INVESTIGATIONS INTO THE AGONISTIC BEHAVIOUR, TERRITORIALITY AND OLFACTORY COMMUNICATION OF THE MONGOLIAN GERBIL (*Meriones unguiculatus*)

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ABSTRACT

The problems of defining territoriality and the functions of scent-marking were reviewed in mammals with particular reference to the Mongolian gerbil and the suggested territorial function of scent-marking. It was concluded, on the evidence presented to date, that it was unlikely that this gerbil displayed territorial behaviour in the strict sense of defending an exclusive area. It was also clear that there was insufficient evidence to associate scent-marking behaviour, in mammals in general and specifically in the gerbil, with the defence of a territory and that this behaviour could serve other functions.

Experiments were then reported which investigated the links between the agonistic behaviour, territoriality and scent-marking in the gerbil. An ethogram of its agonistic behaviour, derived from laboratory experiments under a number of different conditions1), was presented and the possible functions of the behavioural acts and postures observed were discussed. No evidence was found that pairs of gerbils would defend an exclusive territory under laboratory conditions and, although there was evidence of relative exclusivity of use of a home area, it was suggested that this was maintained by mutual avoidance. The role of the scent-marking behaviour was discussed and experimental evidence2) presented which suggested that it could assist in the spacing of individuals in a natural population as a consequence of learning by association with the aversive stimuli of aggressive encounters with conspecifics.

Conc

1) ; 2) FOOTNOTES - see over

Footnotes

[1] The ethogram of the Gerbil was constructed from the results of a series of 5-minute male-male encounters in a small arena. Interactions between two mated pairs were also studied in a series of 11 experiments conducted in a large (12 sq. m) arena under experimental conditions designed to induce "territorial" behaviour.

[2] The use of male scents and sebum as possible cues for behavioural modification was investigated using a shock-escape training procedure.

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CONTENTS

CHAPTER I

INTRODUCTION

1.0.0. INTRODUCTION

The Mongolian gerbil, *Meriones unguiculatus*, is a desert rodent which, since its introduction to the U.S.A. in 1954, has rapidly achieved prominence as an experimental animal in various fields of research.

Much of the behavioural research, carried out using the gerbil, has been centred around an investigation of its scent-marking behaviour, which is an action whereby the secretion from a gland on the ventral surface of this animal is deposted on objects in its environment. This secretion contains a scent which may have certain communicative functions. The scent-marking of the Mongolian gerbil has been frequently referred to as a "territorial behaviour", however there has been no satisfactory evidence to support this suggestion; in fact there is a shortage of evidence to support the claim that the scent-marking behaviour of any mammal has a "territorial" function (Johnson, 1973).

There is perhaps a major difficulty in attempting to investigate the function of scent-marking in the Mongolian gerbil, that is the dearth of adequate information concerning its ecology and social behaviour in its natural habitat, which is so remote that only a few useful reports exist. However, the aim of this study has been to attempt to investigate experimentally the possible function of the scent-marking behaviour of this species of gerbil, using both a semi-natural environment and more conventional laboratory experiments, particularly in relation to its spatial organization and possible territorial behaviour. Thus the review that follows deals briefly with the Mongolian gerbil as an experimental animal. This is followed by a review of the key issues related to spatial organization and territoriality in mammals with particular reference to the gerbil. This provides a framework for a short review of scent-marking behaviour in the gerbil and other mammalian species.

1.1.0. THE MONGOLIAN GERBIL

1.1.1. DESCRIPTION AND CLASSIFICATION

The Mongolian gerbil, *Meriones unguiculatus*, is a small rodent, approximately nine cm. in length. Its natural colouring is agouti, with black-tipped fur covering a slate grey undercoat. The ventral surface of the body and the front paws are an off-white colour. They have large, slightly protruding eyes and the head is short and broad. The tail is between nine and twelve cm. in length and is well covered with fur which is slightly tufted along the ridge with a more pronounced black tuft at the tip. The hind paws have four digits only but the front paws have five, with sharp black claws, which have resulted in this species often being referred to as the "clawed-jird" (Jansen, 1968). When mature, at about ten to twelve weeks, the average body weight of the male is between 70 - 100 gm., the female is lighter at between 60 - 80 gm. (Schwentker, 1964; Nakai et al, 1960).

Gerbils are mammals of the Order *Rodentia*, Sub-order *Myomorpha* and of the Super-family *Muroidea*. A difference of opinion appears to exist as to which Family they should belong. Ellerman (1940) places them in the *Muridae* as does Lay (in Schwentker, 1968), however Simpson (1945) places them in the Family *Cricetidae* but says that they are often given a family rank between the two. They belong to the Sub-family *Gerbillinae* which contains a number of different genera. Lay (op. cit) recognises fourteen different genera

FIGURE I

Classification of the Mongolian gerbil (*Meriones unguiculatus*), adapted from Schwentker (1968) and Simpson (1945). The number of extant species in the genera are shown in brackets. The lines dividing the column of generic names indicate the related groups that exist in the Sub-family.

ORDER Rodentia

SUB-ORDER Myomorpha

SUPER-FAMILY Muroidea

FAMILY Muridae

SUB-FAMILY Gerbillinae

GENERA
Rhombomys (1)
Psammomys (1)
Meriones (14) spp. unguiculatus
Brachiones (1)

Desmodilliscus (1)

Gerbillus (ca 40)

Microdillus (1)

Sekeetamys (1)

Pachyuromys (1)
Desmodillus (1)
Ammodillus (1)

Tatera (15-25)
Taterillus (8-12)
Gerbillurus (3-5)

in this Sub-family. The Mongolian gerbil belongs to the genus Meriones, which was first described by Illiger (1811). The first description and identification of the Mongolian gerbil was credited to Milne-Edwards in 1867. This was later confirmed by Chaworth-Musters and Ellerman (1947), when the genus was revised. This genus is further subdivided into fourteen species, the Mongolian gerbil having the specific name, unguiculatus (see Fig. I).

1.1.2. THE GERBIL IN RESEARCH

The original laboratory colony of Mongolian gerbils was set up in the U.S.A. by Dr. Victor Schwentker in 1954 using animals from a Japanese colony descended from a few wild animals captured in Eastern Mongolia in 1935 (Schwentker,1963). It appears that most of the U.S. stocks have originated from this colony, which is at Tumblebrook Farm, Brant Lake, New York, and it was from this colony that the Laboratory Animals Centre in Britain obtained animals to set up their stock in 1966. Marston and Chang (1965) used animals from the "Lederle Laboratories" in Chicago while studying them in Britain but these animals probably originated from the Tumblebrook Farm colony. It is therefore likely that stocks of these animals set up in Britain are direct descendents of the Schwentker colony in Tumblebrook Farm.

Detailed information on the care and management of *Meriones unguiculatus* has been made available by several authors (Marston and Chang, 1965; Glick, 1970; Schwentker, 1963,1964,1968; Jansen, 1968; Nauman, 1963) and some data is also available for other members of the Gerbillinae (Petter, 1967; Woodcock, 1955). Mortality, organ weights and body weight ratios of *Meriones unguiculatus* have been studied (Schwentker,1968; Norris and Adams,1972d; Wilbur and Gilchrist,1965; Cullen, Parc and Mooney,1971). Its metabolism has also been investigated (Robinson,1959), and much of the medical work using this animal has been reviewed in Rich (1968). Schwentker (1968) also provides a bibliography of the research using this animal.

1.2.0. THE BEHAVIOUR OF THE MONGOLIAN GERBIL

In the past decade the use of the Mongolian gerbil in behavioural research has increased, much of which has been carried out by Delbert Thiessen working at the University of Texas. Prior to 1967 the research on gerbils was mainly physiological in character (Thiessen, 1968), although a number of authors had previously used it in behavioural research (Walters et al, 1963; Webster and Caccavale, 1966; Kuehn and Zucker, 1966). Thiessen and his co-workers chose to study three aspects of the gerbil's behaviour, spontaneous epileptiform seizures (Thiessen et al, 1968 a; Goldblatt, 1968), its apparent lack of depth perception (Thiessen et al, 1968 b; Collins et al, 1969; Thiessen et al, 1969), and finally the scent-marking behaviour with the ventral gland (Thiessen, Friend and Lindzey, 1968; Lindzey et al, 1968). However, in their studies of the scent-marking behaviour the authors suggested that this behaviour was "territorial marking" whereby a scent was laid down which, "acts as chemical signal to avert territorial onslaughts". (Thiessen, 1968, p. 75). This suggestion went unchallenged until Johnson (1973), in his review of mammalian scent-marking, concluded that

> "the term "territorial marking" is often not appropriate because in many instances marking behaviour is clearly unrelated to territory and in no case has its communication value with respect to territorial organization been determined" (p. 531).

It was around this time that my own study was started when it was clear that few attempts had been made to determine if, in fact, the Mongolian gerbil was "territorial" and if a relationship existed between its "territorial" behaviour and scent-marking.

This was perhaps not surprising since there was no appropriate information from field work carried out on this species mainly because of the remoteness and inaccessibility of its habitat. However there were data available from studies of other species of *Meriones*, notably *Meriones hurriannae*, and studies of other genera (e.g. *Tatera* and *Psammomys*). These will be discussed in the appropriate context in the general review that follows but it appears that this information was largely ignored by previous authors. Thiessen (1973) reported attempts to establish populations of gerbils under semi-natural conditions but gave only brief details about possible "territorial" behaviour. Thus to date there have been no experimental studies aimed at determining if this behaviour actually occurs in gerbil populations and its relationship to scent-marking. Schenkel (1966) suggested that the important tasks of ethological research would be to analyse "the order of aggression proper to the species, including the problem of territoriality", and he further suggested that such research should analyse

> "motivation and function of the manifestations of presence - including (scent) marking".

In the absence of complete information about the aggressive behaviour and the "territoriality" of the Mongolian gerbil it was therefore the aim of this study to examine them and also scent-marking.

Thus before reviewing the literature on scent-marking and territoriality in the Mongolian gerbil it is necessary first to review the concept of "territory" in mammals. This will be followed by a review of the evidence for territorial behaviour in the gerbil. A review of mammalian scent-marking behaviour including its relationship to territorial behaviour will then be presented. Finally the scent-marking behaviour of the Mongolian gerbil will be discussed, with particular emphasis on the evidence for its territorial function.

1.3.0. TERRITORY

1.3.1. HISTORICAL PERSPECTIVE

The inclusion of the concept of territory as a recognised subject for organized research is generally attributed to H. Eliot Howard as a result of his book "Territory in Bird Life" (1920). According to Wilson (1975), since that time:

> "the number of studies devoted to territoriality has risen exponentially, until today it ranks with aggression and dominance as one of the several most intensely studied topics of sociobiology" (p. 261).

Yet Howard was by no means the first to record his observations of territorial behaviour.

Ardrey (1967) quotes from the works of Aristotle (384 - 322 BC),

> "A pair of eagles demands an extensive space for its maintenance, and consequently cannot allow other eagles to quarter themselves in close neighbourhood". (p. 53);

and also from the works of Pliny,

> "One pair of eagles needs a very considerable space of ground to forage over, in order to find enough food; for which reason they mark out by boundaries their respective allotments, and seek their prey in succession to one another". (p. 53).

In the seventeenth century references were made to the behaviour of the male nightingale when he occupied or seized a place referred to as his "freehold". Wilson (1975) attributed this expression to G.P. Olina (1622) whereas Carpenter (1958) attributed it to Willugby (1678). In the eighteenth century Goldsmith (1774) seems to have been the first to use the term territory:

> "the fact is, all these small birds mark out a territory to themselves, which they will permit none of their own species to remain in; they guard their dominions with the most watchful resentment; and we seldom find two male tenants in the same hedge together" (quoted in Carpenter, 1958, p. 225).

It was about this time that other authors were expanding the idea of territory beyond that of simple possession and defence of a specific area. Gilbert White (quoted in Ardrey, 1967) related territory to the reproductive behaviour of birds while Count de Buffon (in Ardrey,op. cit) suggested that,

> "... the conduct is not occasioned by rivalship, as some have supposed; it is suggested by the solicitude for the maintenance of their young, and regulated by the extent of ground necessary to afford sufficient food". (p. 54)

In 1820 Naumann also related territory to breeding behaviour in birds.

In 1868 perhaps the first theoretical approach to territory was produced by Altum (in Mayr, 1935) in his systematic description of bird territorial behaviour. He defined territory as an area which was occupied by one male of the species and defended against intrusion by other males of the same species. He also paved the way for the idea of territorial display, particular territorial singing, in birds and included the idea that birds settled at fixed distances from each other to ensure food for themselves and their young. His ideas, however, were largely ignored at the time and in 1903 Moffat produced an independent theoretical formulation of territory based on his observations of birds. Here he suggested that fighting served to "parcel-out" territories. These territories were related to the suitability of nesting sites and the availability of food and thus there were a limited number of territories available. As a consequence the number of breeding pairs in an area was limited and fairly constant and the less powerful individuals who were unable to get a territory were not able to reproduce. The reproductive population was therefore limited to the land that would support it, an idea that Wynne-Edwards (1962) was to pursue later.

In 1906, Brewster observed that territorial possession by one bird was sufficient to cause an intruding bird of the same species to retire when threatened by the resident and thus introduced the idea of dominance-reversal which will be discussed later (see Section 1.3.3.).

In many ways Howard (1920) did not introduce any new conclusions in his study of territory and birds but his contribution was to subject the behaviour of many species of birds to a systematic inquiry thereby highlighting the importance of territory in the life cycle of birds. He described territory in behavioural terms. A male bird sought to obtain a specific area, usually close to its birthplace, at the start of the breeding season and then excluded from it all rival mates. Here it would attract a mate and subsequently the pair would breed and leave. The territory thus served the function of ensuring a food supply; it ensured mating by providing a focus for activity prior to nest building; it served to limit the number of breeding pairs in an area and through fighting made sure that the strongest were the only ones to reproduce. Since that time the concepts of territory have been largely extension and refinements of these original ideas about territory in birds.

Territorial organization amongst other animals, however, was rarely mentioned until Moffat (1903) suggested that his theories about birds could also apply to higher vertebrate animals. Seton (1909) provided probably one of the first accounts of territorial behaviour in mammals in his observations of the Red Squirrel (*Sciurus hudsonicus*), although for the most part his references to "the property instinct" largely related to the possession of food or a mate. Klugh (1927), however, recognised that the fighting between the members of the same species could be over possession of land rather than food or mates. Heape (1931) in his study "Emigration, Migration and Nomadism" clearly considered that defence of an area by an individual or a group of individuals occurred in a majority of species and after reviewing a selection of the literature concerning territory in mammals, Burt (1943) concluded that,

> "... nearly all who have critically studied the behaviour of wild mammals have found this behaviouristic trait (territoriality) inherent in the species with which they worked". (p. 350)

1.3.2. THE DEFINITION OF TERRITORY

Since Howard (1920) gave "some explanation of what the word territory is intended to represent", thereby avoiding a strict definition of the word, a good deal of discussion centring around attempts to develop a single, clear and generally valid definition for territory has taken place.

Howard (op. cit) suggested that the use of the word territory should be based on two dispositions

1. The disposition to remain in a particular place in a particular environment
2. The disposition concerned with the defence of the territory.

His failure to define the concept in general terms, however, meant that it was clearly open to ambiguous usage. Noble (1939) attempted to clarify the term by concentrating on Howard's second "disposition" and thus arrived at probably the most widely accepted definition of territory as "any defended area". His definition was clearly in line with previous suggestions by Tinbergen (1936) where he proposed that the term territory be restricted to the area defended shortly before and during the formation of a sexual bond. Although largely acceptable to other authors Emlen (1957) was critical of it in that he could find no evidence to justify the claim that the area was itself the object of territorial defence. He felt that such a definition ignored other aspects of territoriality i.e. the maintenance of an exclusive area without any obvious defence by the resident. Pitelka (1959) stressed that it was merely this exclusivity of an area that was the important characteristic of territory and not the mechanism by which it was maintained. Brown and Orians (1970) were, however, reasonably satisfied with Noble's definition as being both "adequate and useful" in that it was flexible enough to include the multiple forms that defence could take (e.g. vocalizations, displays, scent-markings) so long as they served to keep rivals out. Thus they identified the essential characteristics of territory as:

> "1. a fixed area which may change slightly over a period of time, 2. acts of territorial defence by the possessor which evoke an avoidance in rivals so that 3. the area becomes an exclusive area with respect to rivals. All of these conditions must be satisfied for an area to be recognised as a territory". (p. 242)

They therefore made quite explicit the notion of exclusivity implied in Noble's original definition.

Vine (1974) pointed out that such general interpretations of the concept meant that if behaviour like advertisement alone lead to exclusion this may be counted as "defence" and thus territoriality may be invoked in almost any instance of relatively exclusive spatial division of habitat. He concluded:

> "Such a re-definition is only legitimate providing that none of the original connotations of the term are surreptitiously retained" (p. 16) (i.e. defence)

However in practice he felt that this requirement would be difficult to adhere to.

Attempts to provide an adequate definition of territory for mammalian species are even more fraught with pitfalls.

Clearly there are important differences between the territories of birds and mammals. While bird territories are commonly relatively specific to the breeding season and the fighting involved in their establishment is readily apparent, the most outstanding feature of mammalian territories is often that individuals or groups of individuals exhibit a relative limitation of movement within their habitat. Nevertheless a number of mammalian species still exhibit remarkably similar territorial behaviour patterns to those more generally associated with birds. Burt (1943) reviewed some of the literature up to the early 40's and gave examples of mammalian species that exhibited territorial behaviour in terms of Noble's "defended area" criterion, where the defence of an area was clearly by aggressive behaviour. More recent studies have revealed similar findings for a number of rodent species. Getz (1961) reported that both the male and female voles, _Microtus pennsylvanicus_ actively defended a relatively fixed area. Eisenberg (1962) in his study of two species of _Peromyscus_, _P_. _maniculatus_ and _P_. _Califomicus_, observed that in the former species males actively defended an area and fought whenever they met, while in the latter species females actively defended an area around their nests. Brown (1966) reported that _Apodemus_ set up social hierarchies where the powerful, dominant male patrolled and defended an area. The females were also observed to defend their breeding ranges and to challenge the movement of males within them. There have been several accounts of laboratory studies using the house mouse, Mus musculus, where areas of exclusive use have been set up and actively defended by the residents (Anderson and Hill, 1965; Mackintosh, 1970; Poole and Morgan, 1976). Armitage (1974) observed that Yellow-bellied marmots defended vigorously a fixed area. Prairie Dogs also appeared to defend a group range by aggression (King, 1955) as did Chipmunks (Yerger, 1953), wild rabbits (Southern, 1948; Lockley, 1961) and captive European rabbits (Mykytowycz and Hesterman, 1975). In certain rodent species the aggressive defence of an area seemed to be correlated with the breeding season, in the squirrels, Spermophilus richardsonii (Yeaton, 1972) and S. undulatus (Watton and Keenleyside, 1974) and in the short-tailed shrew, Blarina brevicauda (Platt, 1976).

It is therefore possible to adopt the definition of territory suggested by Noble (1939) for some mammals and in some cases the behaviour can be as clearly defined as it is in some birds. But such a definition still leaves out a large number of mammalian species whose behaviour would include them as a territorial species in other criteria of territory. Kaufman (1971) suggested that the "defended area" definition of territory was too restrictive in that it ignored:

> "numerous cases of spatially and socially orientated behaviour which clearly belong in a discussion of territoriality". (p. 36)

Certainly some mammalian species have been excluded as territorial species on a strict application of the defended area criterion. Schaller (1965) reported that because gorillas did not appear to defend an exclusive area they were not territorial, Ryszkowski (1966) concluded that the Coypu, *Myocaster coypus* was not territorial on the same criteria and Hornocker (1969) made similar observations in Mountain lions. However, all these species show restricted movements within definite boundaries which is very similar to the effect that is achieved in the species that actively defend an area and thus, in functional terms, such a species is "territorial".

This perhaps raises the question of the extent to which the term "defence" can be applied to behaviours that are not obviously aggressive. Washburn (1966) suggested that what an observer sees in a stable population is the result of avoidance and not the events causing avoidance, thus territorial aggression will be rarely seen in a stable population and will only be apparent when the territorial boundaries are being set up, as is seen in the breeding season in birds. Anderson and Hill (1965) reported that aggression was only seen during the setting up of territories, in their study on laboratory mice, and that once territories had been established no aggression was seen. Such observations imply that other factors may subsequently be maintaining territorial boundaries. Hinde (1956) suggested that learning played an important role and that animals actually learned where the territorial boundaries were. Clearly, however, the learning process could result in the association of other behaviour patterns with the aversive stimuli of overt aggression and thus territorial boundaries could be maintained without any evidence of aggression. Such a function has been proposed for behaviours like scent-marking in mammals where it could act like a substitute threat and thus have a defensive function. Wilson (1975) acknowledged this in his definition of territory:

> "... territory should be defined as an area occupied more or less exclusively by animals or groups of animals by means of repulsion through overt aggression or advertisement. We know that the defence varies gradually among species from immediate aggressive exclusion of intruders to the subtler use of chemical signposts unaccompanied by threats or attacks". (p. 261)

However such a broad definition would seem to be open to the danger pointed out by Vine (1974, see before) where any animal possessing a relatively exclusive area could be said to be territorial and thus any behaviour that an animal did in these situations could be interpreted as "defensive" or "territorial". This could not only lead to observational bias but could clearly impede attempts to study these behaviours in their own right. Moyer (1972) felt that these attempts to encompass divergent behaviours, each of which may have different physiological bases, under one single description implying defence of a territory cast doubt on the value of the concept in helping to understand animal behaviour. In a later section of this chapter these difficulties are highlighted in relation to scent-marking in mammals.

The difficulties inherent in the use of the "defended area" definition of territory with respect to mammalian social and spatial organizations have been tackled by others by simply adopting a very rigid interpretation of the "defended area" criterion. Burt (1943) used the term territory only for that part of an animal's "Home Range" which was actively defended by overt aggressive behaviour. The animal's "Home Range" was that area over which the animal normally travelled in search of food and thus he was able to retain the strict definition of territory but account for the anomalies. Jewell (1966), however, found that the concept of home range needed revising since even that did not adequately cover the variety of behaviour seen in mammalian species. Kaufmann (1962) was forced into using another term altogether to describe the "functional territory" of the coati, Nasua narica. He observed that although a band of these animals had a home range they also maintained an exclusive area in which the animals spent a majority of their time but which they did not actively defend, in fact other bands could penetrate this area but rarely did. He therefore proposed that the term "core-area" should be used to describe this situation. In 1974, Vine proposed that the term territory be used only when "a fixed and clearly bounded area from which an animal or group more or less completely excludes other specified classes of animals". (p. 20) But even then he felt that such a definition did not adequately make the distinction between the "defence" and the "site-attachment" aspects of territorial behaviour. In the previous year Ewer (1973) had emphasised both "defence" and "site-attachments" aspects, in that the term territory could be used of an area which was actively defended but it could also cover clear cut cases of animals holding completely exclusive areas.

