CONCLUSIONS

The structure and composition of groups was observed to be similar to that reported by most previous researchers (eg. Myers and Poole 1959, Lockley 1961, Mykytowycz 1958). Groups contained between 1 and 3 males and between 1 and 4 females. Where the number of males in a particular group is X, the number of females present varied between (X-1) and (X+1). Only 10.6% (N=7) of groups recorded contained (X-1) females and 28.8% (N=19) of groups contained (X+1) females. The largest proportion of groups (60.6%, N=40) contained equal numbers of males and females - the most frequently observed composition being two males and two females. This is a smaller range of variation than that reported by Mykytowycz (1961), Myers and Poole (1959) and Myers and Schneider (1964). A more detailed discussion of the frequency of occurrence of the various group compositions in relation to breeding success is contained in chapter 7.

Warren structure

Over the three year period of the present study, the number of warrens under observation varied slightly. In 1975 seven warrens were studied in three areas, whereas in both 1976 and 1977, ten warrens were under observation in four study areas. A total, therefore of 27 annual warren structures were recorded and the frequency of occurrence of different compositions is shown in fig. 6.17.
Fig. 6.17

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Composition of warrens in the study areas in 1976 and 1977 (measured by number of constituent groups).
Warrens consisting of a single group constituted 26% of warrens observed. This warren structure is similar to that reported by Mykytowycz (1958) and Myers and Poole (1959). A single group of rabbits, consisting of several males and several females inhabit a defended territory. This appears to be accepted by most authors as the fundamental unit of rabbit social organisation. The social behaviour of rabbits in such warrens was observed to follow the pattern described by the Australian researchers. A rough linear dominance hierarchy (as measured by aggressive interactions) appears to exist between the males but the relationships between females and between males and females is more complex.

Between males, intrawarren aggressive interactions followed several common patterns. Both during and outside the breeding season the most frequent form of interaction was simple displacement of one male by another with no physical contact. Chases and fights only rarely developed from these encounters. During the breeding season, many interactions centred around the defence of females. The dominant male was frequently involved in chasing off other males which approached too close to females. However, in some groups non-dominant males formed a partnership with a particular female and spent a great deal of time in her vicinity. Such males often defended these females by either chasing off more subordinate males or by rushing at more dominant males. This latter tactic would result in the more dominant male chasing the subordinate male, often over a large distance. Almost invariably after such an interaction the more dominant male did not return to the female.
Initiation of aggression by females was largely location dependent. Females possessed patches of varying sizes, usually containing the burrow entrance which they defended against other females and most males. During grazing, females only infrequently displaced other adults either within or outwith the breeding season. Some individual females were particularly aggressive but this did not seem to fit into a general pattern across warrens. In general, a linear dominance hierarchy (scored on the outcome of aggressive encounters) did not exist among females but particularly in single breeding group warrens, if one female was aggressive this could appear to be the case.

This phenomenon was reported by Myers and Poole (1961) who note that "some females were by nature aggressive, others very quiet". However observations in the present study suggest that even in the case of these aggressive females the outcome was location dependent.

During the breeding season females were frequently inspected by males and occasionally these inspections were prolonged into the long slow chases noted by Southern (1948), or developed into more aggressive chases. On some occasions the female would attack the male and see him off, but as mentioned above, in most cases a more dominant male intervened. Outside the breeding season the adult females retire from most social interaction but continue to defend their particular "patch" vigorously. However, to some extent personal space is also defended even during grazing particularly by the more aggressive females. In the late summer, adult females are particularly aggressive towards young individuals and were occasionally observed to drive off dominant males.
The relationship between males, therefore, is quite different from that between females. The suggestion by Mykytowycz (1958) that a linear female dominance hierarchy similar to that in males exists is not borne out by observations made during the present study despite the use of similar criteria for dominance. These observations accord with the findings of Myers and Poole (1959) despite their reservations about the artificiality of their study conditions.

These descriptions of single group warrens apply to only 26% of observed warrens. However, it should be noted that areas chosen for study were selected partly because of a high concentration of rabbits, a good field of view and other practical considerations. It seems probable that where the overall density of rabbits or the terrain is different, the various compositions of warrens will occur with different frequencies. Certainly some of the warrens under study were among the largest noted on the island and in a more general survey it is probable that warrens composed of a single group would be more common than is suggested by the present results.

(b) Warrens consisting of Multiple Groups

74% of the warrens studied contained more than one group (range 2-5). In almost all cases a single dominant male patrolled the combined ranges of the component groups on a daily basis. Although the route taken by the dominant male normally passed through each group range, the amount of time spent in each range and the area of the range covered varied from warren to warren. All the males in the area classified as a warren were submissive to the dominant male and in many instances the dominant male would
deviate from his path while patrolling in order to displace a male. In most warrens group ranges overlapped to some extent and therefore members of different groups were in daily contact. This was less true of females which had smaller ranges than the males.

Interactions within groups were described above for single group warrens but intergroup aggressive interactions between males were more flexible. For example, certain males were observed consistently to repulse the dominant male if he approached a female group member but this was by no means a widespread phenomenon. At joint grazing areas there was very little aggression shown between males if females were not involved. In most cases the interactions which did occur closely resembled those in the single group situation. Females again defended particular areas around burrows against other females, either from the same group or from outside and as described above some females were particularly aggressive towards other rabbits. The organisation of a multiple group warren, then, resembles quite closely the organisation of a smaller single group warren. The linear dominance hierarchy among males however is less rigid and in inter-group conflicts the outcome is more situation or location dependent. The single dominant male seen in every multiple group warren displaces other adult males frequently but may sometimes be repulsed if a male is defending a female.

Such a multiple group organisation under a single dominant male was observed by Lockley (1961) for one breeding season before he removed the dominant role from one enclosure and it remained the organisation in the remaining enclosure for the length of the study. It was also recorded by Mykytowycz (1958) during the initial phase of the Canberra study. Again this system collapsed
on the removal of the dominant male but appeared also to do so spontaneously later in the season as the population increased.

(c) Home Ranges

The ranges presented in figs. 6.1 - 6.15 are aggregate adult male daily ranges. Normally these overlapped almost completely within groups but in some groups variations did occur (eg. in the path taken between the burrows and the grazing area) - these are mentioned in the text.

Adult male ranges vary considerably in size. The smallest recorded in the present study was that of the Cross Park 1B group during the spring of 1976. This group consisted of 2 males and 1 female and occupied a range of some 450m². The Cross Park study area was densely populated and there was considerable competition for space between different warrens. This range was recorded after warren 1 had declined in size and much of the previously occupied territory was taken over by members of warren 3. In addition, an adequate grazing area lay almost adjacent to the group burrows. The largest recorded range was that of the Nettle Hollow 1A group in the spring of 1975. This group consisted of two males and three females and occupied a range of 2100m². The burrows in this group lay some distance from the two primary grazing areas and it is possible that access to a grazing site is a prime factor in determining home range size.

Myers and Poole (1959,1961) report that range sizes decrease with increasing population density and results from present observations (see app. 3) confirm that rising overall adult density is significantly correlated with decreasing adult male range size ($p<0.01, r_s=0.76, N=11$). However, it is also apparent
### Table 6.18: Study Area, Year, Number of Groups, Number of Warrens, Overall Density (Adults/acre), Mean Adult Male Home Range Size (acres) (m²)

<table>
<thead>
<tr>
<th>Study Area</th>
<th>Year</th>
<th>Number of groups</th>
<th>Number of warrens</th>
<th>Overall Density (Adults/acre)</th>
<th>Mean adult male home range (acres) (m²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cross Park</td>
<td>1975</td>
<td>6</td>
<td>3</td>
<td>10.43</td>
<td>0.35</td>
</tr>
<tr>
<td>Cross Park</td>
<td>1976</td>
<td>6</td>
<td>2*</td>
<td>12.32</td>
<td>0.30</td>
</tr>
<tr>
<td>Cross Park</td>
<td>1977</td>
<td>7</td>
<td>2*</td>
<td>12.32</td>
<td>0.23</td>
</tr>
<tr>
<td>Nettle Hollow</td>
<td>1975</td>
<td>5</td>
<td>1</td>
<td>6.94</td>
<td>0.44</td>
</tr>
<tr>
<td>Nettle Hollow</td>
<td>1976</td>
<td>5</td>
<td>2</td>
<td>7.76</td>
<td>0.27</td>
</tr>
<tr>
<td>Nettle Hollow</td>
<td>1977</td>
<td>5</td>
<td>2</td>
<td>7.76</td>
<td>0.29</td>
</tr>
<tr>
<td>Thistle Field</td>
<td>1975</td>
<td>7</td>
<td>3</td>
<td>23.28</td>
<td>0.21</td>
</tr>
<tr>
<td>Thistle Field</td>
<td>1976</td>
<td>8</td>
<td>3</td>
<td>26.72</td>
<td>0.16</td>
</tr>
<tr>
<td>Thistle Field</td>
<td>1977</td>
<td>7</td>
<td>3</td>
<td>25.00</td>
<td>0.17</td>
</tr>
<tr>
<td>Tennis Court</td>
<td>1976</td>
<td>4</td>
<td>3</td>
<td>9.39</td>
<td>0.44</td>
</tr>
<tr>
<td>Tennis Court</td>
<td>1977</td>
<td>5</td>
<td>3</td>
<td>9.86</td>
<td>0.40</td>
</tr>
</tbody>
</table>

Mean adult male home range size and the adult density (no./acre), number of groups and number of warrens in each study area in each breeding season of the study (see appendix 3 for statistical treatment of data).

* although only 2 warrens were located within the study area, rabbits from a further warren grazed within the study area and it seems probable that they had an effect upon the distribution and ranges of the rabbits included in this sample.
from fig. 6.18 that the number of groups in an area is inversely correlated with adult male range sizes and in one case (Cross park, 1976/1977) this was independent of increasing density although the situation is complicated by the presence of rabbits from warren 3 grazing in the area (see figs. 6.2 and 6.3).

In three of the study areas, while the walled enclosures do not strictly speaking confine the rabbits they do effectively limit normal expansion and in these areas rising overall density of the adults does seem to compress home ranges. However it is probable that these ranges are elastic only within certain limits and that these are defined by access to a suitable grazing area.

While the results of this section of the present project are similar in many respects to the results of the Australian enclosure studies, it seems clear that there is more variation in a naturally occurring population than is apparent in the captive populations previously studied. Most of the enclosure study populations consisted of small warren systems and a very similar social structure to that reported by Mykytowycz (1974) and Myers et. al. (1971) was observed in small single group warrens in the present study population. However, in the larger multiple group warrens the observed existence of a single dominant male with access to the ranges of all of the component groups is a phenomenon which has not previously been reported. Furthermore, while Myers and Poole (1959) refer to the defence of female group members against intruders rather than territorial defence per se (a phenomenon observed during the present study), this observation appears to have been omitted from more recent summaries of rabbit social organisation. Clearly considerably more research on natural populations is required to clarify the position. Until this is
carried out the currently accepted picture of breeding groups with completely independent dominance hierarchies, inhabiting exclusive territories within the larger framework of the warren must surely be questioned.
CHAPTER 7

REPRODUCTIVE PERFORMANCE
Reproductive Performance

Reproduction in the rabbit is a complex phenomenon and is far from being fully understood. Although the laboratory rabbit has been used extensively in reproductive studies throughout this century, it was not until 1941 that any attempt was made to investigate reproduction in the wild rabbit (Brambell, 1944). The results revealed that much work was still required and Brambell remarked "It might be thought ...... that although precise information is scanty, investigation of the reproduction of the animal in the wild state could add little of importance. Yet such an assumption is unjustifiable for it will be shown that the wild rabbit in fact differs widely from the tame rabbit in its reproductive processes".

Laboratory rabbits, it was known, are contact stimulated ovulators and are capable of breeding throughout the year. However, there is some evidence of a reproductive cycle in wild rabbits based on a 7 day or multiple 7 day period (Myers and Poole, 1958, 1962), and in the UK there is a fairly sharply defined breeding season extending from January to June (Brambell, 1944; Phillips, 1955b, Phillips, Stephens and Worden, 1952; Lloyd, 1970). There are records of sporadic breeding in small numbers throughout the year in most populations and there have been some reports (eg. Phillips 1955b) of autumn breeding in substantial numbers, but this is unusual in the U.K. Lloyd (1970) reports that in the period following the epizootic of myxomatosis, when population levels were greatly reduced, the breeding season commonly extended into August. Brambell (1944) found that the onset of the breeding season could be delayed and the subsequent
season shortened by a particularly severe winter. The presence of frost or snow reduces fertility in rabbits (Myers and Poole, 1962) but whether this effect is primarily on males or females is not known. Brambell (1944) concludes that the onset of the breeding season is determined by the condition of the females but that the cessation of breeding in the summer is determined by the condition of the males. The testes begin to decline in weight at the height of the breeding season and reach a minimum weight with a corresponding reduction in spermatogenesis in July. Lloyd (1970), however, does not mention this finding and suggests that exhaustion of the females may terminate breeding. It seems more likely that loss of libido in the males is the main factor in ending the breeding season as it has been demonstrated that, at least in Australian conditions, providing nutritional requirements are met females can breed in the summer if fertilized (Myers and Poole, 1962).

It is axiomatic in reproduction theory that young mammals are born at a time of the year when food of the required quality and quantity is available either for the nursing mother or for the weaned offspring or both. However as Lloyd (1970) points out, at least by subjective estimates, food is available for rabbits in the U.K. in greater quantity and of better quality in July and August than in January, February or March and he concludes "Thus, the termination of breeding in the season in this species may be unconnected with food availability". The results of studies carried out in Australia go some way toward explaining how this strange state of affairs could have arisen.

In Southern Australia the breeding season of the wild rabbit follows a pattern differing in some important respects from that
seen in U.K. populations. There is a normal spring breeding season which comes to an end abruptly as the pasture dries out in the summer. It seems probable that the very sudden termination of breeding near the beginning of the hot, dry summer is due to the inability of the females to lactate on dry food. There is then a second breeding period in the autumn as the autumn rains allow the growth of fresh pasture. It is suggested (Poole, 1960; Myers and Poole, 1962) that this essentially bimodal breeding pattern may be the ancestral breeding pattern of the European rabbit in the Mediterranean climate of its original home on the Iberian peninsula. The fact that in a Mediterranean type climate the rabbit breeds both on an increasing light schedule in the spring and on a decreasing light schedule in the autumn had led Watson (1957) to argue that it is unlikely that changes in photoperiod directly govern the breeding season. However it is possible that breeding is affected not by increasing or decreasing day length per se, but rather by the ratio of daylight to darkness which is equal at the spring and autumn equinoxes. Certainly, even in the U.K. populations, the males seem to go through a period of sexual activity in the autumn although this usually takes the form of interest in the maturing young females of the year. It seems probable that the important difference between U.K. and Australian populations is that in the U.K., the adult females do not experience a corresponding autumnal period of sexual activity. It is known that the juice of fresh green plants injected into oestrogen primed female rabbits can cause ovulation by triggering secretion of pituitary hormones (Bradbury, J.T., 1944) and it may be that the absence of fresh pasture growth in the U.K. in autumn inhibits ovulation in females at this time. Such an argument goes some way towards explaining the fact that rabbits in the U.K. have
a shorter breeding season than environmental conditions would seem to allow.

Previous studies have reported considerable variation in breeding season length, the mean number of litters per female and the mean number of young per litter in different populations. Lloyd (1970) suggests that population density is a major factor in determining such variation. Myers (1966) reports that both food availability and population density affect overall productivity, although the results suggest that the relationship between numbers, space and breeding success is a complex one. Direct comparison of results is hampered by the fact that breeding success has been recorded in different ways in different studies. Litter size, estimated from examination of embryos in dead females from large scale rabbit clearance schemes in Wales (Phillips, Stephens and Worden, 1952, Stephens, 1952; Phillips, 1955b) varied between 4.36 and 4.6. Litter size has also been estimated from observations of wild populations. In the U.K. Lloyd (1970) found mean litter sizes varied from 2.8 to 5.9 depending on the location of the population and in Australia Myers and Schneider (1964) observed mean litter sizes of 5.14 and 5.5 in different warrens. The total annual productivity or the mean number of young born per female per year has also been reported in various studies. Those carried out in the U.K. report mean figures varying from 3.9 (Lockley, 1961) to 30 in one of Lloyd's (1970) study populations. The remainder of the British studies, however, report a smaller range of mean annual productivity of between 8 and 12 (Brambell, 1944; Lloyd, 1963; Southern, 1940). There is also a suggestion in the literature that litter size may increase throughout the breeding season (Southern, 1940). Stephens (1952) reports that the
The mean number of embryos in pregnant females rises from 3.39 at the start of the season to 5.70 at the peak of the season.

The social organisation of the rabbit and the definitions of certain key terms used in the present study are discussed fully in chapters 5 and 6. However, as several of the points made have direct relevance to this section they are reiterated briefly here.

The "breeding group", consisting of a small number of adult males and females is regarded by many researchers as the fundamental unit of rabbit reproductive activity. The available data on the composition of such groups comes largely from enclosed populations and reflects considerable variation within certain limits. Mykytowycz (1960) reports that breeding groups in the Canberra enclosures consisted of 1-5 males and 1-7 females. Myers and Poole (1959), however, report that breeding groups in the Albury enclosures were limited to 2-3 males and 3-4 females. Lockley (1961) describes smaller groups of 1 male and 1-3 females.

In the present study similar small groups of adults were observed in all of the study warrens but, due to doubts about the exclusiveness of breeding between the members of such groups, they are referred to simply as "groups" rather than as "breeding groups". In warrens consisting of more than one group it was frequently observed that a single dominant male roamed freely throughout the collective ranges of the other members of the warren. Thus, while in the Australian enclosure studies, each breeding group can be viewed as an independent social entity, this was not always observed to be the case in the present free living study population. The frequently observed existence of a dominant male from one of the component groups of a warren which had access
to the ranges of the members of other component groups clearly casts doubt on the reproductive independence of groups.

While the concept of dominance has been the subject of considerable debate over the past twenty years, it has frequently been demonstrated that there is a correlation between social status and reproductive success - "to dominate is to possess priority of access to the necessities of life and reproduction" (Wilson, 1975). This correlation has also been reported in populations of captive rabbits (e.g. Mykytowycz, 1960; Myers et al., 1970). Myers and Poole (1959) suggest that the aggression of the dominant male may have a limiting effect on the number of males in the 'breeding group' and hence on their access to females. However, there is no evidence from studies of wild populations to support such a suggestion.

One further factor which may differentially affect reproductive success is the quality of the home burrows. It has been suggested (Lockley, 1961) that the suitability of the burrow system for giving birth to litters (in terms of warmth, freedom from flooding etc.) may affect the survival of offspring and may permit females to give birth to young earlier in the season than females forced to use isolated breeding stops. Where there is such variation in the quality of burrows (as far as can be ascertained by observers) there is some evidence that dominant rabbits have priority of access to the favoured sites (Mykytowycz, 1961; Lockley, 1961).
AIMS AND HYPOTHESIS

The aim of this section of the present study is to investigate the general pattern of reproductive activity among members of the island population and the factors influencing their reproductive success.

(i) Overall Reproductive Performance: Basic data on the following features of reproductive performance are presented to permit comparisons with other populations:

(a) The times of onset and termination of the breeding season.
(b) The pattern of breeding and in particular the variation in mean litter size throughout the season.
(c) The mean annual productivity of the females in the study warrens.

(ii) Factors influencing interwarren variation in reproductive performance

(a) The number of warren inhabitants - As discussed above, there is considerable evidence that population density is an important determinant of the observed variation in breeding success between populations. In the present study the effect of number on within population variation is examined. The number of rabbits in the warren is used as an index of "density". The reasons for the decision to use such an index are covered in the discussion later in this section. It is hypothesised that the number of rabbits in a given warren is inversely correlated with the mean reproductive success of the member rabbits.
(iii) Factors influencing intrawarren variation in reproductive performance

(a) The size and composition of groups

(b) Social status. Although paternity of litters could not be ascertained with any confidence, it is hypothesized that the mean reproductive success of females occupying the same home as the dominant male burrow system will be higher than that of the females belonging to other groups in the same warren.

Method

The term 'reproductive success' refers to the number of surviving offspring produced by an individual. In ideal conditions it would be advantageous to have a measure of the number of offspring surviving until they in turn reproduced. This is seldom a realistic goal in field studies on unrestricted populations and, in the case of the rabbit, the dispersal of the young at the end of their first summer, as they approach sexual maturity, makes this particularly difficult. In the present study the tracking of young following dispersal was attempted in only one area and the results are discussed in later section of this chapter.

The number of offspring surviving until first observation is used throughout this chapter as a measure of reproductive success. However, the author's presence on the island, and hence the observations, were not continuous throughout the breeding seasons. This means that the interval between the time of birth and first observation of the young was variable and therefore a source of error in any comparisons drawn between the reproductive success of different individuals. The fact that the precise date of birth of litters is, in many cases, unknown makes it impracticable to use a
standardised survival interval as a measure. In general then, the estimates of reproductive success, based on the number of young surviving to first observation, must err on the low side – the error being produced from the following possible sources:
(a) Death or emigration before observation.
(b) Litters born outside the observation area.
(c) Failure to observe litters or individual members of litters.

The study warrens were chosen largely for their ease of observation and, although the warrens were not dug out to enable an accurate census to be taken, error (c) is unlikely to have introduced major bias into the results. Error (b) was more important in certain warrens and, where females were suspected of dropping litters outside the observation area, the data has been omitted from the relevant analyses. Emigration before first observation is unlikely to have contributed much error to the data as observations were frequent enough to record the young before such emigration took place. The major source of error, therefore, is probably due to the death of young before first observation. Tyndale-Biscoe and Williams (1955) in a study of a New Zealand population of wild rabbits estimate that mortality was as high as 41% for the first 21 days of life. However, most deaths were due to predation and the absence of mammalian predators in the present study population undoubtedly reduced the mortality rate considerably. Moreover, the data in this section come from observations of relatively well established warrens and obviously include only a small sample of the rabbits born on the island. Those rabbits born in less well established warrens or in isolated breeding stops may well have suffered considerably higher mortality. However, during the period immediately following
emergence from the breeding burrow the young rabbit is at its most vulnerable and mortality at this time must contribute some error to the data. It must be accepted, then, that estimates of reproductive success in this section do not necessarily accurately reflect the number of young born, but rather give an index of the number of young surviving across a variable interval between birth and the time of first observation.

Any analysis of the distribution of litter production and variability in litter size across the breeding season can only be attempted in those cases where it is possible to calculate the date of birth of the litter. Of the litters born in the study warrens over the two breeding seasons, at least some members survived until they were recorded in 117 cases. Of these litters, in 72 cases at least one member was trapped and weighed, permitting a rough index of age and hence data of birth to be obtained. In a further 4 cases the young were observed within a few days of emerging from the breeding burrows and the date of birth was calculated on the basis that the normal time elapsing between birth and first emergence is approximately 21 days (Thompson and Worden, 1956).

RESULTS

(i) Overall Reproductive Performance

The data stem from observations carried out during the breeding seasons in 1976 and 1977 on seven warrens. Six of these warrens were in existence across both seasons while the Nettle Hollow 2 warren was only formed in 1977. For the purposes of comparison each warren is treated as a separate entity in each of the two years of this section of the study. This means that the same individual may appear in more than one group of data (eg. a
female's productivity in one season may be compared directly with her productivity in the following season). Given that different conditions prevailed during successive breeding seasons, this was regarded as a valid procedure and as the only way of unravelling the effects of variables across seasons. The results, therefore, effectively comprise data from 13 warrens which are, in turn, composed of 37 groups. The total number of adults in the sample is 144, of which 75 are females.

(a) **Times of Onset and Duration of Breeding Seasons**

In both years of the study the first litters were born in February but, possibly due to the particularly severe winter of 1975/76, very few litters were dropped as early as this in 1976. Of the litters for which date of birth could be calculated, only 8 were produced before mid March in 1976 compared with 15 in 1977. However, breeding extended later into the summer in 1976 than in 1977 (see fig. 7.1). The breeding seasons on the island, lasted some 14 weeks in both years with the modal time of birth in each year occurring during April.

(b) **Variation in Litter Size**

As, in most cases, it was not possible to positively assign individual litters to specific adult females, it is not possible to trace the sequence of litters dropped by each females. It is possible, however to examine litter size and survival across time in more general terms (see fig. 7.2). Again the measures used in this analysis is the number of young, in litters for which date of birth could be calculated, surviving until first observation. Fig. 7.2 shows that, when the data from the two seasons is combined, there is a general tendency for mean litter size to be smaller early in the season and for the variability in litter size to be
Fig. 7.1

Distribution of births (individuals and litters) during the 1976 and 1977 breeding seasons. Only those litters for which data of birth could be calculated are included in this analysis.
Fig. 7.2

<table>
<thead>
<tr>
<th>TIME OF BIRTH</th>
<th>Early Feb</th>
<th>Mid Feb</th>
<th>Late Feb</th>
<th>Early March</th>
<th>Mid March</th>
<th>Late March</th>
<th>Early April</th>
<th>Mid April</th>
<th>Late April</th>
<th>Early May</th>
<th>Mid May</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean Litter size</td>
<td>2.5</td>
<td>2.63</td>
<td>2.86</td>
<td>3</td>
<td>3.4</td>
<td>3.38</td>
<td>2.92</td>
<td>3.17</td>
<td>3.2</td>
<td>3.2</td>
<td>2</td>
</tr>
<tr>
<td>Standard Deviation</td>
<td>0.71</td>
<td>0.75</td>
<td>1.07</td>
<td>0.89</td>
<td>0.7</td>
<td>0.51</td>
<td>0.64</td>
<td>0.75</td>
<td>0.63</td>
<td>0.45</td>
<td>-</td>
</tr>
<tr>
<td>Coefficient of Variation (%)</td>
<td>28</td>
<td>29</td>
<td>37.4</td>
<td>29.7</td>
<td>20.6</td>
<td>15</td>
<td>21.9</td>
<td>24</td>
<td>19.8</td>
<td>14</td>
<td>-</td>
</tr>
<tr>
<td>N (total=76)</td>
<td>2</td>
<td>8</td>
<td>7</td>
<td>6</td>
<td>10</td>
<td>8</td>
<td>13</td>
<td>6</td>
<td>10</td>
<td>5</td>
<td>1</td>
</tr>
</tbody>
</table>

Variation in litter size throughout the breeding season (combined data for 1976 and 1977 seasons).

Fig. 7.3

<table>
<thead>
<tr>
<th>WARREN</th>
<th>Mean reproductive success (offspring/female)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1976</td>
</tr>
<tr>
<td>Tennis Court 1</td>
<td>8</td>
</tr>
<tr>
<td>Cross Park 1</td>
<td>6.75</td>
</tr>
<tr>
<td>Tennis Court 2</td>
<td>5.25</td>
</tr>
<tr>
<td>Thistle Field 1</td>
<td>5.14</td>
</tr>
<tr>
<td>Cross Park 2</td>
<td>4.13</td>
</tr>
<tr>
<td>Nettle Hollow 1</td>
<td>3.4</td>
</tr>
<tr>
<td>Nettle Hollow 2</td>
<td>-</td>
</tr>
<tr>
<td>Mean Annual R.S.</td>
<td>4.71</td>
</tr>
</tbody>
</table>

Mean reproductive success within the 7 study warrens for the two years of the study. Note that Warren Nettle Hollow 2 was not in existence during the 1976 breeding season.
greater.

(c) **Mean Annual Productivity**

Of the 6 warrens in existence for the two years in which data was collected, 5 showed a greater mean productivity per female in 1976 than in 1977 (see fig. 7.3). Overall mean reproductive success was slightly higher in 1976 (1.65 litters per female: 4.71 offspring per female) than in 1977 (1.49 litters per female: 4.46 offspring per female). Across the two years of observations a total of 117 litters were born in the study warrens giving an overall annual mean of 1.56 litters per female. This mean litter size of 2.93 results in an overall annual productivity of 4.57 offspring per female. The mean productivity varied considerably from warren to warren, ranging from 3.27 offspring per female at Nettle Hollow 1 to 6.67 offspring per female at Tennis Court 1.

(ii) **Factors influencing interwarren variation in reproductive performance**

(a) The number of warren inhabitants

Warren size is calculated in four different ways.

(a) Number of Groups (range 1 - 4)
(b) Number of Adults (range 5 - 19)
(c) Number of adult females (range 2 - 10)
(d) Number of adult males (range 3 - 9)

Correlations between warren size, using each of these four measures, and mean reproductive success of the member females were calculated using Spearman's correlation coefficient ($\rho$) N=13 (see fig. 7.4 and appendix 4.1).
WARREN

<table>
<thead>
<tr>
<th></th>
<th>Adult Females</th>
<th>Adult Males</th>
<th>Total Adults</th>
<th>Groups</th>
<th>Mean Reproductive Success</th>
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Warren size and mean reproductive success. Summary of data.
(a) The number of groups in a warren is negatively correlated with reproductive success ($r = -0.71$) $p < 0.01$

(b) The total number of adult rabbits in a warren is negatively correlated with reproductive success ($r = -0.75$) $p < 0.01$

(c) The number of adult females in a warren is negatively correlated with reproductive success ($r = -0.79$) $p < 0.01$

(d) The number of adult males in a warren is negatively correlated with reproductive success ($r = -0.68$) $p < 0.05$.

The greater the number of inhabitants in a warren, then, the lower is the mean reproductive success of its members. This finding holds true across all four methods of measuring warren size.

(iii) Intra Warren Variation in Reproductive Success

(a) Group Composition

Considerable variation in both total number of adults and composition of observed groups is evident from fig. 7.5. In general, the number of females in a given group is equal to or greater than the number of males. Only 4 examples were recorded where this is not the case and, as it is probable that the surplus male in each instance was not an active breeding member of the group, these have been recorded in fig. 7.5 along with groups of equal ratios. The most common group structure is two males and two females followed by one male and one female. These are also the most successful group configurations in terms of productivity. The two male/two female composition is slightly more successful than any other (mean annual productivity = 5.18 offspring per female). The results of a Kruskal-Wallis one way analysis of variance reveal that $p < 0.1$, $H = 116.94$ d.f=1 (see appendix 4.2).
Frequency of occurrence of observed group configurations and the mean reproductive success of their members.

* (includes 2 examples of 2 male/1 female group structure)

** (includes 2 examples of 3 male/2 female group structure)

(see appendix 4.2 for statistical treatment of data).
(b) **Social Status**

In this analysis, data from only 6 warrens (5 of which were in existence across the two years of the study) are considered. Tennis Court 1 contained only one group and is therefore not included in the following comparisons. Within a given warren for each season, the mean reproductive success of the members of the group containing the dominant male is compared with the mean reproductive success of the members of the remaining groups. Using a Wilcoxon signed pairs matched ranks test \( N=11 \) (see appendix 4.3) it is found that members of groups containing the dominant male enjoy significantly greater mean reproductive success than members of groups without the dominant male from the same warren in the same season \( T=9 \ p<0.01 \). It must be stated that any error present in the data will tend to bias the results in favour of the above conclusion. This is because the groups containing the dominant male usually occupy a central position in the warren whereas members of groups without the dominant male often occupied more peripheral positions and were therefore more likely to drop litters in less easily observed locations. However, for the reasons stated above in the method section, and because, given the small number of warrens under study the results demonstrate such a strong effect, it is probable that the effect is a genuine one.

Fig. 7.6 gives a summary of the relationship between warren size, based on the total number of adult inhabitants, and the mean productivity both of the females belonging to groups containing a dominant male and of those in groups without a dominant male. The warrens have been divided into "large" and "small" based on those above and below the mean size. The mean productivity is as follows: With dominant male in small warren > with dominant male
Warrens are divided into "large" and "small" based on those containing more or less than the mean number of adults. Warren size is compared with the mean reproductive success of groups containing a dominant male and with those not containing a dominant male.
in large warren > without dominant male in small warren > without dominant male in large warren. The hypotheses that there will be an inverse relationship between warren size and reproductive success and that the presence of a dominant male in a group will increase mean productivity are therefore supported.

It is possible that an increase in the number of inhabitants of a warren affects all the member rabbits equally or alternatively it is possible that there is a qualitative difference in the pattern of breeding in large and small warrens. There is some evidence from studies of other mammals that the value of dominance is enhanced at high population densities (Myers, 1966). It might be expected, therefore, that in large warrens the reproductive success of members of groups without a dominant male is disproportionately affected by the increase in numbers. However, Fig. 7.6 shows that, if anything the opposite is true. This impression is supported by a series of Spearman's correlation coefficients carried out on the data (see appendix 4.4). Groups without a dominant male do not show a significant inverse relationship between mean productivity and warren size. This finding holds true irrespective of the method used to measure warren size. However, groups containing a dominant male do show significant inverse relationships between productivity and warren size across 3 methods of measuring warren size (N=11).

(a) Number of adult females \( (\rho_i = -0.54) \ p < 0.05 \)
(b) Total number of adults \( (\rho_i = -0.55) \ p < 0.05 \)
(c) Number of groups \( (\rho_i = -0.55) \ p < 0.05 \)
(d) Number of adult males \( (\rho_i = -0.50) \ N.S. \)

Members of groups containing a dominant male are therefore more affected by increased warren size than are members of groups.
DISCUSSION

Previous researchers have reported considerable variation in breeding season length and productivity in different populations and in the same population across different seasons. Evidence from studies on British offshore islands suggests that the breeding season tends to be shorter than on the mainland. Lockley (1939) reports that on Skokholm young rabbits did not usually appear until April. Lloyd (1970) however, in a comparative study of populations on several offshore islands, including Skokholm, reports that in the years between 1959 and 1963 the breeding season length varied between 10 and 17 weeks in length. The onset of breeding varied between late January and late March and it ceased between late May and late June. In a comparison study carried out on the Welsh mainland, Lloyd found that while the onset of breeding was only slightly earlier, the season lasted considerably longer into the summer months. In the present study the breeding season lasted some 14 weeks in both years and ended in May, considerably earlier than the time suggested by most mainland reports.