Other authors have emphasised that even these two aspects of territory do not adequately convey the full nature of the concept. Allee et al (1949) suggested that territory had an importance to the resident which could not be accounted for by a definition which was based solely on defence. Defence of an area needed the presence of at least another animal for it to be seen and Crook (1968) argued that without it solitary animals could not be said to be territorial. Marler and Hamilton (1966) regarded territory as an external reference for dominance whereas Davis (1958) regarded territory as social rank without subordinates. Such views of the concept clearly emphasise the need to examine it in terms of the social organization of mammals in general and this will be considered in the next section. However it is also apparent that diversity of animal behaviour and the equal diversity of opinion as regards the possession of an area of relatively exclusive use make it virtually impossible to define territory adequately. Kaufmann (1971) concluded:

> "No simplified definition or explanation of territory yet advanced can cover all of the related kinds of behaviour known, and perhaps it is naive to look for one". (p. 39)

But Carpenter (1958) had already decided that this was the case when he concluded:

> "It would seem advantageous to view territorality primarily as a behaviour system which is expressed in

> a spatial-temporal frame of reference. The organismic mechanisms, the drives and incentives or motives and the sensory-response and learning processes are all different aspects of the behavioural system of territoriality. These are expressed with reference to loci in space, and to the topography of habit areas, as well as to other organisms living in the area. Behavioural systems change over periods of time. Those which constitute territoriality in animals are so complex, and involve so many adaptive and even non-adjustive mechanisms, that they defy adequate description by condensed definitions. Fully systematic and analytic descriptions are required". (Carpenter, 1958, p. 228)

His suggestion that the concept of territory should be described in each case rather than defined has implications for the way in which studies in this area should be carried out. The implications for the studies so far carried out on the so called "territorial scent-marking" of the gerbil will therefore be discussed in a later section. However it is first necessary to look more closely at the concept of territory in relation to the social organizations of mammals in general since if no strict definition is possible the concept must be discussed within an established frame of reference where the types and functions of each behaviour pattern are described as clearly as possible.

1.3.3. TERRITORY AND SOCIAL ORGANIZATION

The difficulties of providing an adequate, all-embracing definition of territory, discussed in the previous section, lead to the conclusion that territory might be best considered in terms of observable behaviour and thus as a concept it is best described rather than defined. However, in the wide variety of types of social organization adopted by different animal species, territory is only one way in which animal populations can be organized. There are nevertheless strong links between the different types of social organization and territory and in this section these will be reviewed with respect to mammalian species so that the available evidence concerning the social organizations of the gerbil can then be discussed later in its proper context. In this respect the discussion will be limited to those species whose social organization is founded on a basis of aggressive interactions since it will become clear later that aggressive behaviour is an integral part of gerbil behaviour.

Lorenz (1966) pointed out that aggression or fighting was an "ever-present process" and asked the question what was its significance. He concluded that it was "an essential part of the life-preserving organization of instincts" (p. 39) and, although his general conclusions were later to be criticised (Ashley-Montague, 1968) it is generally accepted that aggression, in its many forms, plays an important role in the survival of the majority of individuals (Wilson, 1975). Aggression can have a number of effects and may take a number of different forms depending on its underlying physiological bases e.g. sexual, maternal etc. (Moyer, 1972). Wilson (1975) listed eight forms of aggression in animal species: 1) Territorial; 2) Dominance; 3) Sexual; 4) Parental disciplinary; 5) Weaning; 6) Moralistic; 7) Predatory; 8) Anti-predatory, pointing out that aggression is often a mixture of very different behaviour patterns serving very different functions. It is clear however that one effect of aggression in a group of animals is to establish a social organization. Wolfe and Summerlin (1968) reported that aggression in the Cotton rat was greatest in a population which had not established a social organization but that as a result of the aggression a population of caged animals soon became organized and the level of aggression fell. Poole and Morgan (1973) observed that aggression in colonies of mice declined after the colonies had been set up in the laboratory and the animals had established a social organization based on a dominance hierarchy. Similarly the establishment of territories in the populations of mice studied by Anderson and Hill (1965) resulted in a drop in aggressive behaviour in these populations. Thus the initial aggression among groups of strange animals can result in the establishment of a social organization which in turn can result in a drop in aggression (Hodgdon and Larsen, 1973).

The type of social organization that develops as a result of aggressive behaviour in animal populations appears to depend on a number of factors which link social organizations based on a dominance system with those based on territory. Dominance as a concept has been subject to as much discussion over the years as has territory, however in this context it is best considered as defining a relationship between two specified individuals where one animal is dominant to the other when its behaviour is not limited by the other (Deag, 1977). Guhl (1956) exemplified the concept in his reports on the social organization of chickens where a rigid hierarchy existed based on a linear "peck order"; A was dominant to B who in turn was dominant to C who was dominant to D; A was always dominant to B, C and D and D always subordinate (i.e. its behaviour was limited by the other) to A, B and C. However this strict form of a dominance hierarchy has been shown to have little generality across species and has been subject to criticism and modification (Gartlan, 1968; Van Kreveld, 1970; Rowell, 1974). Rigid hierarchies are often limited to species maintained in crowded conditions (Kinsey, 1976) and not all measures of dominance in terms of the above definition e.g. priority of access to food, to mates, to other resources, aggressive superiority and social functions, always go together. Thus the term is more precisely used when both the individuals and the resources or function to which their dominance relates, are specified (Vine, 1974). Thus it is clear that if an animal has priority of access to an area and limits access to that area by other conspecifies not only is the animal behaving in a way that is characteristic of a dominant but the effect is identical to that observed in territorial species. Leyhausen (1971) pointed out that cats operate two systems of social organization depending on the location of an interaction between two individuals. An individual has an area in which he will always be dominant to an intruding animal yet if the same animals meet on neutral ground the status of the animals will depend on their relative strengths and therefore their position in the social rank system of that population. Thus dominance can be related to localities and Leyhausen referred to it as "relative social hierarchy" since the rank of the individual depended on the location. Davis (1959) identified this "territorial rank" in starlings and it has been reported for a number of other birds (Brown and Orians, 1970). In mammalian species, too, the existence of this relationship has also been observed. Farentinos (1970) reported that in the Tassel-eared squirrel, Sciurus aberti ferreus, males that held a dominant position in a group did so only within their respective "home areas". Dunford (1970) also suggested that the mutual exclusiveness of "core areas" and the regular spacing of burrow entrances in a group of Chipmunks, Tamias striatus, was in part due to the dominance of the resident over any intruders and that this dominance regularly coincided with the animal's "core area". Tinbergen (1957) in fact emphasized aspects of territory which made it little more than an area in which the resident had absolute dominance over intruders. Such an emphasis clearly highlights the relationship between dominance and territory and a number of authors, notably Davis (1958) and Fisler (1969) have suggested that dominance systems, in the form of social ranks, and territory are in effect the opposite ends of a continuum of social behaviour related to the density of the population. Crowcroft (1955) was able to illustrate this in house mice and it has more recently been demonstrated in laboratory populations of the Allegheny wood rat, *Neotoma floridana magister* (Kinsey, 1976). It has been observed in such cases that at low densities those species will form territories but when forced to live together they will become organized into dominance orders; the most extreme example being when one animal becomes a despot. Wilson (1975) relates this sort of continuum to the "Sociality" or what Davis (op.cit) referred to as the species-specific "individual-distance tolerance limits", where the more social the species the lower the limits and the more likely they are to form groups and group territories or intergroup dominance orders. Wilson (op.cit) also suggested that such a pattern related to population density occurs very generally among vertebrate animals. It is therefore important to consider the density of laboratory populations of a species and its density in the wild when making inferences about the social organization in nature and about the functions of various behaviour patterns from the evidence of laboratory studies. This will be discussed later with reference to the Mongolian gerbil.

In considering this relationship between territory and dominance, however, it is obvious that territory is also closely related to the phenomenon of "individual distance", that is the distance that one member of a species maintains between itself and other members of the same species. This is seen most clearly in the spacing of starlings when resting on a telegraph wire but is a characteristic of nearly all animals. Leyhausen (1971) linked this phenomenon with dominance,

> "... the size of the area around an animal which it can keep free of others and how far it dares to penetrate into the 'free sphere' of others, is among other things, a very precise indication of the social status of an individual within a group". (p. 23)

and subsequently to territory where the space around the animal becomes related to a particular area to which an animal is attracted. These individual distance "tolerance limits" referred to by Davis (see before) are species specific and can be invoked to account for the way populations of different species are distributed and organized within a given habitat. This approach to territory necessarily implies that within a given population and within its territory an animal will always be dominant. At first this may seem to imply "defence of an area" and lead to a definition of territory which was rejected in the previous section. However, fighting may be important only in the initial stages of assessing dominance status. In a stable population a dominant animal in its territory (i.e.

one whose behaviour is not limited with respect to a specified resource) often need only depend on the behaviour of others in order to remain dominant in the area. The behaviour of others may be modified by learning as a result of the initial aggression (see previous section) and may involve the use of olfactory sign-posts or other means of advertising the owner's presence. It could be simple avoidance by the intruder when the resident is present or when the boundaries are reached (Hinde, 1956). It could involve use of the same area on a time-sharing basis as proposed by Leyhausen (1965) and observed in the Cheetah, by Eaton (1970) and some Australian rodents (Happold, 1976). Frazer-Darling (1937) suggested that there was also a "psychological" component to territory which can be seen in the way the behaviour of an animal is modified when leaving its own territory and entering another.

Such aspects of the behaviour of an individual may be more or less important in describing the social organization of a group in relation to the space available. Certainly in terms of territory, the holder would be seen to restrict its movement more or less to a specific area but may not necessarily be seen to defend this area. Allee (1949) suggested that the territory holder would also show a tendency to "home" towards its area as a consequence of its "site attachment" to it. It may also exhibit forms of "advertisement" behaviour which could include marking behaviour.

The above description by no means implies a definition however, except that in species where interactions between strangers are aggressive, any social organization including territory will often be founded initially on aggression. Individuals will then carve out a space depending on the density of the population and their own relative aggressiveness and strength with regard to the other members of the population. Perhaps the question to be asked is "why do animals form territories?". Since they can obviously adapt their social behaviour and organization to suit the prevailing conditions, territory must bestow some advantage on the holder. In fact most authors suggest that the function of territory is diverse and serves many different purposes for different species. Hinde (1956) listed ten possible functions, Carpenter (1958) listed 32 but commented that these functions should be viewed "as hypotheses yet to be proven" (p. 242). Johnson (1971) listed twelve functions adapted from Carpenter's original list and the following is a resumé of that list.

1) Natural regulation of population density
2) Provision of adequate space thus increasing the availability and efficient use of food resources
3) A mechanism to ensure dispersal
4) Increase of in-breeding. Hinde (1956), however, suggested that territory might reduce in-breeding.
5) Reinforces monogamy and maintenance of the pair-bond which is efficient at rearing the young
6) Reduces disturbance of breeding by establishing a stable organization

7) Reduces stress by establishing a familiar area and security

8) Reduced time spent in aggression once organization is established

9) Predation avoidance possible because of spaced distribution

10) Reduced probability of spread of disease or parasites because of tendency to remain apart

11) Attraction and acquisition of mates

12) Selection of the strongest animals i.e. those able to obtain a territory.

It will be obvious also that some of these functions could equally well apply to any stable social organization.

In summary therefore, it has been shown that territory can be regarded as linked closely to other forms of social organization both in respect of its underlying basis of aggression, relation to space and density of population and in some of its inferred functions. Such close links may make it difficult to isolate territory as a clearly defined form of social organization within one species although the sort of behavioural parameters that could help in describing its presence in a species that is organized on the basis of aggression have been outlined. Such a descriptive method is essentially a means of clearly identifying what type of social organization exists in a given population of a given species. Only after such an exercise can one attempt to infer what function individual behaviour patterns may have in the maintenance of this organization.

In the following section the present state of knowledge concerning the social organization of the Mongolian gerbil is considered particularly with regard to the evidence relating to its possible territorial behaviour.

1.4.0. THE SOCIAL ORGANIZATION OF THE MONGOLIAN GERBIL

1.4.1. FIELD STUDIES

There is very little direct behavioural data available from field studies carried out on the Mongolian gerbil and thus the actual social organization of this species is not clear. However, there are a number of field population studies that have been reported for various species of gerbil, including the Mongolian gerbil, and thus it is possible to suggest a hypothetical social organization for this species.

The Mongolian gerbil inhabits the dry and sandy steppe areas of Eastern Mongolia, Northern China and Western Manchuria (Tanimoto, 1943; Kasuga - in Schwentker, 1968). However, Bannikov (1954) has reported to have found them in damper regions along moist banks of streams penetrating into the desert. There is confusion in these reports about the life-style of the animal and one is inclined to be cautious in accepting them at face value. Typical of the lack of clarity is the difference in the reports. Bannikov (op. cit) stated that these animals most certainly inhabited human dwellings whereas Tanimoto and Kasuga (op. cit) both stated that they were never found in these situations. What is clear is that they are burrowing animals, each burrow being around 3 - 5 metres overall (Bannikov, op.cit). These burrows contain stores of the main food-stuffs of the gerbil which appears to be very diverse, ranging from green parts of plants in summer to mainly seeds in winter

(Bannikov, op. cit; Tanimoto, op. cit).

As suggested in the previous section the density of animals and their sociability may be important factors influencing the social organization of animal species and it is clear that gerbil species vary widely in both density of population and sociability. Tanimoto (op. cit) stated that *M. unguiculatus* lived in groups in a colony, whether it was on a "one animal, one burrow" basis is not specified. Kasuga (op. cit) stated that "they live in herds in a gallery" which suggests a number of animals inhabiting single burrows. Leont'ev (1963) supported this observation and reported that anything from 1-26 animals have been caught in a single burrow but that it was generally 5 or 6. Bannikov (op. cit) provided the most probable explanations of these observations when he observed that both the first and second litters of the adult male and female remained in the burrow through the following winter, however unmated animals may have inhabited a single burrow. In fact a large number of gerbil species that have been studied appeared to be solitary, and a strict definition of individual burrows is often typical, such as in *Psammomys obesus* (Daly and Daly, 1975) and *M.hurriannae* (Prakash, 1962). *Tatera indica* seems to be a species where individuals are found more readily in the same burrow and Prakash and Jain (1971) reported that up to ten individuals have been found in one burrow. However the sympatric gerbil species *Gerbillus nanus* and *G. gleadowi* were all found to be solitary species. Petter

(1961) reported that M. vinogradovi could be found in small groups and suggested that these may have been undispersed litters. He also found that M. persicus stored food for the winter in large chambers and this was shared by groups of animals. Several burrows may be used by a single animal in this species and Petter (1961) remarked on the "apparent absence of individual territorial competition" within the colony. However Eibl-Eibesfeldt (1951) suggested that M. persicus maintained a group territory but his observations were on captive groups and are thus difficult to put into context. Fiedler (1973) suggested that gerbils in the genus Meriones tended to form permanent social groups whereas the phylogenetically more basic forms, such as Gerbillus tend to be solitary. Thus it seems reasonable to believe that Meriones unguiculatus may be a colonial species where family units live together in a single burrow presumably until the young are driven out by the adults or leave on reaching maturity after the winter. Elwood (1975) also suggested that the Mongolian gerbil lived naturally in monogamous pairs and it seems that on the evidence presented so far this is not unlikely.

The variability evident in the studies relating to the sociability of gerbil species is also evident when the density of naturally occurring populations is examined. However it is clear that this data is of considerable relevance to laboratory studies and the conclusions drawn from them, particularly where animals are seen to "defend" their home cage from intruders. Many authors, notably Barnett (1963) and most recently Geissler and Melvin (1977) suggested that the aggression by an animal in its home cage towards an intruder was the laboratory equivalent to the natural phenomenon in which an intruder to a territory was often defeated by the resident. However this interpretation ignores the possible effects of density on the social behaviour of the animals. The space available in a home cage environment may have the effect of increasing the apparent density of animals. Under such conditions these animals may attempt to form an hierarchical social organization. Thus the aggression and the behaviour patterns observed may not be territorial in these cases and to label them as such may be ignoring other possible interpretations.

Petter (1961) studied a number of species in North Africa and Iran and concluded that densities in optimal habitats ranged from 0.1/ha for *M. crassus crassus* to 50-100/ha for *Psammomys obesus*. However in 1968, Petter studied a population of *M. crassus* where the density was only 0.01/ha and Daly and Daly (1975) reported that even in the best habitat *P. obesus* were only found at densities between 3-5/ha. Higher densities have been reported for *M. hurrianae* (Prakash et al, 1971) where the method used was to count burrow openings. By this method a density of around 1000 animals/ha was estimated but from other methods a more conservative estimate of 28/ha was arrived at from the same species. They also estimated a density of 15/ha for *Tatera indica*. Mermod (1970) reported densities for five species in the Sahara; these were, 4/ha for *Gerbillus nanus*, 2/ha for *G. pyramidum* and 1/ha for each of *M. libyus*, *M. crassus* and *Pachyuromys duprasi*. The only estimate of density for *M. unguiculatus* is from Bannikov (1954) who reported that anything from 30 - 2800 burrows/ha were found, whether these burrows reflected the actual densities of animals is unclear, but on the evidence of the other species it may be rather high. It seems therefore that a figure of between 50-100 animals/ha may well be a more accurate reflection of the densities so far reported for gerbil populations.

Of the actual social behaviour and organization systems, in terms of territory or dominance, existing in these species very little is known. Nel (1975) pointed out that very little is in fact known about the social structures of many free-ranging rodents; however a limited amount of observational data is available for wild populations of some gerbil species.

Fitzwater and Prakash (1969) reported that *M. hurrianae* was a solitary species where males and females occupied overlapping home-ranges. These were not strictly defended but there was evidence that animals maintained an individual distance of between 2 - 4 m. Within these limits an "intruder" elicited an aggressive response from a "resident". Activity was centred around the burrow and burrow openings and the aggressive response was more likely from an animal that was close to its burrow. Kirchshofer

(1958) reported that Gerbillus nanus garamantis was a solitary species and that individuals were mutually aggressive, on this basis he labelled them territorial. Daly and Daly (1975) studied Psammomys obesus and described the social organization where typically adult females occupy a single burrow and adult males move freely over a larger range, often including that of several females. They observed some interactions that could be described as territorial where the resident animal was dominant to the intruding animal, however the results of other interactions were frequently not predictable on the basis of where they occurred. In general the dominance of one individual over the other was related to the sex and relative size of the animals. Daly (pers comm) also observed M. libycus, M. crassus and Gerbillus pyramidum where overlapping home-ranges were maintained, were largely undefended and individual dominance was often independent of where an interaction took place.

Nel (1975), in studies carried out on a number of rodents in the Kalahari desert, observed the social group structure of three Gerbillids, Desmodillus auricularis, Gerbillurus paeba and Tatera brantsi. Nel described the social structure of D. auricularis as,

> "Asocial, solitary dispersed: usually single, widely dispersed, adult animals (except for male and female during mating; female with young; two subadults shortly after weaning)"

G. paebe and T. brantsi were described as

> "Social, solitary clustered: individuals living in close proximity to others (e.g. a number of burrows close together each with usually one inhabitant) and

> showing a fair degree of social tolerance and interaction"

although I. *brantsi* may also have been organized as a

> "social, communal but non-colonial (polygamous group and family band): groups of various size e.g. family groups, a number of individuals inhabiting a restricted habitat (i.e. "communal" or "gregarious" species)."

It is therefore apparent that the social organization of many of the species of gerbil so far studied in the wild is quite variable, although it is clear that they live at relatively low densities. Certainly it would be difficult to classify gerbils as "territorial" animals on the basis of this sort of evidence particularly if the strict criterion of a "defended area" were employed. However, although the strict use of this criterion has been discarded by the present author it will be apparent in the next section that this is often the type of definition employed by authors studying the Mongolian gerbil under laboratory conditions.

1.4.2. LABORATORY STUDIES

A majority of authors studying the Mongolian gerbil have made the assumption that this animal is territorial. Thiessen et al (1968) first made this assertion but presented no evidence in their paper, "Androgen Control of Territorial Marking in the Mongolian Gerbil", and it was not until Thiessen (1973) that it became clear that the term was being used strictly according to the "defended area" definition. As a consequence the subsequent literature has become open to Emlen's (1957) criticism of the use of this strict definition in that it could cause observational bias. Ginsburg and Braud (1971) suggested that since they observed that gerbils attacked non-littermates more frequently than littermates that this was evidence of territorial behaviour in the animal. Wechin and Cramer (1971) noted that gerbils were more aggressive in their home cage and concluded from this "... that territorial defence is characteristic of this species". Spatz and Granger (1970) reported that gerbils will perform a behaviour known as "foot-thumping" more frequently in their home cage than in any other cage and thus suggested that this behaviour was territorial. In fact the aggression exhibited by gerbils in their home cage to strange conspecifics that have been introduced has virtually always been interpreted as evidence of territorial behaviour (see previous section; Nyby, Thiessen and

Wallace, 1970; Thiessen et al, 1970; Yahr, 1977). In one experiment (Thiessen and Dawber, 1972) it was claimed that, because a pair of adult gerbils living in a small box fought with and tended to drive away introduced, strange conspecifies, often forcing them to swim across an aquarium filled with water, this was evidence not only of territory maintenance by the exclusion of intruders but of reproductive isolation as a result of territorial behaviour. Such conclusions, stemming from highly contrived experiments and undoubtedly influenced by previous assumptions concerning the territorial organization of the Mongolian gerbil, clearly illustrate the numerous other interpretations that many of the laboratory studies published so far have failed to consider.

It is undoubtedly the case that many of the laboratory studies reported maintained animals at densities far above the estimated range for naturally occurring populations, which was suggested at between 50 - 100 animals/ha (section 1.4.1.). In a study carried out by Thiessen et al (1971) the density of animals was approximately 167,000/ha, in the study reported by Nyby et al (1970) the density of animals was approximately 140,000/ha. Hull et al (1973) studied the behavioural and physiological effects of maintenance density where they supposed that "even our crowded conditions may not have been too different from gerbils' normal population density inside their burrows". The estimated density of animals in these experiments was 930,000/ha. It is therefore certain that under such conditions it would not only be unlikely for animals to adopt a territorial social organization (see Section 1.3.3.) but it is also probable that such conditions may in fact be accompanied by the pathological effects of artificially high densities (see Christian, 1961; Christian and Davis, 1964). In such cases it seems almost naive to draw any valid conclusions about the social organization and behaviour of natural gerbil populations from such experiments.

Gallup and Waite (1970) demonstrated the effects of relatively high density on the social organization of the Mongolian gerbil although they were attempting to gather "information concerning natural behaviour patterns". The density of animals exceeded 13,000/ha and they observed fighting between mates sometimes resulting in death and the subsequent formation of an hierarchical order under a dominant male (despot). Thus it is apparent that at densities of this order animals tend to form an hierarchy and not territories, clearly then at densities above this the social organization of the Mongolian gerbil would be unlikely to be based on territories. The evidence for the social organization at lower densities, closer to the estimated naturally occurring densities, is less easy to discover. Clarke (1969) attempted to induce territorial behaviour in two mated pairs of gerbils. One pair was placed in a large arena and a further pair were introduced into the same arena but protected by an enclosure of wire mesh. Once the mesh was opened the animals fought but after four encounters quickly established a social order where the pairs lived exclusively in their own areas. Dunn (1970) also reported evidence that two dominant gerbils in a large arena showed signs of restricting their movements to one part of a large arena when there were only two pairs of animals in the whole area, conditions she described as "low density". However it is impossible to draw any conclusions from the results of such experiments as the evidence is so limited.

One must therefore conclude that there is no definitive evidence to suggest that the Mongolian gerbil shows territorial behaviour in the sense that it defends an exclusive area. Nevertheless it is obvious that experiments conducted in the laboratory have not so far attempted to study this problem in any depth although it has been largely accepted as fact that the Mongolian gerbil is territorial. In a later Chapter of this thesis (Chapter IV) an attempt will be made to study this aspect of the social organization of the gerbil where its territorial behaviour, according to the definition that has been used by previous authors, will be examined.

1.5.0. SCENT MARKING IN MAMMALS

1.5.1. GENERAL INTRODUCTION

Communication in mammals using odours has recently received an increasing amount of attention, so much so that a number of comprehensive reviews have appeared (Wilson and Bossert, 1963; Eisenberg and Kleiman, 1972; Epple, 1974; Johnson, 1973; Stoddart, 1976). It is therefore not the intention of this discussion to duplicate the findings of these reviews but merely to outline their major conclusions to provide a frame of reference for a discussion of scent-marking behaviour in the Mongolian gerbil.

Scent-marking is behaviour by which glandular secretions are deposited on the ground or onto objects in an animal's environment. In a majority of mammals specialized cutaneous glands, producing apparently odourous secretions have been identified. For example, the anal glands of rabbits (Stoddart, 1976); the lateral glands of the vole, <u>Arvicola terrestris</u> (Stoddart, 1972); the dermal glands of the shrew (Eadie, 1938); the submandibular glands of rabbits (Lyne et al, 1964); the flank-glands of the Syrian hamster (Algard et al, 1966); the pedal glands in <u>Rhinoceros</u> (Cave, 1962). A number of comparative studies have also been carried out, notably Pocock (1910); Quay (1965, 1968); Quay and Tomich (1963); Doty and Kart (1971). Such studies indicate the wide variety of different glands occurring at different locations, such that there is also a wide variety of different marking behaviours between species in terms of the action patterns involved (see Thiessen and Rice (1976) for a comprehensive review of mammalian scent glands and marking behaviours). The deposition of urine and faeces, carrying secretions of the sex accessory or anal glands can also constitute marking behaviour as can the accidental deposition of scent from interdigital glands as animals move through burrows or runways, for example in the shrew Blarina brevicauda (Pearson, 1946), but generally scent-marking is usually associated with some sort of body-rubbing behaviour where the gland is drawn across the ground or object to be marked (Kleiman, 1966). Schenkel (1966) suggested that the term "marking" be used when a mark is deposited which persists and can be detected by other members of the same species.

The chemical composition of some of the scent marks has been investigated in a number of cases and the components have been identified. For example studies have been carried out to identify the composition of the secretion from the tarsal gland of the Black-tailed deer, Odocoileus hemionus columbianus (Brownlee et al, 1969; Muller-Schwarze, 1971 b), the subauricular gland of the male Pronghorn (Muller-Schwarze et al, 1974), and the anal gland of the Indian mongoose, Herpestes auropunctatus (Gorman et al, 1974; Gorman, 1976), and in each case it has been possible to investigate the effects of the isolated components on other members of the same species. Such substances are often referred to as "Pheromones" (Karlson and Lüscher, 1959). Bronson (1971) sounded a note of caution in using this term when he proposed that it should be used only in,

> "situations where there seems a reasonable probability of isolating one or at least a restricted mixture of compounds that could, in turn, be synthesized and where actions could then be reconfirmed experimentally" (p. 345)

He stressed also that a pheromone should serve a "reasonable biological function" in a natural population and continued

> "it is doubtful that the term pheromone can realistically have merit when referring to the melange of odors probably used in individual identification". (p. 345)

However the identification of pheromones in mammalian scent-marks has, as yet, only been carried out in a few species and more often than not the specific action of scent-marks on other members of the same species is far from clear.

The scent-glands themselves are of two types, apocrine, coiled tubular structures that open into hair follicles and produce sweat and lipid secretions (for example the sudoriferous (sweat) glands of the horse or the chin glands of the rabbit) and holocrine, which produce only lipid material (for example the anal glands of rabbits and the lateral glands of hamsters) and are generally known as sebaceous glands (Stoddart, 1976). The apocrine glands are under the control of the "sweat centre" of the brain, controlling the production of sweat, and blood hormones, controlling lipid production. Holocrine glands are almost exclusively influenced by steroid hormones and in most species of animals studied so far the sebaceous glands show sexual dimorphism, where the male gland is generally bigger (Thiessen and Rice, 1976). Glands typically develop at or about the time of birth and continue to develop throughout life. Frequently the glands also show periods of increased activity during the breeding season, as in Arvicola (Stoddart, 1972). In the rabbit, Oryctolagus cuniculus, the chin gland size and secretory activity has been found to fluctuate throughout the year, and both are maximum during the breeding season. The anal gland was also found to be largest at this time and its secretions tended to have the strongest odour (Hesterman and Mykytowycz, 1968). In the short-tailed shrew however, Pearson (1946) found no such variation and their scent glands were active throughout the year. Mykytowycz (1962; 1966) observed that the chin, anal and inguinal glands of the rabbit were also under the control of testosterone (or other androgens). Gonadectomy of immature animals significantly reduced the size of the chin and anal glands in males but increased their size in females which suggests that oestrogens exerted an inhibiting effect on these glands. Rabbits of both sexes have been found to respond to the administration of male hormones with an increase in the size of these glands but the glands of intact males that were given oestradiol decreased in weight (Wales and Ebling, 1971 ; Mykytowycz, 1966). Castration has been observed to bring about atrophy, or shrinking and a reduction of mitotic activity; in the sebaceous glands of a number of other species, for example the flank glands of voles of the genus Arvicola (Stoddart, 1972), the lateral glands of Golden hamsters (Vandenbergh, 1971), the supracaudal patches and perineal gland in Guinea pigs, *Cavia porcellus* (Beauchamp, 1974) and the sebaceous glands of rats, *Rattus norvegicus* (Stoddart, 1976). In their review of scent-marking behaviour Thiessen and Rice (1976) concluded that, in the light of the evidence of the sexual dimorphism and age dependency, seasonal variation along with the direct evidence of hormonal control so far, the scent-glands of nearly all mammalian species were probably under the control of the gonadal hormones, especially androgens and oestrogens.

The performance of scent-marking behaviours in mammals is also partly controlled by the gonadal hormones, although the frequency of the response can vary as a result of social interactions, the status of the animal and the physical novelty of the environment. In the same way that there is sexual dimorphism in scent-gland size there is generally the same dimorphism in marking behaviour, for example male Golden Hamsters mark about three times more than females (Payne and Swanson, 1970), male Ground Squirrels mark more than females (Steiner, 1974) as do male rabbits (Mykytowycz, 1962; 1968) and the male Degus, *Octodon degus* (Kleiman, 1975). There is often, though not always, a seasonal variation in marking behaviour which may relate to the animals' breeding season (Johnson, 1973). Mykytowycz (1965; 1966) reported that the marking behaviour of rabbits increased during the breeding season and Steiner (1974) reported a dramatic increase in marking frequency and intensity during the reproductive period in male Columbian ground squirrels. However Taylor (1968) reported peaks of marking activity, in the squirrel, Sciurus caroliensis, both within and outside the breeding season and Townsend (1953) found that, although marking in Beavers increased in July, this was not clearly related to the animals' breeding season.

This suggests that marking behaviour may be linked, at least in some animals, to hormonal fluctuations connected with reproductive activity and it is certainly true that the gonadal hormones in a number of species play an important part in controlling marking behaviour (Thiessen and Rice, 1976). In general it appears that in males testosterone (or some other androgens) have an important controlling effect. In rabbits for example, castration inhibited scent-gland development and marking, while administration of testosterone reinstated marking behaviour (Coujard, 1947 ; Mykytowycz, 1962, 1965, 1966, 1968). Price (1975) reported that the urine-marking of wild and domestic Norway rats was dependent on testosterone since it could be restored in castrate males by administering this hormone. In female animals there is evidence of changes in the frequency of scent-marking related to oestrus state. Beach and Gilmore (1949) found that female dogs urinated more frequently when in heat and Kleiman (1966) listed several other Canids where the female marks more frequently, or often only marks, when in heat. Grassé (1955) stated that in many species, the glands of the females secreted most at the time of sexual receptivity. Johnston (1977) found that the frequency of vaginal marking by female hamsters reached a peak on the day before oestrus and was almost totally absent on the oestrus day. He concluded that these observations suggested hormonal control particularly by the ovarian hormones but their role was not clear, although it is likely that, on the evidence of this and other species, these hormones may be implicated. However it is clear from other evidence in the hamster (Vandenbergh, 1973) that the flank glands in both sexes are controlled by androgens. Thus the role of the sex hormones in scent-marking behaviour seems to be complex and as yet is not fully understood. These hormones are nevertheless implicated in the relationships that scent-marking has to aggression and social dominance in many species.

The frequency of scent-marking behaviour has been positively correlated with high aggression and high social status (rank) in a number of species. For example in Columbian ground squirrels the dominant male in each community performs nearly all the marking (Steiner, 1970) and this has also been reported for the Sugar-Glider, *Petaurus breviceps papuanus* (Schultze-Westrum, 1970). Dominant males also mark more frequently in the hamster (Eibl-Eibesfeldt, 1953; Drickamer and Vandenbergh, 1973) and the rabbit (Myers and Poole, 1961; Mykytowycz, 1965). Ralls (1971) reviewed the relationship between scent-marking, aggression and dominance and concluded that animals marked frequently in any situation where they were both intolerant of and dominant to other members of the same species. The relationship between these social factors and scent-marking is also apparent at the hormonal level. In males the level of blood androgens have been positively correlated with levels of aggressive behaviour in a number of species (see Drickamer and Vandenbergh, op. cit) and it appears that in the female hamster the ovarian hormones, particularly progesterone, are important in maintaining the level of aggression (Payne and Swanson, 1972). There is also evidence that dominance status can be predicted from the blood levels of certain corticosteroid hormones (Candland and Leshner, 1971). It may be that the relationship between the scent-marking behaviour, aggression and dominance in many animals is therefore based on the same hormonal mechanism as the reproductive behaviour (Thiessen and Rice, 1976).

The frequency of marking, however, can also be influenced by other factors, notably the novelty, strangeness or unfamiliarity of the environment, both physical and olfactory. Martin (1968) noted an intense marking response in the Tree-shrew, _Tupaia belangeri_, both in a new cage and to novel objects placed in its home cage. Johnson (1973) reported on similar observations for a number of other species although more recently Maruniak et al (1974) have suggested that one of the most potent factors in increasing the rate of urinary marking in mice was the environmental novelty. Olfactory novelty and its influence on the frequency of marking behaviour is difficult to determine.

Certainly clean cages or arenas tend to produce high marking rates in many animals (see above) but marking as a response to an unfamiliar scent-mark or marked area involving the same species may not be the same as marking in response to novelty (Johnson, 1973). Animals often show increased marking rates in the presence of unfamiliar scent-marks, for example in the beaver (Aleksuik, 1968); the Tree-shrew (Martin, 1968); the Sugar-glider (Schultz-Westrum, 1970); the mongoose (Rasa , 1973); the Golden Hamster (Johnston, in Ralls, 1971) and the dog (Hart, 1974). Frequently, however, the response to another scent-mark may vary according to the context in which it is encountered. Experiments with rabbits revealed that if alien faecal pellets were placed in a rabbit's home area they elicited intense marking (Mykytowycz, 1968; Mykytowycz and Hesterman, 1970). However in the completely unfamiliar area of another rabbit it did not mark, though in novel, socially neutral areas the rabbit would mark.

In some species Johnson (1973) suggested that an alien scent-mark may be the primary stimulus for marking behaviour and that communal marking sites are often found in colonial species. Eisenberg (1963) observed that heteromyid rodents tended to concentrate their sandbathing at a preferred locus which was used by a group of animals. Lane and Ginswold (1976) recently confirmed that not only were deposits left by sandbathing in the Kangaroo rat, Dipodomys spectabilis, but that the loci were commonly used by other conspecifies to deposit their marks. Communal marking sites have also been reported in the rabbit (Mykytowycz and Gambale, 1969) and the otter (Erlinge, 1968) as well as many other species (Johnson, 1973).

It is apparent therefore that scent-marking is a response which is governed by a number of complex and as yet only partly understood internal and external stimuli. Hormonal and social factors often appear to be linked but frequently interact in a complex manner (Drickamer and Vandenbergh, 1973a, 1973 b) which make a precise understanding of these behaviours difficult. However even without a clear knowledge of the relevant factors involved in scent-marking behaviour a number of suggestions have been proposed for its possible functions; these will be discussed in the following section.

1.5.2. FUNCTIONS OF SCENT MARKING

In recent years the possible functions of scent-marking in the field of olfactory communication have been discussed by a number of authors (Mykytowycz, 1970; Cheal and Sprott, 1971; Ropartz, 1968; Johnson, 1973; Thiessen and Rice, 1976). Johnson (1973) suggested that,

> "Scent marks might act as:
>
> (i) a deterrent or substitute for aggression, to warn conspecifics away from occupied territory;
>
> (ii) a sex attractant or stimulant;
>
> (iii) a system of labelling the habitat for an animal's own use in orientation or to maintain a sense of familiarity with an area;
>
> (iv) an indication of individual identity, perhaps including information on social status, age, dominance, etc;
>
> (v) an alarm signal to conspecifics;
>
> (vi) Wynne-Edwards (1962) has proposed that marking has an epideictic function: an indication of population size." (p. 522)

Thiessen and Rice (1976) suggested that these functions could be condensed into three major classes of signal

> "... those used for (a) aggregation (b) recognition and (c) population control." (p. 506)

In the following discussion however, we will briefly review the evidence in support of each of the functions suggested by Johnson with particular emphasis on the evidence for the territorial function of marking.

(i) TERRITORIAL FUNCTION

Marking behaviour is often referred to as "territorial marking" (see Sections 1.3.2.; 1.4.2.) although Schenkel (1966) has pointed out that a precise definition of the correlation between marking and territory has rarely been given. Some authors (e.g. Ropartz, 1968) claim that there is plentiful evidence to support this relationship, however as yet such evidence is far from conclusive.

Hediger (1949) observed that many species deposit scent where they tend to meet or expect rivals, thus if scent-marks acted as a means of territorial defence it might be expected that they would be more likely to be deposited at the territorial boundaries. There is some evidence in support of this suggestion particularly in the European Lynx, Lynx lynx, and the wild cat, Felis silvestris (Lindeman, 1955, in Ewer, 1968) and more recently reported for the Loris, Galago alleni (Charles-Dominique, 1977). However it is more generally the case that scent-marks occur not only at the borders but throughout an animal's home area (Aleksiuk, 1968; Mykytowycz and Gambale, 1969; Eibl-Eibesfeldt, 1953). Mykytowycz (1965) commented that rabbits probably saturated their whole home area with smell and this is probably the case with most animals. Animals have also been observed scent-marking in neighbours' territories (Myers and Poole, 1961; Eibl-Eibesfeldt, 1953).

The association of marking with aggression and dominance (Section 1.5.1.) has often been used as evidence to support the idea of a "territorial" function for this behaviour. A number of animals have been observed marking during aggressive encounters (see Ewer, 1968; Ralls, 1971) and, although this may suggest that marking might have some function as a threat and therefore play some part in "territorial defence", Johnson (1973) pointed out that not only was there no evidence of its effect during these encounters but there were also many cases where this behaviour was used independently of a territorial context, for example between members of the same colony (Mykytowycz, 1965).

There is very little evidence of the effect that scent-marks have on other conspecifics in relation to territory. It might be expected that if scent-marks act as a deterrent to warn animals to keep out of an occupied area that animals encountering an alien scent-mark would withdraw. However there are no observations of this ever occurring. Leyhausen and Wolff (1959) suggested that scent-marks might act as "railway-signals" to minimize encounters between individuals by signalling how recently an animal has passed but withdrawal from a scent-marked territory was clearly not the usual response. Johnson (1973) suggested that a more likely effect of scent-marks was to predispose withdrawal in the presence of the resident animal as a result of the scent-mark acquiring aversive properties through repeated aggressive encounters with the resident. Harrington (1976) reported a learned avoidance of scent associated with the experience of defeat in mice. However, male scent-marks, far from being aversive to other males, seem to possess attractive properties (Erlinge, 1968; Rowe, 1970; Beauchamp, 1973).

Olfactory cues can be used in the recognition of territorial boundaries in mice (Harrington, 1976) although Mackintosh (1973) stressed that they were only used when they did not conflict with visual cues. It is therefore apparent that as yet there is no clear evidence to suggest that marking has a territorial function in any of the mammalian species studied so far. There is evidence that scent-marks can invoke an aggressive response, usually threat, in another animal (Eibl-Eibesfeldt, 1953, Aleksiuk, 1968; Rasa, 1973) but whether this is related to territorial behaviour is not clear. Thus there remains only limited justification for labelling scent-marking as purely territorial.

(ii) SEX ATTRACTANT OR STIMULANT

Marking appears to be related to several factors which suggest it might have a sexual function. In a number of species it has been found to appear with the onset of sexual maturity, for example the hamster (Dieterlen, 1959). It has been shown to be sexually dimorphic and often to vary in relation to the reproductive period in some species. The females of certain species also show a variation in marking behaviour in association with their oestrus cycle (see previous Section). The evidence for its role in sexual behaviour, however, is still somewhat unclear. Johnson (1973) pointed out that often statements about the sexual function of marking were unsupported by relevant data and generally there seemed to be some disagreement. Recently Darby et al (1975) investigated the effect of the vaginal discharge of the female hamster on males and report that it attracted investigatory interest and, if smeared on an appropriate stimulus object, it would facilitate copulatory behaviour. In the previous section it was reported that the vaginal marking behaviour of the female hamster was at its greatest on the day before oestrus and was absent on the oestrus day (Johnston, 1977), and Johnston therefore suggested that the vaginal marking had a sexual advertisement function, since he also observed that it was performed at a higher rate in the presence of a male. Other authors have suggested that olfactory cues may serve to attract sex partners to each other (Le Magnan, 1952; Godfrey, 1958; Carr and Caul, 1962; Bronson, 1971). It has been observed that a female cat in oestrus will show behaviour typical of her response to a male if placed in a cage recently occupied and marked by a male (Michael and Keverne, 1968). Beach and Gilmore (1949) showed that urine from a female dog in oestrus was more attractive to males than urine from an anoestrus female. Hanes (1976) suggested that the dermal glands in female shrews, _Sorex vagrans_ and _S. obscurus_, might elicit approach and copulatory behaviour by the male when females were in oestrus. Verberne and De Boer (1976) suggested that the urine and cheek gland secretion of female cats contained information about her hormonal status and that tomcats consequently showed a cyclic intensity of interest to marks from these glands corresponding with the female's oestrus state. They concluded that these marks could be used by males to ascertain the female's hormonal state but they reported no evidence of its link with any subsequent sexual behaviour.

It is therefore apparent that, while scent-marks may be used by males to obtain information about the hormonal status of the female, their role as a sexual attractant and stimulant is very vague and so far there is little evidence of this occurring in natural populations.

(iii) HABITAT LABELLING

Marking behaviour performéd in an animal's home area could serve as a means of orientation. Kalkowski (1968) reported that mice leave marks which conspecifies can use as an odour trail for orientation up to 24 hours later. Poelayen-Neuwall (1966) suggested that the Kinkajou, Potos flavus schreber, used scent-marking to indicate colony trails within its home range. Means et al (1971) have reported that rats will use odour trails left by conspecifies as cues in a maze learning experiment and Davis et al (1970) have reported that the odour trails left by one species in a runway experiment could be used as cues by other species. Galef and Heiber (1976) suggested that olfactory cues left by adult cats could be used by weanlings to direct them to their first meals of solid food in their natural environment.

It has been suggested that the saturation of an animal's home area with its own scent (Mykytowycz, 1965) could thereby serve to make the area more familiar and thus provide a sense of security and increased confidence Ewer and Wehner (1974) have recently reported that scent-marking in the Africa civet, Civettictus civetta, is often associated with anxiety or insecurity. Kleiman (1971) has pointed out that animals often spray each other with urine (enurination) particularly rodents and lagomorphs and this may act as a form of reassurance to the owner by giving the other animal a familiar smell. This may also be the function of the high marking rates observed in a number of species in novel environments (see Section 1.5.1.). Eibl-Eibesfeldt (1970) has reported early observations in which a badger, Meles meles, frightened by a strange environment was calmed by the presentation of an object smeared with its own scent. Thus it is possible that, as well as providing cues for orientation within a home range, scent-marks may have a "psychological effect", the smell of "home" acting to reassure the animal.

(iv) INDIVIDUAL IDENTITY AND RECOGNITION

It is quite clear from a number of studies that the scent-marks of individual animals can be identified by conspecifies and could thus be used in individual recognition For example in mice (Bowers and Alexander, 1967; Hahn and Simmel, 1968), in rats (Bloom and Phillips, 1973; Carr et al, 1976), in Guinea pigs (Berüter et al, 1974), in the domestic pig (Meese et al, 1975), in the lemur, *Lemur fulvus*, (Harrington, 1976). Lemurs can also distinguish between male and female conspecifies from the scent-marks (Harrington, 1977) and Heimburger (1959) has reported that in the *Canidae* the marking response of a male dog to the scent of another is greater if the scent is from a rival male, thus demonstrating its ability to discriminate between scent-marks. In the Blacktailed deer it has been shown that it is scent from the tarsal gland that is important in individual recognition (Muller-Schwarze, 1969) and it has also been suggested that this discrimination can be seen between sub-species and thus may be important for sexual isolation in areas where ranges overlap (Muller-Schwarze and Muller-Schwarze, 1975).

The sexual status of the female may also be determined from the olfactory cues in scent-marks (see Subsection 1.5.2. (ii)) and it has been shown that other information may also be contained in the odours of some animals. For example Valenta and Rigby (1968) found that albino rats could reliably distinguish between the odours of stressed and unstressed rats and Morrisson and Ludvigsen (1970) reported that there was clear evidence that rats could produce an "odor of non-reward or frustration" in a T-maze experiment.

The social status (dominance) of an animal may also be indicated by the scent-marking behaviour of an individual.

In general dominant animals mark more frequently than subordinates (Section 1.5.1.). Desjardens et al (1973) also suggested that in mice the pattern of urinary marking was different in dominant males. Dominants tended to mark the entire cage floor while subordinates typically marked in only two or four pools in the corners of their cages. Whether or not dominant animals can be distinguished from the olfactory cues in their scent-marks is not clear although it is likely that the ability to discriminate between individuals on the basis of marks coupled with learned aversion as a consequence of aggression by a dominant may play a part in this.