It is interesting to note that Henderson (1979) was carrying out a study of rabbit population regulation on the nearby Fife mainland in 1976 and 1977. He reports that in both years the first young were not born until April and the modal date of birth was in May. In 1976 the season lasted into July and in 1977 it tailed off more slowly with sporadic breeding taking place into August and September. The season started later in 1976 after the severe preceding winter, as it did in the present study, but continued later in 1977 which was not the case with the island population.
It is possible that the generally milder climate of the Isle of May permitted an earlier start to breeding than on the neighbouring mainland but it is difficult to unravel the reasons for it ending earlier than in other populations. Climate, food availability and population density have all been noted as affecting breeding season length in the rabbit. Climate, certainly in the U.K. however, undoubtedly exerts more influence on the timing of the onset of the breeding season rather than on its termination. Food availability seems, at least subjectively, to have been a relatively unimportant factor in the two years of the study on the island. Although the vegetation in the main feeding areas became very close-cropped during the summer months, it appeared to be present in greater quantity and of considerably better quality than at the start of the breeding season. Lloyd (1970) suggests that populations existing at high population densities have shorter breeding seasons and show lower productivity than low density expanding populations. The overall density of adults in the study warrens was moderately high (15-20/Acre) for U.K. populations, and about half of the maximum density observed on Skokholm (described by Lloyd as "a very high density population"). It is possible, therefore, that the density level on the Isle of May is sufficient to affect the length of the breeding season especially as Lloyd's (1970) results show that populations on Skokholm and Skomer at similar density levels to those on the May, had shorter breeding seasons than those reported here. It is also interesting that in 1976 when the population was smaller due to the effects of the preceding winter the mean productivity was higher, despite a later start to the season, than in 1977.
Density, therefore, may play an important part in curtailing the length of the breeding season. It cannot alone, however, account for the general low productivity of the rabbits. The mean number of litters born to females is low (1.56) but not unusually low. Many previous researchers (e.g. Southern, 1940; Lockley 1961; Brambell, 1942) have reported that in wild U.K. populations females produce roughly 2 litters in a season. The mean number of young born per female, however, is approximately half that reported in other comparable studies even in populations at higher density levels. It is possible that this discrepancy is due to the error sources mentioned above and in particular to juvenile mortality. In other words that a high percentage of young actually born in the island population did not survive until recorded. Alternatively, it is possible that the females simply produce small litters. One explanation for this could be genetic in nature. The island population has, as far as can be ascertained, remained in virtual genetic isolation since the 14th century and there is some evidence that low fertility is genetically determined (Southern, 1940). It is certainly known that the factor for foetal atrophy is recessive and it is possible that isolation and inbreeding may have increased the likelihood of its occurrence in the Isle of May population.

The mean litter size increased throughout the breeding season but it is not known if the females drop smaller litters early in the season or if the litter size is constant and a greater proportion of young survive later in the season. There is certainly some evidence that the former is true (Southern, 1940, Stephens, 1952; Myers and Poole, 1961) although it seems probable that the climate and the poor quality of food in February and
March may result in higher mortality. Results from studies carried out in S.E. Australia showing that young born late in the season suffer higher mortality than those born early in the season (Mykytowycz and Fullagar, 1973) can be explained by the rapid drying up of the pasture and the subsequent food shortage at the start of the summer hot season.

Although overall population density (measured as numbers of animals per unit area) has been referred to in the discussion above to permit comparisons with previous studies, it is of course a very broad generalisation, taking no account of the realities of the social organisation of a colony-dwelling species such as the rabbit - "The rabbit ....... even with unlimited space, will congregate around a central warren area, creating localized minor crowding" (Mykytowycz and Fullagar, 1973). It is, nonetheless, a valuable general concept allowing comparisons to be drawn between populations. However, the present study is limited to within population variation and at this level it ceases to be particularly useful. The environment is not uniform, nor are the rabbits randomly distributed throughout it. Given that the environment is composed of niches of different quality and the population is long established in that environment, it is reasonable to assume, especially in severely limited environment such as the island, that the high quality niches are occupied. One of the choices facing an individual rabbit living in a high quality niche, therefore, is whether to remain in the present niche or to emigrate to an occupied or less populated but lower quality niche. In addition to the fact that the rabbit is a gregarious animal and seems attracted to established groups (Lockley, 1961) there is, by definition, an advantage in deciding
to remain in the high quality niche, but does such a decision also incur a cost? There is a limit to the carrying capacity of a given niche in terms of provision for the physical necessities of life but Myers (1964) has demonstrated that at "moderate" population densities (50 animals/acre), even if food and water are provided in excess, the member rabbits show the effects of stress and productivity declines. One common explanation for the increased stress in high density populations is the increased number of contacts with other members of the population (e.g. Wilson, 1975). Even at very high density levels (200/acre) rabbits remain in their social groups, but the groups become larger, increasing the number of contacts with other animals. Given this, it was decided to look at the effect of the size of warrens on the reproductive success of their members.

The results show clearly that there is an inverse relationship between warren size and reproductive success with the highest negative correlation being with the number of adult females present. The four measures used are obviously inter-related to a high degree and it seems probable that several combined factors give rise to the overall decline in productivity. Females appear to be more space dependent than males in that they are more territorially conservative and defend an area within the warren, particularly against other females. It is probable, therefore, that the number of adult females in the warren system is an important factor in influencing the breeding success of an individual female. Mykytowycz and Fullagar (1973) report a close inverse correlation between the proportion of breeding females in a population and the density of females. This does not rule out the possibility that an increased number of animals in the male's
immediate environment may decrease male fecundity. The series of very carefully controlled experiments by Myers (1966) on captive populations of rabbits demonstrated that at very high densities both sexes show physiological changes. In males the adrenal and spleen weights increase while kidney weights decrease. In females the adrenal, spleen and kidney weights all decrease. Among newly weaned rabbits, body weights are significantly lower and adrenal weights significantly higher in high density populations.

Unfortunately in studies of wild populations such careful controls cannot be recreated and variables may be confounded. In the present study for instance it is possible to argue, although it seems unlikely, that large warrens occur in less favourable locations than small warrens. However, examination of fig. 7.3 reveals that in four of the five warrens which altered in size over the two years, mean productivity was lower in the year of larger warren size than in the year of lower size. The results of the present study, then, show that variations in productivity, while not as marked as those in Myers' artificially controlled environments, are statistically significant in a wild population living at relatively low density. There is, therefore, a cost in terms of reproductive success to continuing to expand the number of animals at an established warren site. It would be interesting to know how the productivity of a large warren compares with the productivity of some of the smaller groups of rabbits living among the rocky outcrops which abound on the island. Such outcrops could permit the digging of only shallow burrows and seem, subjectively, a lower quality niche than the study warrens. Unfortunately such a comparison was not undertaken, primarily due to difficulties of observation. However, analysis of trap/retrap data on young
animals in the Cross Park and Tennis Court areas shows that the young remaining in the study warrens at the end of the summer have significantly higher growth rates than those that emigrate to the rocky area nearby called Ardcarran (see fig. 2.2 and Chapter 3).

The fact that the most successful group composition in terms of breeding success was also the most frequently observed composition, suggests that there may be strong selection pressure on rabbits to limit the number of males and females in a single group. The only previous study on a wild population of rabbits to report 'breeding' group composition and productivity was carried out on a collection of 5 small warrens in Southern Australia (Myers and Schneider, 1964). The results show that 3 of the 5 groups comprised 2 males and 2 females and that at the end of the study these contained a mean of 7.67 surviving offspring per female while the other 2 groups contained a mean of only 4.5 surviving offspring per female. Group composition has not previously been examined as a possible factor affecting breeding success in the rabbit and unfortunately the results of the Australian enclosure studies are not presented in such a way as to permit such an analysis to be undertaken. Thus, it is not known if this result is generally applicable to rabbit populations living under different conditions. Indeed, it is difficult to see why this particular group composition of 2 males and 2 females should be more successful than other configurations and it is a feature of rabbit social organisation which seems to merit further research, particularly on natural populations.

Previous researchers studying the effect of social status on breeding success in enclosed populations (eg. Mykytowycz, 1959; Myers and Poole, 1961) have used the social status of individual
females to draw comparisons between the overall breeding success of dominant and subordinate females. Such data is very difficult to collect in field studies of natural populations and data in the present study permits only between groups comparisons as litters could not be directly attributed to individual females. However, six of the study warrens contained more than one group and in each case, one of these groups contained a dominant male which ranged throughout the entire warren territory. It was felt, therefore, that some index of the influence of social status on breeding success could be obtained by comparing the mean breeding success of members of the group containing the dominant male with that of groups in the same warren which did not contain the dominant male. While it is probable that there is considerable variation between the breeding success of the females within a particular group, the results clearly show that the mean breeding success of females in the group containing the dominant male is significantly higher than that of the females belonging to the other groups in the same warren. Limitations of the present study prevent the assessment of the importance of the various intermediate causal factors. It is possible that genetic differences, resulting in variations in the number of young born, are the prime factor or perhaps the fact that dominant animals have access to higher quality breeding burrows, resulting in a higher survival rate of offspring, is more important. These factors can only be unravelled by a carefully controlled series of experiments in a semi-natural environment.

Having ascertained that warren size is inversely correlated with breeding success it was argued that this reduction in breeding success could afflict all member rabbits equally or alternatively it could afflict a sub-section of the members
disproportionately. In other words it is possible that larger warrens contain a higher proportion of reproductively unsuccessful individuals. If this is so, evidence from other species suggests that these unsuccessful individuals are likely to be the subordinate animals as dominant animals are more resistant to the effects of rising numbers. One might expect, therefore that the mean productivity of those groups containing dominant males would show a lower inverse correlation with warren size than the productivity of other groups. This is not the case. Indeed, the members of groups without a dominant male do not show a significant negative correlation between reproductive success and warren size, while members of groups containing a dominant male show significant negative correlations between breeding success and the total number of adults, the number of adult females and the number of groups constituting a warren.

As the paternity and maternity of offspring could not be directly attributed, there remain several possible explanations for this phenomenon. It is possible, for instance, that the dominant male and his female partner/s are as productive in large warrens as they are in small warrens, while the other members of the group are disproportionately affected by increasing numbers in the warren. The only measure of reproductive success in the present study was at the level of the group – not at the level of the individual. However, while the differential value of belonging to a group containing a dominant male diminishes in larger warrens, it is still better to be in a dominant male's group in a large warren than to be in another group even in a small warren (see fig. 7.6).

Therefore, although groups containing a dominant male are
more affected by warren size, they are not so affected as to reduce their breeding success to the level of members of other groups. But why should increased warren size disproportionately affect groups containing a dominant rule? Increased size seems to negate some of the advantages which some groups have in small warrens. The possibility that the dominant male spends more time in aggressive encounters and therefore less time in reproductive behaviour does not seem probable, as the number of males in the warren seems less important than the number of females. More likely is the possibility that the intermediate effect acts through the females. It is possible that the stress of social interactions (defence of breeding burrows etc.) with a larger number of females has a levelling effect on reproductive success. Again, such factors can only be unravelled in more carefully controlled experiments beyond the scope of the present study.

It must be admitted that this section asks more questions than it answers. An attempt has been made to investigate certain factors affecting reproductive success in a natural population which have hitherto been studied only in captive populations. The problems inherent in the investigation of such factors in the field have been highlighted. However, it is important that the results from artificial populations are corroborated with evidence from natural populations. The answers to many of the questions posed above can come from studies of natural populations if one is willing to accept a greater amount of interference with the population than was deemed desirable in the present study. While such interference may have increased the amount of information available on reproductive performance, it would undoubtedly have decreased the validity of the results of other sections of the study.
CHAPTER 8

ACTIVITY PATTERNS
Activity Patterns

The recording and analysis of the distribution of an animal's activities in time in an essential first step towards the description of that animal's time-energy budget. Very little information towards this end has been collected on the European rabbit in the northern hemisphere. The only British study to concern itself with this problem was that carried out by Southern (1948) at the Sheepstead site. Southern reports in general terms on the general activity and daily variation in behavior of his study population but no systematic sampling of behavioural states is recorded. Seasonal variation of a few social behaviors is reported in more detail. However, due to variations in the amount of observation time across months and other biases, freely admitted by Southern, very few conclusions can be drawn from the data other than that there is a peak in social behavior during the breeding season and another brief peak in August.

Several more detailed studies were carried out in Australia during the 1950's. Dunnet (1957) describes the emergence pattern of adult and young wild rabbits at two locations near Canberra between winter and summer 1953. During observation periods at intervals varying from 2-5 minutes, the number of rabbits which had emerged was recorded. No attempt was made to record the daily or seasonal variation in specific behaviors. One of the prime aims of the study was to assess the validity of using sight counts at different times of the day for population estimates. Rowley (1957) reports an investigation into seasonal and climatic effects on emergence of an enclosed population of rabbits in Tasmania. The main observations reported were carried out over a 28 day period.
in the winter of 1954, although results of an earlier study in the late summer of the same year are briefly reported and compared. Rowley uses an index of activity dubbed "grazing emergence", which is defined at the time of day when 20% of the population was grazing for the first time on a given evening. Use of this index seems to have been partly to counter the fact that surface squatting rabbits confused any straight head count of emerged rabbits.

Taking advantage of the particularly favourable observation conditions in the enclosures at the Canberra site, Mykytowycz and Rowley (1958) carried out three continuous 24 hours observations during an 8 day period in the late spring of 1957. Observations took the form of a sample every 15 minutes with "particular attention ....... paid to certain individuals selected because of their status in the community". The number of rabbits above ground and the number grazing throughout the day are reported. Some data on the amount of time spent basking, grooming, resting etc. is also presented. In addition the percentage time spent in various activities is recorded for certain individual rabbits. The authors admit that the data is limited to only three days during the breeding season, but for the first time an attempt had been made to observe the behaviour of the rabbit across continuous 24 hours periods.

In the following year (1958) at the Albury site, eight continuous observations were carried out, two of which are reported; one in late summer and one at the start of the breeding season (Myers and Poole, 1961). Between the summer of 1957-58 and the summer of 1958-9, Myers and Poole recorded the seasonal variation in behaviour of their captive study population in some
considerable detail. Unfortunately the extensive data collected in the course of the study are of limited value in any discussion of seasonal variation in behaviour in a U.K. population of rabbits. Seasonal conditions in New South Wales differ greatly from those found in the British Isles. Myers and Poole describe the year as being divided into three distinct periods.

(i) The hot dry summer when the dried out pasture offers little food to the rabbits. During this period there is no reproductive activity.

(ii) The autumn/winter period which starts with the onset of the autumn rains, permitting the growth of lush pasture. This is followed by a midwinter shortage of food and a subsequent re-growth of pasture in early spring.

(iii) The spring breeding season, which starts with the birth of the first litters and ends with the last. Food is fairly plentiful during this period.

It is readily apparent that these conditions and their sequence of occurrence bear little relationship to climatic conditions in the British Isles.

These five studies, therefore, supply the only data and seasonal variation in rabbit behaviour. The only British study (Southern, 1948) supplies little detailed quantitative information. The four Australian studies supply information which is severely limited in some way. Dunnet (1957) and Rowley (1957) concern themselves only with time of emergence or with the number of rabbits above ground at a particular time. The Mykytowycz and Rowley (1958) study is confined to only three days during the breeding season and the Myers and Poole (1961) study, while having the virtue of being reasonably comprehensive, suffers the
disadvantage of having limited applicability to U.K. populations of rabbits.

In the present study, the research described in this section was carried out to answer the following questions:

1. How do rabbits distribute their surface activity throughout the day?
2. Is there seasonal variation in this distribution?
3. Is there variation in this distribution across the various age/sex/social classes of animals in the population?
4. While on the surface, how do rabbits distribute the proportion of time spent in different behaviours throughout the day?
5. Is there seasonal variation in this distribution?
6. Is there variation in this distribution across the various age/sex/social classes of animals in the population?

METHOD

The sampling procedure used to collect data in this section involved selecting an observation area, and at hourly intervals, recording the following:

(a) The presence of any marked, and therefore identifiable, rabbits.
(b) Their precise location.
(c) The behaviour in which they were engaged.
(d) If the behaviour was social in nature, the identity of the other individual/s involved.

This procedure has been called variously, "time sampling" (Hinde, 1973; Hutt and Hutt, 1974, Slater, 1978); "point sampling" (Dunbar, 1976); "On-the-dot sampling" (Hinde, 1973; Slater, 1978)
and "instantaneous" and "scan sampling" (Altmann, 1974). Altmann uses the term "instantaneous sampling" when referring to the sampling of the behaviour of a single animal and "scan sampling" when referring to the sampling of the behaviour of members of a group of animals. Scan sampling is therefore simply a form of instantaneous sampling in which several individuals are scanned at predetermined points in time and their behavioural states are recorded. In order that each scan should approximate a collective instantaneous sample, the time between sampling the behaviour of each individual should be kept to a minimum (Altmann, 1974; Lehner, 1979). In the present study observation and recording time amounted to 5-10 seconds per animal. The total time spent on a scan therefore varied depending on the number of animals being sampled. The maximum time spent on a single scan was approximately 120 seconds. The following behavioural states were recorded;

(a) Feeding (normal grazing behaviour or superficial scratching at ground)

(b) Resting (sitting or lying motionless, not engaged in any of the behaviours in other categories)

(c) Grooming (sitting, licking or rubbing paws over head etc)

(d) Active (in motion or excavating a burrow)

(e) Socially interacting (any involvement with another rabbit; chasing, investigation, fighting, grooming etc. which may be sexual, aggressive or parental in nature)

The categories are exhaustive and mutually exclusive in order to facilitate the rapid recording of data, and are of necessity rather broad. Some of the categories encompass quite diverse behaviours; in particular the categories "active" and "socially interacting" do not yield as much information as might
be desired. However, many of the behaviours falling in these categories can better be described as events rather than states and as such do not lend themselves to accurate sampling by this procedure.

Digging or burrowing would seem to be an obvious behaviour to include in the categories but it occurred very infrequently during daylight hours. Myers and Poole (1961) draw a distinction between "actual excavation of a burrow" and "the superficial type of surface scratching evident from food getting and in certain forms of sexual behaviour". Such superficial scratching was classed as "feeding" for the purposes of the present analysis and serious digging (N=4) was classed as "active".

In all, 377 scans were carried out on 52 days across 6 separate months (see fig. 8.1). The distribution of scans throughout the day is shown in fig. 8.2. The low proportion of scans in the early morning and in the evening is due to the shorter period of daylight in several of the sample months. The observations in February and April 1977 took place in four areas: Cross park, Tennis court, Thistle field, and Nettle hollow. In the remaining four months, however, the Thistle field site was not included due to frequent disturbances caused by work by the lighthouse staff and by bird ringers.

Results

Only marked and therefore identifiable rabbits were recorded in the scans, as one of the aims of the observations was to ascertain if the distribution of behaviours differed across the different age/sex/social classes of rabbits in the population. All times referred to are corrected to G.M.T.
Number of scans carried out in each of the sample months and the total number of marked individuals in each age/sex/social class available for sampling in each month.

Distribution of scans throughout the day for each of the sample months (times are GMT).
General Surface Activity

As different numbers of scans were carried out in different areas at different times and on different numbers of animals it was necessary to perform several corrections on the raw data. The figures in this section, therefore, are composed from data points which have been corrected for the number of scans taken at each time and expressed as a percentage of the total number of marked animals in each observation area. Each data point, then, represents the mean percentage of the potential number of marked animals in the particular age/sex/social class in question which were actually observed per scan at each time. This was seen as the only valid method of presenting the data to allowing direct comparisons of the behaviour of the members of the different age/sex/social classes at different times in different areas. The various warrens being sampled showed slight but inconsistent variations in daily activity patterns and such variations have been ignored for the purposes of this analysis. Of course, the data are compiled from samples taken in different weather conditions. This factor is discussed later in this chapter.

Fig. 8.3 shows the daily surface activity of adult and young rabbits averaged over the six observation months. It demonstrates the standard pattern of early morning activity tailing off fairly rapidly between roughly 0700-0900 hours for both adults and young. Throughout the remainder of the morning there are very few adult rabbits above ground and this is followed by a sharp rise in numbers throughout the afternoon. From approximately 1600-1700 hours onwards a fairly stable percentage of the population (50-65%) is above ground at any one time although individual rabbits are coming and going throughout this period. Young rabbits
Overall daily surface activity of adults and juveniles (mean figures across the six observation months). Each data point represents the mean percentage of the total marked members of that class observed per scan sample (see text).
show a more erratic daily activity pattern. During the middle and late morning the percentage of young above ground never falls to the same level as adults and they show a much less clearly defined rise in numbers throughout the afternoon. In general, young rabbits go to ground and re-emerge more frequently than adults in a given space of time.

Fig. 8.4 shows the same data broken to illustrate variations between the various age/sex/social classes. While the afternoon and evening activity patterns are fairly straightforward with the only major variation being the high percentage of dominant males above ground at any given time, the morning pattern shows quite marked differences between the classes. Again the dominant males appear very active at 0500 hours but this may be an artifact resulting from the relatively low number of scans at this time. Females appear to be more active than males in the early morning. Adult and juvenile males show a similar pattern of activity which is quite different from both adult and juvenile females. All classes show a rapid fall in numbers between 0800 and 1000 hours with the young of both sexes remaining above ground throughout the rest of the morning in greater numbers than the adults.

Such figures may be valuable in illustrating the general activity patterns of the various classes of rabbits but obviously any seasonal variation is masked in these treatments of the data. In figs. 8.5-8.10 the data is treated in the same manner as in fig. 8.4 and they show the mean percentage of rabbits in the five age/sex/social classes above ground at each hour of the day for each separate month. No data on young rabbits are included in the figures for February and April due to insufficient numbers being marked.
Overall daily surface activity of the members of the 5 age, sex and social status classes of rabbits (mean figures across the six observation months). Each data point represents the mean percentage of the total marked members of that class observed per scan sample (see text).
February - mean daily surface activity for the sex and social status classes of adult rabbits (insufficient juveniles marked to permit analysis).
April - mean daily surface activity for the sex and social status classes of adult rabbits (insufficient juveniles marked to permit analysis).
Fig. 8.7

June - mean daily surface activity for the five age/sex/social status classes.
Fig. 8.8

August - mean daily surface activity for the five age/sex/social status classes.
Fig. 8.9

September - mean daily surface activity for the five age/sex/social status classes.
November - mean daily surface activity for the five age/sex/social status classes.
Adult activity shows a remarkable consistency across the months although the small number of scans comprising certain of the data points gives rise to more variation within the basic pattern. In most months the dominant males exhibit the most rapid and consistent rise in number in the early afternoon followed by a slight tailing off in the late afternoon or early evening. Adult males and females follow a less pronounced but similar pattern. There is little consistent variation in daily adult activity across seasons except for a marked increase in dominant male activity during the height of the breeding season in April. Young rabbits show much greater seasonal variation in general activity. The activity of the young is very erratic in June but gradually becomes more regular and similar to the adult pattern as the months go by. However, even in November, it should be noted that there is still a greater percentage of young above ground in the middle of the day.

Overall seasonal variation in activity is portrayed in fig. 8.11. In this figure each data point is averaged across time of day and presented as the mean percentage of the potential number of animals of the particular age/sex/social class for that month. The data are arranged to give a picture of variation throughout the calendar year although it should be noted that observations in August, September and November were made in the calendar year preceding that in which the February, April and June observations were made. It is obvious that dominant males spend consistently more time above ground than the members of other classes. In general rabbits are more active on the surface during the summer months but there is little consistent variation in seasonal activity between the other four classes.
Surface activity of the five age/sex/social status classes over the six observation months (mean figures across time of day).
Mean % of all marked rabbits in each activity state at different times of day (mean figures across the six observation months).
Behavioural States

In this section the data refer only to marked animals observed above ground and the data points in each figure express the mean percentage of those animals observed in each of the five exhaustive and mutually exclusive behavioural states. Fig. 8.12 shows the daily variation in activity averaged over the six months and over the five age/sex/social classes. Feeding is by far the most common activity throughout the day except in the early morning when many rabbits are resting or grooming before retiring to their burrows. Resting and grooming show further peaks as the afternoon emergence commences and most individuals spend some time at the mouth of the burrow before moving farther afield to feed. The "active" and "socially interacting" states tend to follow the general pattern of above ground activity. The large peak in the percentage of rabbits feeding in late morning is based on observations of a small number of animals. Most of the rabbits above ground at this time are juveniles and they largely spend the time feeding. It is interesting to note the difference in behaviour at 1100 and 1200 hours when the number of rabbits observed is very similar. At 1100 hours the majority of the rabbits above ground are young and most of those observed are feeding. At 1200 hours the first adults are beginning to emerge giving rise to the high percentage of animals resting.

Figs. 8.13 – 8.17 portray the seasonal variation in each of the behavioural states for each of the five age/sex/social classes. Again, the data points refer to the mean percentage of marked animals observed above ground in each of the behavioural states, but in these diagrams each data point is averaged across the times of day to give a single monthly figure.
Feeding - Fig. 8.13

There is little difference between the age/sex/social classes in the seasonal pattern of feeding behaviour. The main feature of fig. 8.13 is the peak in feeding in the cold winter months of November and February and a gradual decrease in the spring as the quantity and quality of pasture improves. The decrease in the percentage time spent feeding in the late spring and early summer may also partly be a negative effect due to the rabbits simply doing other things at this time of year. Such a negative effect may also account for the observation that dominant males spend a smaller percentage of their time feeding than do members of other classes.

Resting - Fig. 8.14

Adults show a rise in the percentage time spent resting during the summer months. At least part of this increase can be explained by the fact that the category "resting", includes basking behaviour which is obviously correlated with warm, sunny weather. However, perhaps more simply, time above ground in the unfavourable weather conditions of the winter months is probably better spent in activities more directly relevant to survival. Young rabbits clearly spend steadily less time resting as they grow older. For the first month or so after emergence from the nest young rabbits spend most of their time above ground in the immediate vicinity of the burrow. Most of this time is spent feeding but a large proportion is spent sitting immobile, and at a time when they are vulnerable to aerial predators this is probably an effective anti-predator adaptation. Gradually as they grow both in size and in familiarity with their surroundings they become more active and venture farther afield and the amount of time
Feeding - mean % of members of each age/sex/social status class recorded feeding during each of the six observation months (mean figures across time of day).

Fig. 8.13

- - - dominant males
- - - subordinate males
- - - adult females
- - - juvenile males
- - - juvenile females

Mean %/scan

Months
Resting - mean % of members of each age/sex/social status class recorded resting during each of the six observation months (mean figures across time of day).
spent immobile falls steadily.

Grooming - Fig. 8.15

There is little consistent variation in the seasonal pattern of grooming between the different age/sex/social classes. For all classes there is a slight rise in grooming in the summer months paralleling the increase in time spent resting but it remains at a fairly constant level.

Active - Fig. 8.16

Adult rabbits show little consistent seasonal variation in the proportion of time they spend in movement. Adult females are particularly sedentary throughout the year with a slight rise in movement during the breeding season. Dominant males consistently show the highest level of activity. Surprisingly, this is at its lowest level during the breeding season although the locations recorded for each animal on the scans indicate that they spend most time near the warren during this time. Young rabbits show an increase in activity between June and August and this tails off slightly again as the autumn sets in.

Socially Interacting - Fig. 8.17

Fig. 8.17 shows two quite distinct peaks in social activity. The first, in April, coincides with the breeding season and 62.5% of adult male social encounters and 50% of adult female social encounters at this time involved sexual behaviour. In dominant males, however, only 28.7% of social interactions were sexual in nature, the remainder (71.43%) were aggressive. In contrast, only 37.5% of adult male social interactions could be classified as aggressive and in adult females only 31.25%. The remainder of the social encounters in adult females (18.75%) were classified as
Grooming - mean % of members of each age/sex/social status class recorded grooming during each of the six observation months (mean figures across time of day).
Active - mean % of members of each age/sex/social status class recorded in active state during each of the six observation months (mean figures across time of day).
Fig. 8.17

Social - mean % of members of each age/sex/social status class recorded in socially interacting state during each of the six observation months (mean figures across time of day).
maternal and normally involved grooming between mother and young. The second peak in social behaviour occurs in the late summer, in August and September, and is largely due to the involvement of young rabbits. The young females become sexually attractive to males and at this time 50% of their social interactions are sexual in nature and most instigated by adult males. The young males are also maturing, however, at this time of year 25% of their social encounters are sexual investigation or chasing, mainly with young females. The bulk of the interactions between young males and other members of the population at this time of year are aggressive. Both young males and females are chased aggressively by adult females but the young males are also harassed by adult males and 58.33% of their social interactions are aggressive in nature compared to only 12.5% in young females. The remainder of the social interactions in the young (16.67% in males and 37.5% in females) are of a neutral, investigative nature and developed into neither overt aggression nor sexual encounters.

DISCUSSION

The daily activity pattern of the rabbits shows some similarities and some marked differences from that previously reported. Throughout the early morning the number of rabbits above ground falls sharply, but although there was a steady trickle of rabbits returning to their burrows during this period, most would go to ground as the result of some disturbance and would not re-emerge. By late morning very few rabbits remained on the surface. Occasionally one or two adults would emerge during this period but young rabbits did so much more frequently and they normally spent the time feeding on or around the surface of the warren. Dunnet (1957) notes that young rabbits emerge earlier than
adults and follow a more erratic pattern of activity. The main period of emergence starts in early afternoon and the numbers above ground increase rapidly over a period of several hours. Dunnet (1957) suggests that emergence takes place over a short period and that the number above ground thereafter is fairly stable, but because of the lack of information on total population size (it is stated simply that the two warrens were "large") it is impossible to estimate the percentage of the population above ground at any one time. However, using the stable number above ground after "emergence" as a measure, it is evident that a large number of rabbits emerge in an astonishingly short space of time. The number above ground increases from 8 to the stable level of 42 in 10 minutes (i.e. 81% of the stable number emerge in 10 minutes). Rowley (1957) using his "grazing emergence" measure does not give data for comparison but reports that emergence took place over a short period and that the pattern observed was similar to that reported by Dunnet. Mykytowycz and Rowley (1958), however, report a much slower pattern of emergence although the data is averaged over the three days of the study. The percentage of rabbits above ground increased steadily from 5.66% to 54.72% in 8 hours. Some confusion or difficulty of interpretation may arise from the fact that the data for these three studies was collected in different ways and three quite different methods are used to present it but, even accepting this, the results do not seem to be compatible.

In the present study the number of adults above ground rose from 2.5% to 60% over a 4 hour period while the number of young rabbits rose steadily but more slowly over a 10 hour period.

Southern (1948) suggests that rabbits are primarily dawn and dusk feeders although he made no nocturnal observations and
reports that during a normal evening activity period some 30% of the population would be above ground. Myers (1957) reports that during observations made on thirteen small warrens, which were subsequently flooded and the population size determined, 90% of the population were regularly observed during the evening activity period. However, these observations were made during the autumn when no young were present and Myers suggests that the presence of young would lower this proportion considerably. Two further studies are reported in the same paper. In the first, carried out by Rowley, 55-63% of the subsequently determined population were observed on four successive evenings when young were present. In the second, conducted by Dunnet, two warrens of different sizes were observed. In the larger, 55-60% of the population was observed and in the smaller, 75% of the population was observed. Myers suggests that there is an inverse relationship between the accuracy of emergence count population estimates on the one hand, and warren size and presence of young on the other. The warrens under observation in the present study are very small indeed compared to those observed by Australian researchers.

Mykytowycz and Rowley (1958), as a result of their 24 hour observations, report that rabbits are active throughout the night with 42% of the population above ground at dusk, rising to a peak of 54.72% during the early hours of darkness. In these studies no distinction is drawn between adults and young, and if the adults and young are averaged together in the results of the present study, some 50% of the island population are above ground during the evening activity period. However, this is probably an underestimate for a "normal" evening activity period as, throughout the day, the rabbits were subject to "scares" which
sent then to ground for varying periods of time. The warrens were occasionally sampled during such periods and the final results necessarily reflect this. Unfortunately it was impossible to carry out any systematic observations during the hours of darkness, but casual observations did suggest that large numbers of rabbits are above ground throughout the night.

The island rabbits emerged several hours earlier than those reported in previous studies and this more generally diurnal behaviour is probably due to the lack of mammalian predators. Rowley (1957) reports that the mean time of "grazing emergence" during the summer occurred 106 minutes before sunset, whereas during the winter the mean emergence time was 70 minutes before sunset. In the present study the pattern of emergence was quite different. At all times of the year emergence took place steadily throughout the afternoon. Therefore, quite simply, the later the sunset, the longer the period of time between emergence and sunset. During the long summer days of June, for example, using Rowley's measure, emergence took place some 6 hours before sunset. Lockley (1961) transported five rabbits from the island of Skokholm for inclusion in the Orielton study population and reports that they emerged earlier than the mainland rabbits, adding that from his observations on Skokholm, the island rabbits were generally more diurnal in their daily activity. Particularly fascinating is his observation that the dominant mainland adult male, already established in the Orielton enclosure, adapted its daily activity pattern to that of the newly introduced island rabbits within a few days.

Weather

The results of the scan samples were little affected by the
vagaries of the weather. Rain (recorded, if it fell at any time during daylight hours on a particular day) fell on only 23.67% of days and was seldom heavy or prolonged. The climate of the island is drier than the neighbouring mainland with an average annual rainfall of only 22 inches which is fairly evenly distributed throughout the year. The temperature is also remarkably uniform, given the position of the island. The mean temperature for July differs from that in January by only 17.8°F. The low annual rainfall is compensated for by a high relative humidity which permits the surprisingly lush pasture to flourish (Eggeling, 1960). Rowley (1957) noted that the normal pattern of emergence was disrupted by wind or by rain but most frequently by the combination of rain with a strong wind. Southern (1940) reports that in the Sheepstead population feeding behaviour could be disrupted either by heavy rain or by a strong wind, especially if the temperature was low. Lockley (1961), while agreeing that heavy rain disrupts feeding, states that wind has little effect.