(v) ALARM-SIGNAL

There is no experimental evidence that scent-marking behaviour is used to communicate alarm. In the previous subsection it was reported that rats could distinguish between the odours of stressed and unstressed rats (Valenta and Rigby, 1968) and Donovan (1969) has claimed that the domestic dog will avoid the anal gland secretion from a frightened dog. Muller-Schwarze (1971) has reported that the Blacktailed deer released scent from its metatarsal gland when frightened and that this could possibly be laid down as a mark when the animal is in flight, presumably for the use of other deer. Johnson (1973) suggested that a volatile scent discharged directly into the air might be more effective than a scent-mark, in that it was rapid and would not persist for as long as a scent-mark.

(vi) EPIDEICTIC FUNCTION

The communal nature of scent-marking in some species (Section 1.5.1.) has lead to the suggestion that scent-marks functioned as a display providing the necessary feed-back about the density of a population (Wynne-Edwards, 1962). The information contained in scent-marks about the animals that deposited them is thought to be an important feature indicating the size and composition of a given population and there is some evidence that the frequency of marking may in fact be affected by the population density. Erlinge (1968) reported that otters increased their marking and visited more marking sites at times when the population was higher and Koch et al (1969) observed an increase in the size of communal latrines in the lemming, Lemmus lemmus at a time of a population peak. Mykytowycz and Gambale (1969) have shown that, among other factors, population size affected the number of communal dung hills in a rabbit colony. However Myers et al (In Esser, 1971) reported that when fewer rabbits were present in a limited area the marking rate increased, but other factors may have been involved. Ralls (1971) commented that scent-marking could affect the breeding condition of a population of animals through the distribution of primer pheromones, the effects of which have been demonstrated in a number of rodents (see Bruce, 1970; Schultz and Tapp, 1973; Mornex , 1974;

Koller, 1974).

It is apparent therefore from the content of this brief review of the suggested functions of scent-marks that there is some evidence to support a number of different functions for scent-marks. Johnson (1973) concluded his review by pointing out that:

> "A common misconception seems to be that all scent-marking behaviour can be treated as analogous whereas in reality it is obviously a diverse behaviour and scent-marks can have many functions".

He also pointed out that there was a great deal of experimental work to be carried out in this field. It thus seems clear that, in view of the diversity of functions possible for any scent-marking behaviour investigated, the behaviour must be clearly described in the context not only of the animal's normal social behaviour but in relation to its effect on other conspecifies or even other species.

In the following section a review of the scent-marking behaviours in the Mongolian gerbil is presented and the evidence so far for its possible functions discussed.

1.6.0. SCENT MARKING IN THE MONGOLIAN GERBIL

1.6.1. TAXONOMY AND PHYSIOLOGY

The skin of mammals contains lipid-secreting sebaceous glands associated with each hair follicle and it is often the case that certain areas become enlarged and modified to give a sebaceous pad secreting a sebum (Section 1.5.1.). In the Mongolian gerbil there is a mid-ventral sebaceous pad of this type. This mid-ventral gland occurs in at least five other species of *Meriones*, *Rhombomys opimus* and *Psammomys obesus* (Sokolov and Skurat, 1966) as well as other more distantly related Rodents e.g. *Blarina*; *Cricetus*; *Phodopus*; *Neotoma*; *Peromyscus*; *Sigmodon* and *Rattus* (Quay and Tomich, 1963). Other rodents of the subfamily Microtinae have sebaceous glands in the posterio-lateral area of the skin (Quay, 1968) and thus the mid-ventral complex appears to be most common to the family Cricetidae.

In the adult Mongolian gerbil the gland is situated in the midline of the body in the middle of the abdomen and is an elevated fusiform pad of sebaceous elements. It is yellow to orange in colour and is somewhat larger in males than in females and exudes a sebum with a musky odour when squeezed. In young animals the gland is probably not distinguishable to the naked eye until around 28 days and it reaches its maximum adult size after 86 days around the time when the animal becomes sexually mature (Feldman and Mitchell, 1968).

On castration the male gland was found to involute but could be restored by administration of Testosterone (Arluk, 1966; 1969; Mitchell, 1965) and thus appeared to be under the control of androgens which probably act at the cellular level (Arluk, 1969). In the female, gonadectomy also caused the gland to involute and replacement therapy with testosterone proprionate or oestradiol benzoate would also restore it (Owen and Thiessen, 1974 a; Yahr and Thiessen, 1975). It thus appears that testosterone is probably the active hormone in males and oestrogen (or oestrogen plus progesterone) in females (Thiessen and Rice, 1976). Thiessen and Yahr (1969) have also reported the presence of submandibular glands in Meriones unguiculatus. These glands are sexually dimorphic, being larger in the male and appeared to be under the control of testosterone since gonadectomy in the male significantly reduced the size of the gland. In the female gonadectomy had no effect (Mastraccio, 1972).

Associated with both of these glandular areas are marking behaviours when secretions of these glands are deposited on objects in the animals' environment. Marking with the chin gland is probably rare, only occurring when the object is too high to be marked with the ventral gland (Thiessen, Yahr and Lindzey, 1971 a). On the other hand marking with the ventral gland is common and has been investigated quite thoroughly. Both males and females will rub the ventral gland over low-lying objects in their environment and this behaviour is sexually dimorphic, where the male generally marks more frequently than the female. A description of this behaviour has been given by Thiessen et al (1968) as "... highly discrete, involving rapid approach to an object, sniffing of the object, mounting it and then pressing the ventral sebaceous gland against its surface and finally a foreward dismount".

Like the gland itself the behaviour appears to be partly dependent on the gonadal hormones. Gonadectomy in the male, while completely eliminating the gland, does not completely eliminate the behaviour although it is significantly reduced (Thiessen et al, 1968; 1971 a; Whitsett and Thiessen, 1972). The behaviour could be restored to its normal level by the administration of testosterone proprionate, however the degree of marking behaviour exhibited was directly proportional to the dose (Thiessen and Lindzey, 1970 d; Thiessen et al, 1968; Blum and Thiessen, 1971). There is also some evidence that oestrogen can partially restore the marking behaviour of castrate males (Nyby and Thiessen, 1971).

In the female ovariectomy reduced the amount of marking (Yahr and Thiessen, 1975) and both injections of testosterone and oestrogen stimulated marking (Owen and Thiessen, 1974 b). However it appeared that the effect of oestrogen depended very much on the level of marking behaviour of the individual female prior to gonadectomy. Yahr and Thiessen (op. cit) reported that oestrogen or progesterone alone would not stimulate marking in ovariectomized females that were low markers prior to the operation. It appeared that both oestrogen and progesterone were necessary to stimulate these females and that progesterone had a modifying role on the primary stimulus of oestrogen (Owen and Thiessen, 1974 a; 1974 b). This is closely linked to observations that the ventral marking of females increased during pregnancy and lactation and the findings of Owen and Thiessen (1974 b) that injections of the hormone precursor Androstenodione into both intact and ovariectomized females were effective in raising marking levels only of intact animals. This gave rise to the conclusion that the precursors are converted into behaviourally active hormones during late gestation and lactation and give rise to increases in female marking. Thus there appears to be a fairly complex hormonal interactive system at work in the female marking behaviour.

Further investigations into the hormonal basis of marking behaviour in the gerbil have been carried out. It was found that testosterone proprionate, injected into intact males and females could raise levels of ventral marking to very high levels in both sexes (Thiessen et al, 1971; Thiessen and Lindzey, 1970 d) and implants of the hormone in the preoptic area of the brain were found to evoke marking in the male (Thiessen and Yahr, 1970 b; Thiessen et al, 1973; Yahr and Thiessen, 1972). Oestrogen and testosterone appeared to have antagonistic effects when injected together (Nyby and Thiessen, 1971) and adrenalectomy had no effect on marking behaviour of either sex (Thiessen et al, 1971). It thus appears that one of the primary factors influencing the marking behaviour of male and female Mongolian gerbils is the level of gonadal hormones.

The behaviour is also under some exogeneous control and a number of studies have been reported. Baran and Glickman (1970) claimed that excision of the ventral gland caused attenuation in the frequency of the response but studies carried out by Blum and Thiessen (1970) were unable to confirm this.

It also appears that olfactory cues play an important part in the maintenance of ventral-marking behaviour. Olfactory bulb ablation caused the almost total elimination of this response (Baran and Glickman, 1970). Wallen and Glickman (1974) reported that peripheral anosmia induced using zinc sulphate produced similar results indicating that the original findings were due to the deprivation of olfactory cues rather than lesions of the central nervous system. Thiessen et al (1970 c) reported that massive doses of testosterone proprionate could partially restore marking behaviour in operated animals, however Lumia et al (1975) found that they were unable to restore marking with the hormone and that the major effect of these injections was to increase the aggression of the bulbectomized animals.

Nyby and Thiessen (1971) suggested that the physiological control of ventral-marking behaviour in the Mongolian gerbil was through androgens which appeared to be similar to the control of sexual behaviour in many other rodents. However it is clear that olfactory cues are a necessary exogeneous factor for the maintenance of this behaviour, while it is not yet clear how much cutaneous stimulation affects its performance. The type of physiological control that operates with respect to marking with the chin-glands has not been identified, although Thiessen et al (1971 a) believe that it is not influenced by androgens.

Recently Thiessen et al (1974) have carried out studies using conditioning techniques, exploratory tests, thin layer and gas chromatography, and mass spectrophotometry to determine the composition of the ventral-gland secretions. They have suggested that in the male (and probably the female) the primary pheromone in the scent is phenylacetic acid, which they suggest is only one of many other volatile substances present in the sebum. As yet however, none of these has been fully investigated and it is believed that only one pheromone exists.

From the literature reviewed so far it is apparent that the taxonomy and physiology of the ventral-marking behaviour in the gerbil are generally similar to those of a number of mammalian species (Section 1.5.1.). However, although the studies carried out on this gerbil are among the most detailed for any species, the physiological mechanisms of marking behaviour are still only partly understood. Still less clear are the effects of social factors on the performance of the ventral-marking and chinning behaviours and these will be discussed in the next section where the possible functions of marking behaviour in the Mongolian gerbil will be reviewed.

1.6.2. POSSIBLE FUNCTIONS OF SCENT-MARKING IN THE MONGOLIAN GERBIL

Thiessen et al (1970) concluded their study on the ventral-marking of the male Mongolian gerbil by suggesting that,

> "The ventral gland of M. unguiculatus could conceivably be used to aggregate conspecifies, to disperse members of a population, to attract members of the opposite sex, and to afford cues for individual recognition, as well as to mark the home territory of a gerbil or group of gerbils". (p. 30)

Unfortunately the subsequent literature relating to ventral-marking in the gerbil did not always fully consider all these possible functions and thus many studies have been reported where the scent-marking behaviour of the gerbil has been exclusively labelled "Territorial Marking"; see for example Turner (1975), Thiessen et al (1970 c), Thiessen and Yahr (1970 b), Thiessen et al (1970 b), Thiessen et al (1973). However, as Johnson (1973) and Thiessen himself, in the statement quoted above, recognise, scent-marking in the gerbil may have many functions. Thus in this section the functions of scent-marking suggested by Johnson (1973, see Section 1.5.2.) will be discussed with reference to the evidence for each so far obtained for the Mongolian gerbil.

(i) Territorial function

In common with a large number of mammalian species (Section 1.5.2.) the Mongolian gerbil will saturate its home area or cage with the secretions of its sebaceous glands, urine and faeces and when placed in a clean cage will immediately mark any suitable objects using its ventral-gland. Daly and Daly (1975) have reported that although object scent-marking using the ventral gland was seen only rarely in a wild population of Psammomys obesus, sand-bathing behaviour where the flank and ventrum were rubbed in the sand was seen frequently particularly near the home burrow. Thus the odour of a gerbil will be prevalent in and around the area that it inhabits, although the effect of this on others, from observations on wild populations, has never been observed. However a number of laboratory studies suggest that scent-marking in the gerbil may have a function related to the possession of a home area.

Scent-marking behaviour in the Mongolian gerbil has been found to be linked closely with aggressive behaviour and dominance (Thiessen, 1973) and Swanson (1974) suggested that it may be used as a threat behaviour in the male in order to assert dominance over a female where the male was inhibited from using overt aggression. Evidence from other sources also suggests that the marks themselves might become associated with the aversive stimuli of an aggressive encounter and thus may act as a substitute threat. Nyby et al (1970) have reported that subordinate animals rarely mark in the presence of the dominant animal, although they will mark if placed alone in a clean area. However if this area is contaminated with the scent-marks of the dominant the subordinate will not mark. Recently

Yahr (1977) has reported the same effect if the clean area in which the subordinate is placed is visually similar to the area in which it was defeated by the dominant. It is thus obvious that a number of cues may become associated with the dominant and that the scent-marks may not be the primary cue if there are visual cues available. Nevertheless it has been demonstrated that subordinate Mongolian gerbils will show avoidance of the odours from the area or cage where they had previously experienced defeat (Nyby et al, 1970; Thiessen and Dawber, 1972). This suggests that the scent-marks become associated with defeat and thus animals show learned avoidance of these marks or at least show a predisposition to retreat in their presence (see Johnson, 1973). It is therefore possible that,a scent-mark could act as a deterrent, warning individuals away from an occupied home area. This deterrent effect however, is clearly linked with previous experience since strange male odours are very attractive to other males and have no effect on their marking behaviour (Baran, 1973; Thiessen et al, 1970), thus before scent-marks are effective in the maintenance of a home area the resident animals must be able to inflict a defeat on the intruder.

There is unfortunately no evidence to support the claim that gerbils are in fact "territorial" according to the "defended area" definition (see Sections 1.4.1. and 1.4.2.) and it is thus unlikely that the scent-marks of gerbils act in such a clearly defined way in defence of a home area. However, their presence might assist in the maintenance of some form of spatial organization (Daly, pers. camm) possibly by acting as "sign-posts" (Leyhausen and Wolff, 1959). These may modify the behaviour of the individuals that encounter them, by predisposing them to retreat in the presence of a resident (see Johnson, 1973). As yet, however, the laboratory evidence presented here has not been linked with any observations of the effect of scent-marks on individual gerbils in the wild.

(ii) Sex attractant

Marking behaviour in the gerbil is related to a number of factors which might suggest a sexual function. The ventral-gland develops fully at the onset of sexual maturity (Feldman and Mitchell, 1968) and both the behaviour and gland size show sexual dimorphism (see Section 1.5.1.). However there appear to be no seasonal changes in the female gland and excision of the gland in male and female has not been shown to affect the animals' reproductive success (Sokolov and Skurat , 1966; Mitchell, 1967). It must therefore be concluded that it plays no significant part in the gerbils' reproductive behaviour.

The secretions from the ventral-glands of female Mongolian gerbils have not been found to be any more attractive to males than those of the male, and females do not appear to be preferentially attracted to the sebum of the male (Thiessen et al (1970 a). Thiessen et al (1973) have reported similar results for M. tristrami and it is unlikely that the ventral mark of these two species has any function as a sex attractant. However, Daly and Daly (1975) noted that the urine of an oestrus female gerbil, Psammomys obesus, induced prolonged intense sniffing from males and it seems possible that urine marking may play some part in the identification of receptive females although there was no evidence of males following a urine trail towards a receptive female or of any involvement of urine marking in sexual behaviour.

(iii) Habitat labelling

It is clear that the Mongolian gerbil will scent-mark most frequently when it is presented with a novel situation, the highest rates of scent-marking with the ventral-gland being recorded in "moderately" novel environments (Baran and Glickman, 1970). Once the area is saturated with the scent-mark the rate declines until marking is rarely observed in animals in their home cage or home area (Gallup and Waite, 1970). There is little evidence to suggest that gerbils use olfactory cues within their home area for orientation, although Wilz (1975) has suggested that scent-marking operates as a negative feedback device by limiting activity in a previously explored environment. The saturation of the home area with scent could also serve to reassure the resident animal (see Section 1.5.2.) but so far there is no evidence that this happens in the gerbil. Rothenberg (1974) reported that female Mongolian gerbils will fight to defend a premarked area, although it was not clear if the experimental animals were significantly affected by the presence of their own marks or not.

Mongolian gerbils will commonly mark novel objects in their home environment almost immediately but whether this is for reassurance has never been tested.

(iv) Individual identity and recognition

Mongolian gerbils are capable of distinguishing between other gerbils on the basis of the odours of their urine (Dagg and Windsor, 1971). Halpin (1974; 1975) has shown that faeces and the ventral-gland sebum can be used by gerbils for the individual identification of other conspecifics. Recently Thiessen et al (1976) have identified a pheromone in the Harderian gland of M. unguiculatus. This they believe is rubbed onto the face during the facial groom and is investigated during the introductory nose to face sniffing behaviour when two gerbils meet; this may have a function in individual recognition.

Thiessen et al (1976) also believe that the secretions of the Harderian gland are important to the dominance status of the individual but it is not clear whether the status of the animal can be identified by the secretions from this gland, although dominants secrete greater amounts. Nor is it clear whether dominant animals can be distinguished by their scent-marks. Certainly dominant male gerbils have been observed to mark more frequently both during and after aggressive encounters with other gerbils, and subordinates tend to mark less or not at all (Thiessen et al, 1970 a; Nyby et al, 1970; Yahr, 1977). Thus it is possible that for a given group of gerbils the scent-mark of the dominant will be the most prevalent odour. It is more likely, however, that dominants could be recognised through their marks as a result of previous experience and it has already been shown that subordinates will avoid the scent-marks of the dominant animal (Nyby et al, 1970).

Wallace et al (1973) have observed that a gerbil pup carrying the scent-mark from the ventral gland of the mother has an increased chance of retrieval, thus pups may be identified using the scent-marks rubbed off the mother while they are suckling in the nest.

(v) Alarm signal

There is no evidence so far that the gerbil uses a scent-mark as an alarm signal for conspecifics.

(vi) Epideictic function

The use of scent-marks as means of monitoring the population level has never been investigated for the gerbil. There are no reports of communal marking sites or sites for defaecation from the studies so far reported for wild populations of gerbils. The effects of odours from one gerbil on the marking behaviour of another are not clear, although the depression of marking in subordinates in the presence of the dominants' odour reported by Nyby et al (1970) may be significant in this respect and thus may be a function of previous experience.

Gerbils have been reported to show a decrease in their frequency of ventral-marking in a test situation as the numbers housed together increased (Thiessen et al, 1970 a) but the significance of these results is unclear.

The functions of scent-marking in the Mongolian gerbil have not yet been fully investigated and thus there is very little evidence for many of the general functions proposed by Johnson (1973). Clearly there is a need for more research in this area but it appears that much of the work done so far has often accepted unquestioningly that the scent-marking behaviour of the Mongolian gerbil is a territorial behaviour. On the evidence presented previously (Section 1.5.2.) it is clear that scent-marking in other mammals serves a number of diverse functions and neither for other mammals nor for the gerbil has the link between territory and scent-marking been adequately demonstrated, at best a number of assumptions have been made which so far have remained untested. It is therefore the aim of the remainder of this thesis that in the following Chapters some of these assumptions will be tested experimentally with a view to elucidating the questions relating to the social behaviour and scent-marking of the Mongolian gerbil.

PREFACE TO EXPERIMENTAL CHAPTERS:-

THE GERBIL COLONY HISTORY

PREFACE TO EXPERIMENTAL CHAPTERS: THE GERBIL COLONY HISTORY

The animals used throughout the experimental work cited in this thesis were taken from a colony established in the Department of Zoology in 1971. As this was the first colony of *Meriones unguiculatus* to be set up in the department it is useful to give a brief resumé of its history.

In the autumn of 1971 five breeding pairs of *unguiculatus* were obtained from "Fisons Ltd". In May 1972 nine breeding pairs were added from a colony established at Glasgow University. By August 1972 the stock had reached its maximum size of 30 breeding pairs and was subsequently maintained at this level by careful culling. In December 1972 ten breeding pairs were incorporated from "Fisons Ltd" and until 1974, when the experimental work was completed, the stock remained stable.

MAINTENANCE

Animals were housed as breeding pairs in polypropylene cages, as supplied by "North Kent Plastics", which had large wire tops. These gave the pair a cage of 45x28x22 cms. which was found to be adequate for successful breeding. The floor of each cage was covered with wood-shavings and fresh straw was provided for use as a nest-building material. The cages were cleaned and sterilized every two weeks and the animals rehoused in clean cages with fresh straw and wood-shavings. If a litter was present this was transferred to the new cage in the old nest.

The animals were fed on rat pellets of the "Edinburgh University Diet" type and this was supplemented by a handful of mixed grain and some fresh vegetables once a week. Water was provided ad-lib.

As far as possible cages were checked every day for litters so that a fairly accurate date of birth was available for subsequent colony animals. Litters were then removed 28 days after birth, sexed, and selected animals caged as future breeding pairs. This pairing was carried out in such a manner as to reduce inbreeding in the stock.

The colony was maintained in a large, well ventilated animal-house where the temperature was held constant at 24°C (76°F). The colony-room was artificially lit by neon striplights which were controlled through a time-switch to provide a 14 hour day and a 10 hour night out of phase with the natural cycle. This was arranged so that the dark period for the colony was between noon and 10 p.m. each day thus enabling experiments to be carried out in the afternoon and during the animals' night. Cage cleaning was always undertaken during the animals' day as were movements of animals to and from the experimental rooms.

CHAPTER II

THE AGONISTIC BEHAVIOUR OF THE MONGOLIAN GERBIL I: AGONISTIC BEHAVIOUR BETWEEN PAIRS OF ADULT MALE GERBILS

2.0.0. AGONISTIC BEHAVIOUR BETWEEN PAIRS OF ADULT MALE GERBILS

2.1.0. INTRODUCTION

Interactions between adult gerbils that are strangers are characterised by a high incidence of fighting and agonistic behaviour (Schwentker, 1963; Marston and Chang, 1965; Jansen, 1968; Barfield and Beeman, 1968; Marston, 1972; Swanson, 1974). Thus in order to attempt a study of the relationship between territoriality and scent-marking it was necessary to fully understand and classify the various agonistic behaviours observed during adult gerbil interactions.

In 1951 Eibl-Eibesfeldt published data on the agonistic behaviour of the Persian gerbil (Meriones persicus persicus) and Boice et al (1969) published a little on the agonistic behaviour of Meriones unguiculatus as did Clarke in 1969. Since then a few papers have included some ethological data for unguiculatus (Wechkin and Reid, 1970; Wechkin and Cramer, 1971; Ginsburgh and Braud, 1971; Dunn, 1971). However none of these has given a full analysis of agonistic behaviour for this species. The examination of the agonistic behaviour of the Mongolian gerbil by Reynierse (1971) was perhaps the first attempt to provide systematic information for this species, but his use of a personal system of nomenclature made it difficult to apply his ethogram elsewhere and in particular made it impossible to compare the gerbil with other rodents. A similar criticism can be levelled at the study published by Majunder et al

(1974) and in fact neither of these studies provide complete information on the whole range of agonistic behaviours that were evident from observations made as a pilot study to the work reported here. Fiedler (1973) published a more comprehensive account of the agonistic behaviour in two species of gerbil but not unguiculatus. There was therefore a need to establish an ethogram for the agonistic behaviour of the Mongolian gerbil based on some established standard nomenclature, which could be used in experiments studying the territorial behaviour of the Mongolian gerbil.

The system of nomenclature chosen was based on that proposed by Grant and Mackintosh (1963) whose behaviour descriptions were devised from a synthesis of the social postures of four common laboratory rodents, the rat, mouse, guinea pig and hamster. This system was also used by Swanson (1974) in her study of the sex difference in the behaviour of Mongolian gerbils and it is obvious that the use of such standardized descriptions makes comparison easier not only between different studies of the gerbil but also between studies of other rodents that have used the same system. Other systems, notably Eisenberg (1962), are frequently used as central references in the descriptions of rodent behaviours and thus there is still no agreed standard, although a standard nomenclature system may not be feasible for all rodents.

In studying the agonistic behaviour patterns of the male gerbil in these experiments use has been made of the concept of dominance in order to examine the significance of the behaviour patterns observed before, during and after encounters. The nature of the dominance concept has been discussed before in relation to the effects of aggressive behaviour between members of the same species, and dominance was defined as a relationship between two specified individuals where one animal was dominant to the other when its behaviour was not limited by the other (Chapter I, Section 1.3.3.). This is related to aggressive superiority in many species, the more aggressive animal becoming dominant over the other. Often in a group of animals a dominance hierarchy may develop as a result of these aggressive encounters. This has been shown to occur in the Mongolian gerbil under conditions of high density, where a group of male and female gerbils, allowed to interact under semi-natural conditions, formed this type of hierarchical social organization (Gallup and Waite, 1970). It is thus reasonable to assume that when pairs of male gerbils were allowed to interact in the experiments reported here the more aggressive animal of the pair would become dominant over its opponent.

This study also aimed to look at the relationships between the agonistic behaviour and the scent-marking behaviour of the gerbil. For this reason the study was undertaken using adult-male animals only, not only because they have been generally found to have high rates of marking (see Chapter I) but also because male animals were unlikely to exhibit the changes in activity level associated with the oestrus cycle as reported for the female gerbil by Vick and Banks (1969).

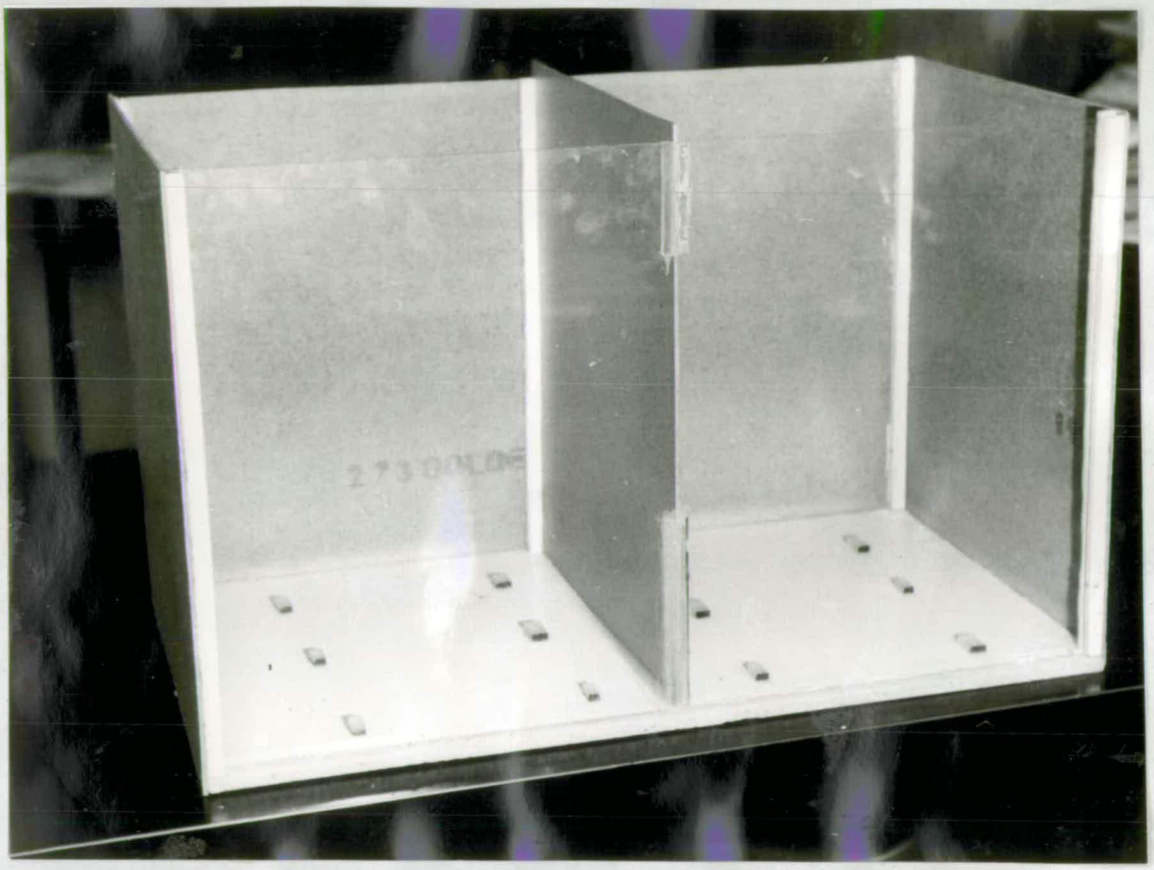


PLATE I

Apparatus used in the experiments reported in Chapter II. The front faces of the perspex pegs, attached to the wooden base of the box, were painted black so as to be visible on the video-tape recordings made during the male-male encounters.

2.2.0. MATERIALS AND METHODS

Sixteen adult male gerbils were used from the main colony. They were housed in pairs with females and were sexually experienced at the time of the experiment. Experiments were carried out in the dark phase of their day-night cycle and in a small room apart from the colony, to which animals were removed one hour before they were used in experiments in order to allow them some time to adapt to the slightly different conditions. Each animal was identified by its cage number and by a system of fur-clippings along its flanks. This clipping removed the surface hairs to reveal the black "guard hairs" which stood out as easily identifiable dark markings during the encounter experiments.

All the experiments were carried out in the apparatus shown in Plate I which consisted of a glass fronted wooden box, 70 cm. long, 40 cm. wide and 43 cm. high, which was divided into two smaller compartments (35x40 cm.) by a central, removable wooden partition. The floor of the box was coated with a white, washable paint and 12 roughened perspex pegs (2x2x0.5 cm.) were fixed to the floor, 6 to each compartment. Figure II gives a plan of the arrangement of the pegs. In each compartment three pegs were aligned close to the partition and were designated "Border" pegs while the other three were aligned close to the side wall and designated "Area" pegs. During the experiments the box was illuminated from above by a single 15 watt red light.

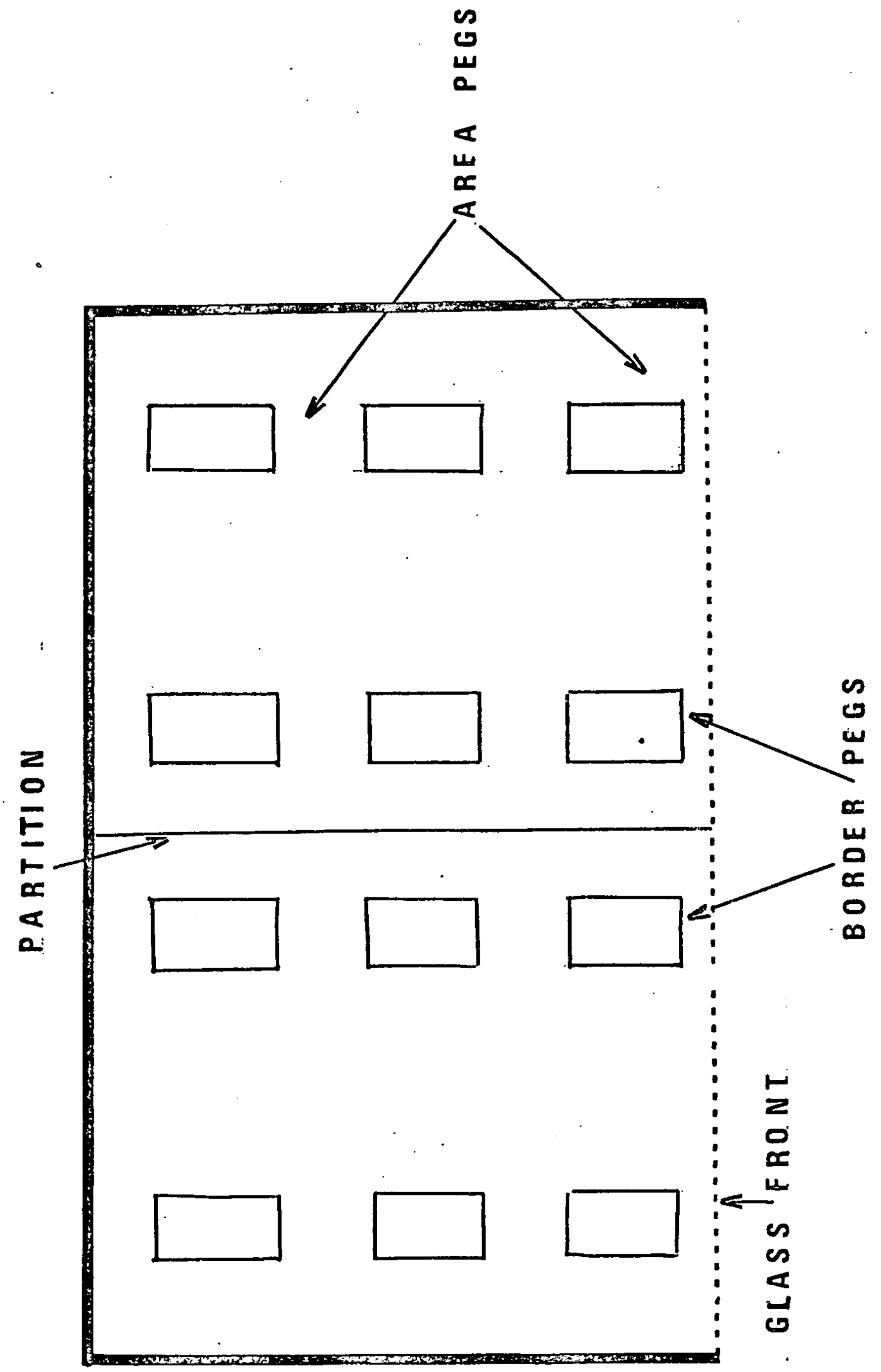


FIGURE II Plan of the test-box used in the male-male encounter experiments and the pre-trial marking sessions.
(Scale: 1cm. : 5cm.)

2.2.1. PRELIMINARY TRIALS

Ten days before the animals were used in the encounter experiments each was given a daily exposure to one compartment of the apparatus for 30 minutes. The compartment to which the animal was exposed was not varied over the ten days and this became its "home" side at the start of the subsequent encounter experiments. By the end of this ten day period eight males had been exposed only to the right hand compartment, the other eight exposed only to the left hand compartment. After each of the daily 30 minute tests the box and pegs were thoroughly washed with water and a weak soap solution, finally being rubbed down with a 70% solution of alcohol which was allowed to dry before another animal was tested in that side of the box. During these trials observations were made on the behaviour of each animal. The frequency of ventral-marking behaviour was recorded as a cumulative total for each minute and a record was kept of the occurrence of other behaviours in each trial. On day ten a recording was also made of the frequency of ventral-marking on each peg in the compartment. Once the animals had completed these preliminary trials they were weighed and an estimate of the area of their ventral sebaceous pad was made, (see Thiessen et al, 1968, Vandenbergh, 1971).

2.2.2. PAIRED ENCOUNTER EXPERIMENTS

On the day following the preliminary trials animals were assigned to pairs such that animals with a "home" side on the left were matched against animals with a "home" side on the right. At the start of the encounter experiment animals were placed in pairs each in its "home" side of the box and a 30 minute pre-trial period was allowed where no recordings were made. After this period the partition was lifted and the animals allowed to interact for five minutes. Animals were then returned to their "home" sides, the partition replaced, and observations continued for a further five minutes. The box was then cleaned, after the animals had been removed and returned to their colony cages, and another pair tested. Pairs were tested every second day in order to minimise the effect of injury during encounters and the trials lasted for 14 days i.e. 7 trials each. Throughout this experiment during the five-minute encounters and the five-minute period after encounters the animals were "filmed" through the glass front of the apparatus using a closed-circuit video camera and recording system. The video-tape recording was then replayed at a later time when the frequencies of each behaviour pattern could be recorded. A behaviour pattern was scored each time it occurred as a separate entity, i.e. if an activity was interrupted in order to engage in a different activity or resumed after a period of inactivity, it was scored again. Total frequencies that each behaviour was performed by each animal were then calculated for every minute and every trial. In the case of ventral-marking only a record of the total frequency of marking for each animal and where this occurred was made. The duration of each separate behaviour was not recorded but a record was kept of the latency in seconds to the first fight in every trial. If the animals did not fight latency was recorded as 300 seconds (Fredricson, 1951).

2.3.0. RESULTS

2.3.1. DESCRIPTION OF BEHAVIOUR CATEGORIES

The system of nomenclature devised by Grant and Mackintosh (1963) necessarily implied a relationship between certain categories since it was based on detailed analyses of social postures in the rat (Grant, 1963) and mouse. In adapting it for the guinea-pig and golden hamster they maintained that,

> "It is, in any case, doubtful whether observations on an animal's behaviour can be made without some interpretation of context".

However, although their system of nomenclature has been used extensively in this work, the same relationships between homologous behaviour categories identified in the male gerbil have not been assumed and thus the nomenclature is used only in as far as it provides a description of the form of behaviour. Full analyses and discussion of the relationships between behaviours have been included in this Chapter and Chapter III.

Although many of the descriptions provided by Grant and Mackintosh could be directly applied to the behaviour patterns observed in the male gerbil during these experiments, some behaviours were seen to be unique to this animal. Therefore in the following descriptions some other nomenclature has been used when necessary.

VENTRAL-MARKING :- A highly discrete behaviour, involving rapid approach to an object, sniffing the object, mounting it and then pressing the ventral sebaceous gland against its surface and finally a forward dismount. (Thiessen et al, (1968).

APPROACH :- Directed movement towards another animal.

INVESTIGATE :- Exploration of all regions of another animal except the face and ano-genital region.

NOSE :- Close contact of the facial region, which resembles the Prairie Dog "Identification Kiss" (King, 1955). (This may also be accompanied by "Mouth-licking" as described in other gerbil species (Fiedler, 1973), but it was not directly observed in *Meriones unguiculatus*).

SNIFF :- Exploration of the ano-genital region.

RETREAT :- Directed movement away from the opponent.

FLEE :- Flight from opponent accompanied by jumping movements.

FREEZE :- A Combination of categories "Freeze" and "Crouch" used by Grant and Mackintosh. The animal remains very still during, before or immediately after an encounter with its opponent.

FIGHT :- The animals lock together biting with teeth and holding with claws while rolling around.

CHASE :- Rapid pursuit of a fleeing or retreating animal.

CHASE-BITE :- Rapid pursuit with biting directed at the nearest part of the fleeing or retreating animal.

AGGRESSIVE GROOM :- Use of teeth and forepaws in vigorous grooming mainly of the shoulder region of the opponent whilst the grooming animal has a tendency to orientate at right angles.

CRAWL-UNDER :- Pushing the head and forepart under the other animal.

UPRIGHT-OFFENSIVE :- Animal stands on its hind legs with the fore paws in the air and head orientated towards the opponent.

UPRIGHT-DEFENSIVE :- Animal in upright position with head up or otherwise turned away from the opponent.

SIDEWAYS-OFFENSIVE :- Animal orientates broadside on to its opponent with head turned to face him.

SIDEWAYS-DEFENSIVE :- Animal orientates broadside on to the opponent with head turned away from opponent.

FOLLOW :- One animal follows the other.

SELF-GROOM :- Animal grooms head and body fur using fore-paws and mouth.

FOOT-THUMP :- (Also called FOOT-STOMP by Routtenberg and Kramis (1969)) This behaviour consists of a rapid pounding of the hind feet against the substrate to produce a staccato thumping sound (Spatz and Granger, 1970).

SQUINT :- A partial closing of an animal's eyes while in close proximity to the opponent (Wechkin and Cramer, 1971).

MOVE-AWAY :- The animal moves away from its opponent unhurriedly and explores the test box.

TAIL-RATTLE :- Originally reported for the Persian gerbil (Eibl-Eibesfeldt, 1951), vole (Clarke, 1956) and mouse (Scott, 1966). The animal's tail is flicked rapidly from side to side often producing a rattling sound on the sides and floor of the test box.

ROLLING :- Animal rolls on to its side or back in the test box and wriggles.

DEFAECATION and URINATION :- Self explanatory terms covering the elimination of faeces and urine.

SCRATCHING :- Animal scratches the test box with its fore-paws generally at the corners or edges of the box. Often accompanied by biting or licking the scratched area.

2.3.11 Analysis and Statistics.

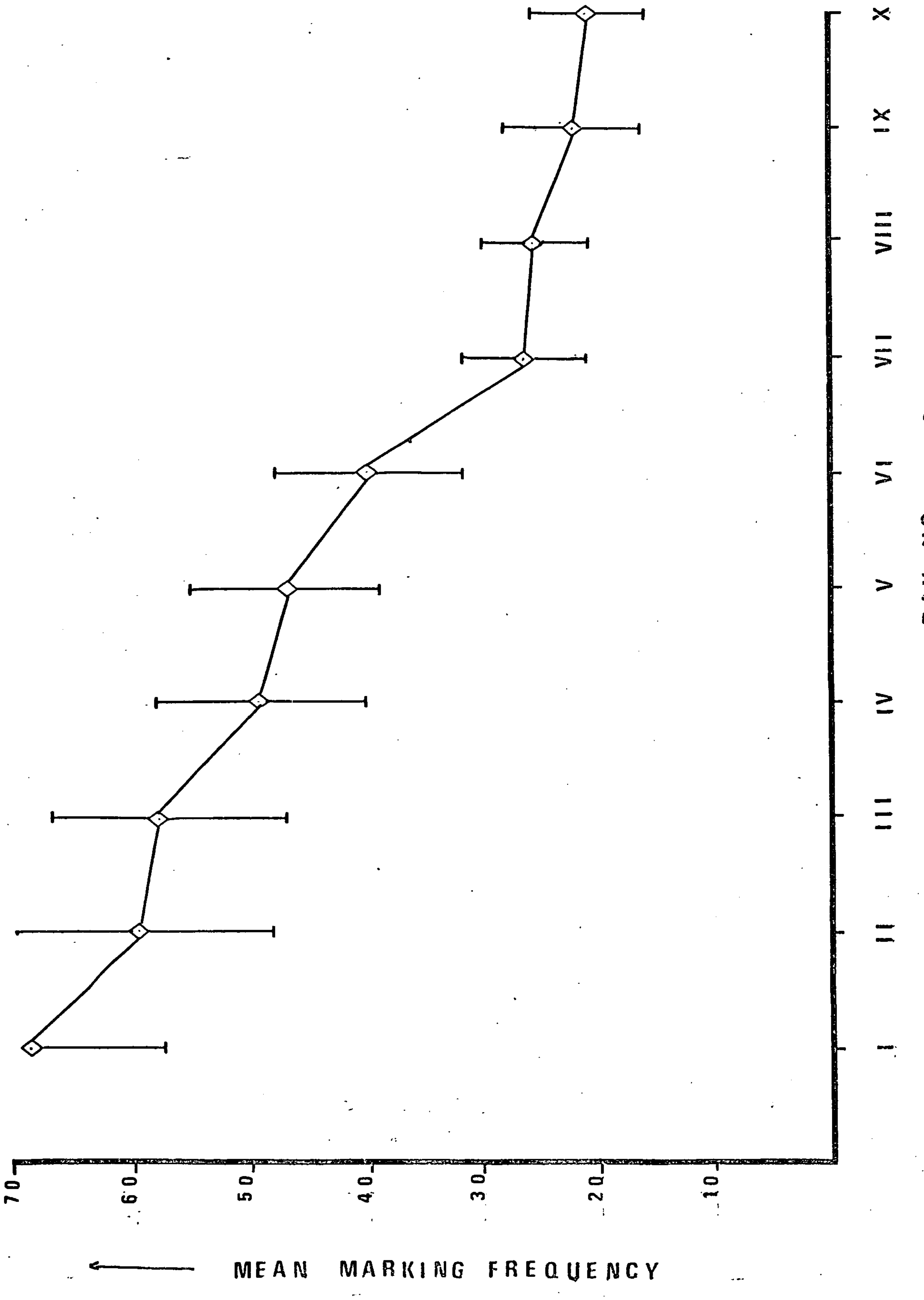
In the following analyses the sample sizes are often very small and the use of the statistics employed, e.g. Chi square, may not be entirely appropriate. They have been given as a guide to the reader and thus the "p" values should not be interpreted as a true representation of significance level.

2.3.2. RESULTS OF PRELIMINARY TRIALS

When first introduced into the experimental box all the animals were very active and explored the area thoroughly while marking almost totally on the perspex pegs. On subsequent days the animals became less active after the first five to ten minutes often performing SELF-GROOM for long periods or SCRATCHING in a corner or on a peg. Towards the end of the ten days some animals attempted to escape from the box by jumping up at the corners and this certainly gave the impression that they had thoroughly adapted to the box to the extent that it no longer offered a suitably engaging stimulus. Some animals exhibited URINATION and DEFAECATION but at low frequencies, and attempts to note the position of urine pools and faecal boli after the trials were unsuccessful since for the most part they were spread around the area by the animals' paws. ROLLING was observed in only two animals and again at low frequencies. It was therefore decided to carry out further analysis only on the data for VENTRAL-MARKING frequencies as this was by far the most frequent behaviour of the gerbils during these trials.

Over the ten days VENTRAL-MARKING frequencies declined significantly. The graph illustrated in Figure III shows the mean value for the total marking frequencies of the sixteen animals on each trial day and a regression analysis performed on this data indicated the significant decline over days ($b = -5.59$; $t = 15.28$; $df = 8$; $p<0.001$).

FIGURE III Graph showing the mean VENTRAL-MARKING frequency for 16 males over the 10, 30 minute preliminary trials.



A similar pattern can be seen if the data for each day is examined. The graphs illustrated in Figure IV indicate the mean cumulative frequencies of all 16 males for each minute for each day. In many respects each day was similar, the bulk of the marking occurring in the first six minutes, however as the days progressed the bulk of the marking appeared to be more compressed into the first 2 or 3 minutes and less and less occurred beyond this time. On Day I there also appeared to be a slight lag in the first minute until marking climbed rapidly to reach the highest value. Subsequent days did not show such an obvious lag and the rise to the highest marking frequency was during the first minute.