In the present study the combination of rain with wind of force 4 or over (beaufort scale) occurred on 11.11% of days but scans took place on only 3 days when such conditions pertained and on all three days the rainfall was light. The prevailing wind is from the West although occasional strong winds from the North East are also a feature of the climate. The gradual slope from the high Western cliffs to the Eastern shoreline results in the study warrens being largely sheltered from the prevailing wind. In addition all study warrens except Nettle hollow are situated around a network of high stone walls (see appendix 1 and maps in chapter 6) and in strong winds the rabbits generally grazed in the lee of these windbreaks. Nettle hollow, contrary to its name, was
situated on an exposed eastern slope and in strong east or north-east winds many of the rabbits ventured down into the relative shelter of a gully to the east or into the lee of the various buildings in the area. Strong wind, therefore, affected the location of rabbits but did not seem to greatly affect either the numbers above ground or the pattern of activity. Heavy, prolonged rain occurred only occasionally and did not coincide with the scan samples. Other observations showed that during such rain numbers above ground were reduced and those above ground spent the bulk of the time feeding.

Daily Distribution of Behaviour

Only two previous studies present quantitative data on the daily distribution of particular behaviours in the rabbit and both were carried out in Australia. Detailed comparisons between studies is again difficult due to differences in sampling methodology and in the definitions of the categories of behaviour under study. However, certain features stand out despite these differences. Myers and Poole (1961) report that feeding was the most common behaviour observed and that it was at its peak during the night. During the early morning a high proportion of the population were resting and grooming before retiring for the day. Throughout the day those few rabbits which were above ground were either feeding or resting until the late afternoon when the main emergence occurred. The proportion of animals feeding rose again from this time onwards into the night. During one 24 hours observation carried out at the start of the breeding season it was observed that social behaviour took place at a fairly constant level (approx. 20%) from late afternoon through the night to early morning with a corresponding drop in the proportion of time spent
feeding. Mykytowycz and Rowley (1958) report a similar daily activity pattern.

This pattern of the distribution of activities is essentially similar to that observed in the island population shown in fig. 8.12. In the early morning when observations commenced at 0500 hours some rabbits were still out at the feeding areas, but many had already returned to the surface of the warren. As individuals returned to the warren they would spend some time sitting grooming at the burrow entrance. Mykytowycz and Rowley (1958) have suggested that this early morning grooming is intensified by the presence of dew on the grass. There was never an occasion when the grass was not damp at this time of the morning on the island and such a grooming bout was almost invariable. This was generally followed by a period of immobility, the rabbit simply sitting at the burrow entrance, and on sunny mornings many animals lay on their sides basking. Occasionally this rest period was spent in the company of another individual but usually this was not the case. Some rabbits would quite spontaneously go below ground at this time but many went to ground as the result of some disturbance and would not re-emerge. During the remainder of the morning those few rabbits emerging or remaining above ground normally fed on the surface of the warren. In the late morning an increasing number of young would emerge, some resting at the warren, and some moving slightly further afield to feed. Around midday the first adults would emerge and sit around the burrows for a time before venturing out to feed. As the afternoon progressed greater and greater numbers would emerge and follow the same pattern of behaviour. Throughout the remainder of the daylight hours over half of the population would normally
be above ground at one time. Individuals would come and go during this period but the young did so more frequently than adults. Social behaviour and general movement were at their peak during the evening and occurred intermittently during more general feeding behaviour. It is not known if the island population continued to feed throughout the night and if so, in what numbers but it appears that the peak in grazing activity occurs much earlier in the day than that reported in the Australian studies.

Myers and Poole (1961) also present quantitative data on seasonal variations in behaviour, however, as already stated, these are not directly applicable to U.K. populations because of very basic differences in the climate. They found that behaviour during the hot, dry summer months is dominated by the shortage of food to the extent that feeding accounts for 90% of the observed behaviour. There is a decrease in the proportion of time spent feeding (to approx. 70%) in the breeding and pre-breeding seasons, when food is more plentiful, with a corresponding rise in reproductive activity. Grooming and resting remain at a fairly constant low level throughout the year.

It is clear from fig. 8.13 that the pattern of feeding in the island population is quite different. The only serious shortage of food occurs in the winter months, and even then feeding accounts for only 60-70% of observed behaviour. So, in the present study population, the proportion of time spent feeding never rises to even the lowest level reported by Myers and Poole. The proportion of time spent resting is more variable in the island population than in the Australian study population. Adults spend a greater proportion of daylight time resting during the summer than in the winter with adult females being generally more
sedentary than other adults. The young show a steady decline in the amount of time spent resting from the time of emergence from the breeding stop until the onset of their first winter. Grooming, however, remains at a fairly constant level throughout the year for all age/sex/social classes. The fact that grooming tails off only slightly during the unfavourable weather conditions in winter suggests that it performs a vital maintenance function for the rabbit.

Southern (1948) discusses seasonal variation in social behaviour and reports an increase during the breeding season and a second peak in late summer. These two peaks were observed in the present study and Southern's suggestion that the second peak is due to the young rabbits reaching maturity is clearly supported (fig. 8.17). After the breeding season adult females play a steadily declining role in the sexual activity of the warren and in August and September the adult males transfer their sexual attentions to the young females. The young males are progressively less tolerated by the adults, suffering an increasing number of chases and aggressive interactions, and many leave the warren altogether at this time of year. Only those remaining within the confines of the warren were included in scan samples and therefore at this time of year the behaviour of only a subsection of the young born within the warren is recorded.

Future Research

The particular island population under observation in the present study appear to be more diurnal than might be expected of a mainland population. Possible generalisation of the results to such populations is therefore limited, although it seems probable that the general pattern of activity and the variation across
age/sex/social classes would be similar. It is possible that the exaggerated diurnal activity pattern seen on the Isle of May is related to the absence of diurnal predators and it would be of interest to compare this population with that of an island where such predators were present.

There is also a need to carry out similar studies on mainland populations of rabbits in the U.K. as much of the Australian data appears to be inapplicable. The choice of site, however, is crucial. It is becoming increasingly difficult to find study sites which are not subject to major disturbances and to particular problems, making it difficult to generalise results.

A major omission in the present study, and one which should be rectified in future studies, is observation throughout the hours of darkness. Nocturnally active animals have always provided problems for observers and the Australian researchers partially overcame these by using floodlights to observe enclosed populations. However, the increasing sophistication of image-intensifiers and other night viewing apparatus should permit such observations to be undertaken with the minimum of disturbance to the animals. Only when such observation is attempted on a wild population can we even come close to obtaining a complete picture of the daily and seasonal activity pattern of the rabbit.
CHAPTER 9

MAMMALIAN OLFACTORY COMMUNICATION
Interest in olfactory communication in mammals has increased dramatically over the past two decades. Early work in this area was stimulated by, and, at the same time it might be fair to say hampered by, the existing extensive research carried out on olfactory communication in insects. Certainly the bulk of the theoretical background to olfactory research was inherited from that source. The principle concept to be carried forward to work on mammals was that of the "pheromone". Pheromones were defined as "substances which are secreted to the outside by an individual and received by a second individual of the same species, in which they release a specific reaction, for example, a definite behaviour or a developmental process" (Karlson and Luscher, 1959). A further distinction, inherent in the above definition, was drawn between "releasing" pheromones which were seen as releasing a specific behaviour, and "priming" phenomones which were seen as resulting in a neuroendocrine or developmental change. The use of the term "releasing" has connotations from early ethological literature inferring that the system has an innate basis and for this reason some authors (e.g. Bronson, 1974) have substituted the term "signalling pheromone" when applied to mammalian communication. However, the term "pheromone" has itself come under increasing criticism when applied to mammalian communication (Beauchamp et al., 1976; Johnson, 1973). The term as used in insect studies implied certain criteria for a substance to qualify as a pheromone. Beauchamp et al. (1976) in an important critical paper suggest that the following criteria have been put forward at different times as necessary for the demonstration of a pheromone.
(1) Species specificity

(2) Well defined specific behavioural or endocrinological function

(3) Large degree of genetic programming

(4) One or a few effective compounds

(5) Uniqueness of these compounds in producing the response

They conclude that these criteria have not been met in any mammalian species and that the criteria are of limited usefulness when applied to mammalian communication systems. They suggest therefore that the term no longer be used when discussing olfactory communication in mammals. It is difficult to disagree with their argument that olfactory communication does not differ fundamentally from communication in other sensory modalities. At the very least it is becoming increasingly apparent that treating olfactory signals as analogous with signals in other modalities is more useful than treating them as analogous with hormones. Argument over whether a given set of olfactory substances do or do not fulfill all the criteria for a pheromone (eg. "It will probably be necessary in the future to distinguish pheromones from olfactory cues which function in a manner closely analogous to pheromones but which are varied or are affected by both the quantity and combination of hormones present within the organism" Gleason and Reynierse, 1969) seems to have become much less common in the literature. Such distinctions based on concepts which are frequently inapplicable to the complex and labile behaviour of mammals are surely less than useful.

The Production of Odours in Mammals

Early study of mammalian scent products was prompted by their commercial importance for the perfume industry. More
recently a few ethologists have attempted to determine the active communicative components in mammalian scent gland secretions eg. Muller-Schwarze (1969), Brownlee et.al. (1969). Using gas-liquid chromatography, these authors separated fractions of Black-tailed deer (Odocoileus hemionus columbianus) tarsal gland scent and succeeded in identifying the major active component. Muller-Schwarze showed that different fractions affected the behaviour of investigating animals to different degrees. Similar studies have been carried out on scent products from a variety of species but as yet the work is in its infancy. Mammalian glandular secretions appear to be considerably more complex than premature extrapolation from the insect work had led researchers to expect. However, because the research is at such an early stage, it is by no means clear if the overall complexity of glandular secretions reflects a corresponding complexity in the actual chemicals necessary for communication. Nevertheless, Beauchamp et.al. (1976) report that recent work on insect pheromones suggests that they may, in many cases, be more complex than expected and, in some instances, interactions between several compounds may be necessary to elicit specific behaviours.

Mammals employ substances from a variety of sources for communicative purposes. Urine and faeces are commonly employed. This is hardly surprising as they are naturally odoriferous and produced with regularity. Many species have developed behaviour patterns to deposit these products in particular locations in order to enhance their communicative function. Faeces are smeared onto objects by eg. the little polecat (Poecilogale albinucha), the giant rat (Cricetomys gambianus) (Ewer, 1968) and some lemurs (Petter, 1965) or are spread onto surrounding vegetation by eg.
the hippo (*Hippopotamus amphibius*) which vibrates its tail rapidly during defaecation (Ewer, 1968). Some species have been observed to deposit faeces regularly at particular sites within their range eg. the white rhino, *Ceratotherium simum* (Owen-Smith, 1972) and the rabbit (Mykytowycz 1968).

Urine is often deposited on conspicuous objects or at other prominent locations, eg. many of the Canidae (Kleiman, 1966), or sprayed onto objects in the environment, eg. many of the Felidae (Ewer 1968). Among the lower primates urine is often transferred to hands or feet and hence spread onto branches, eg. the slow loris (*Loris tardigradus*) (Ilse, 1955).

Many species have, in addition, evolved special glands which produce odoriferous substances. Mykytowycz (1972) reports that scent glands have been found in 15 of the 18 Mammalian orders and that they occur in a wide variety of sites on the body. The commonest odour procuding glands are anal glands (Ewer 1968) and the scent is usually applied directly by rubbing the anal region on the substrate eg. in the red fox, *Vulpes vulpes* (Albone and Fox, 1971) or, in the case of the rabbit, by application to the faecal pellets (Hesterman and Mykytowycz, 1968). Glands have also been commonly reported in the genital area eg. civets, *Viverra, Viverricula* (Ewer, 1968), and at various locations on the head; along the lower edge of the mouth eg. domestic cat; on the chin eg. rabbit; on the cheek eg: pika *Orchotona princeps* (Harvey and Rosenberg, 1960); on the forehead or by the eyes eg. most of the Artiodactyla.

Further glands have been observed on virtually every part of the body surface in different mammalian species and in many cases
these appear to have evolved to permit easy marking of environment as a result of the particular lifestyle of the species involved. For instance many animals which are either burrow dwellers or use runways through vegetation possess lateral glands on the flanks eg. the shrew *Sorex araneus* and many small rodents.

Within the larger mammalian orders there appears to be little uniformity of location of scent glands and similar methods of marking appear to have evolved independently many times in unrelated species. It seems probable that these have evolved a communicative role as a secondary function. Original functions may have been skin care, temperature regulation, salt regulation etc. and, in general, scent glands can be divided into two categories.

1. Holocrine-sebaceous
2. Tubular – (a) apocrine
   (b) eccrine (true sweat glands)

The eccrine glands are best developed in man and the higher primates and amongst the remainder of the mammals sebaceous glands are most commonly found. Sebaceous and apocrine glands may occur separately or in combination within a given gland complex (Mykytowycz, 1972).

As mentioned above, many species have evolved specialised behaviour patterns to deposit faeces, urine and glandular secretions at various locations in their environment. Commonly referred to as "scent marking", this has been the focus for much of the observational research in this area. Kleiman (1966) suggests that the term "scent marking" should be restricted to behaviours which differ from elimination in the case of urination and defaecation and from a comfort movement such as scratching in the case of body rubbing. This distinction has proved, in many
cases, to be difficult to make in practice and is theoretically not particularly useful. Defaecation and urination, although often behaviourally indistinguishable from "mere elimination", may result in products which elicit a predictable behavioural reaction in conspecifics. Mykytowycz (1970) suggests a distinction between active and passive marking depending on whether deposition of scent is accompanied by a specific behaviour pattern. Such a distinction is intended to account for case such as burrowing mammals which may deposit scent from lateral glands while passing along a burrow or certain mammals which have pedal glands. An extensive catalogue of marking behaviour in a wide variety of species now exists (see reviews by Ewer, 1968 and Johnson, 1973).

Information Content of Mammalian Odours

Mutual olfactory investigation is a frequently observed phenomenon among social mammals and in many species intruders to a group range are investigated as a preliminary to further action, if any. Naso-nasal, naso-anal, naso-genital and naso-glandular examinations are commonly reported and there is a growing body of evidence that information permitting identification of mammals is transmitted by odours present both on the body and deposited in the environment.

(1) **species identity:** Evidence for this capability comes mainly from work on small rodents. Moore (1965) reports that *Peromyscus maniculatus* individuals prefer the odour of a conspecific to that of a member of another *Peromyscus* species. Experiments with *Mus musculus* (Bowers and Alexander, 1967) and gerbils, *Meriones unguiculatus* (Dagg and Windsor, 1971) have shown that members of these species are capable of discriminating a conspecific from members of
other rodent species on the basis of odour alone.

(ii) **strain identity:** Several rodent species eg. bank voles, *Clethrionymus* (Godfrey, 1958) and mice, *Mus* (Parkes and Bruce, 1962) have been shown to be capable of discriminating between members of their own strain and members of another strain of the same species on the basis of odour.

(iii) **group identity:** While one may postulate possible genetically controlled variations in the active chemicals or their ratios as a basis for odour discrimination between species or strains, several species of social mammals have been shown to be capable of discrimination between members of their own group and members of a neighbouring group of conspecifics on the basis of odour. In such cases, eg. the common marmoset, *Callithrix jacchus* (Epple, 1970) and the sugar glider, *Petaurus breviceps* (Schultze-Westrum, 1969), while genetic variations are possible, they are less likely to be responsible for easily distinguishable differences in odour common to an entire group. Environmental factors such as diet may play a more important role in varying the odour of eg. urine and faeces. Another possibility in certain cases is that bacterial action on glandular secretions affects their odour, and that groups of mammals living together share similar bacteria which may differ either quantitatively or qualitatively from those possessed by other groups. Finally, in addition to the possibility that frequent body contact between members of a group may create a 'group odour', it has been reported that in several species, eg. the rabbit (Lyne et al., 1964), dominant members of a group mark other members with glandular secretions.
(iv) **sexual identity**: Using simple discrimination tests Bowers and Alexander (1967) have demonstrated that mice can identify the sex of a conspecific by odour. This ability has been reported in a wide range of mammalian species but most studies have concentrated on the discrimination of different reproductive states in both males and females.

(v) **reproductive state**: The release of many odoriferous compounds is under hormonal control and it has been demonstrated that olfactory cues are extremely important for many male mammals to permit discrimination between oestrus and anoestrous females e.g. rhesus monkeys *Macaca mulata* (Michael and Keverne, 1968). It has also been shown that the females of some species e.g. rats (Carr and Caul, 1962) can discriminate between intact and castrated males. It has been suggested by Eisenberg and Kleiman (1972) that discrimination of reproductive state may be dependent on variations in excretion of the steroïds which affect the reproductive system as it is known that several androgen metabolites have a pronounced odour. In many species the presence of the "correct" odour is necessary for normal mating to take place.

(vi) **individual identity**: Work on mice by Bowers and Alexander (1967) and on gerbils by Dagg and Windsor (1971) has shown that these species are capable of distinguishing between individuals on the basis of odour.

(vii) **age**: Most mammals can distinguish juvenile from adult conspecifics by odour since, as the production of many odours is hormone dependent, odour production and associated behaviours do not fully develop until sexual maturity, e.g. rabbits (Mykytowycz 1970). As yet there is no evidence that
mammals can discriminate between adult conspecifics by odours associated with differing ages as opposed to odours differing according to some other variable.

(viii) mood: Fear or stress odours emitted by an individual have been shown to be recognisable by conspecifics in both rats (Valenta and Rigby, 1968) and mice (Sprott, 1969) and commonly elicit avoidance in the investigating animal.

(ix) social status: Rats have been reported to be capable of discriminating between the odour of a dominant male and a subordinate male even when the individuals were unknown to the investigating animal (Krames et al., 1969). A similar ability may also be present in the rabbit (Bell, 1980).

It has been suggested, therefore, that odours may transmit information about a wide range of identifying characteristics. The evidence such for suggestions shows simply that animals are capable of making discriminations between odours produced by different animals. Clearly in most of the studies mentioned above efforts have been made to control for extraneous variables, given the range of discriminative abilities demonstrated, it is not clear if they have succeeded in every case. In addition, while it is one thing to show that mammals are capable of making discriminations based on odour, it is quite another to show the functional significance of such discriminations in a natural setting. It is unclear, therefore, what particular odour characteristic a mammal is using in a given situation to identify a conspecific and if this varies from situation to situation. These problems may not be successfully resolved until it is possible to extract or synthesize the chemicals involved in the transmission of the relevant information.
Theories of Function

Much of the emphasis in olfactory research has been on the odour emitter and in particular in the observation and description of patterns of behaviour involved in scent marking. This is understandable given the very great problems inherent in research in this area. The persistence of an olfactory signal long after the depositing animal has left the immediate vicinity is one of the advantages of the medium for communication. However, this, in conjunction with the fact that many scent stimuli are virtually invisible, creates difficulties for the human observer. The presence of a scent stimulus is often not obvious and in many instances must be inferred from the behaviour of an investigating animal. In addition, as mentioned above, there is the possibility that an overt change in behaviour may not take place as the result of contact with an odour. The animal may simply be primed or predisposed to respond to a further stimulus in a certain manner. In a few cases certain of these problems have been successfully overcome by detailed and sensitive field work but laboratory studies have offered more control over conditions and have permitted more reliable information on reactions to scent stimuli to be collected. However, laboratory research runs the risk of ignoring many of the complexities of olfactory communication. In particular, it is probable that many contextual factors which may modify responses to scent signals are often missing in the laboratory.

Such problems, therefore, have led to a situation where the literature is peppered with speculations about the functional significance of scent stimuli and in most cases the supporting evidence, if it exists at all, is rather weak.
Throughout the 1960s scent marking was commonly referred to as "territorial marking" eg. Mykytowycz (1964, 1968). Most authors cite Hediger (1949, 1950, 1955) as being the originator of the hypothesis that scent, as well as physical threat, was important in the maintenance of a territory in mammals. This hypothesis was accepted by most authors and frequently, in discussing the function of scent marking in a particular species, the maintenance of a territory was stated or implied with little supporting evidence, in some cases even of territoriality. Although scent marking is obviously associated with territoriality in some species, it is now commonly accepted that not all scent marking occurs in a territorial context. Ralls (1971) reports that two species which Hediger used as examples (the black rhinocerous, Diceros bicornis and the chamois, Rupicapra rupicapra) have been more recently studied in the field (Schenkel, 1966 and Kramer, 1969) and that in neither species was marking found to be associated with the possession of a territory.

Kleiman, (1966) suggests that mammalian scent marking may have evolved from automic reactions involving defaecation, urination and glandular secretions in response to unknown terrain. This then served to make the terrain more familiar. It is argued that voluntary control over these processes developed at some later stage and that the behavioural postures commonly observed in mammalian scent marking have developed for directing scent onto conspicuous landmarks. From this it is argued that the further social functions which have been postulated may have developed secondarily. Eisenberg and Kleiman (1972) suggest that each individual mammal may have an "optimum odor field" composed of olfactory stimuli from the individual, from the environment and
from conspecifics. This field provides the optimum level of reassurance and will depend upon the age, sex, mood and reproductive state of the individual. It is argued, therefore, that scent deposition by individuals may be an attempt to bring about or restore the odour field to its optimum level.

Ewer (1968) agrees that the evolution of the structures involved in scent marking and the associated behaviours may have begun purely in relation to the marker but adds the hypothesis that the presence of a foreign mark may also have increased readiness for flight. She argues that the two functions of reassurance and threat are complementary especially in areas where population density is such that the animals' ranges are adjacent, and concludes that the evolutionary transition from the individual function of self assurance to the social function of threat is an easy one and has probably been made independently many times.

Ralls (1971) indicates that most of the evidence from species studied so far suggests that the threatening, aggressive component of marking seems to predominate. Eisenberg & Kleiman (1972) however, suggest that the argument put forward by Ralls is based on evidence of vigorous marking, primarily in agonistic situations and therefore, to some extent, begs the question. Ralls herself admits that the correlation between marking and aggression declines with the vigour and frequency of the marking and she states: "Little can be said about the motivation of less vigorous marking - it may be entirely different".

Although one can readily accept the correlation between scent deposition and the maintenance of territory in many species, the debate about reassurance and threat continues unresolved.
Using the concept of the "optimum odor field" it is possible to postulate that an animal depositing scent is simultaneously altering his own field towards an optimum level while altering an intruder's field away from its optimum level. As the easiest way for the intruder to restore his own field is to withdraw to an area where the odour field is nearer optimal, such deposition of scent can simultaneously serve the dual function of reassuring the resident and increasing the probability that the intruder will withdraw. On the motivational level therefore, it is possible that an individual deposits scent in order to reassure itself which does not preclude the possibility that on the functional level this scent acts as a threat to a conspecific.

There is some evidence that individuals may avoid the scent deposits of conspecifics, particularly in the case where the scent originates from another animal which has previously defeated them in a fight eg. in hamsters, *Mesocricetus auratus* (Dieterlin, 1959). However much of the available evidence suggests that scent deposits actually attract the attention of other members of the same species. Mammals entering a strange territory may modify their behaviour and perhaps show a predisposition to withdraw on encountering the resident. Certainly, the tendency for an individual to emerge as the winner from contests fought on its home ground is a very widely reported phenomenon. Nevertheless the function of scent marks deposited around an animal's home area remains unclear. The interest shown in them by intruding animals may stem from their information value. Eisenberg and Kleiman (1972) suggest that we should move away from the emphasis on the connection between territory and scent marking and should rather view scent deposition as a means of information exchange important
in the orientation of individuals and in the regulation of social behaviour. Clearly it is important to an intruder to ascertain if an area is occupied and, if so, by what sort of individual or group.

There is considerable evidence that in many species a common reaction to encountering a scent mark is to deposit scent at the same site. Indeed, in some colonial species, eg. the rabbit (Mykytowycz, 1968) and the desert cavy, Microcavia australis (Rood, 1970) communal marking sites exist and are visited by most group members. It has been suggested that such sites act as a focus for the general exchange of information between group members (eg. Johnson, 1973). It is possible in group living species that social status, while often established as the result of aggressive encounters, may be maintained through the medium of odour. As reported above, mammals are capable of making a wide range of discriminations based on the odour characteristics of conspecifics and there is an obvious advantage in keeping up to date with information on the presence, status, reproductive state etc. of the other members of a group. In experiments carried out on rabbits in which the dominant male of a group was removed, another male quickly assumed dominance and a general reorganisation of social relationships took place (Mykytowycz, 1958; Lockley, 1961). One may speculate that a sudden drop in the level of odour deposited by the dominant male may have contributed to such changes. However, this is clearly an area for further research.

Odours released as a result of fear or stress may also elicit avoidance in conspecifics and thus function as alarm signals but it is not clear, as yet, how widespread a phenomenon
The ability of many species to determine the sex and reproductive state of conspecific from odours has obvious functional significance to both the sender and receiver of the information but there is also considerable evidence that the reproductive system of some mammals can be affected in a number of ways by exposure to the odour of conspecifics.

(i) Lee-Boot effect: Lee and Boot (1955) reported an increase in the incidence of pseudopregnancy among grouped female mice, Mus as opposed to singly housed females. Furthermore, housing female mice in groups of thirty produces a significant increase in the incidence of anoestrous (Whitten, 1959). Both effects have been shown to be odour dependent.

(ii) Whitten effect: The introduction of an adult male, his urine or his general body odour to a group of female mice rapidly brings them into oestrous and synchronizes their cycles (Whitten and Bronson, 1970).

(iii) Bruce effect: Bruce, with various co-workers has demonstrated that the introduction of the odour of a strange male to a recently inseminated female mouse inhibits the development of pregnancy by blocking implantation (eg. Parkes and Bruce, 1962).

(iv) Acceleration of puberty: Female mice reach puberty significantly earlier when exposed to the odour of adult males (Vandenbergh, 1959).

Eisenberg and Kleiman (1972) raise the possibility that in mice all of these effects may be caused by a single substance in adult male urine. The majority of studies on physiological changes induced by exposure to conspecific odours have concentrated on
changes in the reproductive system of small rodents in a laboratory setting. It is not clear, therefore, how widespread these effects are, or if they occur under normal conditions in a natural setting.

Finally, odour may play an important role in stimulating maternal behaviour in many mammals. Often a combination of visual, auditory, tactile and olfactory cues from offspring are necessary for eliciting normal maternal behaviour. However, it has been reported that in mice (Gandelman et al., 1971) and in rats (Fleming, 1971, PhD thesis cited in Eisenberg and Kleiman, 1972) rendering mothers anosmic can completely eliminate normal maternal behaviour under laboratory conditions.

The idea that the deposition of scent in the environment by mammals serves a single primary function does not appear to be supported by the available evidence. Rather, the evidence suggests that the transmission of odour may fulfill a wide range of functions. Whether it fulfills the same functions in different species and whether scents from different sources in the same species fulfill different functions unfortunately remain unanswered questions. In the past decade a considerable amount of research effort has generated a great deal of speculation but very few answers. Partly this has been due to the inherent difficulties in such research described above but, certainly in the earlier work, it was also partly due to couching the questions within an inappropriate theoretical framework. The practical difficulties in olfactory research remain and, more generally, considerable confusion exists in the theoretical systems of classification of both the semantics and function of animal signals. However, clearly continued observation and description of mammalian
behaviour can only aid the development of a sound theoretical background.

In particular, information on the differential frequency of deposition of scent by animals of varying age, sex and social status, and on the behavioural context in which it was deposited is urgently required. Only when information of this nature is collected by observation of free living mammals can we have confidence in the laboratory findings on information content of signals and can begin to unravel the meaning and function of olfactory signals.

In the present study an attempt has been made to examine aspects of olfactory communication in a free living population of rabbits. In the rabbit, the secretions of various gland complexes in addition to urine and faeces have been implicated in olfaction. The submandibular (chin), anal, inguinal and Harderian glands have all been the subject of considerable laboratory research (e.g. Mykytowycz, 1966a, 1966b, 1966c).

The Harderian and inguinal glands were not studied in the present project. The role (if any) of the Harderian glands (situated near the eye) in olfactory communication is by no means clear (Mykytowycz, 1966c). The inguinal glands (situated in the groin) have been implicated in olfactory communication. Mykytowycz (1966b) suggests that inguinal secretions may serve as a sexual attractant in both rabbits and hares (Lepus europaeus). However, in hares the glands are found to be larger in adult females than in adult males whereas the opposite is true in the rabbit. It is possible that the social systems of the two species (solitary v colonial) may be responsible for such a discrepancy, but it is not
clear if the glands perform a similar role in both species. Release of scent from the inguinal glands is not accompanied by a recognisable behaviour pattern and it was not regarded, therefore, as amenable to study by field observation.

The present study, therefore, concentrated on anal gland scent and faeces, submandibular (chin) gland scent, urine and behaviour known as "pawscrapping" which Bell (1980) suggests may be connected with scent marking.

In each of these cases data on the overall frequency of, and seasonal variation in, deposition of scent by members of different age, sex and social status classes of rabbits is presented. In addition, the behavioural context of acts related to olfactory communication is analysed and, where appropriate, the spatial distribution of scent-related artifacts if examined.
CHAPTER 10

ANAL GLAND SECRETION
Defaecation in the rabbit takes two forms as some food is passed through the digestive system twice. Rabbits excrete small, soft, mucus covered pellets which are reingested, and larger, fibrous, dark coloured pellets are coated with secretion from the anal gland which is a paired organ situated around the end portion of the rectum with secretory ducts opening into the anus at the border of the mucus membrane of the rectum and the epidermis of the skin. Mykytowycz (1966a) reports that the secretion is apocrine. Suggestions that the function of anal gland secretion is primarily that of a lubricant for the faeces are rejected by Takaki and Tagawa (1961) who report that removal of the gland does not significantly affect defaecation.

The size of the gland increases with the age of the rabbit and is generally larger in males than in females. In addition the size varies with the social status and sexual activity of the individual and with season (Mykytowycz and Dudzinski, 1966). These findings, combined with the observation that gland size and activity diminish in castrated males strongly suggest that the gland is under androgenic control (Mykytowycz, 1966a). Mykytowycz also demonstrated that size and activity of the anal gland are inhibited in oestrous females and that these increase after castration, suggesting that oestrogen has an inhibiting effect.

More recently, studies on the chemical composition of anal gland secretion (Goulrich and Mykytowycz, 1972) have revealed that it contains proteins and carbohydrates and that lipid extracts from homogenized glandular tissue contain hydrocarbons,
nonglyceryl esters, free fatty acids and cholesterol. It is further reported that clear differences in hydrocarbon composition were found in the extracts from male and female glands. Hesterman, Goodrich and Mykytowycz (1976), extending this work, found that acid and neutral soluble fractions of anal gland extract contain behaviourally important components and that reactions of 2-3 month old rabbits to faecal pellets treated with such fractions were "mainly of an avoidance type".

Hesterman and Mykytowycz (1968) have suggested that faecal pellets produced in response to the presence or odour of a conspecific ("marking pellets") are more odoriferous than pellets produced without such stimulation ("non-marking pellets"). Using a forced choice paradigm, human judges rated pellets on the basis of their relative odour intensity. It is suggested that marking pellets are coated with more anal gland secretion than non-marking pellets but the possibility that the difference is qualitative rather than quantitative has not been adequately tested. While marking pellets from dominant males were rated more odoriferous than non-marking pellets, those from subodinate males were actually rated less so in 59% of tests. In general, anal swabs and gland extracts from males were rated more odoriferous than those from females. This implies that dominant males produce more scent in response to a conspecific than do members of other sex/social status groups. The fact that subordinate males produced pellets of a lower odour intensity when confronted with the odour of a conspecific is certainly interesting and warrants further study. However, in general, the results of the organoleptic panel tests support the previous findings of variation in weight and activity of anal glands. Odour intensity of anal swabs was found to
decrease in the following order; intact males castrate females castrate males intact females. In addition, the odour intensity of anal swabs increases with the age of the rabbit: Results from tests on homogenized gland extracts indicate that in both sexes the anal glands are more odoriferous in the breeding season.

On the basis of these findings Mykytowycz (1966a, 1968) has suggested that anal gland secretion is involved in the maintenance of territory in the rabbit.

Mykytowycz and Ward (1971) tested the reactions of nestlings to a variety of odours collected from conspecifics and report that the anal gland secretion from the mother was the only odour to consistently attract the nestlings. It is stated that it is "obvious that the rabbit learns to recognise the odour of the mother's anal gland during its earliest life". They suggest that, as adult females and juveniles frequently attack strange young, it is important for young individuals emerging from the nest to remain within the area permeated by the odour of the mother's faeces. Thus young rabbits may recognise the role of faeces in defining territorial boundaries very early in life.

The confidence enhancing properties of anal gland secretion were studied by Mykytowycz (1973) using rabbits which were normally housed in breeding pairs. Two rabbits of the same sex were placed in an arena which contained faeces collected either from one of the rabbits themselves or from their partner. Faeces from males enhanced both their own confidence and that of their partner. Faeces from females enhanced both their own confidence and that of their partner to a lesser extent. An extended study by Mykytowycz, Hesterman, Gambale and Dudzinski (1976) investigated
the confidence enhancing effects of a variety of glandular secretions produced by rabbits using similar methods. They report that male chin gland secretion was more effective than faecal pellets in enhancing the confidence of both the males themselves and their partners. However, it is not clear under what conditions the faecal pellets were collected for such tests. It seems probable that they were obtained from the donors while in their home cages. Schalken (1976) reports that rabbits spend significantly more time investigating pellets produced in response to conspecific odour than pellets produced in the home cage. This finding reflects the difference between marking and non-marking pellets reported by Hesterman and Mykytowycz (1968) and raises the possibility that in the confidence enhancement experiments non-marking pellets rather than marking pellets were used as test material. Further work is evidently necessary to determine if marking pellets are more effective than non-marking pellets in enhancing confidence in this type of situation, and furthermore, if marking pellets are more effective than chin gland secretion.