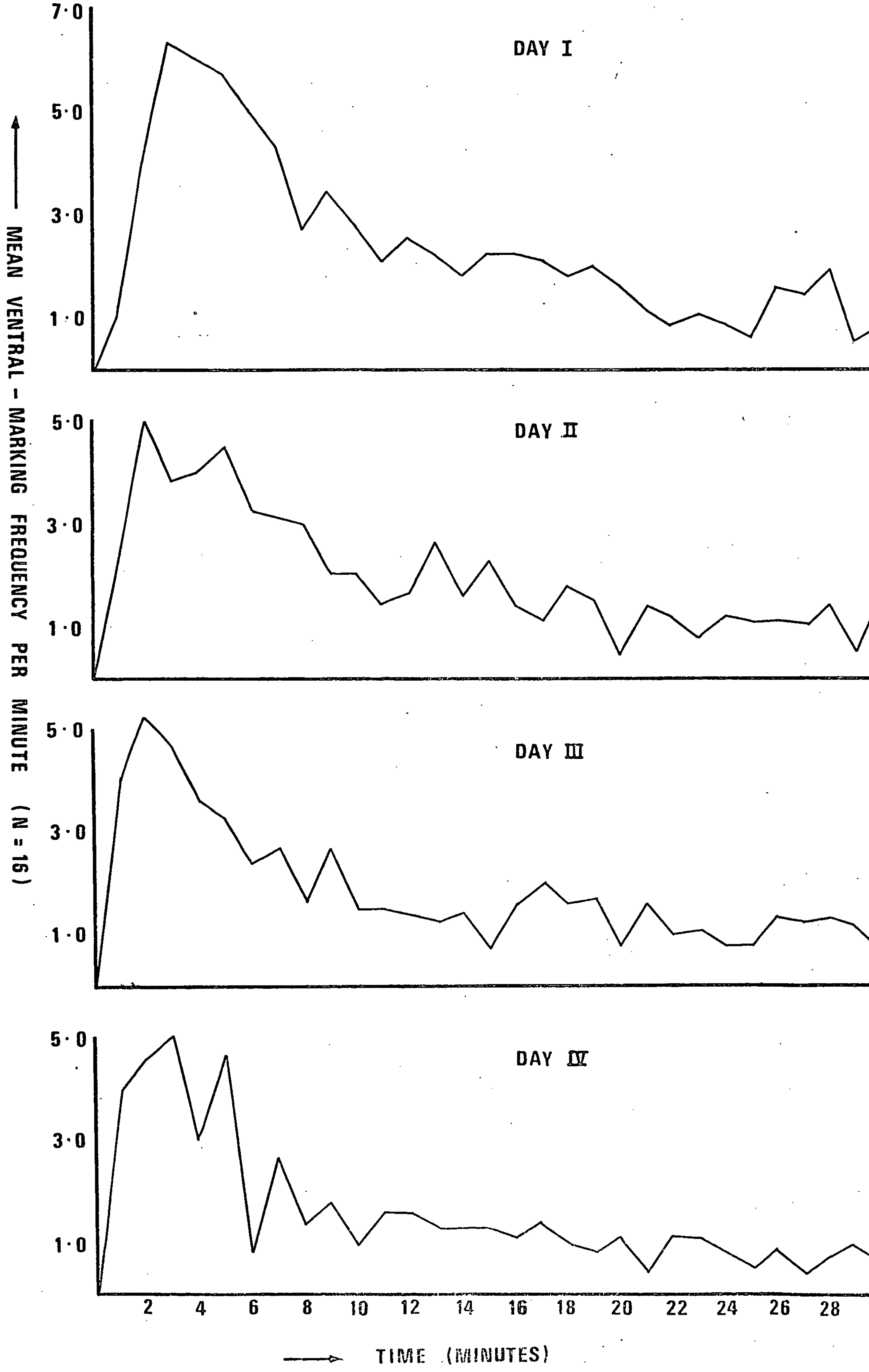
The relationships between VENTRAL-MARKING the weight and gland size of animals as recorded on Day 10 are shown in Table 2.1. The analysis was carried out on the individual totals in each case using a Spearman Rank Correlation (Siegal, 1956).

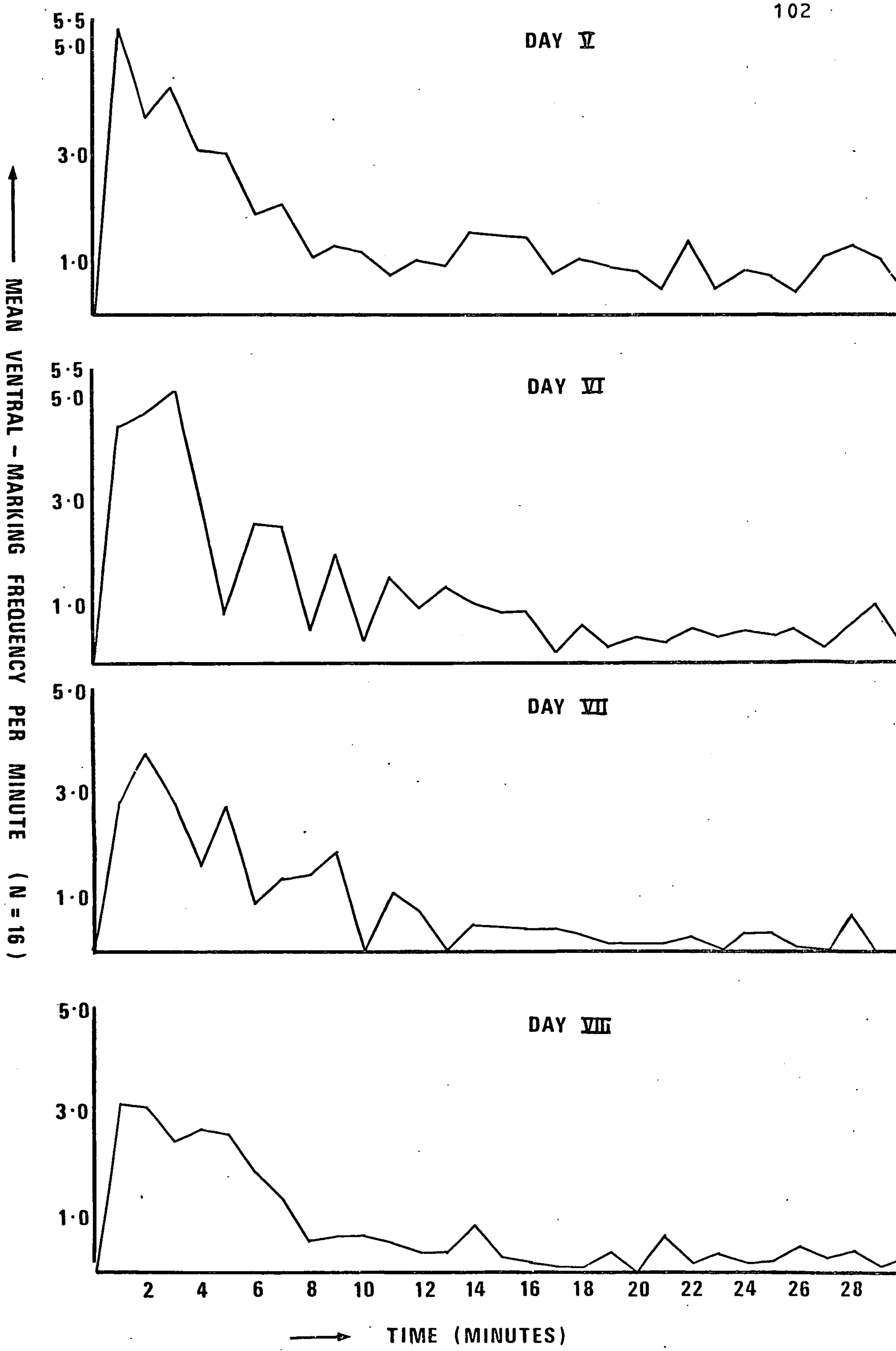
	VENTRAL MARKING (DAY I)	VENTRAL MARKING (DAY X)	GLAND SIZE (DAY X)
WEIGHT (DAY X)	0.71**	0.62*	0.69**
VENTRAL MARKING (DAY I)		0.79***	0.35
VENTRAL MARKING (DAY X)			0.42

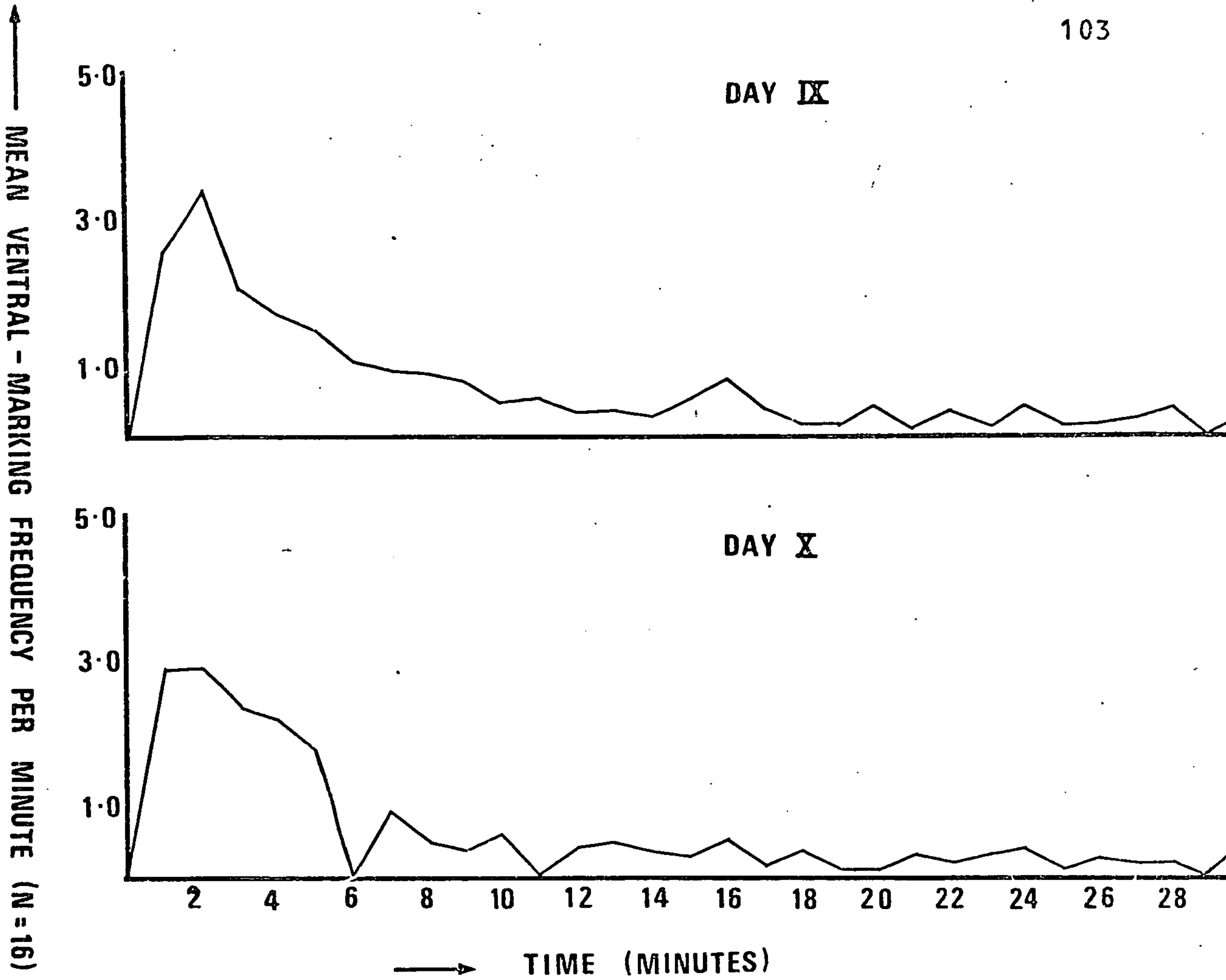
Table 2.1. Results of Spearman Rank Correlation analysis carried out between data for individuals' total marking scores on Day I and X and their weights and gland sizes on Day X.

* $p < 0.1$
** $p < 0.005$
*** $p < 0.001$

FIGURE IV. Graphs showing the mean frequency of VENTRAL-MARKING per minute for 16 males for each of the 10 preliminary trial days.


DAY I
DAY II
DAY III
DAY IV
7·0
5·0
3·0
1·0
MEAN VENTRAL - MARKING FREQUENCY PER MINUTE (N = 16)
2
4
6
8
10
12
14
16
18
20
22
24
26
28
TIME (MINUTES)


MEAN VENTRAL - MARKING FREQUENCY PER MINUTE (N = 16)
DAY V
5·5
5·0
3·0
1·0
DAY VI
5·5
5·0
3·0
1·0
DAY VII
5·0
3·0
1·0
DAY VIII
5·0
3·0
1·0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
TIME (MINUTES)


DAY IX
DAY X
MEAN VENTRAL - MARKING FREQUENCY PER MINUTE (N = 16)
5·0
3·0
1·0
5·0
3·0
1·0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
TIME (MINUTES)

It can be easily seen that the total frequency of marking on Days I and X̲ is significantly correlated to weight but not to gland size after the trials. However weight and gland size are significantly correlated as are the marking frequencies for each animal on Day I and Day X̲.

2.3.3. RESULTS OF PAIRED ENCOUNTERS

In each of the 56 encounters observed both animals were very active. In 25 encounters no FIGHT was recorded although even in these the animals chased and jumped around the box displaying a wide variety of behaviours. In thirteen encounters FIGHT occurred immediately and in the remainder it occurred sooner or later during the trial period. The latencies to the first FIGHT in every encounter are shown in Table 2.2. but the frequency of this behaviour thereafter was not recorded, chiefly because of the grossly varying lengths of individual bouts, which meant that the frequency of this behaviour during trials was not strictly the best measure of aggression. Fredricson (1951) reported that latency to fighting in aggressive encounters was a good measure of aggression, and, since data on the duration of behaviours was not collected, it was felt to be the best measure of aggression in these experiments.

TRIAL NO		1	2	3	4	5	6	7
EXPERIMENTAL PAIR	A	21	296	0	0	0	0	4
	B	15	10	12	0	0	0	0
	C	39	252	300	300	300	300	300
	D	300	300	19	65	0	5	25
	E	24	70	0	0	0	3	0
	F	300	300	300	300	300	300	300
	G	300	300	300	300	300	300	300
	H	143	295	209	300	300	300	300
		(35.5)	(38.5)	(29)	(26)	(27)	(30.5)	(32.5)

Table 2.2. Latencies (in seconds) to first FIGHT during male-male encounter trials. The latencies are given for each of the eight pairs (A - H) for each of the seven trials. An immediate FIGHT is scored as 0 while no recorded FIGHT during the trial is scored as 300. The figures in brackets beneath the trials represent the sum of ranks for each trial calculated for the Friedman Two-Way Analyses of Variance which was carried out on this data. With df = (R-1) = 6 and N = 8 x_r^2 = ~~181.6~~ 4.01 which was not significant ~~p<0.001~~.

The results of a Friedman Two-Way Analysis of Variance (Siegal, 1956) carried out on the data from Table 2.2. indicates that there are no significant differences in the time to the first FIGHT and a look at the data reveals that, of those that fought, there was a tendency for those pairs to FIGHT almost immediately in the later trials. With the exception of the category FIGHT the remaining behaviour categories were analysed in order to discover the relationship that existed between them and the concept of Dominance, which has been found to be useful in discussing agonistic behaviour and scent-marking in many species (see Chapter I).

Since there was no attempt to identify winners and losers in the relatively short encounters the criterion of dominance chosen was the frequency of CHASE behaviour. The frequency of this behaviour has been used by many authors to identify the dominant animal in encounter experiments. In the Golden Hamster Vandenbergh (1971) equated aggression with high frequencies of CHASE. Payne and Swanson (1970) defined CHASE as being indicative of a winner in a "round-robin" series of paired encounters between Hamsters of the same and opposite sex. Allin and Banks (1968) used the frequencies of CHASE and "attack" to identify dominant Lemmings in their investigations, high frequencies of these behaviours being indicative of the dominant animals. Banks and Popham (1975) used only the frequency of CHASE to identify the dominant animal in their work on the agonistic behaviour of the Lemming and Sadlier (1970) used the frequency of CHASE behaviour in Peromyscus as one of the behaviours which could be used to rank animals in order of dominance when no clear winner or loser could be observed. In Thiessen et al (1970 a) the authors report that the criterion for dominance of male gerbils in paired encounters most heavily relied on was the order of chasing. Thus it is clear that the frequency of CHASE behaviour can be used as a criterion for dominance when analysing the agonistic behaviour of rodents.

The relationships between the behaviours recorded in these encounters and the dominance criterion were examined using the Spearman Rank Correlation statistic (Siegal, op. cit. p. 202) which was used to compare the total frequencies of each behaviour for each animal with the total frequency of CHASE. Table 2.3. summarizes the results of this analysis.

BEHAVIOUR	R
APPROACH	0.69 **
INVESTIGATE	0.09
VENTRAL-MARKING	0.69 **
SNIFF	0.10
NOSE	-0.49 *
RETREAT	-0.75 **
FLEE	-0.63 **
FREEZE	0.39
CHASE-BITE	0.62 **
AGGRESSIVE GROOM	-0.04
SQUINT	0.69 **
CRAWL-UNDER	0.38
UPRIGHT-OFFENSIVE	-0.24
UPRIGHT-DEFENSIVE	-0.81 **
SIDEWAYS-OFFENSIVE	0.76 **
SIDEWAYS-DEFENSIVE	-0.62 *
FOLLOW	0.30
FOOT-THUMP	-0.51 *
SELF-GROOM	0.20
MOVE-AWAY	0.29
TAIL-RATTLE	0.77 **

Table 2.3. Summary of the results of a Spearman Rank Correlation analysis comparing total frequencies of each behaviour in each animal with total frequencies of chase. N = 16; * = $p<0.05$; ** = $p<0.01$

As a result of this analysis the behaviours were classified according to their correlation with the dominance criterion of CHASE. Table 2.4. summarizes this classification. Behaviours with significant positive correlations with CHASE are labelled dominant, those with significant negative correlations with CHASE are labelled subordinate. The remaining behaviours were not significantly correlated with this dominance criterion to allow classification in this way.

DOMINANT	SUBORDINATE	OTHERS
APPROACH	RETREAT	INVESTIGATE
VENTRAL-MARKING	FLEE	SNIFF
CHASE-BITE	UPRIGHT-DEFENSIVE	FREEZE
SQUINT	SIDEWAYS-DEFENSIVE	AGGRESSIVE-GROOM
SIDEWAYS-OFFENSIVE	FOOT-THUMP	UPRIGHT-OFFENSIVE
TAIL-RATTLE	NOSE	FOLLOW
		CRAWL-UNDER
		SELF-GROOM
		MOVE-AWAY

Table 2.4. Classification of behaviours based on the results of Spearman Correlation Coefficient analysis (see Table 2.3.). Those classified as dominant behaviours had significant positive correlations with CHASE, those classified as subordinate had significant negative correlations with CHASE. The others showed no significant correlation.

In a recent paper Dow et al (1976) highlighted the importance of describing changes in the frequencies of behaviour patterns with time. They pointed out that most functional systems in behaviour, like courtship or aggressive behaviour, are structured in time, where the frequencies of the elements comprising such systems change during the performance of the behaviour. It thus appeared necessary to examine the temporal patterns during the aggressive behaviour observed in these experiments with male gerbils and consequently further analysis was carried out on the data after identifying the dominant animal in each of the original pairs. This was done using the frequency of CHASE, the dominant animal being the one with a significantly higher frequency of CHASE on a Chi-square analysis (see Siegal, p. 42); where the frequencies of CHASE were too low a Binomial test was carried out, (Siegal, p. 36). With the exception of VENTRAL-MARKING data, which was collected differently, the mean total frequency of each behaviour for each minute and for each trial was then calculated separately for dominant and subordinate animals. Regression analyses on the data for minutes and trials were then carried out for the dominants and subordinates. Table 2.5. summarizes the significant values.

REGRESSION OVER MINUTES

DOMINANT BEHAVIOUR	b	t
APPROACH	-1.38	3.24 *
CHASE	-2.39	4.03 *
SQUINT	-0.71	4.39 *
SIDEWAYS-DEFENSIVE	0.05	3.46 *

SUBORDINATE BEHAVIOUR	b	t
FLEE	-2.58	6.17 ***
FREEZE	-0.56	6.44 ***
UPRIGHT-DEFENSIVE	-0.88	3.51 *

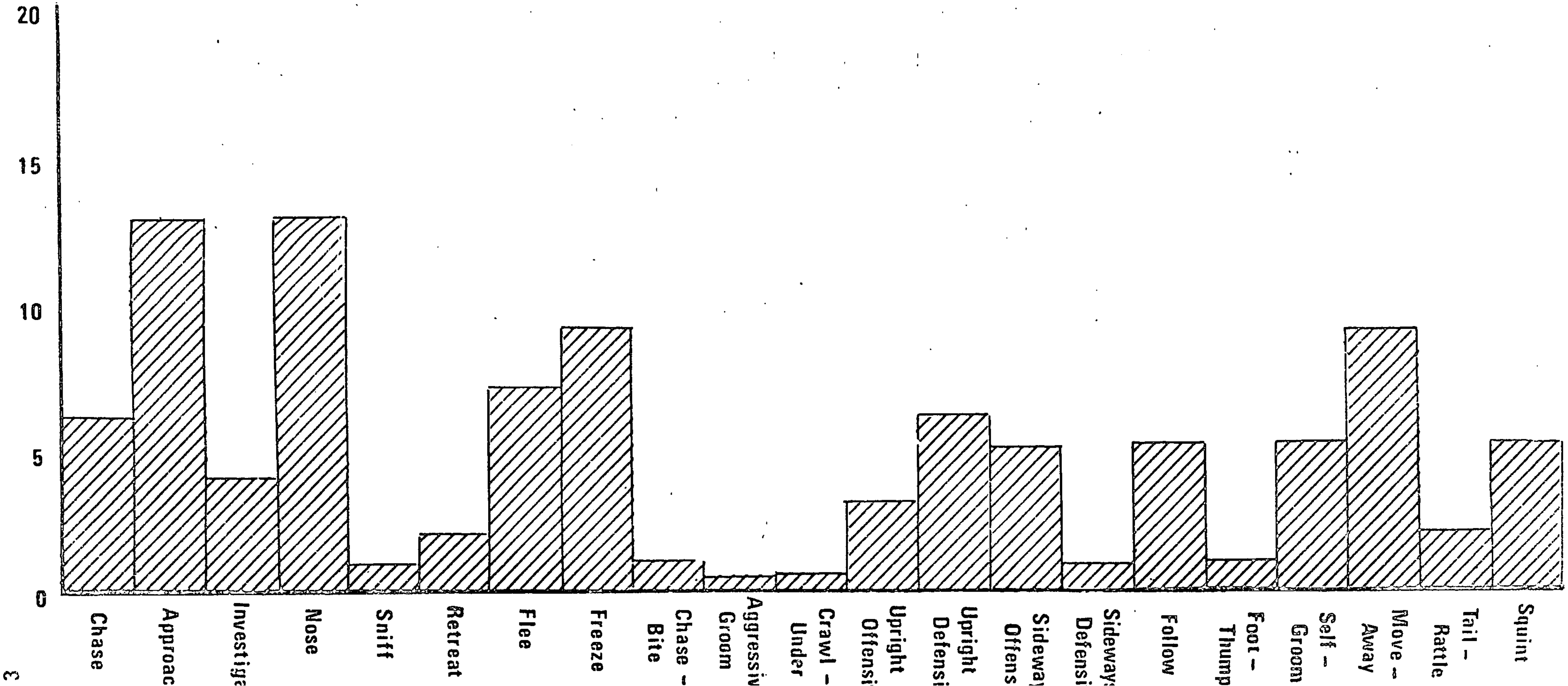
REGRESSION OVER TRIALS

DOMINANT BEHAVIOUR	b	t
RETREAT	-0.07	2.69 *
FREEZE	0.49	3.52 **
UPRIGHT-OFFENSIVE	-0.31	2.96 *
SIDEWAYS-OFFENSIVE	0.82	2.93 *
FOLLOW	-0.30	4.52 ***
FOOT-THUMP	-0.18	3.42 **
SELF-GROOM	0.23	3.35 *
AGGRESSIVE-GROOM	-0.07	3.09 *
TAIL-RATTLE	0.71	5.37 ***
NOSE	-0.52	4.63 ***

SUBORDINATE BEHAVIOUR	b	t
INVESTIGATE	-0.17	2.69 *
UPRIGHT-DEFENSIVE	1.35	9.53 ***
FOLLOW	-0.15	2.79 *
NOSE	-0.71	5.25 ***

Table 2.5. Summary of significant values of the regression analyses carried out on the mean total frequencies of each behaviour for dominants and subordinates over minutes and trials. Significance levels are indicated thus,
* $p<0.05$; ** $p<0.02$; *** $p<0.01$.

FIGURE V Male behaviours during encounters expressed as a percentage of total frequency of all behaviours except ventral marking.



Overall it can be seen that dominants showed more changes with time than subordinates. Over the seven trials the dominant animals showed decreases in the frequencies of RETREAT, UPRIGHT-DEFENSIVE, FOLLOW, FOOT-THUMP, NOSE and AGGRESSIVE GROOM, while their frequencies of FREEZE, SIDEWAYS-OFFENSIVE, SELF-GROOM and TAIL-RATTLE increased. Subordinates showed significant decreases in their frequencies of INVESTIGATE and FOLLOW as the trials progressed but increased their frequency of UPRIGHT-DEFENSIVE. Within trials dominants approached, chased and squinted less during the five minutes but showed an increase in SIDEWAYS-OFFENSIVE. Subordinates showed decreases in the amounts of FLEE, FREEZE, NOSE and UPRIGHT-DEFENSIVE over the five-minute trial periods.

A full summary of the behavioural data, excluding VENTRAL-MARKING, giving the percentage of the total behaviours that each category represented is given in Figure V.

The analysis of the data for VENTRAL-MARKING was first carried out on individual total marking frequency scores on Day X of the preliminary trials and on Day I of the paired encounter trials, both during and after the encounters. Dominants and subordinates were treated separately and total frequency scores were converted to a score of marks per minute since Day X trials were longer than both the encounter trials and the observation period after the encounters. Table 2.6. summarizes these data and a Friedman Two-Way Analysis of Variance performed on the data from dominant animals reveals that there are no significant differences in the marking rate in these three periods (x_r^2 = ~~89.81~~ 4.19, N = 8, k = 3, $p<0.$~~0000036~~20). Thus the marking rate declines from Day X levels during encounters and returns to a value slightly above these levels in the period after encounters. Subordinate animals do not mark during or after the first encounter and no analysis was necessary.

DOMINANT ANIMALS - MARKING SCORES PER MINUTE

DAY X OF PRELIMINARY TRIALS	DAY I OF ENCOUNTER TRIALS	DAY I OF POST-TRIAL OBSERVATION
2.37	2.60	4.40
0.17	0.00	0.00
1.33	0.40	2.40
1.20	0.00	0.00
0.97	0.00	2.20
1.73	4.40	5.20
0.10	0.00	0.00
1.23	0.6	7.20
(18)	(10.5)	(19.5)

SUBORDINATE ANIMALS - MARKING SCORES PER MINUTE

0.03	0.00	0.00
0.03	0.00	0.00
0.06	0.00	0.00
0.30	0.00	0.00
0.13	0.00	0.00
0.13	0.00	0.00
0.10	0.00	0.00
1.37	0.00	0.00

Table 2.6. VENTRAL-MARKING rates, expressed as a score per minute, for dominant and subordinate animals comparing rates on Day X of the preliminary trials to Day I during the paired-encounter phase and Day I during the observation phase after encounters. Figures in brackets indicate total rank scores for Friedman Analysis of Variance carried out on data from dominants.

Further analysis of the VENTRAL-MARKING data was carried out to discover if marking occurred at different locations before and after the paired-encounters. For this purpose data from Day X of the preliminary trials for the frequencies of marking on the "border" and "area" pegs for each individual was compared using the "Wilcoxon Matched-Pairs Signed-Ranks" test. This was done separately for dominant and subordinate animals and the same analysis was carried out on the data for the observation periods after encounters when individual data was totalled for all seven periods. Table 2.7 summarizes the data. The results of the Wilcoxon tests revealed no significant differences in the location of marks either before or after the encounters.

DOMINANT ANIMALS - MEAN MARKING FREQUENCIES

	BORDER PEGS	AREA PEGS	WILCOXON
DAY X	$\bar{x}$ = 17.88 SD = 13.48	$\bar{x}$ = 19.25 SD = 13.21	NS.
POST-ENCOUNTER OBSERVATIONS	$\bar{x}$ = 32.25 SD = 18.38	$\bar{x}$ = 31.88 SD = 30.93	NS.

SUBORDINATE ANIMALS - MEAN MARKING FREQUENCIES

DAY X	$\bar{x}$ = 4.88 SD = 4.37	$\bar{x}$ = 6.13 SD = 6.19	NS.
POST-ENCOUNTER OBSERVATIONS	$\bar{x}$ = 1.88 SD = 3.48	$\bar{x}$ = 2.00 SD = 5.29	Insufficient Data.

Table 2.7. Mean frequencies of VENTRAL-MARKING for dominant and subordinate animals in terms of their location before and after encounters. The locations are given as "border" and "area" referring to the perspex pegs in each animal's home area. None of the Wilcoxon tests was significant.

A similar analysis was carried out on the VENTRAL-MARKING data collected during the paired-encounter trials. The frequency of VENTRAL-MARKING for each individual was totalled over all seven encounters and the scores for marking in the "home" area compared to the scores for marking in the "opponents" area using the Wilcoxon test as before. The analysis was performed separately for dominant and subordinate animals and table 2.8. summarizes the results which show that dominant animals mark more in their opponents' area during the encounters. The data for subordinate animals were insufficient for analysis since few subordinate animals mark in these encounters.

MEAN TOTAL FREQUENCIES OF VENTRAL-MARKING DURING ENCOUNTERS

	HOME AREA	OPPONENTS' AREA	WILCOXON
DOMINANT ANIMALS	$\bar{x} = 16$ $SD = 19.67$	$\bar{x} = 45.63$ $SD = 45.71$	$p<0.05$
SUBORDINATE ANIMALS	$\bar{x} = 1.25$ $SD = 2.38$	$\bar{x} = 2.25$ $SD = 4.38$	Insufficient Data

Table 2.8. Mean total frequencies of VENTRAL-MARKING for dominant and subordinate animals during paired-encounters expressed in relation to animals' "home" area before the encounters. The results of the Wilcoxon test are also given.

The final analysis was carried out to explore the relationship between variables measured before the encounter phase of the experiment and the subsequent classifications of dominance and subordination. The data for weight, ventral-gland size and VENTRAL-MARKING score on Day I and Day X of the preliminary trials were compared between animals subsequently classified as dominant and subordinate animals using the "Mann Whitney U" test. Table 2.9. summarizes the data. The only significant difference between dominants and subordinates on these variables was in their marking scores on Day X when dominants marked significantly more.

		MARKING SCORES		
	WEIGHT	DAY I	DAY X	GLAND SIZE
DOMINANT	$\bar{x}$ = 60.80	$\bar{x}$ = 89.50	$\bar{x}$ = 34.13	$\bar{x}$ = 88.25
	SD = 2.11	SD = 52.23	SD = 21.12	SD = 32.58
SUBORDINATE	$\bar{x}$ = 59.54	$\bar{x}$ = 49.63	$\bar{x}$ = 8.13	$\bar{x}$ = 69.50
	SD = 2.80	SD = 41.41	SD = 12.65	SD = 32.19
MANN-WHITNEY "U"	NS	NS	u = 10.5 $p<0.01$	NS

Table 2.9. Data on variables prior to paired-encounter trials comparing dominants and subordinates using the Mann-Whitney "U" statistic.

2.4.0. DISCUSSION

This study was carried out in order to provide an ethogram of the agonistic behaviour of the male Mongolian gerbil. It also examined the scent-marking behaviour of this animal in relation to its behaviour during agonistic encounters. Thus for the sake of clarity the results of the main study of the agonistic behaviour and the results of the analysis of the VENTRAL-MARKING data are discussed separately.

2.4.1. AGONISTIC BEHAVIOUR

There is no doubt that the behaviour patterns exhibited by male gerbils during the paired-encounter trials are probably homologous with patterns which occur in most other rodents, particularly the laboratory rat, guinea-pig, mouse and hamster. However it is not clear whether all patterns and acts have the same significance in gerbil agonistic behaviour as they do in these other rodents.

APPROACH has been considered generally to be part of an introductory phase in the social interactions of other rodents along with the behaviours INVESTIGATE, SNIFF and NOSE (Grant and Mackintosh, 1963; Swanson, 1974). Both APPROACH and NOSE have the highest percentage of occurrence during encounters (see Fig. V) and together account for 26% of all behaviour patterns seen. If the percentage of the behaviour INVESTIGATE and SNIFF are included, these introductory acts account for 31% of all behaviours, excluding VENTRAL-MARKING. The positive correlation of APPROACH behaviour with dominance appears to agree with the findings of Reynierse (1971) who used the category "dominance-approach" in his investigations of gerbil agonistic behaviour, and it is clear from this that dominant animals exhibit higher frequencies of APPROACH and would thus be more likely to initiate interactions with the subordinate animal. The significant decline in the frequency of APPROACH by dominants during the five minutes of a trial would indicate that the dominant animals start each trial with high frequencies of APPROACH towards the subordinate possibly to identify it at least in the initial trials. However, from the analysis of the data on the latency to fighting in each trial (see Table 2.2.) it seems that as the trials progress the fighting starts earlier and thus whereas the APPROACH in the initial trials may be for the purposes of identification in the later trials APPROACH by the dominant is more likely to be to FIGHT the subordinate.

The negative correlation with dominance and NOSE behaviour is perhaps unusual, certainly if this is an introductory act as suggested it would possibly be seen more frequently in the dominant animals who would be more likely to initiate such an interaction. The significant decline in this behaviour over the seven trials for dominants and subordinates also supports the findings of Halpin (1976) who reports that the frequency of NOSE behaviour is highest in unfamiliar pairs of gerbils and thus, in the experiments reported here, as the animals become more familiar with each other over the seven trials therefore the frequency of NOSE behaviour declines. Thiessen et al (1976 a) have identified a pheromone in the Harderian glands of the Mongolian gerbil's face which stimulates investigation by conspecifics and it is probable that the investigation of the facial region in the behaviour NOSE is for the purpose of individual recognition (see Chapter I). However its association with subordination in this experiment may indicate other functions for the postures associated with NOSE in the subordinate animal which are worthy of further investigation.

Neither of the two behaviours INVESTIGATE and SNIFF show any significant association with dominance or subordination. INVESTIGATE would certainly aid in individual recognition since the fur and ventral gland of a gerbil contains odours from scent-gland pheromones, faeces and urine from the bedding material and gerbils have been shown to be capable of discriminating between such odours from different animals (Halpin, 1974). SNIFF behaviour would also provide similar information to the animals but its low frequency of occurrence in these male-male encounters seems to support the suggestion that this behaviour has a function during male-female sexual behaviour (Grant and Mackintosh, 1963).

The behaviours that were positively correlated with dominance can also be viewed as being equated with aggression in these encounters (see Section 2.3.3.). There is no doubt that CHASE-BITE is a highly aggressive act, in the Guinea-pig and Hamster Grant and Mackintosh (op. cit.) observed that this behaviour replaced attack and Allin and Banks (1968) include the element CHASE-BITE in their definition of attack behaviour in the Collared-Lemming. Lerwill and Makings (1971) point out that there is an exaggeration of CHASE behaviour in the Golden Hamster when agonistic encounters occur in confined areas and thus the absence of a behaviour classified as "ATTACK" in the experiments carried out here may be a combination of the tendency for gerbils to CHASE-BITE rather than attack in confined areas and the classification system used which puts CHASE-BITE as a separate element from one labelled ATTACK.

The partial closing of the eyes in the behaviour SQUINT is also related to the dominance status of the individual. Reynierse (1971) and Swanson (1974) both found that this behaviour in the gerbil was indicative of a defensive animal, yet Johst (1967) reports that partial eye closure in Clethrionomys is also related to dominance. During the trials it was noticed that SQUINT often occurred during the SIDEWAYS-OFFENSIVE posture and this has also been observed in the gerbil by Dunn (1971). The SIDEWAYS-OFFENSIVE posture was also found to be correlated with dominance in these trials and it is likely that this behaviour is indicative of an aggressive animal as it is in other rodents (Grant and Mackintosh, 1963). SQUINT may therefore be part of an aggressive behaviour sequence performed by an animal on the offensive.

The behaviour pattern TAIL-RATTLE is the final behaviour that correlated significantly with dominance. This behaviour has been observed in other species of gerbil (Eibl-Eibesfeldt, 1951; Fiedler, 1973) but its function appears to be unclear. Eibl-Eibesfeldt (1950) described it as an expression of excitement in the mouse related to the activation of the "aggressive drive" and Clarke (1956) invoked a similar suggestion for the same behaviour in the vole. In the mouse it has been suggested that tail-rattling is a signal which elicits fighting (St. John, 1973), although recent authors do not believe that it has any function in communication but merely acts as an external indicator of general stress (Haber and Simmel, 1976).

Of those behaviours that were negatively correlated with dominance, FLEE, RETREAT, SIDEWAYS-DEFENSIVE and UPRIGHT-DEFENSIVE, it would seem that these findings are in general agreement with the findings for other rodents. One would expect subordinate animals to be less aggressive in the presence of the dominant and thus the finding that subordination is characterized by higher levels of these defensive postures is not surprising. Chance (1962) believes that the UPRIGHT and SIDEWAYS-DEFENSIVE postures, where the head is turned away from the opponent, act as a "cut-off" mechanism in an aggressive situation. The turning away is a means of cutting-off the aggressor from the view of the subordinate thereby reducing the tendency to retreat particularly where there is limited space in which to retreat.

FOOT-THUMP, the staccato drumming of the hind feet on the floor of the test box, was also associated with subordination. Reynierse (1971) observed that this behaviour was indicative of a dominant animal. Routtenberg and Kramis (1967) observed that the foot-thumping occurred after cessation of a rewarding brain stimulation, during sexual behaviour (before and between intromissions) and in association with foot-shock. They concluded that FOOT-THUMP was an aversive response to cessation of reward. Swanson (1974) found it to be generally associated with the responses to threat by other animals and it would seem that this would support the findings here since subordinates would be more likely to be threatened than dominants.

With regard to the temporal patterning of behaviour in both dominant and subordinate animals (Table 2.5.) it is apparent that different trends occur both during trials and over trials between the two animals. Dominant animals show significant decreases over trials in behaviours associated with subordination (RETREAT and FOOT-THUMP) while significant increases are seen in certain of the dominant elements (SIDEWAYS-OFFENSIVE and TAIL-RATTLE). Perhaps in response to the increase in SIDEWAYS-OFFENSIVE subordinates show a significant increase in their frequency of UPRIGHT-DEFENSIVE.

Within trials the dominant animals start each trial with high levels of CHASE and subordinates with high levels of FLEE, both of which decrease over the five minute trial period along with SQUINT and UPRIGHT-DEFENSIVE. It would seem therefore that the decrease in the aggressive element CHASE would suggest a general decrease in aggression by the dominant as a trial progresses which is mirrored in the subordinates' decrease in the frequency of FLEE.

From these findings it would appear that as the trials continue dominant animals become more dominant, increasing certain offensive elements in their behaviour, while decreasing defensive subordinate elements. The subordinates become more defensive over the trials. However at the start of each trial the highest levels of CHASE and FLEE are seen probably associated with fighting and thus occur closer and closer to the start of every trial. This could be seen as a way of re-establishing the dominance relationship between the pairs, as it is in Polecats (Poole, 1974), after which the relationship is maintained by an increase in the ritualized, offensive-defensive postures while the tension of this situation is reflected in the increases in TAIL-RATTLE and FOOT-THUMP over the trials. The familiarity of the opponents during these encounters would also be important. Poole and Morgan (1975) found that male mice attacked familiar opponents less than unfamiliar ones over a period of 25 days and Davis (1975) found that the highest frequencies of attack were in the first few trials of paired-encounter experiments using male Degus (Octodon degus). Both authors suggest that familiarity is responsible for the variability of aggression observed in encounters of this type where animals are repeatedly exposed to each other.

2.4.2. VENTRAL-MARKING

When placed in the experimental apparatus during the ten preliminary trials, the VENTRAL-MARKING response of the male gerbil was easily the most striking behaviour pattern. After Day I, however, it is clear that the frequency of this response declines eventually (see Fig. III) and some animals no longer mark in the area. Over the same period Thiessen et al (1969 a) reported that male gerbils show a significant increase in marking but his results come from trials of five minute duration using a much larger area than that used here and thus are probably not directly comparable. However the decreases seen in these experiments agree with the observations of Higgins et al (1967) who report that in a thoroughly familiar home cage the VENTRAL-MARKING rate of male gerbils is low. Baran and Glickman (1970) suggest that the novelty of an environment is one factor that might affect the VENTRAL-MARKING response and report that the highest rates of marking are seen in gerbils placed in moderately novel environments. In their observations on the marking of male gerbils they report a time lag at the start of the initial day of testing and this was also observed here (see Fig. IV, Day I). Baran et al (op. cit) suggest that the novelty value of a perfectly strange environment does not immediately produce marking because of the competing responses of olfactory, visual and locomotion exploration. Once the area is familiar these competing responses for exploration decline and marking with the ventral gland becomes the dominant response until it habituates with repeated exposure to the test situation.

The social and physiological factors involved in the marking behaviour of the gerbil revealed in the other data point to a more complex explanation for the causal factors and function of marking. Although there was no significant correlation between marking frequencies and the size of the ventral gland Thiessen et al (1968) found that not only were gland size and marking rates correlated but both were directly related to the amount of testosterone administered to castrate males. Mykytowycz (1965) reports a similar correlation between gland size and marking in his study of the chin-marking behaviour of the rabbit and further reports that marking frequencies were positively correlated with weight. This second finding is supported by the results of this experiment for the weight of the gerbil on Day X was correlated with marking frequencies at the start and finish of the trials.

However neither weight nor gland-size measures were directly associated with the outcome of the paired-encounter trials and dominant animals showed significant differences from subordinates in their marking rates only on Day X. Thiessen et al (1970 a) also report similar findings for the male gerbil where neither weight nor gland-size correlated with dominance during paired encounters. Weight and flank-gland size have been demonstrated to be good predictors of the outcome of social encounters in Golden Hamsters where the heavier animal with the larger gland is most likely to become dominant (Payne and Swanson, 1970; Drickamer et al, 1973). Nevertheless the correlation between VENTRAL-MARKING frequency and dominance agrees with other observations on the gerbil (Thiessen et al, 1971 b) and in general with data for other species e.g. Guinea pig (Beauchamp, 1974), Hamster (Johnston, 1975 a, 1975 c) and rabbit (Mykytowycz, 1962). Ralls (1971) suggests that in general marking frequency is positively correlated with dominance. It is interesting to speculate why this might be the case in these experiments particularly since the dominant animals could not be identified by their initial marking rates on Day I of the preliminary trials. One might postulate that these final marking rates were directly related to the levels of testosterone in these animals because the stimulus of the arena, i.e. the novelty value of the arena, was virtually nil. That testosterone is both related to marking frequency and aggression has been shown by Lumia et al (1975) and Thiessen et al (1970 a) found that high marking animals tend to become dominant particularly if they have high androgen levels. The marking behaviour of dominants and subordinates during and after the first encounter is also very different. It is clear that subordinate animals do not mark at all on the first day although dominant animals show significant differences in the amount of marking before, during and after the encounter (see Table 2.6.). Maruniak et al (1974) suggest that the increase in urinary marking in mice with exposure to other males, after this response had been habituated, is a direct result of the increase in novelty value of the apparatus due to the presence of a strange animal. This may account for the increase in marking by dominants after the first encounters observed here particularly as a result of the olfactory stimuli left by the subordinate in the area. Maruniak et al (1975) report that olfactory cues are a primary modality in detecting biological novelty for mice and it may well be similar in the gerbil, particularly as dominant animals also mark more frequently in the opponents' (subordinates) home area than their own during encounters, and this would be where the most novel olfactory stimuli would be. Nevertheless this does not preclude the possibility that marking by the dominant has some significance for the subordinate. The fact that subordinate gerbils do not mark during or after encounters may well be as a result of the dominants' olfactory markings. Nyby et al (1970) proposed that olfactory cues from dominants inhibited the marking of a subordinate animal after its defeat by the dominant although recently Yahr (1977) reports that visual cues i.e. those provided by the area in which the subordinate was defeated play an important part in subordinate marking rates. She found that although the test area was cleaned subordinates refused to mark although they would do so in a neutral area even when odours from the dominant gerbil were present.

2.5.0. CONCLUSIONS

During five-minute paired-encounter trials male Mongolian gerbils exhibit a variety of agonistic behaviours which are probably homologous with agonistic behaviour patterns which have been identified in a number of other common laboratory rodents. It is possible, using the criterion of dominance based on the frequency of CHASE behaviour, to identify clusters of behaviour patterns that characterize the agonistic behaviour of dominants and subordinates in these situations although many of the behaviour patterns identified do not appear to relate so obviously to dominance in these situations. The familiarity of opponents in these experiments may be one factor influencing the changes in frequency of certain behaviours in particular the increase of the ritualized offensive-defensive postures over the trials.

As in agreement with the findings reported for other species, VENTRAL-MARKING was found to be correlated with dominance, but neither weight nor the size of the animals ventral-gland pad were found to be correlated with dominance. The direct association of the marking frequencies of males on the final day of the preliminary trials with their eventual status in the encounter trials may be connected with the level of testosterone in these animals. However the factors influencing marking behaviour may be a combination of social status and the novelty value of the environment. Changes in the marking frequency with time can be explained on the basis of the declining novelty of the environment. The fact that dominant animals mark more frequently in the subordinates' home area during encounter trials could be due, at least in part, to the relative olfactory novelty of that area.