In addition to depositing faecal pellets apparently at random throughout the home range, rabbits also deposit pellets at special sites within that range. These large accumulations of pellets are referred to either as "dunghills" in the Australian literature (eg. Mykytowycz, 1968) or "latrines" in the U.K. literature (eg. Southern, 1948). Mykytowycz and Gambale (1969) observed a population of adult rabbits in an 85 acre enclosure and report that latrines are mainly formed and maintained by males and that dominant males visit latrines more frequently than subordinate males. The amount of time spent marking while on latrines is roughly equal in dominant and subordinate males.
despite the fact that visits by subordinate males are substantially longer. It is suggested that dominant males visit many latrines, depositing scent quickly on each, whereas subordinate males visit fewer and spend longer there. Latrines of varying age and size were observed over a period of two months and the daily incidence of defaecation at each was recorded. The mean number of pellets per day varied between 2.9 and 9.3. As Taylor and Williams (1956) report that an adult wild rabbit can produce up to 820 pellets per day, clearly these latrines are not simply areas where rabbits prefer to defaecate, but fulfil some particular function.

Again, Mykytowycz (1968) suggests that they are important in the demarcation of territory. However, while Mykytowycz and Gambale (1969) report that in some cases where two warrens were adjacent, latrines tended to be clustered between them and suggest that latrines condition an invading animal to "respect" any member of the resident group, in the light of the laboratory research mentioned above, they stress the confidence enhancing rather than repellant qualities of latrines: "The identification of an animal with its home range is probably a more important role of dung-hills". It is further claimed that while pellets deposited at random are non-marking pellets, latrines are composed of marking pellets. However, there is no convincing evidence that this is the case and the authors admit that diffuse deposition of faeces does not necessarily mean that they contain no information.

In an attempt to determine the reaction of rabbits of known age, sex and social status to latrines, Mykytowycz and Hesterman (1970) introduced either strange latrines or sods of grass into a laboratory pen containing 29 rabbits of mixed sex and age. The
reaction of a single individual was recorded in each test. The results indicate that rabbits spent more time exploring and marking latrines than sods of grass. In general exploring and marking increased with age and while in males dominant individuals marked more than subordinates, the reverse was true in females. One of the problems with the group test procedure was that on occasion dominant males prevented subordinates from approaching the stimulus material. However there are clearly more serious criticisms to be levelled at this study. Introducing such test material into an unnatural laboratory pen where no latrines already exist is a highly artificial situation. If, as Mykytowycz and Gambale (1969) suggest, these relatively static features of a rabbit's range are important in its orientation and confidence enhancement, it is unlikely that collections of strange pellets placed in the home pen are perceived as "latrines" by the investigating rabbit.

The available evidence, then, suggests that anal gland secretion in rabbits varies with the age, sex and social status of the individual and with season. Pellets deposited in response to conspecific odour appear to differ either in strength or quality of scent from "normal" pellets. Laboratory experiments have shown that rabbits act in a more confident manner when in the presence of their own or even their "partners" anal gland odour. Males are mainly responsible for the maintenance of latrines.

However, if anal gland odour is confidence-enhancing, why do rabbits deposit marking pellets at localised sites which are used by other rabbits rather than depositing such scent throughout the home range? If, alternatively, latrines are sites for information exchange, why are they visited by only a subsection of the
resident group? Mykytowycz and Gambale (1969) report that only 23 per cent of the adult female population visited latrines during 80 hours of observation. It is possible that odour deposited at latrines is of interest only to males, but if this is so, why do some adult females visit latrines while others do not? There is no behavioural evidence of seasonal variations in visits to, or behaviour on, latrines or of the role, if any, played by young rabbits in their maintenance. Clearly there is much still to be learned about the function of anal gland secretion in the rabbit, particularly among free living populations.

In the present study, although defaecation was occasionally seen when observation conditions were particularly favourable, it was not invariably accompanied by any recognisable posture or behaviour. On some occasions a tail-flick was present, but defaecation did occur without this behaviour. Thus, no accurate record of the frequency of defaecation was possible. For this reason it was decided to focus attention on latrines and on behaviour on and around them.

In this section of the present study an attempt is made to find answers to the following questions.

1) Observation of free living rabbits on latrines.
   a) In a natural population, do adult rabbits of different sex and social status groups show a similar pattern in the frequency and duration of visits to latrines and behaviour on latrines to that reported by Mykytowycz and Gambale (1969) for an enclosed group of rabbits?
   b) Do young rabbits differ from adults in their behaviour towards latrines? No young rabbits were present in the population studied by Mykytowycz and Gambale.
c) Does the pattern of behaviour involved in visiting and maintaining latrines show seasonal variation?

d) In what behavioural context do visits to latrines by members of different age, sex and social status groups occur?

2) Examination of the spatial distribution of latrines. Are latrines grouped in any way with respect to warrens and known territories?

3) Manipulation of odour characteristics at latrine sites. What are the effects of pellet deposition of the following manipulations?

a) Clearing existing latrines of pellets,

b) Removing latrines and replacing them with turf,

c) Removing latrines and replacing them with turf plus pellets collected at random from another area,

d) Removing latrines and replacing them with turf plus pellets collected from a latrine in another area.

METHOD

Data for this section come from transcripts of focal animal samples carried out on rabbits in the Cross Park, Tennis Court and Nettle Hollow study areas in six separate months in 1976 and 1977. Details of method and limitations are discussed more fully in Chapter 5. For this and subsequent sections of the study, only marked animals are used in the compilation of results. Thus the sex, social status and approximate age of all animals is known. Each sample lasted for 50 minutes and data from 115 samples are used giving a total observation time of approximately 96 hours. 27 samples were carried out between 0600 and 0900 hours and the remaining 88 were carried out between 1500 and 2200 hours. Seasonal distribution of samples is shown in fig. 10.1. A total of
Distribution of focal animal samples across time of day, month and the age/sex/social status class of the target animal.
62 different individuals were observed; 7 dominant males; 16 adult males; 17 adult females; 10 juvenile males; 12 juvenile females. Clearly the number of dominant males available for sampling in the study areas was lower than the number of members of the other classes. This data was augmented in certain sections by data collected from observations of marked individuals by ad lib sampling. These observations are described in more detail in the relevant sections below.

RESULTS

1. Frequency of Visits to Latrines

The overall number of visits to latrines and the mean number per hour of observation for members of each age, sex and social status class are shown in Fig. 10.2. Each class shows a higher frequency of visits during the evening activity period than in the morning.

Chi-square tests were carried out on the total number of visits by members of the 3 adult classes. Expected frequencies are based on the assumption that the rates of latrine visits are independent of class, and were calculated using a formula suggested by Altmann and Altmann (1977). Such tests were not possible on the data for young rabbits as the expected frequencies are too low.

The frequency of visits between the three adult classes varied significantly ($X^2 = 14.3, p < 0.001$). There was no significant difference between the frequency of visits by dominant and subordinate males ($X^2 = 1.01, \text{N.S.}$). Use of such tests may be questioned as the data are not necessarily independent,
Mean frequency and rates of latrine visits for the 5 age/sex/social status classes in the morning and evening activity periods.
particularly in the case of the dominant male class. However, a clear difference in the frequency of latrine visits between all adult males and adult females is evident in fig. 10.2.

Direct comparison with results reported by Mykytowycz and Gambale (1969) is difficult. The authors present data showing the mean number of visits per animal for each class, but these figures refer only to the mean number of visits by the subsection of the population actually observed visiting latrines (i.e. animals with a zero score are omitted from the data). In the present study, zero scores are included in the results. As the authors provide information on the total number of animals of each class in the sample population it is possible to calculate the overall mean frequency of visits for members of each class (see fig. 10.3). While this is useful for comparative purposes, it is also surely a more realistic indicator of relative frequency given that, while all dominant males visited latrines only 23% of females did so. From these amended figures, it is possible to calculate the mean rate of latrine visiting (mean number of visits per hour of observation) by members of each class (see fig. 10.3).

The absolute rates of visits for all three classes are considerably higher in the present study than those calculated from the Australian data. Mykytowycz and Gambale carried out observations between 1500 and 1900 hours when "the rabbits were active in only a portion of their total home range" and although some observations in the present study were made in the morning, the majority were between 1500 and 2200 hours. Due to the more diurnal activity cycle of the island population, it seems probable that observations were conducted when the rabbits were generally more active than in the Australian study. Mykytowycz and Gambale
Mean frequency of latrine visits reported by Mykytowycz and Gambale (1969) and a transformation of that data to include the "zero scores" omitted in the original. The amended data is then used to compute mean latrine visit rate for comparison with results of present study (see text).
do not report the time of year when their study was undertaken but they do state that only adult rabbits were present, so it is probable that it took place outside the breeding season. In the present study data collected during the breeding season are included in the results. Therefore daily and seasonal variations in the general level of activity may partially account for differences in the rates of latrine visits observed. Although the absolute rates found in the two studies differ considerably, the relative rates of latrine visiting for the two classes of adult males are very similar. The relative rate of visits by adult females, however, is higher in the present study and may be due to the capture method employed. All animals in the sample were marked and most had been snared. It is possible that his capture method selects for less sedentary females and therefore the sample may not be a totally representative one.

Young males show a higher frequency and rate of latrine visits than young females although the difference is not as marked as in adults. Juvenile females visit latrines more frequently than adult females and this may simply reflect their generally less sedentary behaviour.

2. Seasonal Variation in Latrine Visits

Data on the seasonal distribution of visits to latrines are presented in the form of rates (visits per hour of observation) to correct for the imbalances in observation in each of the six months (see figs. 10.4 and 10.5). A comparison of figs. 10.1 and 10.4 shows the unavoidable variation in the number of observation periods carried out on members of each age, sex and social status class in the six months.
<table>
<thead>
<tr>
<th></th>
<th>FEBRUARY</th>
<th>APRIL</th>
<th>JUNE</th>
<th>AUGUST</th>
<th>SEPTEMBER</th>
<th>NOVEMBER</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dominant males</td>
<td>1</td>
<td>1.25</td>
<td>0.71</td>
<td>0.67</td>
<td>0.29</td>
<td>0</td>
</tr>
<tr>
<td>Subordinate males</td>
<td>0.6</td>
<td>1.67</td>
<td>0.5</td>
<td>0.2</td>
<td>0.17</td>
<td>0</td>
</tr>
<tr>
<td>Adult females</td>
<td>0</td>
<td>0.17</td>
<td>0.14</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Juvenile males</td>
<td>-</td>
<td>0</td>
<td>0.29</td>
<td>0.5</td>
<td>0.67</td>
<td>0</td>
</tr>
<tr>
<td>Juvenile females</td>
<td>-</td>
<td>-</td>
<td>0.17</td>
<td>0.25</td>
<td>0</td>
<td>-</td>
</tr>
</tbody>
</table>

Mean Rate of latrine visits (visits/hour of observation) for members of the five age/sex/social status classes across the 6 sample months.
Fig. 10.5

Monthly variation in rate of latrine visits (visits/hour of observation) for the five age/sex/social status classes.
A Kruskal-Wallis one-way analysis of variance by ranks reveals that there are significant differences between the rates of visits by the different adult classes across the 6 sample months ($H = 7.291$, d.f. = 2, $p < 0.025$). Post-hoc pairwise comparison (Scheffe's method) show that dominant males and females differ significantly at the 0.01 level.

Clearly, although adult females show a low rate of latrine visiting throughout the year, all adults show a peak in visits during the breeding season. However, the data indicate, surprisingly, that at this time subordinate males have a higher rate of visiting than dominant males. April is the only month in which this is the case. Dominant males spend more time in social behaviour than subordinate males during the breeding season, and it is possible that this leaves correspondingly less time for latrine maintenance. Young males show a steady increase in the rate of visits to latrines in the first few months of their lives. No latrine visits were recorded in five hours of observation in November. The low number of samples conducted in November reflects the low number of rabbits above ground during the day. The shortage of daylight hours means that much of the normal period of greatest activity occurs after dark. If facilities enabling night observation had been available, undoubtedly a more realistic assessment of behaviour at this time of year would have been possible.

3. **Temporal Patterns of Latrine Visits**

While the above data give an indication of the overall frequency of visits by different groups at different times of the year they do not show whether visits were grouped or isolated. Thus animals may show the same overall frequency of visits even
though the pattern of such visits is quite different. This is particularly relevant given the observation (Mykytowycz, 1958) that dominant males conduct scent marking "tours" of their range, briefly visiting many sites in a relatively short time. Although this observation referred primarily to chin marking it is possible that similar phenomenon occurs with respect to latrine visits. Although, obviously, it is unlikely that the 50 minute observation periods coincided with entire sequences of such behaviour, it was felt that further analysis of the data from samples where at least one visit was recorded might yield more information (see appendix 5.1 for frequency of occurrence over sample months). Latrine visits were placed in one of the two following categories.

(i) Instances where the latrine visit was the only visit made by the target animal in the 50 minute sample period.

(ii) Instances where the latrine visit was not the only visit made by the target animal in the 50 minute sample period.

No occurrences of an animal visiting the same latrine more than once in a 50 minutes sample were recorded.

Fig. 10.6 shows a summary of this data. A chi-square test conducted on the data for dominant and subordinate males shows that dominant males exhibit significantly more grouping of latrine visits than subordinates (chi-square = 4.78, d.f. = 1 p < 0.05 one tailed). However, it should be noted that the maximum number of visits observed in a single observation period was 3 (see appendix 5.1).

The proportion of observation periods in which no visits were recorded is similar for dominant males (55.56%) and subordinate males (60%). The difference, therefore, in the overall frequency of visits by members of these two classes can largely be
Fig. 10.6

<table>
<thead>
<tr>
<th></th>
<th>Single visits</th>
<th>(%)</th>
<th>Multiple visits</th>
<th>(%)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Dominant males</strong></td>
<td>7</td>
<td>38.89</td>
<td>11</td>
<td>61.11</td>
</tr>
<tr>
<td><strong>Subordinate males</strong></td>
<td>10</td>
<td>71.43</td>
<td>4</td>
<td>28.57</td>
</tr>
<tr>
<td><strong>Adult females</strong></td>
<td>2</td>
<td>100</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><strong>Juvenile males</strong></td>
<td>5</td>
<td>100</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><strong>Juvenile females</strong></td>
<td>2</td>
<td>100</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

Overall frequency of single and multiple latrine visits within single observation periods for the 5 age/sex/social status classes.
accounted for by the tendency of dominant males to make more 
latrine visits during some observation periods rather than 
regularly making single visits in more observation periods.

4. **Duration of Latrine Visits**

Data on visit duration from focal animal samples are 
augmented by data from observations in the Tennis Court and Cross 
Park areas during the summer of 1977. These data were collected on 
an "ad lib" basis, by observing all animals above ground at the 
study warrens during evening activity periods and recording visits 
to latrines by marked individuals as and when they occurred. 
Visits recorded for each age/sex and social status class by both 
methods are presented in appendix 5.2. Mean durations of visits 
for each class and comparisons with data reported by Mykytowycz 
and Gambale (1969) are shown in fig. 10.7.

A Kruskal-Wallis one-way analysis of variance by ranks was 
carried out on the data from the present study and reveals a 
significant difference between the 5 age/sex and social status 
classes in the duration of latrine visits ($H = 47.423$, d.f. = 4, $p$ 
$< 0.001$). Post hoc pairwise comparisons (Scheffe's method) show 
that the latrine visits of dominant males are significantly 
shorter than those of any other class ($p < 0.01$). Furthermore the 
visits of subordinate adult males are significantly longer than 
those of all other groups ($p < 0.05$) except juvenile males. 
Subordinate adult males however, also show greater variation in 
visit duration than any other class (see appendix 5.3 for raw 
data). Visit durations of members of the other classes generally 
fall between the two extremes shown by dominant and subordinate 
adult males.
<table>
<thead>
<tr>
<th>Age/sex/social status</th>
<th>N visits</th>
<th>Mean Duration (secs)</th>
<th>Range</th>
<th>Mean Duration (secs) (Mykytowycz and Gambale)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dominant males</td>
<td>29</td>
<td>43</td>
<td>8-114</td>
<td>31</td>
</tr>
<tr>
<td>Subordinate males</td>
<td>25</td>
<td>208</td>
<td>15-380</td>
<td>263</td>
</tr>
<tr>
<td>All Adult males</td>
<td>54</td>
<td>119</td>
<td>8-380</td>
<td>174</td>
</tr>
<tr>
<td>Adult females</td>
<td>6</td>
<td>94</td>
<td>46-185</td>
<td>86</td>
</tr>
<tr>
<td>All adults</td>
<td>60</td>
<td>117</td>
<td>8-380</td>
<td>163.54</td>
</tr>
<tr>
<td>Young males</td>
<td>10</td>
<td>162</td>
<td>114-221</td>
<td>-</td>
</tr>
<tr>
<td>Young females</td>
<td>5</td>
<td>133</td>
<td>63-172</td>
<td>-</td>
</tr>
<tr>
<td>All young</td>
<td>15</td>
<td>152</td>
<td>63-221</td>
<td>-</td>
</tr>
</tbody>
</table>

Mean duration of latrine visits (N=75) by members of the 5 age/sex/social status classes. Data from Mykytowycz and Gambale (1969) is presented for comparison.
The results broadly support the findings of Mykytowycz and Gambale for an enclosed population. Bell (1977, unpublished PhD thesis) in a study of a wild population on Skokholm reports that the mean duration of latrine visits for all rabbits in her sample was 120 secs. It is not clear if this sample included young rabbits.

5. Behaviour on Latrines

In this section the focal animal sample data are again augmented by data from the observations in Cross Park and Tennis Court described above. Mykytowycz and Gambale (1969) present data on the behaviour of rabbits on latrines in the form of time spent in each behaviour expressed as a percentage of total time on the latrine. In the present study it was found that such an approach was only feasible for certain behaviours eg. resting and grooming, where the bout duration is relatively long. A single observer in the field without sophisticated event recording apparatus cannot accurately determine bout length for many behaviours which occur in rapid, rather confused sequences. Frequently, sequences of sniffing, sitting alert, grazing, pawscrapping and chinning occurred during visits to latrines. These were not fixed sequences and did not invariably contain all of these elements, therefore they could not be regarded as single units and the overall duration of sequences recorded. Thus, for mainly practical reasons, the occurrence of behaviours was recorded in three different ways. Bout durations of resting, grooming and sitting alert were recorded. All occurrences of chin marking were recorded as events. Pawscrapping and feeding were recorded in the form of one-zero occurrences for each visit. This was felt to be a realistic approach as these behaviours were frequently interrupted.
by sniffing, chinning, etc., but are probably best viewed as single bouts. For reasons described earlier defaecation and urination were not recorded.

a) Chinning

Deposition of scent from the submandibular gland onto pellets was recorded on 52% of visits by rabbits in the sample. Fig. 10.8 shows the mean frequency and rate (bouts/minute on latrine) of chinning for each of the age, sex and social status classes. Chinning uninterrupted by another behaviour is recorded as a single bout. Mykytowycz and Gambale report relative times spent in chinning for members of different adult classes and indicate that dominant males spend approximately seven times as much of their time on the latrine in chinning as subordinate males. While percentage duration data are not directly comparable to event data, it is clear from fig. 10.8 that dominant males chin more than subordinate males and, furthermore, given the shorter duration of their visits (see fig. 10.7), their rate of chinning while on latrines is considerably higher. Chi square tests reveal that while the different age/sex/social classes do not differ significantly in the number of visits in which chinning was recorded ($p < 0.2$, d.f. = 4, chi square = 5.948), they do differ significantly in the number of chinning bouts recorded ($p < 0.01$, d.f = 4, chi square = 13.353). The main difference between the classes would therefore appear to be in the number of chinning bouts per visit. The results of the Australian study also indicate that females spend a higher percentage of their time on latrines in chinning than subordinate males. While the frequency of chinning, observed in the present study, is much higher for subordinate males, the rate of chinning for subordinate males and
Chinning on latrines: Total chinning bouts for each age/sex/social class, the number of visits and percentage of visits on which chinning was observed. Chinning rate is calculated from visit duration data (see fig. 10.7).

<table>
<thead>
<tr>
<th></th>
<th>N Visits</th>
<th>Chinning bouts</th>
<th>Visits on (%) chinning recorded</th>
<th>Mean bouts per visit</th>
<th>Chinning rate (bouts per minute on latrine)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dominant males</td>
<td>29</td>
<td>38</td>
<td>21</td>
<td>72.41</td>
<td>1.31 has 1.82</td>
</tr>
<tr>
<td>Subordinate males</td>
<td>25</td>
<td>17</td>
<td>14</td>
<td>56</td>
<td>0.68 has 0.2</td>
</tr>
<tr>
<td>Adult females</td>
<td>6</td>
<td>1</td>
<td>1</td>
<td>16.67</td>
<td>0.17 has 0.11</td>
</tr>
<tr>
<td>Young males</td>
<td>10</td>
<td>3</td>
<td>3</td>
<td>30</td>
<td>0.3 has 0.11</td>
</tr>
<tr>
<td>Young females</td>
<td>5</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

Fig. 10.8
adult females is similar due to the longer duration of the male visits. Differences between the results of the two studies may again be due to the inclusion in the present study of data collected during the breeding season.

(b) Feeding

Feeding was simply scored if it occurred during a latrine visit. Data is presented in fig. 10.9 and a chi square test shows that there are no significant differences in the incidence of feeding per visit between the different age/sex/social classes (chi square = 1.263, d.f. = 4, N.S.).

The recorded frequencies of feeding are low, however, and if the scores are converted into percentage of visits on which feeding occurred, it does appear that subordinate males feed on a slightly higher proportion of visits than either dominant males or adult females. The results for adults mirror the findings of Mykytowycz and Gambale on the percentage time spent feeding. Feeding while on latrines was generally rather desultory and was frequently interrupted by other activities, therefore the slightly higher frequency of feeding shown by subordinate males may simply be an artifact of the longer duration of their visits. It has been suggested that feeding in this context may be regarded as gustatory investigation (Mykytowycz and Hesterman, 1970).

(c) Pawscraping

Pawscraping is the term commonly applied to short bursts of scraping at the ground in order to distinguish the activity from the "more serious" digging observed when rabbits are excavating burrows or breeding stops. Again this behaviour was simply scored if it occurred during visits to latrines. Fig. 10.10 shows that
### Feeding on latrines

Data show the number of visits on which feeding occurred and the percentage of total recorded visits on which feeding occurred.

<table>
<thead>
<tr>
<th></th>
<th>N Visits</th>
<th>Visits in which feeding recorded</th>
<th>% Visits in which feeding recorded</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dominant males</td>
<td>29</td>
<td>7</td>
<td>24.14</td>
</tr>
<tr>
<td>Subordinate males</td>
<td>25</td>
<td>10</td>
<td>40</td>
</tr>
<tr>
<td>Adult females</td>
<td>6</td>
<td>1</td>
<td>16.67</td>
</tr>
<tr>
<td>Young males</td>
<td>10</td>
<td>3</td>
<td>30</td>
</tr>
<tr>
<td>Young females</td>
<td>5</td>
<td>2</td>
<td>40</td>
</tr>
</tbody>
</table>

### Pawscraping on latrines

Data show the number of visits on which pawscraping occurred and the percentage of total recorded visits on which pawscraping occurred.

<table>
<thead>
<tr>
<th></th>
<th>N Visits</th>
<th>Visits in which Pawscraping recorded</th>
<th>% Visits in which Pawscraping recorded</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dominant males</td>
<td>29</td>
<td>3</td>
<td>10.34</td>
</tr>
<tr>
<td>Subordinate males</td>
<td>25</td>
<td>5</td>
<td>20</td>
</tr>
<tr>
<td>Adult females</td>
<td>6</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Young males</td>
<td>10</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Young females</td>
<td>5</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>
only adult males were observed pawscraping at latrines. Clearly the data does not lend itself to statistical analysis. Mykytowycz and Gambale report that dominant males spend a higher percentage of visit time in digging. In the present study subordinate males were observed pawscraping on more visits than dominant males and, although individuals varied in the amount of pawscraping per visit, the impression gained was that dominant males did not spend more time in this activity than subordinates. The possible link between pawscraping and olfaction is discussed more fully in chapter 13.

d. Sitting Alert, Resting and Grooming on Latrines

"Sitting alert" and "resting" both describe situations when an animal is immobile but are easily distinguishable in practice. "Sitting alert" refers to an animal in a sitting posture with ears up, nostrils dilating etc, whereas "resting" refers to an animal either sitting or lying in a relaxed posture often with eyes closed. "Grooming" refers to a variety of maintenance activities; licking fur on body and legs; scratching; rubbing forelegs on the head etc. Time spent in each activity per visit was recorded and is shown in fig. 10.11 expressed as the mean percentage of visit time. Most rabbits spend a considerable proportion of their time on latrines sitting alert. As this behaviour frequently includes dilation of the nostrils it is probable that olfactory information is being gained. Black-Cleworth and Verberne (1975) suggest that rabbits may exhibit a behaviour analogous to "flehman", shown in the felidae and other mammals with a well developed vomeronasal organ, after sniffing a scent stimulus. However in the present study "sitting alert" was not invariably preceded by sniffing at the substrate and there is no evidence that the vomeronasal organ
<table>
<thead>
<tr>
<th></th>
<th>Mean % of visit time spent in each activity</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N Visits</td>
</tr>
<tr>
<td>Dominant males</td>
<td>29</td>
</tr>
<tr>
<td>Subordinate males</td>
<td>25</td>
</tr>
<tr>
<td>Adult females</td>
<td>6</td>
</tr>
<tr>
<td>Young males</td>
<td>10</td>
</tr>
<tr>
<td>Young females</td>
<td>5</td>
</tr>
</tbody>
</table>

Resting, sitting alert and grooming on latrines; data show mean percentage of visit duration spent in each activity.
is involved. The proportion of time spent resting is lower in all groups except adult females. Mykytowycz and Gambale suggest that during sitting and lying, the scent characteristics of the latrine may be transferred to the body of the animal. However, rolling on a latrine, observed on one occasion in the Australian study was not observed during the present study. Although Mykytowycz and Gambale do not distinguish between "alert" and "relaxed" postures in immobile animals they do draw a distinction between sitting and lying. If these are combined to give a total "time immobile" figure, the results for subordinate males and adult females correspond fairly closely to the results presented in fig. 10.11. However, although it appears that dominant males in the present study spent approximately twice as long immobile on latrines as those in the Australian study they still spend considerably less time than members of other classes. Although the absolute levels of grooming in the present study are slightly higher than those reported by Mykytowycz and Gambale, the relative percentage (Adult females subordinate males dominant males) are the same. Young rabbits spend a higher proportion of their time on latrines grooming than adults.

e) Sniffing
The percentage of time on latrines devoted to sniffing is presented by Mykytowycz and Gambale but in the present study it was found that the duration of sniffing was very difficult to record as it occurred in short bouts interspersed by other behaviours. To record individual sniffs as events would have required slow motion recording apparatus to gain anything like an accurate tally. For these reasons the frequency of sniffing was not quantitatively measured.
6. Behavioural Context of Latrine Visits

It has been suggested that the complexity of mammalian chemosensory communication is greater than the potential complexity of the active chemicals and that identical chemical signals may take on various different meanings depending on the context in which they are received (Beauchamp et al., 1976). Thus the possibility exists that members of different age, sex and social status classes visit latrines in different contexts and may not be "using" latrines for the same reasons. Analysis of the behavioural context of activities related to olfactory communication has rarely been attempted, although several researchers have concerned themselves with the causation of scent marking behaviour (e.g. Johnston, 1977).

There are several problems inherent in the analysis of context, the first being in deciding what behaviours actually constitute the context. An animal may be observed going through a sequence of chasing, grooming and scent marking. If grooming invariably follows chasing then it may validly be regarded as a chase-groom unit, but if this is not the case, which of these preceding behaviours does one regard as the "context" in which the scent marking occurred? The problem here is that if the observer ignores the grooming he is in effect regarding the chasing as more "relevant" or "interesting" than the grooming and is thus prejudging the issue of context. At what point, then, in the preceding behaviour does one select the behaviour to record as the context? In this section of the present study the behaviour immediately preceding a latrine visit has been recorded.

Bell (1980) reports the results of an analysis of the behavioural context of latrine visits. However, it appears that
the data from a free living population on Skokholm were collected by ad lib sampling. This procedure has several drawbacks as the observer's attention is naturally drawn to more "interesting" or noticeable behaviours. The event being analysed is thus more likely to be recorded as following more noticeable behaviours. The only valid method of approaching this problem is to sample all behaviour for a single animal at a time. Therefore data presented in this section are obtained only from focal animal samples - see fig. 10.1 for distribution.

Many of the behavioural categories used in this analysis have already been given operational definitions in this chapter, but several may need a few words of explanation.

"Exploration" is a term sometimes used to refer to investigatory behaviour outside the normal geographical range of the animal (i.e. investigation of an 'unknown' area). In the present study however, it has been used to refer to investigatory behaviour (movement interspersed with bouts of sniffing) irrespective of location. In fact the greatest amount of such behaviour took place within the home range of the animal concerned.

"Intrawarren social interaction" is used to describe any social interaction between the animal concerned and another resident of the same warren. Such behaviour may be aggressive, sexual or parental and involve chasing, grooming, fighting, olfactory investigation etc.

"Interwarren social interaction" - as above but involving any interaction between the animal concerned and a resident of a different warren.
Behaviour occurring prior to latrine visits is shown in fig. 10.12. The sample sizes are obviously very small for all but the adult male groups and consequently only a small variation in behaviours was recorded.

The categories of behaviour as presented in figs. 10.12 and 10.13 are not amenable to statistical testing for differences between the five age/sex/social status classes and it was decided to collapse the behavioural categories into 2 variables called 'active' and 'passive', and to compare dominant male scores with the combined scores of the remaining 4 classes. Within the "active" category are included scores for exploration, intra and inter warren social interactions, chinning and pawscraping. Within the "passive" category are included feeding, grooming and resting. Thus the 'active' category contains social behaviour, behaviour related to scent marking and movement throughout the environment.

Clearly, the collapsing of the data into such categories is a post hoc expedient to permit statistical testing and the membership of the categories is open to question. For instance it might be argued that 'exploration' is more investigatory and therefore "passive" with respect to olfaction. However, as animals engaged in scent marking or social behaviour were more likely to be recorded actively moving around their environment than animals feeding, resting or grooming, it was felt that exploration fitted more satisfactorily into the 'active' category. It has been suggested that pawscraping may be related to scent marking (see chapter 13) and it was also included in the 'active' category.

Dominant males are significantly more likely to have been engaged in an 'active' behaviour immediately prior to a latrine.
<table>
<thead>
<tr>
<th></th>
<th>Dominant males N (%)</th>
<th>Subordinate males N (%)</th>
<th>Adult females N (%)</th>
<th>Young males N (%)</th>
<th>Young females N (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total Visits</td>
<td>18 (33.3)</td>
<td>14 (14.3)</td>
<td>2 (14.3)</td>
<td>5 (20)</td>
<td>2 (100)</td>
</tr>
<tr>
<td>Exploration</td>
<td>6 (33.3)</td>
<td>2 (14.3)</td>
<td>0 (0)</td>
<td>1 (20)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>Feeding</td>
<td>4 (22.2)</td>
<td>5 (35.7)</td>
<td>1 (50)</td>
<td>2 (40)</td>
<td>2 (100)</td>
</tr>
<tr>
<td>Intrawarren Social Interaction</td>
<td>3 (16.7)</td>
<td>1 (7.1)</td>
<td>0 (0)</td>
<td>1 (20)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>Interwarren Social Interaction</td>
<td>1 (5.6)</td>
<td>1 (7.1)</td>
<td>1 (50)</td>
<td>0 (0)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>Chinning</td>
<td>2 (11.1)</td>
<td>1 (7.1)</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>Pawsraping</td>
<td>1 (5.6)</td>
<td>1 (7.1)</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>Grooming</td>
<td>1 (5.6)</td>
<td>2 (14.3)</td>
<td>0 (0)</td>
<td>1 (20)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>Resting</td>
<td>0 (0)</td>
<td>1 (7.1)</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
</tr>
</tbody>
</table>

Behaviour immediately preceding latrine visits (N=41) by members of the age/sex/social status classes. Data expressed as frequency and % frequency.
<table>
<thead>
<tr>
<th></th>
<th>Dominant males</th>
<th>Subordinate males</th>
<th>Adult females</th>
<th>Young males</th>
<th>Young females</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N (%)</td>
<td>N (%)</td>
<td>N (%)</td>
<td>N (%)</td>
<td>N (%)</td>
</tr>
<tr>
<td>Total Visits</td>
<td>18 (16.7)</td>
<td>14 (7.1)</td>
<td>2 (100)</td>
<td>5 (20)</td>
<td>2 (50)</td>
</tr>
<tr>
<td>Exploration</td>
<td>3 (16.7)</td>
<td>1 (7.1)</td>
<td>0 (0)</td>
<td>1 (20)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>Feeding</td>
<td>6 (33.3)</td>
<td>8 (57.1)</td>
<td>2 (100)</td>
<td>2 (40)</td>
<td>1 (50)</td>
</tr>
<tr>
<td>Intrawarren Social Interaction</td>
<td>3 (16.7)</td>
<td>1 (7.1)</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>Interwarren Social Interaction</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>Chinning</td>
<td>1 (5.6)</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>Pawscraping</td>
<td>1 (5.6)</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>Grooming</td>
<td>0 (0)</td>
<td>1 (7.1)</td>
<td>0 (0)</td>
<td>1 (20)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>Resting</td>
<td>4 (22.2)</td>
<td>3 (21.4)</td>
<td>0 (0)</td>
<td>1 (20)</td>
<td>1 (50)</td>
</tr>
</tbody>
</table>

Behaviour occurring immediately following latrine visits (N=41) by members of the 5 age/sex/social classes. Data expressed as frequency and % frequency.
visit than are members of other classes (chi square = 3.216, d.f. = 1, p < 0.05). It is clear from fig. 10.12 that dominant males show a higher incidence of exploration, social behaviour and chinning before visiting latrines than do members of the other 4 classes. Among members of these other classes, the most frequent pre-visit activity is feeding.

Behaviour occurring immediately after visits to latrines is shown in fig. 10.13. Again, collapse of behavioural categories into 'active' and 'passive' variables permits comparison between dominant males and the combined scores of the other classes. Dominant males are significantly more likely to show active behaviour after latrine visits than are members of other classes (chi square = 3.598, d.f. = 1, p < 0.05). Fig. 10.13 shows that dominant males show a higher incidence of exploration and social interactions following latrine visits than other classes but all classes show a high incidence of feeding and resting after visits. Comparison of pre and post-visit behaviours for all rabbits is given in fig. 10.14. The incidence of feeding and resting increases after visits but the incidence of all other behaviours, several of which can be regarded as scent related, decreases. Bell (1980) suggests that a high proportion of latrine visits take place in an aggressive context (after chases) and are usually performed by the aggressor. In the present study a much lower proportion of visits followed social interactions of any kind and while dominant males were invariably the aggressor (either chasing or approaching a conspecific) in their interactions, this was not necessarily the case for members of other classes.

It seems probable that the problems inherent in ad lib sampling, discussed above, account for much of the disparity
between the two sets of results (see fig. 10.14). If attention is inadvertently drawn to chases between rabbits, then latrine visits following chases will be recorded. Latrine visits following, for instance, feeding are less likely to be recorded. The fact that post-visit behaviours correspond much more closely supports this argument.

In dominant males, therefore, latrine visits appear to take place in an "active" context. Exploration, scent-marking and social interactions account for a larger proportion of both pre and post-visit behaviour than is the case in other groups. For other classes feeding constitutes a higher proportion of both pre and post-visit behaviour.

7. Latrine Distribution

The distribution of latrines in the Cross Park and Tennis Court areas was mapped in the summer of 1977. Figs. 10.15, 10.16 show the locations and sizes of latrines in relation to territorial boundaries. Latrine sizes were assessed by counting the pellets very roughly. Although this is only a crude guide to absolute size it does give a reasonable indication of relative size. The location of major latrines appeared to be remarkably stable over the three years of the study. It can be seen from fig. 10.15 that in the Tennis Court area, the location of latrines corresponds closely with territorial boundaries and the two largest latrines were visited by members of both warrens 1 and 2. In fact the territorial boundaries could be fairly accurately deduced from the distribution of latrines (see photos). The situation in the Cross Park area was much less straightforward. In addition to several latrines along territorial boundaries, the majority of latrines were scattered throughout territories,
Fig. 10.14

<table>
<thead>
<tr>
<th></th>
<th>Pre-visit behaviour (%)</th>
<th>Post-visit behaviour (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Feeding</td>
<td>34.15</td>
<td>12</td>
</tr>
<tr>
<td>Exploration</td>
<td>21.95</td>
<td>19</td>
</tr>
<tr>
<td>All social interactions</td>
<td>19.52</td>
<td>42</td>
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<tr>
<td>Intrawarren social</td>
<td>12.2</td>
<td>-</td>
</tr>
<tr>
<td>Interwarren social</td>
<td>9.76</td>
<td>-</td>
</tr>
<tr>
<td>social interactions</td>
<td>7.32</td>
<td>-</td>
</tr>
<tr>
<td>Chinning</td>
<td>7.32</td>
<td>4</td>
</tr>
<tr>
<td>Pawscraping</td>
<td>4.88</td>
<td>-</td>
</tr>
<tr>
<td>Resting</td>
<td>2.44</td>
<td>4</td>
</tr>
</tbody>
</table>

Behavioural context of latrine visits (N=41). Pre and post visit behaviours expressed as % of frequency and data from Bell (1980) to permit comparison.
Latrine distribution - Tennis Court study area summer 1977
Latrine size (approx. no. of pellets) • 500 □ 500-1000 □ 1000-1500 ★ 1500
........ Daily ranges of adult males (composite for each warren)

Latrine distribution - Cross Park study area summer 1977
Latrine size (approx. no. of pellets) • 500 □ 500-1000 □ 1000-1500
........ Daily ranges of adult males (composite for each warren)
particularly in warren 2. Mykytowycz and Gambale (1969) also found considerable variation in latrine distribution although they suggest that when warrens are adjacent there is always a concentration of latrines between them. This is largely supported by the present findings although obviously a more extensive field study of latrine distribution is necessary.

8. Experimental Manipulation of Latrine Characteristics

Mykytowycz and Gambale (1969) examined the incidence of defaecation on latrines by the simple expedient of examining existing latrines and counting the number of fresh pellets on a daily basis. This procedure may be possible in the dry heat of S.E. Australia where pellets dry out very quickly, but was simply not feasible on the Isle of May. Fresh pellets were not always easily distinguishable from the existing mass of pellets and an accurate assessment of daily pellet deposition would have been quite impossible. A further measure of visits to latrines used in the Australian study was "signs of urination". Assuming that this means the wetting of existing pellets or ground by urine, this again may be possible in the dry climate of Australia but not on the Isle of May.

Therefore it was necessary to clear latrines to gain some idea of pellet deposition. This technique was undertaken with certain misgivings as Mykytowycz and Gambale in referring to work by Taylor and Williams (1956) claim that "rabbits ...... tended to avoid defaecation of areas from which their own fresh pellets were removed". However, examination of the Taylor and Williams paper shows that they removed pellets from a non-latrine area and obtained rather strange results. The day after pellets were initially removed there was normal deposition of pellets. These
were also removed and over the following nine days very few pellets were deposited. Why rabbits should have deposited pellets normally after initial clearance but not thereafter is not known. Taylor and Williams conclude that "the animals avoidance of cleared areas cannot be regarded as established".

Established latrine areas on the Isle of May differ from non-latrine areas in that beneath the pile of surface pellets lies a mass of decomposed pellet material which has permeated the underlying substrate. Therefore it is probably true to say that removal of the surface pellets does not remove the "latrine". It simply removes the most recently deposited pellets and permits counting of newly deposited pellets. This is quite a different situation from removing randomly deposited pellets from an area of grass or earth as in the Taylor and Williams study.

In this section of the present study the daily incidence of defaecation was recorded at latrine sites after various manipulations:

a) latrines were cleared of surface pellets
b) latrines were dug out and replaced with a sod of turf, which had been cleared of pellets, obtained from another area
c) latrines were replaced with a sod of turf with 20 fresh pellets collected at random from another area
d) latrines were replaced with a sod of turf with 20 fresh pellets collected from a latrine in another area.

Latrine sites were selected on the basis of size and location. All sites were located on fairly level ground in the southern half of the island outside the main study areas. The original latrines at these sites were of roughly equal size.
(approximately 1000 pellets). There is the possibility in all of the tests that pellets were blown on or off the test sites. Pellets end to be blown around much more when they age, dry out and become lighter (both in weight and colour). Fresh pellets deposited at test sites were therefore seldom dislodged by wind, and pellets blown onto the sites were generally lighter in colour and therefore distinguishable. No attempt was made to observe behaviour at any of these latrine sites.

(a) Cleared Latrines. Latrines at 10 sites were initially cleared of pellets and subsequently, before 1200 hrs each day for 9 days, fresh pellets were counted and removed. There is considerable variation in the level of defaecation at different sites and across days. The mean daily pellet deposition varied between 3.2 and 15.9 with an overall mean of 10.2. The range in numbers of pellets deposited/day/site is 0-23. The mean percentage of days on which pellets were deposited is 84.4%. Variation across days does not show any clear pattern although defaecation did decrease on 2 occasions during prolonged heavy rain and increased again the following day (see fig. 10.17). Mykytowycz and Gambale (1969) suggest that defaecation increases after rain in order to replace the odours leached out by the rain. This is one possible explanation for increased defaecation after heavy rain, however such variation may simply reflect the overall level of above ground activity. The number of rabbits above ground is greatly reduced during prolonged heavy rain and this if often followed by an unusually large proportion of the population feeding on the surface. It rained all day on day 3 (see fig. 10.17) and the lowest pellet count was recorded, but the highest count was recorded the following day. Mykytowycz and Gambale recorded daily
Total pellets deposited on 'cleared' latrines.
defaecation at latrines of different ages and sizes. They found that mean daily pellet deposition varied between 2.9 and 9.3 and that defaecation took place on 50% - 88% of days. All latrines used in the tests in this section correspond to their "new-small" category for which mean daily pellet deposition was 5.5 with defaecation occurring on 63% of observation days.

(b) Latrines replaced with sods of grass. Latrines were dug out of the ground and replaced with sods of turf from a different area of the island. The turf was cleared of any pellets already present. Ideally the replacement turf for this test would have been collected from a rabbit free area to ensure that no scent products were present, but it was found that if areas were fenced of to exclude rabbits the vegetation grew long very quickly and changed in character. Latrines at 4 sites were replaced with turf and for the 8 subsequent days freshly deposited pellets were counted and removed before 1200 hours each day. The mean pellet count varied between 0.25 and 0.63 at different sites. The overall mean daily pellet count was 0.44. Defaecation occurred on a mean of 15.63% of days. Although defaecation did not occur at any site on the first day after replacement of latrines, there was no discernable pattern to the subsequent daily level of defaecation at any site.

The higher incidence of defaecation in the previous test compared to the present test suggests that "clearing" latrines of pellets does not effectively remove the latrine. The very low incidence of defaecation in this second test is surprising given that the replacement turfs were located on the sites of latrines. Evidently the odour of the latrine is important in stimulating defaecation.
(c) Latrines replaced with turf and randomly collected pellets. As in the previous test 4 latrines were dug out and replaced with turf. For each test site 20 pellets, which were judged to be reasonably fresh, were collected from non-latrine areas in another location and scattered on the replacement turf. For the 8 days following replacement, any additional pellets were counted and all pellets removed before 1200 hours each day. As it was impracticable to remove only freshly deposited pellets, all pellets were removed and a fresh supply of stimulus pellets replaced at each site daily.

The mean daily count varied from 1.5 to 2.38 at different sites and the overall mean daily pellet count was 1.88. Defaecation occurred on a mean of 46.9% of days. As in the previous test, defaecation did not occur on the first day following removal of the latrine and there was no clear pattern to subsequent defaecation.

(d) Latrines replace with turf and pellets collected at latrines. The test procedure was similar to that described for the previous test. For each site, 20 pellets which were judged to be reasonably fresh were collected from latrines in other areas and scattered on the replacement turf. At each site pellets from a single latrine were used on each test day, but this was not the case across days. Therefore rabbits were confronted with pellets from a single latrine each day but in the course of the test they encountered pellets from 8 latrines.

The mean pellet count varied between 2.38 and 5.88 at different sites and the overall mean daily pellet count was 3.91. Defaecation occurred on a mean of 62.5% of days.
The results of the four test conditions are summarized in fig. 10.18. Clearly the presence of faecal pellets or the odour of pellets stimulates defaecation. The "turf alone" condition resulted in a very low rate of pellet deposition but rather surprisingly the pellets collected from non-latrine sites stimulated considerably more defaecation. Thus, the designation of such pellets as "non-marking pellets" (Hesterman and Mykytowycz, 1968), suggesting that they do not carry olfactory information appears to be misleading. The clear difference between the level of defaecation stimulated by "random" pellets and latrine pellets may therefore be due to relative intensity of odour, supporting Bell's (1980) suggestion that anal gland odour on pellets is not an "all-or-none" phenomenon.

Mykytowycz and Gambale (1969) added "a few" foreign pellets (although it is not stated, it is assumed that these were from other latrines) to 35 latrines and compared the incidence of defaecation at these with that at a similar number of untreated latrines. They report that the incidence of defaecation was higher at the treated latrines (6.6 pellets per day) then at the untreated latrines (5.0 pellets per day). While the results of the present tests indicate that rabbits deposit more pellets on their own cleared latrines than they do on turf treated with strange pellets, the conditions in the two studies clearly differ in several respects. Here, in condition (d) the latrine had been removed, there was a greater number of strange pellets present at any time on the latrine site than "known" pellets and any pellets deposited by the rabbits were removed and replaced with a fresh group of strange pellets every 24 hours. The interesting alternative of permitting deposited pellets to accumulate was
<table>
<thead>
<tr>
<th>LATRINE SITE CONDITION</th>
<th>Number of Sites</th>
<th>Mean number of pellets deposited per day</th>
<th>Mean incidence of defaecation (% of days)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cleared of pellets</td>
<td>10</td>
<td>10.2</td>
<td>84.4</td>
</tr>
<tr>
<td>Replaced by Turf</td>
<td>4</td>
<td>0.44</td>
<td>15.63</td>
</tr>
<tr>
<td>Replaced by Turf &amp; random pellets</td>
<td>4</td>
<td>1.88</td>
<td>46.9</td>
</tr>
<tr>
<td>Replaced by Turf &amp; latrine pellets</td>
<td>4</td>
<td>3.91</td>
<td>62.5</td>
</tr>
</tbody>
</table>

Summary of results of latrine replacement experiments.

A series of t-tests was carried out on the data from the 4 conditions. Defaecation at sites simply cleared of pellets was significantly higher than at any of the sites in the other 3 conditions, p<0.001, d.f. = 14 (t = 9.263, t = 7.468, t = 4.711). However, although sites with turf and latrine pellets elicited significantly higher pellet deposition than sites with turf and random pellets (p<0.05, d.f. = 14, t = 2.415), sites with turf and random pellets elicited significantly higher deposition than sites with turf alone (p<0.01, d.f. = 14, t = 3.345). See appendix 5.4 for raw data.
unfortunately not practicable. The sods of turf in conditions b, c and were not replaced each day and it is possible that other scent deposits eg. urine, accumulated over the period of the tests.

Discussion

Despite the discrepancies mentioned above, where data are comparable the results of the present study on frequency and duration of visits and behaviour on latrines generally support the findings of Mykytowycz and Gambale (1969) for an enclosed population of rabbits. The finding that all adults show a peak in latrine visits during the breeding season partly accounts for the differences in the overall frequencies of visits reported in the two studies. There was no clear seasonal variation in the duration of visits and the absolute figures correspond closely with those reported in the Australian study.

Dominant males visit latrines more frequently, visit more latrines per observation period and spend a shorter time there than members of other age, sex or social status classes. During visits to latrines they chin much more and rest, sit alert and groom less than other rabbits. They visit latrines in a more social or exploratory context than members of other classes.

Subordinate males generally visit latrines less often than dominant males and spend a longer time there at each visit. During visits they do not chin mark frequently but paws scrape often and spend a considerable proportion of their visit time feeding and sitting alert. They tend to visit latrines while feeding or exploring or after grooming.

Adult females visit latrines only infrequently and during visits spend a considerable proportion of their time resting and
grooming. The low number of visits makes visit context difficult to assess.

These differences in visit frequency and duration, behaviour on latrines and visit context support the argument that members of different adult sex and social status classes may visit latrines for different reasons. The pattern of dominant male visits and their behaviour before and during latrine visits suggest that they regularly deposit scent on a relatively large number of latrines. Subordinate males visit fewer latrines for a longer time and, if the suggestion that feeding on latrines is a form of gustatory exploration is correct, they appear to be investigating odours on a large percentage of their visits. Furthermore, if the nostril dilation, characteristic of the "sitting alert" posture, is indicative of odour reception, then it may be argued that the overall emphasis of subordinate male latrine visits is on odour investigation. Adult females do not visit latrines regularly and, when they do, they spend a higher proportion of their visit time resting out and grooming than adult males. Sitting and lying on the faecal pellets may permit scent to be directly transferred to the body and grooming may transfer odours on the forepaws to other parts of the body. Thus it is possible that the emphasis of adult female latrine visits is on acquiring odours deposited primarily by dominant males.

Young males visit latrines more frequently and stay longer than young females. However both groups show similarities in their behaviour on latrines and in the contexts of their visits. In both classes feeding occurs on a high percentage of visits and sitting alert accounts for a high proportion of visit time. It is possible, therefore, that young rabbits visit latrines primarily
to investigate odour. The peak in the frequency of visits for young males in September coincides with a period of increased social activity when young males are progressively less tolerated by adults and many are forced to leave the warren. As young males spend a high proportion of visit time grooming, it is possible that they are also acquiring the odour of dominant males.

While the latrine replacement tests obviously present the rabbits with an unnatural situation by removing a relatively stable element of their environment, they demonstrate that the odour of an existing latrine is important in eliciting continued defaecation at the site. Removal of latrines immediately reduces pellet deposition. They also show that there is a difference between pellets deposited at latrines and those deposited throughout the range, but the effect of the latter in stimulating defaecation is by no means negligible. It seems probable that all faecal pellets carry olfactory information but that more anal gland secretion is carried by those deposited on latrines. Given that limitless quantities of glandular secretion are not available to each rabbit and that their synthesis involves an energy cost, however small, it is reasonable to suggest that the deposition of highly odoriferous pellets at specific sites visited by a high proportion of conspecifics is an efficient method of olfactory communication.

While much of this discussion is speculative, it is clear that members of different age, sex and social classes behave in different ways towards latrines. As they are of obvious importance to the members of the resident group it is unlikely that the sole function of latrines is in territorial demarcation. The distribution of latrines in the study areas was varied and it is
possible that in small warrens the location of latrines around the territorial boundary is also adequate for the exchange of information between group members, whereas in larger warrens additional latrines within the territory are necessary. A more extensive study of the relationship between warren size and latrine distribution would undoubtedly yield valuable information.
CHAPTER 11

CHIN GLAND SECRETION
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CHIN GLAND SECRETION

During studies of the social behaviour of enclosed populations of rabbits, it was observed that rabbits frequently rub their chins on ("chinning") blades of grass, burrow entrances, the edges of posts etc. and occasionally on other rabbits (Myers and Poole, 1961). Mykytowycz (1962) first suggested that rabbits deposit scent from the submandibular cutaneous (chin) gland during this characteristic behaviour and that this permits marking of objects in the environment which could not easily be marked with faeces or urine.

The gland complex is mainly composed of modified sweat glands of the apocrine type (Lyne et.al., 1964). Thin layer chromatography of lipid extracts of gland tissue revealed the presence of hydrocarbons, nonglycerylesters, free fatty acids, cholesterol, triglycerides, diglycerides and monoglycerides (Goodrich and Mykytowycz, 1972).

There is no sexual dimorphism in the weight and activity of chin glands in rabbits up to 2 months of age, but at sexual maturity a clear difference emerges. In adult rabbits the glands are much better developed in males than in females. Hair on the chin is often matted with a yellowish encrustation and drops of glandular secretion are easily expressed in adult males, but not in females (Lyne et.al., 1964). While proteins were found in gland extracts from both sexes, carbohydrates bound to proteins occurred at a much higher level in male samples and there were clear differences in the hydrocarbon composition of samples from males and females (Goodrich and Mykytowycz, 1972).
The level of gland activity appears to be under androgenic control. Castration of males reduces the size and activity of the gland and inhibits chinning. Testosterone restores the functioning of the gland in castrates, stimulates its activity in females and increases chinning in both groups (Mykytowycz, 1962). In castrated females, the gland size increases but the level of chinning is not affected. The observation that chinning continues to occur in males castrated as adults but not in those castrated as kittens suggests that experience is also an important factor (Mykytowycz, 1965). In normal adults Mykytowycz (1962, 1965) reports that wild males chin approximately ten times more frequently than females and that laboratory males chin roughly seven times more frequently than females.

Rabbits taken from populations maintained at a high density demonstrated that, in general, the weights of dominant male glands were twice that of sexually inactive subordinate male glands which were, in turn twice as heavy as those of adult females. There was however, considerable variability in female gland weights. Most females did not chin but some females had chinning frequencies and gland weights comparable to those of subordinate males. Generally rabbits taken from low density populations show higher chin gland weights than those from high density populations (Mykytowycz and Dudzinski, 1966). The relationship between social status and chinning frequency was investigated by Mykytowycz (1965). Using laboratory rabbits, it was found that chinning frequency in an arena could be used as a predictor of subsequent dominance in contests with other rabbits.

In addition to these differences between animals of different sex and social status, the frequency of deposition of
chin gland secretion also varies with time of year and time of day, being generally highest during the breeding season and shortly after emergence in the afternoon.

The suggestion that chin gland secretion plays a part in the demarcation of territory was first put forward by Mykytowycz (1962). The reported differences in gland activity between sex and social status groups have been regarded as evidence for this view. Mykytowycz (1965) reports that rabbits in their own territory move around in a "confident" manner with the body close to the ground, eating, sniffing and chinning, whereas rabbits in a completely strange territory move about with body raised in an "alert" attitude and do not chin. In a neighbouring territory, it is reported that rabbits adopt a similar alert posture but do not suspend chinning altogether. Marsden and Holler (1964) report that chinning is observed in the Swamp rabbit, Sylvilagus aquaticus which is territorial, but not in the Cottontail, Sylvilagus floridanus which is not territorial. The chin gland is much more highly developed in the gregarious rabbit than in the solitary hare, Lepus europaeus. Mykytowycz (1965) suggests that these observations support the argument that the chin gland is important in territorial marking.

The emphasis in early papers (eg. Mykytowycz, 1962) was on territorial warning or in advertising that space is occupied in order to minimise aggressive encounters, but in later work (eg. Mykytowycz, 1973) the emphasis shifted to the argument that chin gland secretion enhances the confidence of the animal depositing the scent. A series of experiments by Mykytowycz (1975) demonstrated that the confidence of rabbits is higher when in the presence of their own chin gland secretion than when in the
presence of another rabbit's chin gland secretion. Field trapped animals and laboratory males were tested in a contest arena which contained the chin gland secretion of one of the contestants. Confidence was assessed by measuring the level of chasing, aggression, sniffing the other rabbit and exploration of the arena. Laboratory females were tested in an arena containing the chin gland secretion of the male partner of one of the contestants. In all cases the rabbits showed greater confidence in the "home" situation than in the "away" situation, and it is reported that the difference was greater in field trapped males than in laboratory males. Using a similar paradigm Mykytowycz et al. (1976) showed, furthermore, that chin gland secretion is more effective in enhancing confidence than urine or anal gland and inguinal gland secretions.

Chin gland secretion is odourless to man and it had been suggested that the secretion may simply act as a fixative for other odoriferous substances with which the rabbit comes into contact while chinning e.g. faeces, urine (Goodrich and Mykytowycz, 1972). However, the experiments reported above used chin gland secretion expressed directly from the gland and therefore this is unlikely to be the case. Several species produce glandular secretions which are odourless to man e.g. cheek glands of the Pika Ochotona princeps and side glands of the musk shrew, Suncus murinus, and there is no reason to suppose that such substances are also odourless to the animals which produce them.

It has been observed that rabbits frequently mark over existing scent deposits (faeces, urine and chin marks) with their own chin gland secretions. It has further been demonstrated that male rabbits chin the faecal pellets, urine and chin marks of
other animals more frequently than neutral stimuli or their own odour products (Black-Cleworth and Verberne, 1975; Schalken, 1976). It appears, therefore, that rabbits attempt to mask odours deposited in the environment by other animals with their own chin gland secretion, perhaps in order to enhance their confidence.

However, chinning is not always directed towards inanimate objects, it is sometimes directed at a conspecific. In particular, adult males chin young rabbits and occasionally adult males and females chin each other during amatory behaviour or copulation. It is suggested by Mykytowycz (1965) that the chinning of young rabbits may make them acceptable to members of the groups because they acquire a familiar odour. He reported that on occasions when young females were enurinated and chinned by an adult male from another warren, they were attacked on returning to their own warren. In an investigation into aggression of adults towards young rabbits of various ages, Mykytowycz and Dudzinski, (1972) found that males tended to chin young rabbits more than females do and that the frequency of chinning decreased with increasing age of the young. In general, "strange" kittens were chinned more often than "own" or "own group" young. Adult females very seldom chinned young rabbits and then only very young kittens which would normally have been nestlings (21 days of age).

The aim of this section of the present study is to ascertain if the results of previous research on chin marking in laboratory rabbits or on wild rabbits in a laboratory setting are applicable to free living populations of wild rabbits. An attempt is made to answer the following questions.
A. **Chinning Directed at the Substrate**

(1) In a free living population, do members of different age, sex and social status groups show differences in their frequency of chin marking?

(2) Are there differences in the temporal patterns of chin marking in the different age, sex and social status groups?

(3) Is there seasonal variation in the frequency of chin marking in rabbits? Are there differences in the seasonal variation in the different age, sex and social status groups?

(4) In what behavioural context does chin marking by members of the different age, sex and social status groups occur?

B. **Chinning Directed at Conspecifics**

(1) Are there differences in the frequency of chin marking conspecifics between members of different age, sex and social status groups?

(2) At which group of rabbits is such marking most commonly directed?

**METHOD**

The data presented in this section come from transcripts of focal animal samples. Details of the samples and observation areas are given in the previous chapter.

Data refer to chinning bouts. A chinning bout was scored when a rabbit chin marked an object or a conspecific at a single location. Most bouts consisted of a single act of chin marking but up to 4 chinning acts were recorded in a single bout. The number of acts per bout was not correlated with age, sex, social status or time of year and it was felt that the bout was a more realistic indicator of chinning frequency than individual marking acts. Bout
duration was not recorded.

RESULTS

A. Chinning Directed at Inanimate Objects

1. Chinning Frequency

The overall number of observed chinning bouts and the mean number of bouts per hour of observation for members of each age, sex and social status group are shown in fig. 11.1. Each group shows a higher frequency of chinning during the evening activity period than in the morning.

Chi square tests were carried out on the total number of bouts recorded for members of the different groups.

Dominant males chin considerably more frequently than other adults (v. subordinate males, \(X^2 = 13.64, p < 0.001\); v. adult females, \(X^2 = 19.46, p < 0.001\)). This result supports earlier findings on chin gland weights and on chinning activity of laboratory rabbits (Mykytowycz, 1965).

Subordinate males and adult females chin more frequently than young rabbits (\(X^2 = 4.85, p < 0.05\)). Again this result reflects earlier findings on gland weights. However, it should be noted that these data refer to overall frequencies and that in young rabbits they cover a period up to and including the development of sexual maturity. Young rabbits show a rapid increase in chinning activity during the summer months.

There is no significant difference in the overall chinning frequencies of subordinate males and adult females (\(X^2 = 0.57, \text{N.S.}\)). This result is surprising in the light of previous findings on gland weight and activity. However, further analysis of the
Mean frequency and rates of chinning for the 5 age/sex/social status classes in the morning and evening activity periods.

(N) = No. of individuals of each class included in the sample.
data reveals that there is considerable variation in the chinning frequency of females. In adult females chinning occurred in only 22.58% of observation periods whereas in subordinate males chinning occurred in 50% of observation periods. Analysis of the frequency of bouts per observation period shows a considerable difference in the standard deviation for the two groups (subordinate males, $S = 0.877$; adult females, $S = 1.149$). The difference between the coefficients of variation (subordinate males, C.V. = 1.25; adult females, C.V. = 3.8) was tested for significance using the test statistic $C$ (Lehner, 1979). There is considerably greater variation in the frequency of chinning by different females than in subordinate males ($C = 9.9$, $p < 0.001$).

Thus, it is clear that a small number of females account for a large proportion of the observed chinning. This finding supports reported results on variation in chin gland weight and activity in adult females (Mykytowycz and Dudzinski, 1966). That the overall level of chinning in females is found to be higher relative to males in the present study than reported elsewhere may again be due to the possibility that the capture method biases the sample in favour of more active females.

2. **Temporal Patterns of Chinning Bouts**

The commonly reported observation that dominant males perform scent marking "tours" usually seen after emergence in the afternoon (eg. Mykytowycz, 1958) was discussed in the previous chapter. In order to determine if there are differences in the temporal patterns of chin marking in the 5 age, sex and social status classes, observed chinning bouts were divided into the following two categories:

(i) Instances where only a single chinning bout was observed in
the 50 minute sample period.

(ii) Instances where other chinning bouts were also observed in the 50 minute sample period.

Fig. 11.2 shows that there is considerable variation between the 5 classes in the temporal patterns of chinning. This is highly significant (chi square = 25.239, d.f. = 4, p < 0.001). It seems clear that if dominant males were observed chinning in an observation period, then they usually chinned more than once, (range 1-6). On two occasions the observation period coincided with what could indeed be described as a scent marking 'tour', when the rabbit moved purposefully around its range, pausing briefly to chin mark or displace other rabbits. However, most of the observed chinning bouts took place during 'normal' active behaviour. When dominant males are active above ground, they frequently interrupt other behaviours to chin tufts of vegetation or other objects nearby.

While adult females also show a high proportion of multiple chinning bouts this was, as discussed above, due to a small number of females chinning relatively frequently. Dominant males chinned on 59.26% of observation periods whereas adult females were observed chinning on only 22.58% of observation periods when they were the target animals. Thus, while a high level of chinning was a regular feature of dominant male behaviour, this was clearly not the case for most adult females. However, even among the small number of females responsible for most of the chin marking, the impression gained was that this was a much more sporadic behaviour than the regular chinning of dominant males. Subordinate males, in general, chin regularly but at a fairly low level, with a high proportion of chinning bouts occurring singly during observation
Frequency and % frequency of single and multiple chinning bouts within single observation periods for the 5 age/sex/social status classes.

<table>
<thead>
<tr>
<th></th>
<th>Single bouts</th>
<th>(%)</th>
<th>Multiple bouts</th>
<th>(%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dominant males</td>
<td>3</td>
<td>6.25</td>
<td>45</td>
<td>93.75</td>
</tr>
<tr>
<td>Subordinate males</td>
<td>11</td>
<td>52.38</td>
<td>10</td>
<td>47.62</td>
</tr>
<tr>
<td>Adult females</td>
<td>2</td>
<td>11.76</td>
<td>15</td>
<td>88.24</td>
</tr>
<tr>
<td>Juvenile males</td>
<td>3</td>
<td>60</td>
<td>2</td>
<td>40</td>
</tr>
<tr>
<td>Juvenile females</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>100</td>
</tr>
</tbody>
</table>
periods. The low number of bouts recorded in young rabbits do not permit any meaningful analysis of grouping to be undertaken.

3. **Seasonal Variation in Chinning**

Data on seasonal variation in chinning are presented in the form of rates (bouts per hour of observation), as the numbers of samples were not equally distributed across the six observation months.

A Kruskal-Wallis one-way analysis of variance by ranks reveals that there are significant differences between the rates of chinning by the members of the different adult classes ($H = 10.725$, d.f. = 2, $p < 0.0003$). Post hoc pairwise comparisons (Scheffe's method) show that dominant males differ from subordinate males ($p < 0.1$) and from adult females ($p < 0.01$).

Figs. 11.3 and 11.4 show clearly that dominant males chin at a higher rate than other classes throughout the year. All adults show a peak in chinning rate during the breeding season and it is at this time that the higher rate of chinning by dominant males is most noticeable. The level of chinning falls off for all rabbits throughout the summer and autumn, reaching a low point in November. However, as discussed in chapter 10, the November data may be unrealistically low due to the lack of observations during the times of peak activity in that month.

The relatively low number of observations on young rabbits in each of the observation months may cast doubts on the validity of the absolute levels of chinning shown in fig. 11.4, but a trend of increasing chinning during the summer months as they reach sexual maturity is evident.
### Seasonal variation in chinning rate (bouts/hour of observation) for the 5 age/sex/social status classes.

<table>
<thead>
<tr>
<th></th>
<th>February</th>
<th>April</th>
<th>June</th>
<th>August</th>
<th>September</th>
<th>November</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dominant Males</td>
<td>2.99</td>
<td>4.5</td>
<td>1.72</td>
<td>1.8</td>
<td>1.37</td>
<td>1.2</td>
</tr>
<tr>
<td>Subordinate Males</td>
<td>0.72</td>
<td>1.6</td>
<td>0.9</td>
<td>0.72</td>
<td>0.8</td>
<td>0.4</td>
</tr>
<tr>
<td>Adult Females</td>
<td>0.96</td>
<td>1.0</td>
<td>0.69</td>
<td>0.51</td>
<td>0.24</td>
<td>0</td>
</tr>
<tr>
<td>Young Males</td>
<td>-</td>
<td>0</td>
<td>0.17</td>
<td>1.2</td>
<td>0.8</td>
<td>0</td>
</tr>
<tr>
<td>Young Females</td>
<td>-</td>
<td>-</td>
<td>0</td>
<td>0</td>
<td>0.8</td>
<td>-</td>
</tr>
</tbody>
</table>
Fig. 11.4

Monthly variation in rate of chinning bouts (bouts/hour of observation) for the five age/sex/social status classes.
4. Behavioural Context of Chinning

The behavioural context of chinning was analysed following the procedure outlined in the previous chapter. Again, the behaviours occurring immediately before and after a chinning bout are regarded as constituting the context. It should be noted that most of the observations recorded in the category "latrine visit" in figs. 11.5 and 11.6 refer to chinning by rabbits while on a latrine (N = 27). In these cases the rabbit was on the latrine both before and after chinning and therefore there is little difference in the recorded pre and post chinning behaviour. It was felt that in these instances, "latrine visit" was a more realistic indicator of context than a record of the actual behaviour occurring before and after the chinning bout. The small differences in pre and post chinning results are caused by 3 observations of rabbits visiting a latrine immediately after chinning and only 1 observation of a rabbit chinning immediately after leaving a latrine. Operational definitions of the remaining behavioural categories are discussed in Chapter 10.

Behaviour occurring prior to chinning bouts for the 5 age, sex and social status classes is shown in fig. 11.5. Again, as in the case of latrine visits discussed in the previous chapter, the data on behavioural context was not immediately amenable to statistical testing. Thus, the same transformation was performed on the data, collapsing the behavioural categories down to 2 variables called "active" and "passive" and comparing the scores of dominant males with the combined scores of all other classes on these 2 variables. (see chapter 10).

Dominant males are more likely to have been engaged in an "active" behaviour immediately before a chin marking bout than are
<table>
<thead>
<tr>
<th>Behavior</th>
<th>Dominant Males (N=48)</th>
<th>Subordinate Males (N=21)</th>
<th>Adult Females (N=17)</th>
<th>Young Males (N=5)</th>
<th>Young Females (N=2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total Bouts</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Exploration</td>
<td>13 (27.1)</td>
<td>3 (14.3)</td>
<td>5 (29.4)</td>
<td>1 (20)</td>
<td>1 (50)</td>
</tr>
<tr>
<td>Feeding</td>
<td>2 (4.2)</td>
<td>3 (14.3)</td>
<td>6 (35.3)</td>
<td>0 (0)</td>
<td>1 (50)</td>
</tr>
<tr>
<td>Pawscraping</td>
<td>7 (14.6)</td>
<td>3 (14.3)</td>
<td>1 (5.9)</td>
<td>1 (20)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>Latrine Visit</td>
<td>19 (39.6)</td>
<td>8 (38.1)</td>
<td>0 (0)</td>
<td>1 (20)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>Intrawarren Social</td>
<td>5 (10.4)</td>
<td>3 (14.3)</td>
<td>2 (11.8)</td>
<td>2 (40)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>Interaction</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Interwarren Social</td>
<td>2 (4.2)</td>
<td>1 (4.8)</td>
<td>1 (5.9)</td>
<td>0 (0)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>Social Interaction</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Resting</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>Grooming</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>2 (11.8)</td>
<td>0 (0)</td>
<td>0 (0)</td>
</tr>
</tbody>
</table>

Behaviour immediately preceding chinning bouts (N=93) by members of the 5 age/sex/social status classes. Data expressed as frequency and % frequency.
<table>
<thead>
<tr>
<th></th>
<th>Dominant Males (%)</th>
<th>Subordinate Males (%)</th>
<th>Adult Females (%)</th>
<th>Young Males (%)</th>
<th>Young Females (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total Bouts</td>
<td>48</td>
<td>21</td>
<td>17</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td>Exploration</td>
<td>8 (16.7)</td>
<td>0 (0)</td>
<td>2 (11.8)</td>
<td>1 (20)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>Feeding</td>
<td>9 (16.7)</td>
<td>6 (28.6)</td>
<td>8 (47.1)</td>
<td>2 (40)</td>
<td>1 (50)</td>
</tr>
<tr>
<td>Paw scraping</td>
<td>2 (4.2)</td>
<td>1 (4.8)</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>Latrine Visit</td>
<td>20 (43.8)</td>
<td>9 (42.9)</td>
<td>0 (0)</td>
<td>1 (20)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>Intrawarren Social Interaction</td>
<td>3 (6.3)</td>
<td>1 (4.8)</td>
<td>1 (5.9)</td>
<td>1 (20)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>Interwarren Social Interaction</td>
<td>1 (2.1)</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>Resting</td>
<td>2 (4.2)</td>
<td>0 (0)</td>
<td>2 (11.8)</td>
<td>0 (0)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>Grooming</td>
<td>3 (6.3)</td>
<td>4 (19.1)</td>
<td>4 (23.6)</td>
<td>0 (0)</td>
<td>1 (50)</td>
</tr>
</tbody>
</table>

Behaviour immediately following chinning bouts (N=93) by members of the 5 age/sex/social status classes. Data expressed as frequency and % frequency.
members of the other classes (chi square = 7.52, d.f. = 1, p < 0.01). However, although dominant males chin more frequently than subordinate males, the behavioural context of chinning in these 2 classes is very similar. Dominant males tend to chin more often while exploring and subordinate males chin more often while feeding but the majority of chinning bouts are preceded by a similar pattern of behaviours in both classes. Adult females show a higher proportion of feeding and grooming prior to chinning than do adult males, but show a lower proportion of pawscraping and latrine visits. The data on young rabbits are included for completeness, but the number of observations is too low to reveal any pattern.

Fig. 11.6 shows behaviour observed immediately following chinning bouts. Again dominant males are more likely to follow chin marking with an "active" behaviour than are members of other classes, (chi square = 8.96, d.f. = 1, p < 0.01). Dominant males show a higher level of exploration and a lower level of feeding than subordinate males, and adult females again show a higher level of feeding, grooming and resting than adult males, but a lower level of pawscraping and latrine visits.

Overall pre and post chinning behaviours are compared in fig. 11.7. Excepting "latrine visits" which constitute a rather anomalous category for reasons discussed above, it is clear that the incidence of "active" behaviours decreases after chinning. The proportion of chinning bouts preceded by social behaviour, exploration and pawscraping is higher than the proportion of chinning bouts followed by these behaviours. However, the proportion of feeding, grooming and resting increases after chinning.
Fig. 11.7

<table>
<thead>
<tr>
<th>Behavioural Context</th>
<th>Pre-chinning behaviour (%)</th>
<th>Bell (1980) (%)</th>
<th>Post chinning behaviour (%)</th>
<th>Bell (1980) (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Exploration</td>
<td>24.7</td>
<td>17.5</td>
<td>11.8</td>
<td>17.5</td>
</tr>
<tr>
<td>Feeding</td>
<td>12.9</td>
<td>11.25</td>
<td>26.9</td>
<td>25</td>
</tr>
<tr>
<td>Pawscreaping</td>
<td>12.9</td>
<td>16.25</td>
<td>3.23</td>
<td>12.5</td>
</tr>
<tr>
<td>Grooming</td>
<td>2.15</td>
<td>-</td>
<td>12.9</td>
<td>-</td>
</tr>
<tr>
<td>Resting</td>
<td>0</td>
<td>-</td>
<td>4.3</td>
<td>-</td>
</tr>
<tr>
<td>Intrawarren Social Interaction</td>
<td>12.9</td>
<td>-</td>
<td>6.45</td>
<td>-</td>
</tr>
<tr>
<td>Interwarren Social Interaction</td>
<td>4.3</td>
<td>-</td>
<td>1.1</td>
<td>-</td>
</tr>
<tr>
<td>All Social Interactions</td>
<td>17.2</td>
<td>38.75</td>
<td>7.5</td>
<td>23.75</td>
</tr>
<tr>
<td>Latrine Visits</td>
<td>30.1</td>
<td>1.25</td>
<td>33.33</td>
<td>5.0</td>
</tr>
</tbody>
</table>

Behavioural context of chinning bouts (N=93), Pre and post chinning bout behaviours expressed as % frequency and data from Bell (1980) to permit comparison.
The results of an analysis of the behavioural context of chin marking in a free living population of rabbits on Skomer (Bell, 1980) are included in fig. 11.7 for comparison. These data also indicate that while feeding increases after chinning, both social interactions and pawscraping decrease. The obvious differences in the reported levels of occurrence of several behaviours in the two studies may be due to differences in the sampling methods. In addition, the variation in the behavioural context of chinning for members of each of the age, sex and social status groups means that, if one is presenting the overall mean results for a population of rabbits, the structure of that population will have a considerable influence. The structure of the population studied by Bell is not reported but it remains possible that the actual levels of occurrence of behaviours reported in the two studies may be influenced by differences in population structure.

The social interactions reported in figs. 11.5 and 11.6 have been further subdivided into sexual or aggressive interactions. All social interactions observed in relation to chinning were judged to fall into either of these categories. Social interactions in this context normally took the form of either displacements or chases. Sexual and aggressive chases are quite distinguishable. Sexual chasing or courtship chasing (Southern, 1948) is less intense than aggressive chasing and is characterised by frequent pauses. The chinning animal is shown in fig. 11.8 as the active (+) or passive (-) participant in either sexual or aggressive encounters. It should be noted that only one of the participants in a social interaction was necessarily identifiable although in several cases the other rabbit was also marked.
Fig. 11.8

<table>
<thead>
<tr>
<th></th>
<th>Dominant males</th>
<th>Subordinate males</th>
<th>Adult females</th>
<th>Young males</th>
<th>Young females</th>
<th>Total bouts</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Pre-Chinning</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Social Interactions</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aggressive</td>
<td>++++</td>
<td>+++</td>
<td>++</td>
<td>-</td>
<td></td>
<td>11</td>
</tr>
<tr>
<td>Sexual</td>
<td>++</td>
<td>+</td>
<td>-</td>
<td>+</td>
<td></td>
<td>5</td>
</tr>
<tr>
<td><strong>Post-Chinning</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Social Interactions</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aggressive</td>
<td>+++-</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td></td>
<td>7</td>
</tr>
<tr>
<td>Sexual</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0</td>
</tr>
</tbody>
</table>

Frequency of aggressive and sexual social interactions before and after chinning bouts (+ = active participation, - = passive participation).

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Clearly, when chinning follows a social interaction of either an aggressive or sexual nature, it is usually performed by the active participant. Chin marking occurs more frequently in an aggressive context than in a sexual context. On 3 occasions chinning bouts which had been preceded by chasing or displacement were followed by chasing of the same animal. On all 3 occasions the chinning animal was the active participant. The single observation of a dominant male being chased following chinning occurred when the male chinned in a neighbouring territory and was chased by an unidentified resident.

In general, chin marking of the substrate, therefore, tends to be preceded by exploration, pawsraping or social interactions, most of which are of an aggressive nature and is performed by the aggressor. Adult males perform a high percentage of their chinning bouts on latrines. A higher incidence of more passive behaviours such as feeding and grooming follows chinning. As discussed in the previous chapter, grooming may have a scent related function and it has been suggested that feeding may, in certain circumstances, be regarded as gustatory exploration. Goodrich and Mykytowycz (1972) suggest that the presence of carbohydrates and proteins in chin gland secretion may indicate that gustation is involved in the detection of deposits from the chin gland. They also report that "food in all forms" is particularly frequently chinned by rabbits and suggest that communication may be established during ingestion of chinned food. However if rabbits are indeed detecting glandular deposits during feeding, in the light of the finding that rabbits feed more often after rather than before chinning, it seems likely that it is their own deposits which they are detecting.
B. CHINNING DIRECTED AT CONSPECIFICS

Chinning of conspecifics was observed sporadically throughout the year and was particularly common during the summer months when the population contained a high proportion of young rabbits. Such marking normally took place in a non-aggressive context, although one aggressive chase terminated with a subordinate male sitting motionless and being chinned by a dominant male. No further aggression followed this act. On 2 occasions sexual chases were similarly terminated with the male chinning the head of the female. Typically, however, chinning occurred following approaches to rabbits which were feeding, resting or grooming during the evening activity period.

Fig. 11.9 shows that most conspecific chinning is performed by dominant males and that the most common targets are young rabbits. Although the rate of chinning in young males is almost as high as that of subordinate adults, young rabbits were observed rubbing their chins on the heads of other young rabbits at an age when the chin gland is by no means fully developed. In young rabbits therefore this behaviour may be manifest without fulfilling the same function as it does in adults.

Fig. 11.10 shows the number of conspecific chinning bouts when the chinning animal approached the target animal and vice versa. Apart from 2 unidentified adults, the only animals to approach adults and be chinned were young rabbits. It seems probable that such a behaviour is an act of submission as such approaches were most often made to dominant males. The 2 instances in which young rabbits approached adult females and were chinned were cases of offspring approaching their mother. In 3 cases when a male and female were observed sitting adjacent to one another,
Frequency of conspecific chin marking by members of the 5 age, sex and social status groups.

<table>
<thead>
<tr>
<th>MARKED RABBIT</th>
<th>Marking Rabbit</th>
<th>Dominant male</th>
<th>Subordinate male</th>
<th>Adult female</th>
<th>Young male</th>
<th>Young female</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dominant male</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0</td>
</tr>
<tr>
<td>Subordinate male</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
</tr>
<tr>
<td>Adult female</td>
<td>3</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>5</td>
</tr>
<tr>
<td>Young rabbit</td>
<td>5</td>
<td>3</td>
<td>2</td>
<td>3</td>
<td></td>
<td></td>
<td>13</td>
</tr>
<tr>
<td>Adult (sex unknown)</td>
<td>1</td>
<td>2</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td>5</td>
</tr>
<tr>
<td>Total</td>
<td>10</td>
<td>7</td>
<td>4</td>
<td>3</td>
<td>0</td>
<td></td>
<td>24</td>
</tr>
</tbody>
</table>

| Rate of marking (Bouts /hour of Observation) | 0.44 | 0.28 | 0.15 | 0.26 | 0 |

Fig. 11.9
Instigator of interactions involving conspecific chin marking of subordinate male(s), adult females (F), young rabbits (Y) and adults of unknown sex (U).
the male chinned the head of the female. This has been described by several authors as a feature of "amatory behaviour" and in each of the cases observed here, it occurred between adult members of the same group.

Chinning a conspecific therefore, may be a positive act of reassurance or bonding between rabbits. It is normally performed in a non-aggressive context and is actively elicited by young rabbits. The possession of the odour of a dominant male by a young rabbit may also reduce the chances of being the target for aggression either by other adults or by the dominant male.

DISCUSSION

The relative frequencies of chin marking in the 5 age, sex and social status classes in this free living population mirror the previously reported differences in chin gland size and activity. Dominant males chin more frequently than members of other classes and adults chin more frequently than young rabbits. The absolute levels of chinning found in the present study are lower than those reported previously, but the observed frequency of chinning depends on many factors such as the time of day and time of year when the observations are made, on the population structure, and so on. Mykytowycz (1965) discusses the relative frequencies of chin marking by adult males and females of differing social status. However, the only data referring to wild rabbits in enclosures are based on 2 hours of observations and are obviously included for illustrative purposes only. The data nevertheless highlight the variation in chinning frequency in individual females. This is strongly supported by the results of the present study. A small number of females was found to be responsible for a large proportion of female chinning. Mykytowycz
(1965) has suggested that dominant females show a much higher frequency of marking than subordinate females. In the present study, for reasons outlined in chapter 5 such a distinction is not drawn, but the dominant females as described by Mykytowycz are part of a "dominant pair" and thus belong to the same group as the dominant male. Analysis of the present data partly support this suggestion. The number of observations is small but three females belonging to dominant male groups account for 58.8% of all female chin marking observed. However the question of why certain females chin so much more frequently than others remains unanswered and this is an area that warrants further study.

The finding that all adults show a peak in chinning activity during the breeding season is in accord with previously reported results on chin gland weight and activity. This peak coincides with the time of maximum competition for mates and for space but there is no second peak in adult chinning corresponding to the increase in social behaviour in the late summer. Young rabbits, however, do show a peak in chinning at this time, as they reach sexual maturity.

Any area inhabited by rabbits must possess a composite odour deposited by members of the resident group. However, the differential frequencies of chin marking by the various classes and individuals must mean that the chin gland component of the composite odour is largely composed of the odours of certain individuals. For most of the time in most groups this odour will be dominated by the scent of the dominant male. If one accepts the concept that each individual mammal has an "optimum odour field" (Eisenberg and Kleiman, 1972) then it may be suggested that the optimum odour field of dominant male rabbits contains a higher
proportion of personal odour than is necessary for other members of the group. Thus there may be a greater need for dominant males to mask odours deposited by other group members.

Although chinning was observed to occur in a wide variety of behavioural contexts, the high levels of exploration prior to chinning suggest that in many instances the presence of existing odours was being investigated before personal odour was deposited. If the suggestion that feeding may contain an element of gustatory exploration is accepted then, in the light of the finding that feeding occurs with a much higher frequency in all classes after chin marking, it seems that rabbits also frequently investigate their own gland secretions. This investigation of personal odour may serve to reassure the depositor.

The high level of chinning occurring in the context of latrine visits in males may also be due to attempts to mask the anal gland odour of pellets deposited there. However, the fact that differences have been reported in the hydrocarbon composition of chin gland extracts from males and females suggests that at least sexual identity may be discernible from chin gland deposits. Thus it is possible that information contained in chin gland secretion is added to the information contained in anal gland secretion on pellets at latrine sites.

Chinning also occurs in the context of mainly aggressive social interactions and, as it is normally performed by the aggressor, it may serve to reinforce the outcome of the interaction or serve as a threat.

Thus chinning of the substrate may fulfil more than one function. It may permeate the rabbit's range with familiar odour.
and mask the odour deposited by conspecifics. Chin gland secretion may contain information about the identity of the depositor and it is frequently deposited by males at latrines which may serve as focuses of information exchange. Finally chinning may reinforce acts of aggression or function as a threat following aggressive interactions.

Conspecific marking is most frequently performed by dominant males and the most common recipients are young rabbits. Marking of adults in the same group with a familiar odour may reduce aggression and permit closer social contact. Similarly young rabbits may help reduce the likelihood of being the target of aggression by acquiring a familiar odour. This suggestion is supported by the finding that young rabbits elicit such marking particularly from dominant males.

Thus, the suggestion that a single scent product has a single function irrespective of context and that different scent products necessarily fulfill quite separate functions would appear to be unrealistic.

Unfortunately chin marks are not visually identifiable and therefore unlike the case of latrines the emphasis in this case is inevitably on the sender rather than the receiver of information contained in chin gland odour. Many of the previous findings of laboratory studies are supported by the results of the present studies and, while there is clearly a need for further field research on aspects of chinning in rabbits, much useful research can be carried out under laboratory conditions. Indeed, research into aspects of chin marking, such as reactions to chin gland odour, may only be practicable under such conditions.
CHAPTER 12

URINE
The evacuation of urine in the rabbit takes three distinct forms. "Normal" deposition of urine in both sexes is performed in a stationary, sitting position, accompanied by a raising of the tail and rear end. Urine may also be squirted out to the rear from a stationary or moving position. These urine squirts are generally aimed at inanimate objects in the environment. Finally urine may be directed at a conspecific. This behaviour has been labelled epuresis or enurination (Southern, 1948), or urine-spraying (Bell, 1980). This behaviour is performed while moving and normally involves a twisting/leaping movement of the hind quarters, directing the flow of urine towards the target animal. In these latter two behaviours the amount of urine expelled is small.

Mykytowycz (1968) suggests that urine is one component of the odour demarcating territory and that it is important in aggressive and courtship displays (Mykytowycz et al., 1976). It has been demonstrated that in a contest situation both males and females show greater confidence in the presence of their own urine, although the effect was greater in females. The urine of the sexual partner also had a significant effect on the confidence of contestants, (Mykytowycz et al., 1976). However, it is suggested that for males, urine may be less important in the maintenance of territory than either chin gland or anal gland secretions.

Two laboratory studies have investigated reactions of adult male rabbits to urine (Schalken, 1976; Bell, 1977 unpublished PhD thesis). Bell reports that rabbits show a stereotyped sequence of
investigation and scent marking in response to urine. Chinning was the most commonly observed response although some males also defaecated or urinated. Both studies were based on a simultaneous two-choice discrimination paradigm and although there are minor differences in the reported results in general the findings of the 2 studies are in accord. Rabbits investigate and chin mark "strange" urine more than water or "own" urine and fresh urine more than old urine.

Bell reports that adult males show more interest in urine from subordinate males than from dominant males and notes that dominant males produce viscous "smelly" urine whereas subordinate males produce pale, watery urine. Whether this is an artifact of the laboratory conditions under which the animals were housed is not known, but she indicates that subordinate males had a much higher water intake than dominant males. It is further reported that adult males show more interest in adult female urine than adult male urine and in urine from old males rather than from younger males.

However, use of the simultaneous preference paradigm poses several problems when it comes to interpreting this data. It is difficult to unravel the attractive/aversive qualities of the 2 stimuli in any test and a rabbit may spend less time with a particular stimulus because it is either aversive or simply contains little information. Nevertheless it is clear from these studies that rabbits can discriminate sex, age and social status on the basis of urine odour and that they can distinguish their own urine from conspecific urine.

Field observation of "normal" urination and of the reactions
of conspecifics to urine deposits are necessarily rather limited. As in the case of "normal" defaecation, it is a very difficult behaviour to positively identify. Mykytowycz (1974) reports that after visiting breeding stops containing their offspring, adult females plug the entrance with soil and deposit a small quantity of urine. He remarks that breeding stops are seldom disturbed by other rabbits and Bell (1977) suggests that the urine may act as a "keep away" signal. However if this is the case then the attractiveness of female urine presumably alters during the various phases of the reproductive cycle as Lockley (1961) reports that he observed a male rolling on the ground after an oestrous female had urinated there.

Several authors have noted urine being squirted at inanimate objects in the environment (e.g. Lockley, 1961) and the phenomenon is a common feature of rabbit behaviour in laboratory arenas (Heath, 1972; Black-Cleworth and Verberne, 1975). However, in wild populations the behaviour occurs relatively infrequently and reports tend to be anecdotal. Lockley (1961) remarks that the presence of a conspicuous plant stimulated enurination perhaps because "it vaguely resembled another rabbit".

While this is clearly a rather far-fetched supposition, the observation that rabbits spray urine over conspecifics is frequently reported. Southern (1948) describes the behaviours involved in some detail. He reports that enurination is usually performed by males and targeted at females and that it occurs most frequently during the breeding season and in the late summer. Males were observed squirting urine at a female from a stationary position, while running past a female and twisting the hind quarters towards her, or occasionally while jumping over a female.
Many instances of enurination appear to occur in the context of courtship behaviour. Myers and Poole (1961) report that it was most commonly observed performed by males which were "circling" females in a standard courtship sequence. Normally females take little notice other than to shake their fur and sometimes to move away.

Enurination has also been observed in an aggressive context; by an unreceptive female on a male which was "pestering" her (Southern, 1948); by males on other males during disputes at territorial boundaries (Myers and Poole, 1961); by a female approaching parturition on the members of her previous litter to disperse them (Mykytowycz and Rowley, 1958); and by an adult male on a young male followed by an aggressive chase (Southern, 1948). Southern suggests that in the latter case, the male may have been treating the young male as a female and that enurination may be released by the sight of a submissive animal. Myers and Poole suggest that enurination may be a substitute activity occurring when the male is highly excited. Lockley (1961) remarks that enurination of plants and other animals was "clearly significant in releasing tension", but adds that it probably also fulfills a scent-marking role.

Mykytowycz (1968) however, suggests that the smell of foreign urine elicits aggression and reports that females may attack their own young if they have been smeared with foreign urine. A similar case is reported by Mykytowycz and Rowley (1958) of a young female copulating with an adult male from a neighbouring warren. During the course of copulation the female was enurinated several times and on returning to her own warren was attacked and chased out by 2 adult females. The female was
observed back in the warren with no further signs of aggression after 4 days and the authors suggest that the odour of the foreign male urine may have worn off in that time.

Enurination of conspecifics, particularly in a sexual context has been reported in many mammalian species and Mykytowycz (1974) reviews the argument that such behaviour may be regarded as an extension of the male's territorial behaviour. It has been suggested that enurination is a "symbolic take over" of the sexual partner. This argument has been criticized in the light of the discovery of enurination in species in which urine is not used as a territorial marker. However, Mykytowycz argues that, accepting the distinction between the maintenance of territory and personal space, a male in enurinating a conspecific in an aggressive or a sexual context may be attempting to reinforce or broaden his personal "sphere of influence". Ewer (1968) reports that rats and mice frequently enurinate defeated opponents following an aggressive encounter. Mykytowycz further suggests that the enurination of young rabbits may similarly benefit the marker by extending the sphere of influence of his odour and may benefit the young in a similar way to that suggested for chin gland secretion. That is, that the young may reduce the likelihood of being the target of aggression by possessing a familiar adult odour.

In an aggressive context enurination may serve to reinforce dominance or to act as a threat and in a sexual context a receptive female may be enurinated to repel other males. In a similar way the enurination of young rabbits may have the effect of repelling other males. Thus reported observations suggest that, in general, urine directed at conspecifics is aversive, although the possibility remains that in certain cases, when urine is
deposited on the ground (e.g. the urine of oestrous females) that its odour is actually attractive. However it is clear that the observations, upon which such suggestions are based, are limited and in many cases consist of anecdotes referring to single cases.

The aim of this section of the present study is to examine both enurination of conspecifics and the squirting of urine at inanimate objects in a more systematic manner than has been previously undertaken. An attempt is made to answer the following questions.

A. Enurination of Conspecifics
   (1) Do members of different age, sex and social status classes show differences in the frequency with which they enurinate conspecifics?
   (2) Is there seasonal variation in the frequency of enurination?
   (3) At what conspecifics is enurination directed?
   (4) In what behavioural context does enurination of conspecifics occur?

B. Squirting of Urine at Inanimate Objects
   (1) Do members of different age, sex and social status classes show differences in the frequency of urine squirting?
   (2) In what behavioural context does urine squirting occur?

METHOD

The data presented in this section again come from transcripts of Focal Animal samples. Details of the samples and of the observation areas are given in chapter 10. "Normal" eliminative urination was not recorded due to difficulties in positively identifying the behaviour in the field.

Data on conspecifics enurination refer to "bouts" rather
than to individual acts. Only 2 observed bouts contained more than one act of enurination (max N = 3) and these are noted in the relevant sections below.

Results

A. Enurination of Conspecifics

A total of 21 bouts of enurination involving 24 instances of enurination were observed. In 19 of these instances the stream of urine was actually observed and in the 5 remaining cases the movement of the animal obscured vision and enurination was inferred from the characteristic twisting/leaping behaviour.

(1) Variations in Overall Frequency of Enurination

The overall number of observed bouts of enurination and the mean number of bouts per hour of observation for each age, sex and social status class are shown in fig. 12.1. All bouts took place during the evening activity periods (1500 - 2200 hrs). As there were no differences in overall enurination rate between dominant and subordinate males, a chi square test was carried out on the number of bouts recorded for all adult males and those recorded for adult females. Adult males enurinate conspecifics more frequently than adult females ($X^2 = 6.08, p < 0.025$). Young rabbits were not observed enurinating conspecifics.

(2) Seasonal Variation

To counteract imbalances in sample numbers in the observation months, data on seasonal variation in enurination frequency are presented in the form of rates (bouts per hour of observation). Data for adults are shown in figs. 12.2 and 12.3. Enurination occurs most frequently in all classes during the breeding season although the data for females consist of very few observations. A Kruskal-Wallis one-way analysis of variance by
Fig. 12.1

<table>
<thead>
<tr>
<th></th>
<th>N Bouts</th>
<th>Observation Time (hours)</th>
<th>Bouts per hour</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dominant males</td>
<td>9</td>
<td>22.5</td>
<td>0.33</td>
</tr>
<tr>
<td>Subordinate males</td>
<td>10</td>
<td>25</td>
<td>0.33</td>
</tr>
<tr>
<td>Adult females</td>
<td>2</td>
<td>25.83</td>
<td>0.06</td>
</tr>
<tr>
<td>Young males</td>
<td>0</td>
<td>11.66</td>
<td>0</td>
</tr>
<tr>
<td>Young females</td>
<td>0</td>
<td>10.83</td>
<td>0</td>
</tr>
</tbody>
</table>

Overall frequency and rate of enurination for the 5 age, sex and social status classes.
Seasonal variation in the rates of enurination bouts (bouts per hour of observation) for the 5 age, sex and social status classes.
Fig. 12.3

Monthly variation in rate of enurination bouts (bouts/hour of observation) for the three adult classes.
ranks reveals that the seasonal patterns of rates of enurination are not significantly different for the three adult classes (\( H = 3.751, \text{d.f.} = 2, \text{N.S.} \)). The number of bouts for all classes falls off during the summer and rises again in August and September. The low number of recorded bouts undoubtedly accounts for the rather erratic nature of the results.

Southern (1948) presents data on the seasonal variation in the frequency of occurrence of enurination. The results show similar peaks in the spring and late summer. While the data are rather misleading as they are not corrected for imbalances in observation time across months, if this correction is made they still show a similar pattern to that found in the present study.

(3) Targets of Enurination

Enurination targets are shown in fig. 12.4. Clearly adult males enurinate a wide variety of conspecifics although the commonest targets are adult females and young rabbits. Adult females were only observed enurinating adult males. The 3 adult targets of unknown sex were unmarked animals whose behaviour did not serve to positively identify their sex.

(4) Behavioural Context of Enurination

The behavioural context was analysed following the procedure described in chapter 10. The behaviours occurring immediately before and after enurination are regarded as constituting the context. In the former case the behaviour of the enurinating animal was recorded and in the latter case the behaviour of both the enurinating animal and the target were recorded.

Fig. 12.5 shows pre-enurination behaviour. The 2 observed occurrences of females enurinating males were preceded by the male
Frequency of enurination directed at different target classes by the 3 adult classes.

<table>
<thead>
<tr>
<th>Target Rabbit</th>
<th>Dominant male</th>
<th>Subordinate male</th>
<th>Adult female</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dominant male</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Subordinate male</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>Adult female</td>
<td>3</td>
<td>4</td>
<td>0</td>
<td>7</td>
</tr>
<tr>
<td>Young rabbit</td>
<td>2</td>
<td>3</td>
<td>0</td>
<td>5</td>
</tr>
<tr>
<td>Adult (sex unknown)</td>
<td>2</td>
<td>1</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td>Total</td>
<td>9</td>
<td>10</td>
<td>2</td>
<td>21</td>
</tr>
</tbody>
</table>
Fig. 12.5

Prior behaviour of enurinating rabbit

<table>
<thead>
<tr>
<th>INTERACTION</th>
<th>chase target</th>
<th>chase by investigate target</th>
<th>investigate target</th>
<th>approach by target</th>
<th>TOTAL</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male enurinates male</td>
<td>3</td>
<td>0</td>
<td>2</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Male enurinates female</td>
<td>2</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Female enurinates male</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Male enurinates young</td>
<td>4</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Male enurinates unknown adults</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>TOTAL</td>
<td>10</td>
<td>4</td>
<td>3</td>
<td>3</td>
<td>1</td>
</tr>
</tbody>
</table>

Frequencies of behaviours of enurinating rabbits immediately prior to enurination bout.
chasing the female but in males, enurination was more commonly performed by the chasing animal. A total of 14/21 (66.7%) bouts were preceded by chases. In the case of aggressive chases (N = 7), enurination was performed by the chasing animal on 5 occasions and after courtship or sexual chases (N = 7) enurination was performed by the chasing animal also on 5 occasions.

On 3 occasions the enurinating rabbit approached and sniffed the target animal, usually around the ano-genital region. In a further 3 cases the ground where the target animal had been sitting was investigated by sniffing. Both behaviours were most common prior to a male enurinating a female and it seems possible that in the latter cases the male was investigating either urine or inguinal gland secretion deposited on the ground.

Figs. 12.6 and 12.7 show the behaviour of enurinating animals and target animals after the act. Only bouts containing a single act of enurination are included in the data for clarity. The 2 remaining bouts both involved males enurinating females (one containing 2 acts of enurination and the other 3). In the first bout the male enurinated the female, sat motionless, enurinated again and shook/groomed after the second. In the second bout the male enurinated and then approached the female who continued feeding. The male enurinated her again and then sat still while the female moved off. The male approached the female and again enurinated her. The female moved off again and the 2 rabbits fell to feeding some distance apart.

The number of chases following enurination is lower than the number recorded prior to the act. Only 35.5% of chases continued after enurination. In all cases in which the chasing animal was
### Fig. 12.6

<table>
<thead>
<tr>
<th>INTERACTION</th>
<th>chase</th>
<th>sit</th>
<th>feed</th>
<th>chin ground</th>
<th>pawscape</th>
<th>approach</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male enurinates female</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>5</td>
</tr>
<tr>
<td>Male enurinates male</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>4</td>
</tr>
<tr>
<td>Female enurinates male</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>Male enurinates young</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>1</td>
<td>5</td>
</tr>
<tr>
<td>Male enurinates unknown adult</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>5</td>
<td>4</td>
<td>4</td>
<td>3</td>
<td>1</td>
<td>2</td>
<td>19</td>
</tr>
</tbody>
</table>

Frequencies of post enurination behaviours of enurinating animals.

* Only bouts containing a single act of enurination are included (see text).

### Fig. 12.7

<table>
<thead>
<tr>
<th>INTERACTION</th>
<th>Escape</th>
<th>Sit</th>
<th>Feed</th>
<th>Shake/groom</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male enurinates female</td>
<td>2</td>
<td>0</td>
<td>1</td>
<td>2</td>
<td>5</td>
</tr>
<tr>
<td>Male enurinates male</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td>Female enurinates male</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Male enurinates young</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>5</td>
</tr>
<tr>
<td>Male enurinates unknown adult</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>6</td>
<td>1</td>
<td>3</td>
<td>9</td>
<td>19</td>
</tr>
</tbody>
</table>

Frequencies of post enurination behaviours of enurinated animals.
enurinated (N = 4) chases stopped, and in those cases in which the chasing animal enurinated (N = 10) chases resumed afterwards in 5 (50%) instances. In no cases did chases start as a result of enurination. On many occasions the enurinating animal remained close by the target animal feeding or sitting. In 3 cases, males were observed chinning the ground near the target animal.

The most common reaction to being sprayed with urine was shaking of the fur and grooming (N = 9). Instances of animals becoming "excited" as the result of being the target of enurination, previously reported by Southern (1948) and Lockley (1961) were not observed. In most cases except for a shaking of the fur, target animals showed little noticeable reaction.

Overall, 11 enurination bouts occurred in a courtship or sexual context, although 2 of these (by females being chased) might be regarded as aggressive acts. A further 8 bouts took place in an aggressive context and the remaining 2 were neither preceded nor followed by aggression or courtship activities although the acts themselves may have been aggressive. The number of observed social interactions dropped considerably after enurination and the impression was gained that frequently enurination was the final act of an interactive sequence between 2 individuals.

B. Urine Squirted at Inanimate Objects

This behaviour is distinguished from normal eliminative urination by the directing of a relatively small stream of urine backwards at an object or feature of the rabbit's environment. Bell (1980) has described such evacuation as "urine squirting". The urine is squirted out behind the animal while either moving or stationary. If it occurred while a rabbit was stationary it was often followed by a short forward leap.
Fig. 12.8

<table>
<thead>
<tr>
<th></th>
<th>Exploring</th>
<th>Feeding</th>
<th>Grooming</th>
<th>Social Encounter</th>
<th>TOTAL</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Pre Urine Squirt</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dominant Males</td>
<td>4</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>6</td>
</tr>
<tr>
<td>Subordinate Males</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td><strong>TOTAL</strong></td>
<td>4</td>
<td>2</td>
<td>0</td>
<td>1</td>
<td>7</td>
</tr>
<tr>
<td><strong>Post Urine Squirt</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dominant Males</td>
<td>3</td>
<td>2</td>
<td>1</td>
<td>0</td>
<td>6</td>
</tr>
<tr>
<td>Subordinate Males</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td><strong>TOTAL</strong></td>
<td>3</td>
<td>3</td>
<td>1</td>
<td>0</td>
<td>7</td>
</tr>
</tbody>
</table>

Behavioural context of urine squirting in adult males. Frequency of behaviours occurring immediately before and after the urine squirt act are presented for dominant and subordinate adult males.
(1) **Overall Frequency of Urine Squirting**

During the focal animal samples only 7 instances of urine squirting were observed. Six were performed by dominant males and one by a subordinate male. The targets for such urine squirts were usually prominent features of the rabbits’ home range. Three squirts were directed at heaps of soil displaced by warren excavation near a burrow entrance. A further 3 were directed at hummocks of vegetation (Armeria etc.) and the remaining observed occurrence was directed at a piece of driftwood.

(2) **Behavioural Context of Urine Squirting**

Behaviour occurring immediately prior to and following urine squirting is shown in fig. 12.8. Operational definitions of behavioural categories are given in chapter 10.

On 2 occasions urine squirting occurred during scent marking tours by dominant males. Only one occurrence took place in a social context and in general urine squirting appeared to be a solitary activity, taking place while an animal was exploring or feeding.

The fact that urine squirting is not invariably accompanied by an easily recognisable stereotyped behaviour pattern, raises the possibility that many occurrences were simply missed. Therefore it is quite probable that urine squirting occurs more frequently than the present results suggest.

**Discussion**

As has been mentioned, because of difficulties of observation in the field, only enurination of conspecifics and squirting of urine at inanimate objects were recorded. There were no difference in overall enurination frequencies in dominant and
subordinate males and adult males accounted for over 90 per cent of observed bouts of enurination. Adult females performed only two bouts and young rabbits were not observed enurinating conspecifics.

The peak in enurination recorded in the breeding season coincides with the high incidence of sexual and aggressive behaviour at that time. The smaller peak in the late summer coincides with the increase in social activity, largely due to the maturation of young rabbits. These peaks were observed in all adult classes but were most pronounced in subordinate males.

Enurination was not directed predominantly at a single class of rabbits and occurred in a variety of behavioural contexts. It was performed in both sexual and aggressive situations and in 14 (67%) cases was preceded by chasing. In only 5 of these cases was chasing resumed after enurination. These findings support results reported by Bell (1980). In 5 cases enurination of a chasing or approaching conspecific terminated the social interaction and therefore it may be postulated that in this context enurination is aversive. It may act as a threat or may be, as suggested by Bell (1977, PhD thesis), a "keep away" message. However, enurination was more frequently observed being performed by the chasing animal in both sexual and aggressive interactions and the situation here may be more complex.

Several explanations of enurination have been put forward by different authors. The first, that it is a "keep away" message has already been mentioned. The second, that it may be viewed as an attempt by the enurinating animal to widen its personal "sphere of influence" by imparting its odour on to the target animal, has
been suggested by Mykytowycz (1974). The act of enurination presumably both spreads the odour of the enurinating animal and masks the odour of the target animal. Certainly there is evidence that rabbits are capable of discriminating various conspecific characteristics from urine (eg. Schalken, 1976) and therefore urine appears to carry information about the depositing animal. Thus enurination may be a facet of more general scent marking behaviour by which the marking individual increases the level of its personal odour in the environment. Thirdly, it has been suggested that enurination in a courtship context may be an incidental product of the male's highly excited condition (Myers and Poole, 1961), or that it reflects a state of frustration in the male (Lockley, 1961).

It should be noted that these three explanations belong to different levels of analysis. The first refers to the "meaning" of the message being transmitted and possibly to the reaction of the target animal. The second refers to the possible function of the behaviour and the third refers to the underlying motivation for the behaviour. Because of this, these three explanations are not necessarily mutually incompatible. Thus the first two explanations may be linked by the supposition that having their personal odour masked by that of another individual is aversive to target animals.

Enurination during courtship behaviour has been observed occasionally in a variety of mammalian species. Ewer (1968) reports that it is not a normal component in the courtship behaviour of the chinchilla, Chinchilla spp. or the hare-mouse, Lagidium peruanum but may be performed by the male if the female fails to adopt the mating position. It is suggested that in most...
species in which it has been observed, enurination has a repellant rather than a stimulating effect on the female. A commonly reported feature of mammalian courtship behaviour, however, is the presence of sexually attractive but unreceptive females. Female odour may attract males for some time before the female comes into oestrous. In this situation, the motivation for enurination by the male may indeed be frustration, but it is possible that the odour of the male's urine either directly renders the female less attractive to other males or partially masks the females own attractive odour. Thus, the disadvantage of performing an act which is immediately aversive to the potential mate may be outweighed by the longer term advantage of rendering the female less attractive to other males.

Alternatively, it is possible that the aversive element is lessened by the courtship context in which it occurs or by the accompanying behaviour of the male. Male guinea pigs may extrude the testes during courtship - a behaviour which is also performed during threat displays. Ewer (1968) however, reports that the accompanying postures are not identical in the two contexts. A detailed analysis of the behavioural sequences involving enurination in different contexts in the rabbit would require slow motion recording equipment which was not available during the present study. Females attempted to escape from the male after enurination on only 2 occasions and the most common response was shaking of the fur and grooming.

A further possibility is that enurination is a display indicating the aggressiveness or status of the male. Previous reports of females becoming stimulated as a result of enurination (eg. Southern, 1948) would seem to give some support to such a
suggestion. However this was not observed in the present study and Ewer (1968) remarks that in rodents "there is nothing to suggest that urine spraying has a sexually stimulating effect".

Clearly a more detailed study of the behavioural and contextual variables accompanying enurination is necessary before these alternative suggestions can be realistically assessed.

The small number of observed occurrences of urine being squirted at inanimate objects were mainly performed by dominant males. Urine squirts were directed at prominent features of the rabbits range and most bouts took place following solitary olfactory investigation or during scent marking tours. The deposition of urine at prominent sites has been reported in a wide variety of mammalian species and is commonly interpreted as being a feature of territorial behaviour. The sites at which urine was squirted by rabbits were on no occasions situated at territorial boundaries. They appeared to be selected for their physical properties rather than for their location. The possible information carried by urine has been discussed above and it may be deposited within the range to reassure the depositor and to indicate his presence to other members of the group. It is probable that urine deposited on objects between 6 and 12 inches high increases the effective dispersal of the odour. The low observed frequency of urine squirting may reflect the limited number of objects or features in the study areas which might elicit such behaviour. Alternatively it is possible that the behaviour occurred more frequently but was not observed.
CHAPTER 13

PAWSCRAPES
Pawscrapes are small shallow holes normally only a few cm. deep and up to about 15 cm. long which are found in considerable numbers in any area inhabited by rabbits. They are formed by relatively superficial scratching with the forepaws, a behaviour which is easily distinguishable from that employed in the more extensive excavation of burrows or breeding stops.

Southern (1940) first reported the existence of such scrapes and added that, while they are to be found at all times of the year, they are particularly common during the winter. He concluded that they were dug in order to permit feeding on plant roots. However in a later paper (Southern, 1948) he reported that a common reaction among males that had been rebuffed by a female was to fall to excited and rapid scratching of the ground. Myers and Poole (1961) report that in their study of an enclosed population in S.E. Australia, normal feeding on pasture was interspersed with frequent scratching for roots and that during the summer, when the pasture dried out, this increased to a continuous scratching and loosening of the surface soil in a search for roots and seeds. However Myers and Poole also observed scratching by males while in the presence of an oestrous female or a rival male. They suggest that this is a displacement activity and is often a sign of high excitement. Lockley (1961) also viewed scratching behaviour in agonistic situations as displacement activity.

Mykytowycz (1965), however, noted that chinning of the ground was frequently preceded by scratch digging. The behaviour of one dominant male over a period of one hour during the breeding
season is reported and, of 16 observed occurrences of chinning, 5 were preceded by digging. In two other lagomorph species, the cottontail, *Sylvilagus floridanus* and the swamp rabbit *S. aquaticus*, males have been observed scratching at the ground when in the presence of a rival male (Marsden and Holler 1964) and it is suggested that this behaviour is a "dominant gesture".

In a wide variety of mammalian species scratching at the ground has been reported as being associated with scent marking. In *Thryonomys* (Ewer, 1968) the victor in a fight often scratches the ground and deposits scent. In the guinea pig, *Cavia porcellus* a fight is often preceded by ground scratching accompanied by the deposition of anal gland odour (Kunkel and Kunkel, 1964). In these cases, Ewer (1968) suggests that the marking animal is intensifying the threat component of the scent marking by the addition of a visual signal.

Bell (1980), in a study of free living wild rabbits on Skomer, found that a large proportion of pawscraping sequences were performed in an aggressive context and that scent was deposited in a substantial number of cases.

There is considerable variation, therefore in published reports of the behavioural context in which pawscraping occurs and in suggested functions. Bell (1980) is the only previous study in which quantitative evidence if presented to support any of these suggestions but unfortunately the rabbits were not marked in any way and therefore the type of data which could be collected was limited.

In this section of the present study an attempt is made to answer the following questions.
A. Pawscraping Behaviour

(1) Do members of different age, sex and social status classes show differences in the frequency of pawscraping?
(2) Is there seasonal variation in the frequency of pawscraping?
(3) In what behavioural context does pawscraping occur?

B. Distribution of Pawscapes

(1) In addition the distribution of pawscapes was investigated at several locations on the island.

METHOD

Data presented in this section again come from transcripts of focal animal samples. Details of the samples and of the observation areas are given in chapter 10. Data on pawscraping refers to bouts of scraping at a single location. Occasionally pawscraping was interrupted by other behaviours but on no occasion did an animal which had left the location of a pawscrape return to that pawscrape within the 50 minute observation period.

RESULTS

A. Pawscraping Behaviour

A total of 61 bouts of pawscraping were observed during 115 focal animal samples. In 15 of these samples the rabbit pawscraped more than once (Max N = 3) at different locations during the 50 minutes observation period. In 27 samples the rabbit pawscraped only once during the observation period.

(1) Overall Frequency of Pawscraping

The overall number of observed bouts and the mean number of bouts per hour of observation for each age, sex and social status class are shown in fig. 13.1. Only 6 bouts were observed in the morning observation periods (0600-0900), the remainder occurring
Overall frequency and rates of pawscraping for the 5 age, sex and social status classes.
between 1500 and 2200 hours. Members of all classes paw scrape more in the afternoon and evening than in the morning. This different was most pronounced in dominant males and least so in adult females.

Chi square tests were carried out on the overall observed frequencies of paw scraping in the different classes. Among adults there was no significant difference in paw scraping frequency between dominant males and subordinate males or between subordinate males and adult females, but dominant males paw scrape more frequently than adult females. \( \chi^2 = 4.99, \ p < 0.05 \). Adult rabbits paw scrape more frequently than young rabbits \( \chi^2 = 4.89, \ p < 0.05 \) but, if dominant males are excluded from the adult data, there is no significant difference in paw scraping frequency between the remaining adults and young rabbits. Dominant males paw scrape more frequently than young rabbits \( \chi^2 = 9.32, \ p < 0.01 \).

(2) Seasonal Variation

Again, to counteract imbalances in sample numbers in the observation months, data on the seasonal variation in paw scraping frequency are presented in the form of rates, (bouts per hour of observation). Data for the 5 age, sex and social status classes are shown in figs. 13.2 and 13.3. A Kruskal-Wallis one-way analysis of variance by ranks does not reveal any statistically significant differences between the seasonal distribution of paw scraping rates in the 3 adult classes \( H = 3.425, \ d.f. = 2, \ N.S. \). There is not enough data on the young rabbits to permit such a test.

It is clear, however, from fig. 13.3 that dominant males
### Fig. 13.2

<table>
<thead>
<tr>
<th>Age, Sex, Social Status</th>
<th>February</th>
<th>April</th>
<th>June</th>
<th>August</th>
<th>September</th>
<th>November</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dominant males</td>
<td>2.08</td>
<td>1.04</td>
<td>0.48</td>
<td>0.28</td>
<td>0.72</td>
<td>1.67</td>
</tr>
<tr>
<td>Subordinate males</td>
<td>0.5</td>
<td>0.56</td>
<td>0.32</td>
<td>0.33</td>
<td>0.56</td>
<td>0.83</td>
</tr>
<tr>
<td>Adult females</td>
<td>0.83</td>
<td>0.83</td>
<td>0.12</td>
<td>0</td>
<td>0.17</td>
<td>0</td>
</tr>
<tr>
<td>Young males</td>
<td>-</td>
<td>0</td>
<td>0.12</td>
<td>0.42</td>
<td>0.56</td>
<td>0.83</td>
</tr>
<tr>
<td>Young females</td>
<td>-</td>
<td>-</td>
<td>0.14</td>
<td>0</td>
<td>0.28</td>
<td>-</td>
</tr>
</tbody>
</table>

Seasonal variation in the rates of pawscrapping bouts (bouts per hour of observation) for the 5 age, sex and social status classes.
Fig. 13.3

Monthly variation in the rate of pawscraping bouts (bouts/hour of observation) for the 5 age/sex/social status classes.
show very marked peaks in pawscraping activity in the winter months of November and February with a relatively low rate during the summer months. Subordinate males also pawscrape less during the summer months, and show a similar peak in November but not in February. Young males show a steady increase in pawscraping after their emergence from the nest and from the late summer onwards they show a similar rate to that of subordinate adult males. Adult females show a peak in pawscraping activity during the breeding season, in February and April, and the observed rate then declines throughout the summer. The number of bouts observed in young females is not large enough to reveal any consistent picture.

(3) Behavioural Context of Pawscraping

The behavioural context of pawscraping was analysed following the procedure outlined in chapter 10. Again, the behaviours occurring immediately before and after a pawscraping bout are regarded as constituting the context. Pre and post pawscraping behaviours are shown in figs. 13.4 and 13.5 respectively. In fig. 13.4 the category "latrine visit" refers to pawscraping on a latrine or immediately after a latrine visit. In fig. 13.5 the same category refers to pawscraping on a latrine or immediately before a latrine visit. Operational definitions of the remaining behavioural categories are discussed in chapter 10.

Statistical analysis was also conducted by the procedure outlined for behavioural context of latrine visits in chapter 10. "Latrine visits" are included in the variable "active" in both pre and post pawscraping analyses. Chi square tests on scores of dominant males versus the combined scores of the other classes across the "active" and "passive" variables showed no significant differences between dominant males and other rabbits in either the
<table>
<thead>
<tr>
<th>Behaviour</th>
<th>Dominant males</th>
<th>Subordinate males</th>
<th>Adult females</th>
<th>Young males</th>
<th>Young females</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N (%)</td>
<td>N (%)</td>
<td>N (%)</td>
<td>N (%)</td>
<td>N (%)</td>
</tr>
<tr>
<td>N Bouts</td>
<td>24 (37.5)</td>
<td>17 (47.06)</td>
<td>13 (38.46)</td>
<td>5 (60)</td>
<td>2 (100)</td>
</tr>
<tr>
<td>Feeding</td>
<td>9 (37.5)</td>
<td>8 (47.06)</td>
<td>5 (38.46)</td>
<td>3 (60)</td>
<td>2 (100)</td>
</tr>
<tr>
<td>Exploration</td>
<td>3 (12.5)</td>
<td>2 (11.76)</td>
<td>5 (38.46)</td>
<td>1 (20)</td>
<td>0</td>
</tr>
<tr>
<td>Chinning</td>
<td>2 (8.33)</td>
<td>1 (5.88)</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Grooming</td>
<td>0</td>
<td>1 (5.88)</td>
<td>1 (7.69)</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Resting</td>
<td>0</td>
<td>0</td>
<td>1 (7.69)</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Intrawarren Social Interaction</td>
<td>5 (20.83)</td>
<td>2 (11.76)</td>
<td>1 (7.69)</td>
<td>1 (20)</td>
<td>0</td>
</tr>
<tr>
<td>Interwarren Social Interaction</td>
<td>3 (12.5)</td>
<td>1 (5.88)</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Latrine Visit</td>
<td>2 (8.33)</td>
<td>2 (11.76)</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

Behaviour occurring immediately before pawsraping bouts (N=61) by members of the 5 age, sex and social status classes. Data is expressed as frequency and % frequency.
<table>
<thead>
<tr>
<th>Behaviour</th>
<th>Dominant males</th>
<th>Subordinate males</th>
<th>Adult females</th>
<th>Young males</th>
<th>Young females</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N (%)</td>
<td>N (%)</td>
<td>N (%)</td>
<td>N (%)</td>
<td>N (%)</td>
</tr>
<tr>
<td>N Bouts</td>
<td>24 (50)</td>
<td>17 (58.82)</td>
<td>13 (61.54)</td>
<td>5 (80)</td>
<td>2 (100)</td>
</tr>
<tr>
<td>Feeding</td>
<td>12 (50)</td>
<td>10 (58.82)</td>
<td>8 (61.54)</td>
<td>4 (80)</td>
<td>2 (100)</td>
</tr>
<tr>
<td>Exploration</td>
<td>1 (4.17)</td>
<td>0</td>
<td>3 (23.08)</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Chinning</td>
<td>7 (29.17)</td>
<td>3 (17.65)</td>
<td>1 (7.69)</td>
<td>1 (20)</td>
<td>0</td>
</tr>
<tr>
<td>Grooming</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Resting</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Intrawarren Social Interaction</td>
<td>2 (8.33)</td>
<td>1 (5.88)</td>
<td>1 (7.69)</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Interwarren Social Interaction</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Latrine Visit</td>
<td>2 (8.33)</td>
<td>3 (17.65)</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

Behaviour occurring immediately after pawscraping bouts (N=61) by members of the 5 age, sex and social status classes. Data is expressed as frequency and % frequency.
pre or post pawscrape situations (chi square = 1.458, d.f. = 1, N.S.; chi square = 0.786, d.f. = 1, N.S.).

All classes of rabbits show a high incidence of feeding both before and after pawscraping although in all classes the incidence of feeding is higher after pawscraping bouts than before. Adult males also show a high incidence of social behaviour before pawscraping. Of the intrawarren social interactions for all classes, 5 were aggressive chases and in 4 of these the pawscraping was performed by the aggressor. In the 4 remaining instances pawscraping followed sexual interactions and in 3 of these cases was performed by the male. Interwarren interactions preceding pawscraping bouts occurred, in all cases, at territorial boundaries and were aggressive in nature. In 2 instances mutual pawscraping by the two antagonists took place. Social interactions following pawscraping were observed less frequently and in 2 of the 4 recorded instances these were continuations of aggressive chases which had started before the pawscraping bouts. Adult males also show a relatively high incidence of chin marking after pawscraping. Adult females frequently pawscrape while exploring, that is during investigative movement within the home range.

The overall pre and post pawscraping behaviours are compared in fig. 13.6 and it is clear that feeding and chinning occur considerably more frequently after pawscraping than before. More active behaviour such as exploring and social interactions decrease after pawscraping. The results of Bell's (1980) study of a free living population on Skomer are included in fig. 13.6 for comparison. These data also indicate that while feeding and chinning increase, exploration and social behaviour decrease after pawscraping. The differences in absolute levels of occurrence of
### Fig. 13.6

<table>
<thead>
<tr>
<th>Behavioural Context</th>
<th>Pre-pawscraping Behaviour (%)</th>
<th>Bell (1980) (%)</th>
<th>Post pawscraping behaviour (%)</th>
<th>Bell (1980) (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Present Study</strong></td>
<td>Present (%)</td>
<td>Bell (1980) (%)</td>
<td>Present (%)</td>
<td>Bell (1980) (%)</td>
</tr>
<tr>
<td>Feeding</td>
<td>44.26</td>
<td>10</td>
<td>59.02</td>
<td>54</td>
</tr>
<tr>
<td>Exploration</td>
<td>18.03</td>
<td>8</td>
<td>6.56</td>
<td>6</td>
</tr>
<tr>
<td>Chinning</td>
<td>4.92</td>
<td>0</td>
<td>19.67</td>
<td>32</td>
</tr>
<tr>
<td>Grooming</td>
<td>3.28</td>
<td>-</td>
<td>0</td>
<td>-</td>
</tr>
<tr>
<td>Resting</td>
<td>1.64</td>
<td>-</td>
<td>0</td>
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Behavioural context of pawscraping. Pre and post pawscraping behaviour of all rabbits (% frequency) plus data from Bell (1980) for comparison.
behaviours in the two studies are again probably due to differences in sampling methodology. The largest discrepancy is in the reported proportions of pre pawscraping social behaviour. However the behaviour occurring prior to 26% of Bell's observed pawscraping bouts was not recorded, and she freely admits "It seems probable that most of the remaining 13 animals for whom no record of pre pawscraping behaviour had been collected had been engaged in some form of passive behaviour such as resting or feeding rather than active social engagements since the latter seldom passed unnoticed during field scanning" (Bell, 1977). This suggestion is supported by the closer correlation in post pawscraping behaviours recorded in the two studies, although it is possible that differences in the structure of the 2 populations and differences in the seasonal distribution of observations may also have had a major influence on the two sets of results.

B. Distribution of Pawscrapes

The number and distribution of pawscrapes appeared to vary considerably in different areas. Most scrapes were found on sloping, ground but on flat ground (eg. the Tennis Court area) pawscrapes were relatively rare. It was difficult to assess the age of pawscrapes with any accuracy. Very old scrapes could be distinguished from more recent scrapes by the regrowth of vegetation or by the number of old faecal pellets which had accumulated in the hole. Bell (1977) used the presence of freshly displaced soil as an indicator that a pawscrape had been recently dug, but in most areas of the Isle of May the material underlying the turf surface layer was a peaty mixture of plant remains. Thus the material displaced from a pawscrape was not a loamy soil but rather a light fibrous material which was quickly dispersed by the
Pawscraped area to the east of Thistle Field study area.
wind. No attempt was made, therefore, to subdivide pawscraps into "old" and "new" categories. Furthermore, no attempt was made to quantitatively analyse the distribution of pawscraps across large areas of the island. Rather, two areas on the southern half of the island were found to contain high concentrations of pawscraps and as the distribution of scrapes at the 2 sites was quite different, they are described here as illustrative examples.

The first area was located on the east facing slope lying below the eastern boundary wall of thistle field. The site was a grazing area for a group of about 12 rabbits and did not contain any territorial boundary. The pawscraps were evenly spread over a considerable proportion of the slope (see fig. 13.7) and appeared to be dug to give access to roots.

The second site (an area of approx. 2350 m²) constituted the western arm of Cross Park (see figs. 6.3 and 13.8) and contained the boundary between Cross Park warrens 1 and 3. This territorial boundary was one of the least stable in any of the study areas across the 3 year period of observations. As described in chapter 6 frequent "territorial disputes" between members of the two warrens took place around the boundary area and during 1977 warren 1 was re-expanding into the area. Fig. 13.8 shows the distribution of adult male ranges during 1977. A band of approximately 360 m² which included this boundary region was drawn between the two gaps in the surrounding wall which were the only points of entry to the area for members of warren 3. In September 1977, the band contained 280 pawscraps (0.78/m²). The area to the southwest of the boundary area (approx. 375 m²) contained only 11 pawscraps (0.03/m²) and the remaining area to the northeast of the boundary zone contained 110 pawscraps (0.07/m²).
Western arm of the Cross Park study area. Paw scrape distribution.

- adult male ranges - warren 1
- adult male range - warren 3
- fencing containing smeuses
- area b

Area a - 375 square metres contained 11 pawscrapes
Area b - 360 square metres contained 280 pawscrapes
Area c - 1620 square metres contained 110 pawscrapes
While part of the band overlapped with a grazing area for rabbits from warren 3, none of the warren 1 rabbits grazed within the boundary zone and it is difficult to explain the distribution of the pawscrapes solely in terms of obtaining food.

DISCUSSION

While there are differences in the overall frequency of pawscraping in the different age, sex and social status classes, much useful information is missing from such a crude analysis. Data on the seasonal distribution and the behavioural context of pawscraping reveal that there is considerable variation in the pattern of pawscraping in different classes. Most of the previously published suggestions relating to the function of pawscraping receive some quantitative support from the results of the present study. Pawscraping occurs in a variety of behavioural contexts and it seems probable that it fulfills several quite distinct functions.

The general low frequency of pawscraping during the summer months, when food is relatively plentiful suggests that it may be important for obtaining roots etc. when there is little nutritional value in the surface vegetation. In addition, a high proportion of observed bouts took place in the behavioural context of feeding, and feeding on the extracted plant material was commonly observed following pawscraping.

Adult females show a different pattern of pawscraping from that observed in other classes of rabbits. A high proportion of bouts took place while exploring and after the scraping bout, exploration often continued. The majority of adult female pawscraping took place during the breeding season and it is
possible that pawscraping may simply be exploratory digging for breeding stops or may reflect an increased drive in females to dig at his time of year.

The high incidence of chinning after pawscraping by males, and by dominant males in particular suggests that in some cases pawscrapes may act as a visual addition to an olfactory signal. The large proportion of pawscrapes preceded by social interactions may also support Ewer's (1968) suggestion that pawscraping is a component of a threat display. This suggestion may also explain the high concentration of pawscrapes along the disputed territorial boundary in Cross Park. Alternatively, scraping at the ground in such contexts may simply be a displacement activity reflecting a conflict of drives.

It is probable therefore that pawscraping is a behaviour which appears superficially similar in a variety of situations, but which fulfills several different functions. Analysis of the behavioural context in which pawscraping occurs is clearly essential for an understanding of its function in any given instance.
CHAPTER 14

GENERAL DISCUSSION AND CONCLUSIONS
CHAPTER 14
General Discussion and Conclusions

The behaviour of the European rabbit has been studied extensively since the 1940s, with the majority of the published work emanating from Australia. The choice of the Australian researchers to study semi-natural enclosed populations has resulted in the situation where most of our knowledge about rabbit social behaviour is based upon results of observations of enclosed populations in a quasi-Mediterranean climate. Thus, although the volume of research is large, this seems an unusually narrow foundation upon which to base our understanding of such a widespread and economically important mammal. One of the principal aims of the present study then, was to examine the applicability of previous findings on several aspects of rabbit behaviour to a free living population in a northern temperate climate, and hopefully in the process, to widen the existing knowledge base.

As explained above, the initial impetus for the present study was a desire to investigate aspects of olfactory communication, but clearly considerable preliminary information must be available concerning the identity, social organisation and behaviour of a population before meaningful analysis of olfactory behaviour can be attempted. The contents of the present thesis inevitably reflect this process and consequently cover a rather wide range of aspects of rabbit behaviour. Each chapter of the thesis is concluded with a discussion of its results and, given the diverse nature of these results, an attempt has been made in this concluding section to pick up some of the threads running through these previous discussions rather than presenting an overall synthesis of the results based around a single common
While the findings of the present study provide support for many of those of the Australian studies, it appears that there is considerably more variation in the social organisation of the rabbit in a naturally occurring population than has been reported for the captive populations previously studied. Although some variations were reported in the original papers by Mykytowycz (e.g. 1958, 1959) and by Myers and Poole (e.g. 1959) these have been ignored in more recent summaries of the research (e.g. Mykytowycz, 1973; Myers et al., 1971). This seems a rather curious development which has led to the accepted picture of rabbit social organisation being less complex than some of the original evidence would suggest.

Most of the enclosure study populations consisted of small warren systems and the social structure reported is similar to that observed in small single group warrens in the present study population. Such small warrens may be more common generally than was the case in the study areas on the Isle of May, as these were chosen partly because there was a reasonably high density of rabbits present. However, the observation that the accepted description of rabbit social organisation (i.e. small breeding groups with independent dominance hierarchies inhabiting exclusive defended territories) did not appear to apply to larger warrens must cast doubts on the generality of the previously published studies. Clearly, more research on naturally occurring populations is needed to clarify the issue.

Interpretation of the present results on variations in reproductive success is hampered by the fact that the measure of
reproductive success was based on the mean productivity of adult females in each group. The accurate recording of individual reproductive success was not possible without considerably greater interference with the study warrens. Analysis of the data at the level of the group, therefore, was regarded as an unfortunate necessity and is not intended to imply that selection operates at this level.

The finding that mean female reproductive success is inversely correlated with warren size is in support of previous results from enclosed populations (Myers et al., 1971). However, the observation that the optimum group composition is two males and two females has not previously been reported. Interpretation of the comparisons drawn between groups containing a dominant male (ie. the group occupying the burrows in which the dominant male resided) and other groups in the same warren, is rendered particularly difficult by the measure of reproductive success used. Clearly analysis at the level of the group rather than at the level of the individual results in several interpretations of the data being possible. However, the findings that groups in which the dominant male is resident have a higher mean female R.S. than other groups in the same warren, and that such groups are more affected by increasing warren size are interesting and prompt further questions about variations in R.S. within groups under such conditions. Such questions should be amenable to study in a situation where more interference with the population is deemed acceptable.

The published literature contains very little information on the activity patterns of the rabbit in a northern temperate climate. The present results indicate that the seasonal variations
in general surface activity differ markedly from those reported in Australian studies (Myers and Poole, 1961: Mykytowycz and Rowley, 1958). However, it seems probable that such differences result directly from differences in the climates. Climatic differences are probably also responsible, either directly or indirectly, for differences in the seasonal distribution of specific behaviours; eg. the behavioural category 'resting' includes basking in the sun, and the proportion of daily surface time spent feeding must surely be affected by the quantity and quality of the food available. The rabbits on the Isle of May appear to be more diurnal than their mainland counterparts and this may be due to the absence of diurnal predators.

In addition to the reservations, noted above, about the narrow range of conditions under which many previous studies have been conducted, it became apparent that the methods employed, where any details are given, give some cause for concern. For instance in the two previously published studies on naturally occurring populations (Myers and Schneider, 1964; Bell, 1980) the researchers relied on naturally occurring variations between individuals to permit identification. Ideally, every animal in a study population should be individually recognisable. In practice this is only a realisable goal in the study of certain species but as a minimum requirement the researcher must be able to ascertain each individual's membership of any classes which he hopes to employ as variables in the study. For instance, if one is interested in sex differences in behaviour then it is obviously essential to be able to place each of the observed animals into either the male or female category. It is not sufficient to use behavioural criteria to distinguish between classes of animals.
which are subsequently to be compared on measures of similar behaviour - this introduces an unacceptable circularity into the study. When questions are to be asked about differences in behaviour between males and females, juveniles and adults, and dominant versus subordinate individuals the problem of accurate identification becomes paramount. The rabbit is a species which exhibits little sexual dimorphism and few individually recognizable characteristics and therefore marking of individuals is an indispensable prerequisite to the study of their behaviour. In the studies conducted by Myers and Schneider (1964) and Bell (1980) it is difficult to see how enough individuals were recognisable on the basis of naturally occurring variations to permit some of the conclusions of the studies to be validly drawn.

Furthermore, there is little information available in any of the previously published reports on the methods used to sample behaviours in their study populations. This is an important omission as, clearly, the validity and general applicability of conclusions drawn from such studies are dependent on the sampling techniques employed. Lack of strict sampling is less important in the early, generally descriptive studies, but becomes increasingly important when detailed quantitative data are used as the foundation for more general conclusions.

This is clearly illustrated in the data published by Bell (1980) on the behavioural contexts of scent marking activities. As discussed in chapters 10 and 11, the use of inappropriate sampling procedures may result in some behaviours having a higher probability of being recorded than others, biasing the results in favour of more 'eye-catching' activities. The lack of details of sampling methods used in several other studies of rabbit behaviour
must cast doubts over at least some of their more specific conclusions.

Olfaction

In the majority of field studies on mammalian olfaction, the focus of observation is on the odour depositor rather than on the investigator (or on the signal emitter rather than the signal receiver). This is understandable in terms of the efficiency of observations. The practice of sitting observing the site of a scent mark on the offchance that another animal will venture up to investigate it would tax the patience of the must diligent observer. Thus the observer generally concentrates his attention of an animal rather than on a scent mark and when the animal investigates an odour deposit, the identity of the depositor is not normally known. The observer may record deposition of scent therefore, and have little access to information and about the receiver/s, or he may record investigation of scent and have little access to information about the depositor/s.

In general this was the case in the present study. Chinning and specific cases of urine deposition were recorded as they were accompanied by consistent recognisable behaviour patterns. However, in the case of anal gland secretion and defaecation it was not possible to record the deposition of scent and the focus was rather on the reactions of the target animal to a visible landmark (the latrine) which was assumed to be an olfactory stimulus. In this case, therefore, the rabbits were always recorded reacting to a visually identifiable odour source (depositor/s unknown) and the reaction may or may not have involved deposition of scent. In the case of chinning, however, the rabbits were always recorded depositing scent, but not
necessarily in response to an odour source (or at least a visually identifiable odour source). In the case of urination, the rabbits were recorded as depositing urine only if it was accompanied by a specific recognisable behaviour pattern. Thus only a small subsection of all urine deposition was recorded, again not necessarily in response to an odour source.

The results of these sections of the present thesis are not strictly equivalent, therefore, and must be pieced together carefully to form any coherent picture of rabbit olfactory communication. For example while chinning and urine squirting are acts of scent deposition latrine visits are not necessarily so. Mykytowycz and Gambale (1969) and Bell (1977), who were unable to record instances of defaecation, report that pellets were deposited on 42% and 31% of visits respectively. Rabbit visits to latrines may have 3 distinct although not mutually exclusive outcomes related to olfactory communication. They may deposit scent, investigate scent or acquire previously deposited scent. Without being able to realistically record defaecation or 'normal' urination the outcome of most latrine visits can only be surmised by analysis of other behaviours.

These caveats should be borne in mind therefore during the following discussion.

It is obvious from the results of the present study that various scents may be deposited at the same location, eg. chinning and defaecation at latrine sites. It seems probable that differences in the mode of deposition and physical characteristics of the scent (eg. decay rate) result in the effectiveness of different scents varying in different situations. However, is it
the case that these scents carry different information and fulfill
different functions or do the different scents simply reinforce
each other—fulfilling the same function of functions?

The results of observations made during the present study on
seasonal variation and behavioural context of scent-related
activities provide little evidence for the idea of functional
specialisation between different scent products. There is a peak
in chinning, latrine visits and enurination during the breeding
season for adults with a rise in the frequency of chinning and
latrine visits in young rabbits in the late summer as they reach
sexual maturity. There are also marked similarities in the overall
behavioural contexts in which scent-related activities take place
(i.e. in the behaviours occurring immediately before and after
these activities irrespective of age, sex or social status class).
There is a high incidence of exploration and of social
interactions before latrine visits, chinning and urine squirting,
and a higher overall probability of each of these activities being
followed by feeding. Thus while it is clear that each
scent-related activity may occur in different contexts, e.g. either
social or solitary, there is a great deal of similarity between
scent-related activities.

Mykytowycz et al. (1976) report that anal, chin and inguinal
gland secretions and urine influence the confidence of rabbits to
different degrees. They placed pairs of rabbits in an otherwise
neutral arena along with one of the scent products obtained from
one of the pair and compared the performance of each rabbit when
in the presence of its own odour with its performance when in the
presence of its opponents odour. The authors used this finding to
support the idea of functional specialisation, claiming that
inguinal gland odour functions for individual recognition while chin and anal gland secretions are important in territorial demarcation. As Bell (1980) has pointed out however, the results of the experiment might just as easily be used to support the opposite contention – that there is no functional specialisation. The results indicate that a rabbit's confidence is increased by the presence of it's own odour, but to differing degrees depending on the particular odour present ie. the odours from different sources appear to differ quantitatively rather than qualitatively in their effect. Given the practical difficulties in presenting quantitatively equivalent amount of different types of scent to the rabbits in such trials, it is possible to argue that the odours all serve the same function (enhancement of the donor's confidence) and that the quantitative differences in behaviour observed are due to the experimenter's difficulty in assessing, for instance, the chin gland secretion equivalent of 5 faecal pellets.

There is little evidence as yet, therefore, that in the rabbit scent products from different sources have different functions. Furthermore, results from a considerable number of laboratory studies suggest that scent from urine and from anal, inguinal and chin gland secretions may all carry information about the identity of the individual. Certainly there is some evidence that rabbits are capable of discriminating between sex, age, reproductive status, social status and individual identity on the basis of any of the four scents (eg. Mykytowycz and Ward, 1971; Mykytowycz and Dudzinski, 1972; Mykytowycz, 1975; Black-Cleworth and Verberne, 1975; Schalken, 1976; Bell, 1977).

However, although similar identifier information may be
carried by all four scents, this does not necessarily imply that deposition of scent always has the same functional significance.

The most common suggestion about the function of mammalian scent marking has been that it is important in territorial demarcation, and that the scent deposited by one individual is repellent, or acts as a threat to others (eg. Lorenz, 1966; Ewer, 1968; Johnson, 1973; Mykytowycz, 1968). However, Mykytowycz (eg. 1973) has more recently argued that the emphasis when discussing the function of scent deposition, should be on the confidence enhancing effect which the scent has on the depositor rather than on the repellent effect which it is assumed to have on other individuals. As discussed in chapter 9, these possible effects are very difficult to unravel in practice and it seems reasonable to argue that the dichotomy is a false one resulting from arguments on two different levels. On the motivational level, it is possible that an individual deposits scent in order to reassure itself which in turn does not preclude the possibility that on the functional level the scent functions as a threat to a conspecific.

Does the deposition of scent by rabbits, therefore, fulfill only one function? There is evidence from the present observations that individuals, or at least members of the same age, sex or social status class deposit even a single scent in a variety of different behavioural contexts. For example, chinning of the substrate is performed by solitary individuals during exploration and feeding, and is performed in a social context during sexual and aggressive interactions, usually by the 'active' participant. Chinning of conspecifics is most frequently performed by dominant males and in 33% of observed instances, chinning was elicited by the animal being chinned. It seems probable that the functional
significance of the scent is not identical in each of these situations.

An odour carrying identifier information deposited on the substrate in a solitary context may simply serve to indicate the depositor's continued presence to other individuals. Certainly the results of studies conducted by Mykytowycz (1958) and Lockley (1961) indicate that when a dominant male was removed from the enclosures, another male quickly assumed the dominant role. Mykytowycz suggests that odour may play an important role in informing rabbits about the presence or absence of individuals. In addition, the overall level of personal odour in the immediate environment may affect the general confidence of the depositor and have more specific effects on the individuals' interactions with others.

In aggressive interactions, the deposition of scent may increase the marker's confidence while simultaneously acting as a threat to the opponent. In this situation it was observed that deposition of scent by one animal increases the likelihood of withdrawal by the opponent. Such an effect may be understood either in terms of the inherent aversive nature of another's odour or in terms of a learned aversive association between the identifier odour and the outcome of a previous agonistic encounter. If a learned association is involved then the effectiveness of odour deposition as a functional threat would be dependent on the outcome of previous interactions. In other words, there would be little point in an animal which was low in a social hierarchy scent marking in an aggressive interaction as the scent would not constitute an effective threat.
In sexual encounters the deposition of scent on the substrate by a male may act as an attractant to females, particularly if the male scent is familiar and constitutes a large proportion of the scent pervading the home range. High ranking males deposit a disproportionately large amount of scent and there are good reasons for females to mate with such a male. Some of the characteristics which permitted the male to assume a dominant role may be inherited by, particularly, her male offspring. Again, however, the effectiveness of such marking in this context is likely to be dependent on the identity of the marker.

Observations indicated that direct marking of females by males in a sexual context commonly took the form of enurination, although chinning was also recorded. In the case of enurination, the response of females indicated that it was aversive. The seemingly anomalous features of performing an aversive action during what is ostensibly courtship behaviour may be explained by postulating that the short term disadvantage of immediately repelling the female may be outweighed by the longer term advantage of reducing the attractiveness of the female to potential rival males either by masking the female's own odour or by imparting an odour which is aversive to other males.

Chinning of conspecifics did not appear to be aversive and in 30% of recorded instances it was actively elicited. In the majority of these cases the animal eliciting marking was a juvenile and the marking animal was a dominant male. Mykytowycz and Dudzinski (1972) report that in a laboratory situation, adult females act aggressively towards 'strange' young rabbits (i.e. young from different breeding colonies). Adult males however, are more tolerant of such young and even protect them from the
aggression of females. In addition to being protective towards strange young, adult males were frequently observed chinning and licking them. Mykytowycz and Dudzinski (1972) suggest that in a natural setting "it is obvious that in the course of licking, chinning and enurination by the males, the strange kittens become impregnated with the odours familiar to all members and gradually become accepted into the group". Thus, eliciting scent marking, particularly from a high-ranking male may assist young rabbits in acquiring an odour which is familiar to other adults and therefore in reducing the level of aggression directed at them.

The advantage of adult males in marking juveniles may simply be in increasing the level of their personal scent in the environment, especially on a mobile carrier, but such interactions may also reinforce the dominant/subordinate relationship between the pair.

Mykytowycz and Dudzinski (1972) also report that while adult females were more aggressive towards strange young then young from their own breeding colony, they were in turn more aggressive to young from their own breeding colony than to their own progeny. Thus, two levels of discrimination are being performed in this case. It seems probable that individual recognition is important within the group or within the warren while discrimination between group members and strangers may be based on detection of a more general group odour.

The possibility that members of social groups may share aspects of their odour permitting olfactory discrimination at a group level is discussed in chapter 9. In free living rabbits such sharing of scent may take place partly by direct marking of
conspecifics and partly by the acquisition of the odour of others through the communal use of burrows or by frequenting localised scent marking sites such as latrines. Certainly the present results suggest that in certain cases the patterns of behaviour observed at latrines were more easily explained in terms of odour acquisition rather than odour deposition.

In addition to the observation that a scent may be deposited in a variety of different behavioural contexts by members of a single sex, age or social status class, it is clear that there is considerable variation in the behavioural context of scent related activities between classes.

For example, over 30% of adult male chin marking was performed on latrines whereas adult females were never observed chinning on latrines. Analysis of the behavioural context of latrine visits show similar variations - 67% of all pre-visit exploration and 50% of all pre-visit social interactions were exhibited by dominant males. The most frequently observed pre-visit behaviour exhibited by members of other classes was feeding. Unfortunately, analysis of the data at this level may not permit us to draw any conclusions about the function of scent marking. It seems probable that these variations simply reflect differences in the general level of participation in these behaviours. For instance dominant males spend a higher proportion of their surface time in exploration or social behaviour than do members of other classes and it is therefore not surprising that a higher proportion of scent related activities are preceded by such behaviours. At this level then, the behavioural context of marking may be less useful as an indicator of function than had previously been supposed.
Differences in the frequencies and temporal patterns of scent-related activities between classes, however, are much more clear cut. The results indicate that males spend more time in scent-related activities than females and that dominant males deposit a disproportionately large amount of all scents. It seems probable that a higher level of marking by subordinate males would elicit aggression from the dominant male although if learned associations play any part in the rabbit's reactions to an odour stimulus it is also possible that marking by subordinate males would be less effective and the lower benefit/cost ratio of such activity might lead us to expect a lower frequency of occurrence.

If all rabbits deposit scent (albeit to differing degrees) which carries identifier information, and which may fulfill different functions in different contexts, what are the benefits of using a variety of different scent products to transmit similar information?

Bell, (1980) lists several theoretical advantages of a 'multi-scent signal' expressed in terms of variations in mode of release or in the physical properties of different odour products; eg. differences in the effective life or range of single scents or the possibility that one odour product may have additive or fixative properties when mixed with another.

Clearly each scent product is not equally effective in a given situation; eg. urine may be directed at objects or conspecifics from a distance; chin gland secretion may be applied to tall vegetation or prominent landmarks; anal gland secretion, which is deposited as a coating on moist faecal pellets may be less volatile than other products. However, rabbits also deposit
multiple scents in a single situation in the case of latrines. There is evidence that urine, faeces and chin gland secretion are all deposited at latrines. Furthermore, the pellets deposited there appear to carry more anal gland secretion than those deposited throughout the range. One explanation of such behaviour is that depositing a large amount of scent at these localised sites which are visited by a large proportion of conspecifics represents an efficient use of limited resources. It seems probable therefore that the employment of several scent products with different physical or chemical properties might increase the overall effectiveness of information transmission, although clearly considerably more research is required in this area.

Conclusions

The practical difficulties of collecting meaningful data from fieldwork on a free-living population of rabbits have been highlighted. The present study was instigated with the limited aim of investigating olfactory communication under natural conditions. However, a considerable amount of detailed data on the identity, social organisation and behaviour of the study population had to be available before any analysis or interpretation of the results on olfaction could be attempted. Most field studies on free-living populations of mammals are lengthy and time consuming endeavours, and the three year span of the present study permitted only a limited amount of information to be collected. It is to be hoped that some of the lessons learned during this project will aid future investigators to avoid some of the more important pitfalls encountered in such an undertaking.

The need for careful consideration of methodology has also been stressed. The employment of appropriate sampling methods in
the observational study of behaviour is a factor which has often been discussed in theoretical papers but has been too often ignored in studies of behaviour.

The results of the present study do not support the suggestion that scent marking fulfills a single function and there is little support for the idea of functional specialisation of different scents in the rabbit. Rather, the deposition of odour seems to fulfill a variety of different functions in different contexts, and it seems probable that the different scents carry similar information.

The previous laboratory research on rabbit olfaction has demonstrated the value of control over extraneous variables and has yielded a wealth of interesting results. However, further research on free-living populations is required to permit observation of scent related activities within the context of the full range of rabbit behaviour. Only by piecing together the results of several different studies will we begin to understand the functions of scent marking.

Myers and Schneider (1964) assert that "there is no major difference between the basic pattern of social behaviour of confined rabbit populations and of free-living wild rabbits". This assertion is not supported by the results of the present study. It seems possible that in choosing to reap the benefits of ease of observation, extensive background knowledge about the population and control over the population structure, the researchers conducting studies on captive populations have sacrificed some of the complexity and variation in social behaviour which occurs in free living rabbits.


Bell, G.S. (1958) The vegetation on the Isle of May, Firth of Forth, in 1957, relative to exposure features, Coturnix.


Appendix 1

(a) Tennis Court warren 1; a small warren in which fencing and use of box traps was very successful in capturing rabbits. The traps are shown with perspex doors propped open, to acclimatise the rabbits to using them as tunnels.

(b) Thistle Field study area showing tall summer vegetation. View looking North east.
(c) Tennis Court and Cross Park study areas. In the foreground is the raised area to the north of Tennis court and the hide used for observation of that area. In the background is the Cross Park and to the left is the rocky Ardcarran area.

(d) A latrine in the Tennis Court study area. The photograph was taken in unusually dry weather.
APPENDIX 2

FREQUENCY AND OUTCOME OF INTRAWARREN AGONISTIC INTERACTIONS BETWEEN ADULTS

WARREN: CROSS PARK 1
MAY 1976
Total Number of Adults Present = 7

<table>
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<td>f</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Total losses</td>
<td>1</td>
<td>2</td>
<td>4</td>
<td>0</td>
<td>7</td>
<td>12</td>
</tr>
</tbody>
</table>

Total intrawarren agonistic interactions between adults observed in 4 hours observation = 31. M47 was involved in 18 (58%) of all agonistic interactions and "won" 17 (94.44%) of these. Identification numbers in parenthesis indicate rabbits which were not marked at the time of these observations. Identification was by some physical characteristic.

WARREN: TENNIS COURT 1
MAY 1976
Total Number of Adults Present = 5

<table>
<thead>
<tr>
<th>LOSER</th>
<th>M50</th>
<th>F23</th>
<th>(M71)</th>
<th>M39</th>
<th>f</th>
<th>Total Wins</th>
</tr>
</thead>
<tbody>
<tr>
<td>M50</td>
<td>1</td>
<td>6</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>13</td>
</tr>
<tr>
<td>F23</td>
<td>0</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>6</td>
<td>6</td>
</tr>
<tr>
<td>Winner</td>
<td>(M71)</td>
<td>0</td>
<td>1</td>
<td>5</td>
<td>2</td>
<td>8</td>
</tr>
<tr>
<td>M39</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td></td>
<td>1</td>
</tr>
<tr>
<td>f</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Total losses</td>
<td>0</td>
<td>2</td>
<td>7</td>
<td>11</td>
<td>9</td>
<td>29</td>
</tr>
</tbody>
</table>

Total intrawarren agonistic interactions between adults observed in 4 hours observation = 29. M50 was involved in 13 (45%) of all agonistic interactions and "won" 13 (100%) of these.
WARREN: TENNIS COURT 1
MAY-JUNE 1977
Total Number of Adults Present = 6

<table>
<thead>
<tr>
<th>LOSER</th>
<th>M50</th>
<th>M97</th>
<th>F56</th>
<th>F63</th>
<th>(M145)</th>
<th>F97</th>
<th>Total Wins</th>
</tr>
</thead>
<tbody>
<tr>
<td>M50</td>
<td>4</td>
<td>1</td>
<td>2</td>
<td>7</td>
<td>3</td>
<td>17</td>
<td></td>
</tr>
<tr>
<td>M97</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>3</td>
<td>1</td>
<td>6</td>
<td></td>
</tr>
<tr>
<td>F56</td>
<td>0</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>F63</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>(M145)</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
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<tr>
<td>F97</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Total losses 1 6 3 2 14 5 31

Total intrawarren agonistic interactions between adults observed in 4 hour observation = 31. M50 was involved in 18 (58%) of all agonistic interactions and "won" 17 (94.44%) of these.
WARREN:- CROSS PARK 2
MAY 1976
Total Number of Adults Present = 17

<table>
<thead>
<tr>
<th>Marked or recognisable individuals</th>
<th>Opponent</th>
<th>Total Wins</th>
<th>Opponent</th>
<th>Total Losses</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>male</td>
<td>female</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(M74) black</td>
<td>10</td>
<td>5</td>
<td>7</td>
<td>22</td>
</tr>
<tr>
<td>m (mottled)</td>
<td>3</td>
<td>2</td>
<td>2</td>
<td>7</td>
</tr>
<tr>
<td>m (scar eye)</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>F30</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>F24</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>f (large)</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td>m (satellite)</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
</tbody>
</table>

Interactions in which marked or recognisable individuals emerged as winner.

Interactions in which marked or recognisable individuals emerged as loser.

Total intrawarren agonistic interactions between adults observed in 4 hours observation = 63.
(M74) was involved in 22 (34.92%) of all agonistic interactions and "won" 22 (100%) of these.

WARREN:- TENNIS COURT 2
MAY 1976
Total Number of Adults present = 9

<table>
<thead>
<tr>
<th>Marked or recognisable individuals</th>
<th>Opponent</th>
<th>Total Wins</th>
<th>Opponent</th>
<th>Total Losses</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>male</td>
<td>female</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M38</td>
<td>9</td>
<td>5</td>
<td>0</td>
<td>14</td>
</tr>
<tr>
<td>M48</td>
<td>4</td>
<td>4</td>
<td>0</td>
<td>8</td>
</tr>
<tr>
<td>M44</td>
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<td>0</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>m (mottled)</td>
<td>1</td>
<td>2</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td>f (torn ear)</td>
<td>2</td>
<td>1</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td>m (unmarked)</td>
<td>2</td>
<td>2</td>
<td>0</td>
<td>4</td>
</tr>
</tbody>
</table>

Interactions in which marked or recognisable individuals emerged as winner.

Interactions in which marked or recognisable individuals emerged as loser.

Total intrawarren agonistic interactions between adults observed in 4 hours observation = 58.
M38 was involved in 16 (27.59%) of all agonistic interactions and "won" 14 (87.5%) of these.

371
WARREN: NETTLE HOLLOW 1
MAY 1976
Total Number of Adults Present = 16

<table>
<thead>
<tr>
<th>Marked or recognisable individuals</th>
<th>Opponent</th>
<th>Total Wins</th>
<th>Opponent</th>
<th>Total Losses</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>male</td>
<td>female</td>
<td>?</td>
<td></td>
</tr>
<tr>
<td>M51</td>
<td>13</td>
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<td>8</td>
<td>29</td>
</tr>
<tr>
<td>M25</td>
<td>4</td>
<td>1</td>
<td>3</td>
<td>8</td>
</tr>
<tr>
<td>(M59)</td>
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<td>1</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>M22</td>
<td>4</td>
<td>3</td>
<td>4</td>
<td>11</td>
</tr>
<tr>
<td>F07</td>
<td>3</td>
<td>2</td>
<td>3</td>
<td>8</td>
</tr>
<tr>
<td>F35</td>
<td>2</td>
<td>2</td>
<td>3</td>
<td>7</td>
</tr>
<tr>
<td>f (mottled)</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>F38</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>4</td>
</tr>
</tbody>
</table>

Total intrawarren agonistic interactions between adults observed in 4 hours observation = 97.
M51 was involved in 31 (31.96%) of all agonistic interactions and "won" 29 (93.55%) of these.

WARREN:- THISTLE FIELD 1
MAY 1976
Total Number of Adults Present = 14

<table>
<thead>
<tr>
<th>Marked or recognisable individuals</th>
<th>Opponent</th>
<th>Total Wins</th>
<th>Opponent</th>
<th>Total Losses</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>male</td>
<td>female</td>
<td>?</td>
<td></td>
</tr>
<tr>
<td>M45</td>
<td>10</td>
<td>4</td>
<td>11</td>
<td>25</td>
</tr>
<tr>
<td>M28</td>
<td>2</td>
<td>1</td>
<td>2</td>
<td>5</td>
</tr>
<tr>
<td>M37</td>
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<td>0</td>
<td>3</td>
</tr>
<tr>
<td>F05</td>
<td>0</td>
<td>4</td>
<td>2</td>
<td>6</td>
</tr>
<tr>
<td>F22</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>4</td>
</tr>
</tbody>
</table>

Total intrawarren agonistic interactions between adults recorded in 4 hours observation = 81.
M45 was involved in 28 (34.57%) of all agonistic interactions and "won" 25 (89.29%) of these.
WARREN: THISTLE FIELD 2  
MAY 1976  
Total Number of Adults Present = 5

<table>
<thead>
<tr>
<th>Marked or recognisable individuals</th>
<th>opponent</th>
<th>Total</th>
<th>opponent</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>male</td>
<td>female</td>
<td></td>
<td>male</td>
</tr>
<tr>
<td>M40</td>
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<td>0</td>
</tr>
<tr>
<td>(M61)</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>3</td>
</tr>
</tbody>
</table>

Total intrawarren agonistic interactions between adults recorded in 4 hours observation = 14.  
M40 was involved in 7 (50%) of all agonistic interactions and "won" 7 (100%) of these.

WARREN: THISTLE FIELD 3  
MAY 1976  
Total Number of Adults Present = 13

<table>
<thead>
<tr>
<th>Marked recognisable individuals</th>
<th>Opponent</th>
<th>Total</th>
<th>Opponent</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>male</td>
<td>female</td>
<td></td>
<td>male</td>
</tr>
<tr>
<td>M15</td>
<td>5</td>
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<td>15</td>
<td>24</td>
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<tr>
<td>M30</td>
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<tr>
<td>F01</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>2</td>
</tr>
</tbody>
</table>

Total intrawarren agonistic interactions between adults recorded in 4 hours observation = 61.  
M15 was involved in 24 (39.34%) of all agonistic interactions and "won" 24 (100%) of these.
WARREN: CROSS PARK 1
MAY-JUNE 1977
Total Number of Adults Present = 13

<table>
<thead>
<tr>
<th>Marked or recognisable individuals</th>
<th>Opponent</th>
<th>Total Wins</th>
<th>Marked or recognisable individuals</th>
<th>Opponent</th>
<th>Total Losses</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>male</td>
<td>female</td>
<td></td>
<td>male</td>
<td>female</td>
</tr>
<tr>
<td>ragged ear (M129)</td>
<td>8</td>
<td>13</td>
<td>11</td>
<td>32</td>
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<tr>
<td>M94</td>
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<td>3</td>
<td>4</td>
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<tr>
<td>F21</td>
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<td>5</td>
<td>4</td>
<td>11</td>
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<tr>
<td>F57</td>
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<td>0</td>
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<td>1</td>
</tr>
<tr>
<td>F99</td>
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</tr>
<tr>
<td>F77</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>2</td>
</tr>
</tbody>
</table>

Total intrawarren agonistic interactions between adults observed in 4 hours observation = 75.
(M129) was involved in 35 (46.67%) of all agonistic interactions and "won" 32 (91.43%) of these.

WARREN: CROSS PARK 2
MAY-JUNE 1977
Total Number of Adults present = 13

<table>
<thead>
<tr>
<th>Marked or recognisable individuals</th>
<th>Opponent</th>
<th>Total Wins</th>
<th>Marked or recognisable individuals</th>
<th>Opponent</th>
<th>Total Losses</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>male</td>
<td>female</td>
<td></td>
<td>male</td>
<td>female</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
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<td>15</td>
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<td>6</td>
<td>27</td>
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</tr>
<tr>
<td>M123</td>
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<td>2</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>M69</td>
<td>3</td>
<td>2</td>
<td>2</td>
<td>7</td>
<td>3</td>
</tr>
<tr>
<td>F24</td>
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<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>F52</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>2</td>
</tr>
</tbody>
</table>

Total intrawarren agonistic interactions between adults observed in 4 hours observation = 68.
M38 was involved in 27 (39.71%) of all agonistic interactions and "won" 27 (100%) of these.
### WARREN: TENNIS COURT 2

**MAY-JUNE 1977**  
**Total Number of Adults Present = 11**

<table>
<thead>
<tr>
<th>Marked or recognisable individuals</th>
<th>Opponent</th>
<th>Total Wins</th>
<th>Opponent</th>
<th>Total Losses</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>male</td>
<td>female</td>
<td>?</td>
<td>male</td>
</tr>
<tr>
<td>M66</td>
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<td>M120</td>
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<td>1</td>
</tr>
<tr>
<td>F67</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
</tbody>
</table>

Total intrawarren agonistic interactions between adults observed in 4 hours observation = 43.  
(M129) was involved in 16 (37.21%) of all agonistic interactions and "won" 15 (93.75%) of these.

### WARREN: NETTLE HOLLOW 1

**MAY-JUNE 1977**  
**Total Number of Adults present = 12**

<table>
<thead>
<tr>
<th>Marked or recognisable individuals</th>
<th>Opponent</th>
<th>Total Wins</th>
<th>Opponent</th>
<th>Total Losses</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>male</td>
<td>female</td>
<td>?</td>
<td>male</td>
</tr>
<tr>
<td>M121</td>
<td>9</td>
<td>5</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>M114</td>
<td>3</td>
<td>2</td>
<td>1</td>
<td>4</td>
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<tr>
<td>M73</td>
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<td>F35</td>
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<tr>
<td>F93</td>
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<td>F91</td>
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</tr>
<tr>
<td>F95</td>
<td>2</td>
<td>0</td>
<td>1</td>
<td>1</td>
</tr>
</tbody>
</table>

Total intrawarren agonistic interactions between adults observed in 4 hours observation = 53.  
M38 was involved in 21 (39.62%) of all agonistic interactions and "won" 19 (90.48%) of these.
WARREN:-- NETTLE HOLLOW 2
MAY-JUNE 1977
Total Number of Adults Present = 7

<table>
<thead>
<tr>
<th>Marked or recognisable individuals</th>
<th>Opponent</th>
<th>Total</th>
<th>Opponent</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>male</td>
<td>female</td>
<td></td>
<td>male</td>
</tr>
<tr>
<td>m (scar nose)</td>
<td>5</td>
<td>5</td>
<td>2</td>
<td>12</td>
</tr>
<tr>
<td>M96</td>
<td>2</td>
<td>1</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td>f (circle face)</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
</tbody>
</table>

Total intrawarren agonistic interactions between adults observed in 4 hours observation = 23.
"scar-nose" M was involved in 12 (52.17%) of all agonistic interactions and "won" 12 (100%) of these.

WARREN:-- THISTLE FIELD 1
MAY-JUNE 1977
Total Number of Adults present = 13

<table>
<thead>
<tr>
<th>Marked or recognisable individuals</th>
<th>Opponent</th>
<th>Total</th>
<th>Opponent</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>male</td>
<td>female</td>
<td></td>
<td>male</td>
</tr>
<tr>
<td>M145</td>
<td>13</td>
<td>7</td>
<td>8</td>
<td>28</td>
</tr>
<tr>
<td>M113</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>M115</td>
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<td>2</td>
</tr>
<tr>
<td>M98</td>
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<td>4</td>
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<td>F90</td>
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<td>2</td>
</tr>
<tr>
<td>F69</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>4</td>
</tr>
</tbody>
</table>

Total intrawarren agonistic interactions between adults observed in 4 hours observation = 80.
M45 was involved in 29 (36.25%) of all agonistic interactions and "won" 28 (96.55%) of these.
Total Number of Adults Present = 6

<table>
<thead>
<tr>
<th>Marked or recognisable individuals</th>
<th>Opponent</th>
<th>Total</th>
<th>Opponent</th>
<th>Total</th>
</tr>
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Total intrawarren agonistic interactions between adults observed in 4 hours observation = 20.

M61 was involved in 16 (80%) of all agonistic interactions and "won" 14 (87.5%) of these.
Appendix 3

Comparison of overall adult density and the mean size of home ranges of subordinate adult males.

<table>
<thead>
<tr>
<th>Study area</th>
<th>Year</th>
<th>Adult/density (N/acre)</th>
<th>Rank</th>
<th>Mean range sub, males (sq.m.)</th>
<th>Rank d</th>
<th>d²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cross Park</td>
<td>1975</td>
<td>10.43</td>
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<td>1400</td>
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</tr>
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<td>1180</td>
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<td>3.5</td>
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<td>864</td>
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<td>1</td>
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\[\rho_{5} = 0.76, \ N = 11, \ p < 0.01\]
Appendix 4

4.1 Reproductive success and warren size (measured as N adult females, N adult males, N total adults and N groups)

(a) adult females

<table>
<thead>
<tr>
<th>Warren</th>
<th>Year</th>
<th>Adult Females</th>
<th>Rank</th>
<th>Mean R.S.</th>
<th>rank</th>
<th>$d^2$</th>
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<tbody>
<tr>
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<td>9.5</td>
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<td>12.25</td>
</tr>
<tr>
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<td>2</td>
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Spearman's correlation coefficient
\[ \rho_s = 0.79, \quad N = 13, \quad P < 0.01 \]
4.1 (contd).
(b) adult males

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<th>Warren</th>
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<th>Rank</th>
<th>Mean R.S.</th>
<th>Rank</th>
<th>( d^2 )</th>
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</thead>
<tbody>
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\( \rho_2 = 0.68, N = 13, p < 0.05 \)
4.1 (contd)
(c) total adults

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<th>Rank</th>
<th>Mean</th>
<th>R.S.</th>
<th>rank</th>
<th>d^2</th>
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<td>5.29</td>
<td>5</td>
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\[ \rho_0 = 0.75, \ N = 13, \ P < 0.01 \]
(d) groups

<table>
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<th>Year</th>
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<th>Rank</th>
<th>Mean R.S.</th>
<th>Rank</th>
<th>$d^2$</th>
</tr>
</thead>
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<td>5.14</td>
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<td>6.25</td>
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<td>20.25</td>
</tr>
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</table>

$\rho = 0.71, N = 13, p < 0.01$
4.2 Group Composition and Reproductive Success

The 2 male/2 female composition is compared with the combined R.S. of all other compositions in a Kruskal-Wallace one way analysis of variance by ranks.

(1) 2 male/female groups

<table>
<thead>
<tr>
<th>Group Identity</th>
<th>R.S. (mean no. of offspring/female)</th>
<th>Rank</th>
</tr>
</thead>
<tbody>
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<td>33</td>
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<td>1976 Tennis Court 2B</td>
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<td>12</td>
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<td>1977 Tennis Court 2C</td>
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<td>18</td>
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<tr>
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</tr>
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</tr>
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<td>1977 Nettle Hollow 1B</td>
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N = 14  \( R = 308.5 \)

(2) Remaining groups.

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<th>Composition</th>
<th>R.S.</th>
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<td>3m 3f</td>
<td>3.67</td>
<td>8</td>
</tr>
<tr>
<td>1976 Nettle Hollow 1B</td>
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<td>24</td>
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<tr>
<td>1976 Nettle Hollow 1D</td>
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<td>12</td>
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<td>18</td>
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<td>1m 1f</td>
<td>6</td>
<td>30</td>
</tr>
<tr>
<td>1976 Cross Park 2D</td>
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<td>2</td>
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<td>2m 3f</td>
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<tr>
<td>1977 Cross Park 2D</td>
<td>1m 1f</td>
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N = 23  \( R = 394.5 \)

Overall N = 37  \( H = 2.94 \) (with correction for ties; Siegel, 1956)
\( d.f. = 1 \)  \( p < 0.1 \)
4.3 Effect of residence of dominant male in group on mean R.S.

<table>
<thead>
<tr>
<th>Warren</th>
<th>Year</th>
<th>Mean R.S. with dominant male</th>
<th>Mean R.S. without dominant male</th>
<th>A-B Rank</th>
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<tbody>
<tr>
<td>Tennis Court 2</td>
<td>1976</td>
<td>6.5</td>
<td>4.0</td>
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<td>4.5</td>
<td>4.75</td>
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<tr>
<td>Nettle Hollow 1</td>
<td>1976</td>
<td>3.67</td>
<td>3.29</td>
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<td>1977</td>
<td>4.5</td>
<td>2.6</td>
<td>1.9</td>
</tr>
<tr>
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<td>1977</td>
<td>7.0</td>
<td>4.5</td>
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</tr>
<tr>
<td>Thistle Field 1</td>
<td>1976</td>
<td>5.0</td>
<td>5.0</td>
<td>0.0</td>
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<tr>
<td>Thistle Field 1</td>
<td>1977</td>
<td>4.0</td>
<td>3.5</td>
<td>0.5</td>
</tr>
<tr>
<td>Cross Park 1</td>
<td>1976</td>
<td>6.5</td>
<td>7.0</td>
<td>-0.5</td>
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<td>1977</td>
<td>5.33</td>
<td>5.25</td>
<td>0.8</td>
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Wilcoxon matched pairs signed ranks test.
T = 6.5, N = 11, p < 0.01.
4.4 Ranked mean R.S. for groups with dominant male resident and groups without dominant male resident. Comparison with ranked scores for 4 methods of measuring warren size (appendix 4.1)

<table>
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Spearman's correlation coefficient $N = 11$

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<td></td>
<td>rho</td>
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<tr>
<td>adult females</td>
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<td>adult males</td>
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<td>total adults</td>
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Appendix 4.5

SEQUENCE OF LITTERS

WARREN: CROSS PARK 1

YEAR: 1976

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SEQUENCE OF LITTERS

WARREN: CROSS PARK 1

YEAR: 1977

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SEQUENCE OF LITTERS

WARREN: CROSS PARK 2

YEAR: 1976

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WARREN:- CROSS PARK 2

YEAR:- 1977

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## SEQUENCE OF LITTERS

### WARREN: TENNIS COURT 1

**YEAR: 1976**

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**YEAR: 1977**

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WARREN:-- TENNIS COURT 2

YEAR:-- 1976

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YEAR:-- 1977

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SEQUENCE OF LITTERS

WARREN:— THISTLE FIELD 1

YEAR:— 1976

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WARREN: THISTLE FIELD 1

YEAR: 1977

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**WARREN:-- NETTLE HOLLOW 1**  
**YEAR:-- 1976**

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WARREN:- NETTLE HOLLOW 1

YEAR:- 1977

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WARREN: NETTLE HOLLOW 2

YEAR: 1977

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Appendix 5.1

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Single and multiple latrine visits. Distribution of focal animal samples containing one or more latrine visits. The range of visits in samples where a visit occurred is 1-3.
Appendix 5.2

Latrine visits recorded during focal animal samples and visits recorded during ad lib samples (used only for analysis of visit duration and behaviour on latrines).

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Appendix 5.3

Latrine visit durations (seconds) - raw data

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N=29, x=43s  range=8-114s  N=25, x=208s  range=15-380s  N=6, x=94s  range=46-185s  N=10, x=162s  range=114-221s  N=5, x=133s  range=63-172s
Appendix 5.4

Pellets deposited at cleared latrines - 9 days at 10 latrines

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Pellets deposited at latrines replaced with turf

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Pellets deposited at latrines replaced with turf & random pellets

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