The findings reported in this Chapter give an outline of the agonistic behaviour patterns observed in male gerbils during the paired-encounter trials. Chapter III further examines these behaviours in an attempt to obtain a more complete picture of these behaviour patterns using both male and female animals under different conditions.

CHAPTER III

THE AGONISTIC BEHAVIOUR OF THE MONGOLIAN GERBIL: II

AGONISTIC BEHAVIOUR BETWEEN TWO PAIRS OF ADULT MALE AND FEMALE GERBILS

3.0.0. AGONISTIC BEHAVIOUR BETWEEN TWO PAIRS OF ADULT MALE AND FEMALE GERBILS

3.1.0. INTRODUCTION

Chapter II investigated the agonistic behaviour patterns of adult male gerbils in confined conditions. In this Chapter the agonistic behaviour patterns of both male and female gerbils under different conditions are studied.

Colvin (1973) in his study of the agonistic behaviour in five species of the vole Microtus reported that, although there was no difference in the character of the postures and movements of the agonistic behaviour when different amounts of space were available for interaction, he observed differences in the frequency of occurrence of these postures and movements when the area in which encounters took place was reduced. Lerwill and Makings (1971) suggested that in confined spaces Hamsters show an exaggeration of the chasing phase during agonistic encounters. As yet no study of the effect of the amount of available space for interaction on the agonistic behaviour patterns of the gerbil has been carried out although it has been suggested that the density of animals may be an important factor influencing the social behaviour of gerbils (Chapter I, Section 1.3.3.).

The differences between the aggressive behaviours of male and female gerbils have been studied by a number of authors. Norris and Adams (1972 a) reported that the incidence of fighting between pairs of unfamiliar gerbils was significantly higher in male-male encounters (70%) than in male-female encounters (16%) or female-female encounters (10%). In contrast Spencer et al (1973) observed the same frequency of fighting between pairs of gerbils, whether of the same or opposite sex; the main variable which influenced fighting was whether the animals had been isolated before. Nyby et al (1970) and Thiessen and Dawber (1972) reported that female gerbils defended their home cage against intruders as actively as males and Norris and Adams (1972 b) found that males were often attacked and killed by females particularly if she was older. Swanson (1974) suggested that gerbils resemble hamsters insofar as females are as aggressive as males and reported that in mixed-sex-encounters the agonistic behaviour was markedly increased due to the aggressiveness of the female, usually in response to sexual investigation by the male.

Swanson (1974) also reported that males never attacked females during mixed-sex encounters and this inhibition of attack on a female appears to be common to males in a number of species (Moyer, 1972). Payne (1974 a) observed that intact female hamsters evoked little aggression from males and suggested that this was due to hormone-dependent odour cues possibly in the urine or flank-glands of the female which inhibited attack by the male (see also Mugford and Nowell, 1970 a; 1970 b; Stehn et al, 1976; Dixon and Mackintosh, 1975, 1976).

The aggressiveness of the female gerbil may also be influenced by her hormonal state and in particular whether she is pregnant or lactating. Moyer (1968) listed maternal aggression as a major type of agonistic behaviour and Gandelman (1972) reported that, when pregnant or lactating, female mice may become aggressive, although they rarely show any aggressive tendencies at other times. Noirot et al (1975) also reported that pregnant female mice showed significantly more aggressive behaviour towards male intruders than did virgin females. So far, however, there has been little attention paid to possible changes in female gerbil aggressive behaviour during pregnancy or lactation. Vick and Banks (1969) observed activity changes during the normal oestrus cycle of female gerbils and found that wheel-running activity peaked during vaginal oestrus and it is possible therefore that other behavioural changes may occur during pregnancy and lactation.

The hormonal state of the female may also affect the behaviour of the male in particular in relation to female pregnancy and the presence of the young. Elwood (1977) observed that naive males, housed with non-pregnant females, when presented with a gerbil pup, treat it as food. However they respond in a paternal manner when their mate becomes pregnant. Rood (1974) reported that male mongooses play an important role in guarding young at the den while the female forages for food. In the Mongolian gerbil Thiessen (1968) noted "that while the male may take no active part in the care of the offspring, it can safely be left with the female throughout the reproductive cycle". Fiedler (1973) also observed extensive involvement of the male in nesting with the young in *M. crassus* and *M. tamariscinus* suggesting that such behaviour may be widespread in this genus. She also reports that males of these two species defend the young. It is likely therefore that changes in the aggressive behaviour in both sexes may be observed when the female is pregnant, or lactating when young are present.

Gallup and Waite (1970) observed that in a group consisting of eight male and seven female gerbils, maintained under "semi-natural" conditions in the laboratory, an hierarchical dominance order formed. It was therefore possible that,under the laboratory conditions that would exist in the experiments to be reported here, a dominance hierarchy would form within a group of gerbils. These experiments, however, had been designed not only to study the agonistic behaviour between pairs of gerbils, but also in an attempt to examine possible territorial behaviour in this species. (These results will be reported in Chapter IV.) Therefore the methods adopted in the design of these experiments were necessarily a compromise, where the balance between whether the animals formed territories or hierarchies, given a finite amount of space (see Chapter I), was shifted as far as possible to try to induce the formations of territories and reduce the possibility of the formation of dominance hierarchies. Thus the use of a concept of dominance to examine the agonistic behaviours of the two sexes would not be appropriate. Instead the data would be analyzed on the basis of an animal's relative aggressiveness towards another specified animal.

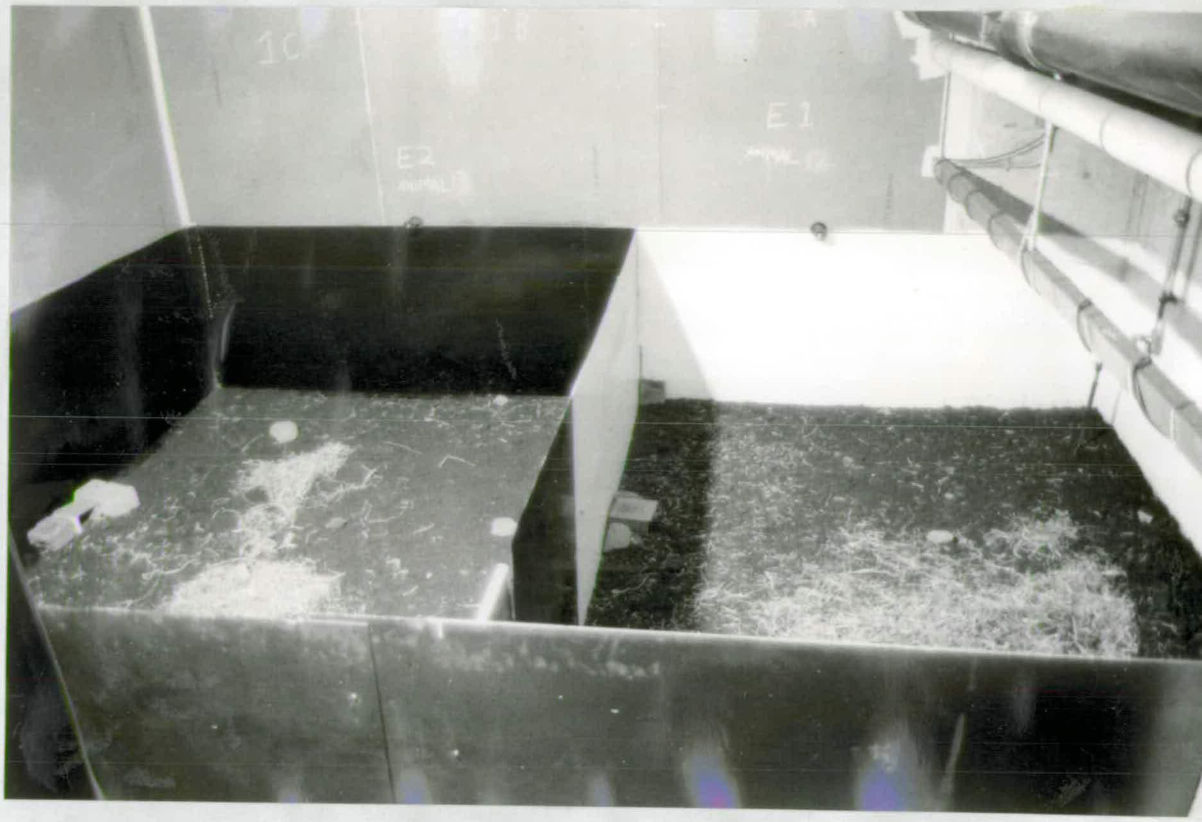


PLATE II

Arena used in experiments reported in Chapters III and IV viewed from behind position normally taken up by the observer. The top of the removeable wooden partition between the two areas is just visible. The alternative nest site X2 in area E2 has been displaced to give a view of the entrance. The nest boxes (NB) and water holders (W) are obscured by the front of the arena in the foreground.

FIGURE VI KEY.

E1 and E2 - Large areas making up the main body of each half of the arena.

B1 and B2 - Border areas adjacent to the partition and of equal size (900 sq. cm.)

B - That area that was obscured by the partition when the areas were closed and more precisely the border area when the areas were open.

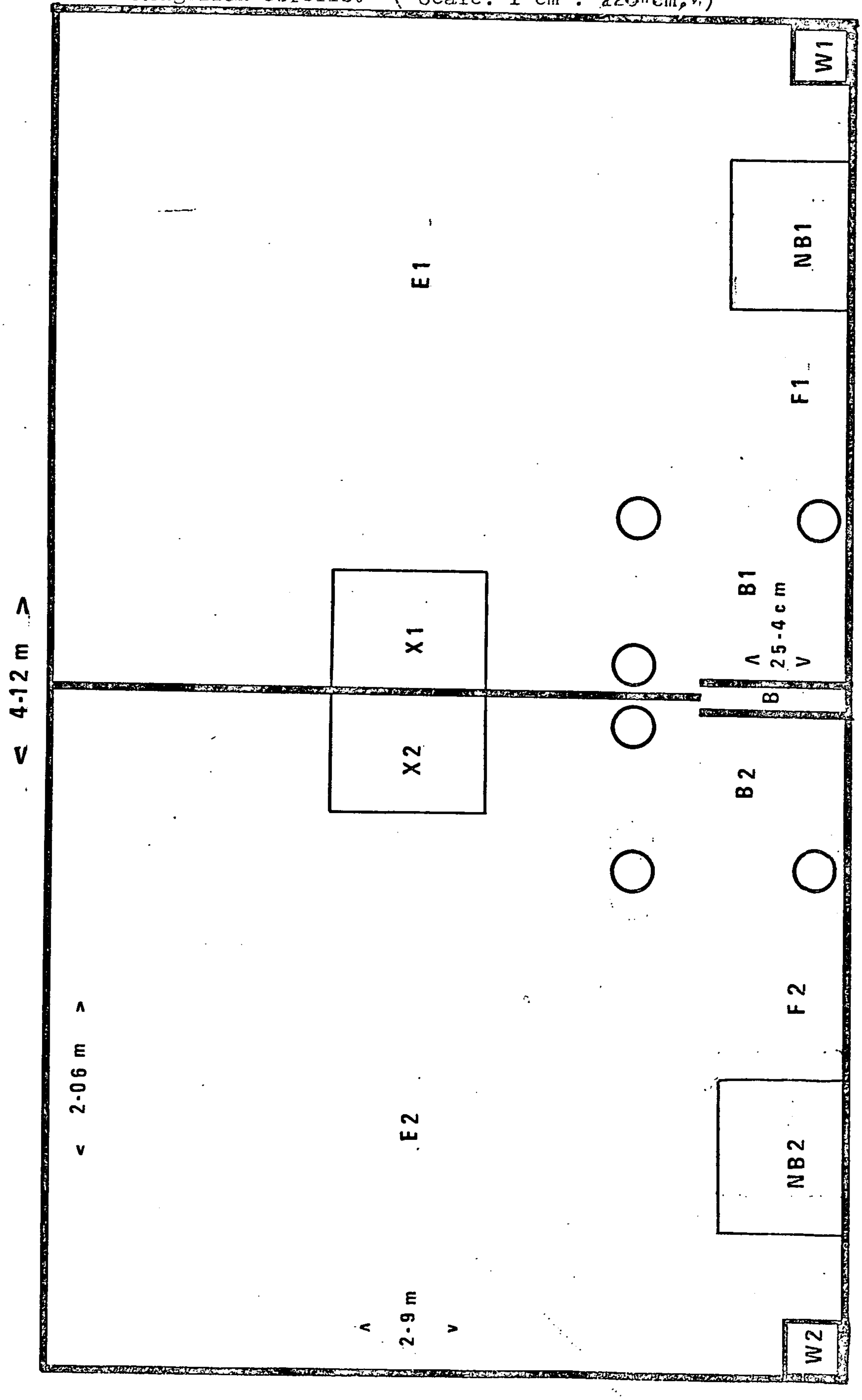
NB1 and NB2 - Two large wooden boxes, filled with straw and with three access holes bored in their sides. These acted as nesting boxes for the pairs.

X1 and X2 - Areas surrounding smaller wooden and rock shelters which had only one entrance and were provided as alternative nesting sites.

F1 and F2 - Those areas where food was placed.

W1 and W2 - Wooden holders for the glass water bottles.

FIGURE VI Diagram of the arena used in the experiments on the Induction of Territorial Behaviour between pairs of Mongolian Gerbils. (Scale: 1 cm : 220 cm)



3.2.0. MATERIALS AND METHODS

3.2.1. EXPERIMENTAL CONDITIONS

22 adult, breeding pairs of Mongolian gerbils, of known age, were used. All were from the Zoology Department colony (see Preface to Experimental Chapters) and were identified by clip-marks on the fur of their flanks and head. During the experiment these animals were maintained on the same diet as the colony.

The apparatus consisted of a large rectangular arena with a total area of 11.94 sq. m. and bounded by sheet-metal walls approximately 90 cm. high (see Plate II and Fig. VI). This area was divided in half by a sheet-metal wall, 90 cm. high, and a single, removeable, wooden partition (see "B" in Fig. VI) connected the two areas giving an access of 25.4 cm. wide and 90 cm. high. This narrow partition, once removed, localised interactions and facilitated observations.

It proved impractical to subdivide the two areas using a grid system because of the difficulties of recording detailed behaviour and detailed position with one observer; instead a number of areas were specified according to the plan shown in Figure VI. B1 and B2 were designated border areas and were marked with three large stones (shown in Fig. VI as circles) to give equal areas of approximately 900 sq. cm. on each side of the partition. Region B was that area where the partition was normally placed and was more precisely the actual border between Areas 1 and 2.

F1 and F2 were small areas where the food was regularly placed during the experiment and NB1 and NB2 were large wooden nest boxes, filled with straw and having three access holes bored in them. W1 and W2 were two wooden holders containing glass water-bottles. Areas X1 and X2 surrounded two shelters of rocks and wood provided as alternative nesting sites; these were smaller than the nest boxes and had only one entrance. The remaining space in the arenas was simply designated E1 or E2 but was by far the largest area. The floors of the arenas were covered in a layer of peat one inch thick and straw and small stones were scattered randomly around it.

The arenas were contained in a room in the basement of the Zoology Department which was next to the boiler house. This provided a constant temperature in the room of 25°C (80°F) which was slightly warmer than the colony room. The room was light-proof and kept on the same dark/light photoperiod as the main colony; however, during the dark phase, illumination was provided by four 60 watt, red bulbs which remained on throughout. Because conditions in the experimental room were slightly different a one month acclimitization period was allowed for the animals to adjust to these different temperatures and the constant "red-light" dark phase before observations were made.

3.2.2. EXPERIMENTAL METHODS

Each experiment lasted seventeen days and involved two pairs of gerbils, one pair in each half of the arena. The experiments were started during the dark phase of the day/night cycle when the animals were weighed and one pair was introduced into one half of the arena. This pair was then observed for one hour and the process immediately repeated for the second pair. For the next six days observations were continued for a period of half an hour for each pair per day. These observation periods started at the same time each day during the animals' "night" and at the same time of "night" as the initial, hourly observations. In case the experimenter disturbed one pair while observing the other, each pair was observed first on alternate days. Thus observations were continued over a period of seven consecutive days during which time the frequencies of VENTRAL-MARKING, URINATE and HIND-DIG (a digging behaviour described in Section 3.3.1.) were recorded for each animal. When both pairs had been observed on each day the nest-boxes in the areas were checked for the presence of litters.

On the eighth day the second phase of the experiments was started. At the same time of "night" as the previous seven days of observation the wooden partition between the two areas was raised giving the animals access to each other. Once this had been done the experimenter recorded the behaviour of the four animals by speaking quietly into a taperecorder, a method which did not disturb the animals at all. Recordings continued until the trial was terminated, which was for one of the following reasons:

a) A fight occurred, lasting more than 30 secs., when the animals were separated, returned to their own areas and the partition replaced.

b) An animal was being chased, bitten and exhibited a high frequency of submissive behaviour (as identified in Chapter II), the trial was then terminated after fifteen minutes [as in (a)] .

c) Animals interacted, without fighting and without exhibiting high frequencies of dominant or submissive behaviours, for one hour [as in (a)] . This time limit was based on the limitation imposed by the length of tape on the cassette taperecorder used and on the difficulty of maintaining accurate observations continuously on four animals for over an hour.

Once each trial was concluded the animals were returned to their own areas and the partition replaced, observations were then continued for a further fifteen minutes and the frequencies of the behaviours VENTRAL-MARK, URINATE and HIND-DIG were recorded. These observations were made on each pair simultaneously during this fifteen minute period. At the end of this period the nest-boxes and where necessary other nesting sites were checked for litters.

These trials continued for ten consecutive days and then the experiment was terminated. In some cases the whole experiment was terminated after a trial had continued for an hour (see (c)) and the rationale for this is described in Chapter IV. Once the experiment was over the animals were removed from the arena, together with any litters, weighed and returned to the main colony room. The floor and walls of the arena were then thoroughly cleaned with soap and water, fresh peat, straw and stones laid down and another two pairs of gerbils introduced one week later. Eleven replicates of this experiment were carried out.

The frequencies of each behaviour performed by each animal were transcribed verbatim into specially prepared check sheets. This gave data of a sequential nature but it was not accurate enough for sequential analysis since a time base was only provided every 30 secs. when a pulse from a timing device was automatically recorded onto the tape while observations were being made. Much of the data was then prepared for analysis by computer as described in the next section.

3.3.0. RESULTS

3.3.1. BEHAVIOUR CATEGORIES

In order to assist the analysis of the data by computer, the behaviour patterns observed were designated "Directed" or "Non-directed". Directed behaviours were those where both the animal performing the behaviour (the subject) and the animal to whom the behaviour was directed (the object) could be identified (e.g. subject, male A CHASE object, male B). Non-directed behaviours were those where only the performing animal (the subject) could be identified (e.g. subject, male A FOOT-THUMP). A list of each of these types of behaviour pattern is given below. Many of these behaviours had been identified and described during the male-male encounter experiments reported in Chapter II but some had only occurred in this experiment. Accordingly a description is only provided for those behaviours that were only seen here. As in the previous experiments the basic nomenclature system used was that of Grant and Mackintosh (1963).

3.3.1. a. DIRECTED BEHAVIOUR

APPROACH
NOSE
CHASE
FLEE
RETREAT
FIGHT
SIDEWAYS-OFFENSIVE
SIDEWAYS-DEFENSIVE

SQUINT
FOLLOW
INVESTIGATE
CHASE-BITE
UPRIGHT-OFFENSIVE
UPRIGHT-DEFENSIVE
CRAWL-UNDER
SNIFF
AGGRESSIVE-GROOM

ATTACK:- An animal rapidly approaches its opponent, often leaping on the opponent, biting at the face or neck while kicking with the hind feet. This behaviour is probably replaced by CHASE and CHASE-BITE when the interaction takes place in confined conditions (Chapter II).

AVOID:- An animal watches the movements of its opponent closely while in the FREEZE posture then moves-away from the vicinity of the opponent even though no interaction has taken place.

ATTEMPT-MOUNT:- Any attempt at mounting an animal in which there are pelvic thrusts, but falling short of a complete copulatory act.

FULL-AGGRESSIVE:- Comparable to the behaviour of the same name in the rat, the aggressive animal orientates at right angles to and over the opponent's body without biting.

3.3.1. b. NON-DIRECTED BEHAVIOURS

VENTRAL-MARK
FREEZE
TAIL-RATTLE
SELF-GROOM
FOOT-THUMP

HIND-DIG:- The performance of this behaviour seems to be related to the availability of a sawdust or peat substrate and has been seen previously in mice and Collared Lemmings (Allin and Banks, 1968) where it has been best described. It is different from digging in both form and intensity. The head is typically held up nearly level with the back while vigorous strokes of the forelegs propel peat backwards past the side of the animal. Peat may be piled up under the body and the hind feet are then used to expel it. This display does not appear to be directed at the sides or corners of the arena and occurs away from obvious places used for ordinary digging.

DIGS:- This is the ordinary digging referred to above and replaces the category SCRATCHING in Chapter II.

EXPLORE:- An animal moves around its environment sniffing at objects, sometimes digging around or biting them.

URINATE:- A specific behaviour sequence associated with the elimination of urine (Reider and Reynierse, 1971). Seen in both sexes, the animal squats on its hind legs while urine is passed. The front paws are then used to scratch peat over the urine pool. The whole sequence may take up to fifteen seconds after which the animal moves off. Although urine pools could not be seen, because of the absorbent peat substrate, it was assumed that when this behaviour sequence occurred urine had been passed.

SQUEAK:- A high-pitched sound given when an animal was being chased or when it was threatened while cornered.

FEED:- An animal holds food in its forepaws while gnawing with its teeth. These acts also occur in other circumstances e.g. paper shredding or straw shredding, but were only scored as FEED when they occurred with obvious food material e.g. grain, vegetable, rat pellets.

FULL-SUBMISSIVE:- The animal lies on its back completely motionless. On one occasion it was seen to continue after the opponent had moved off but more generally it occurs when the more aggressive opponent is in the FULL-AGGRESSIVE posture. This behaviour has been described previously for the rat and the golden hamster (Grant and Mackintosh, 1963).

SIT:- Animal sits on the floor of the arena on its hind legs often with the front paws off the floor and the body almost upright.

3.3.2. RESULTS OF SEVEN-DAY FAMILIARISATION PROCEDURE

There was a marked difference between the behaviour of the pairs on day 1, during their first hour in the arena, and the other six days, during the half-hour observation periods. When first introduced the pairs began exploring their new environment, thus exhibiting long bouts of the behaviour pattern EXPLORE, covering the whole of the area available. This was accompanied by high levels of VENTRAL-MARKING throughout the whole area. There were few signs that the animals were fearful of the larger and novel environment although one or two animals went into seizure when first placed in the arena. Goldblatt (1968) and Thiessen et al (1968) report that these seizures are fairly common throughout colonies of Mongolian gerbils. These seizures lasted up to ten minutes in some cases and the start of observations was delayed until the animals had recovered. At the same time the other animal of the pair was removed to its cage until its mate had fully recovered. The animals did not establish a nest in this first hour but on the following day a nest had always been established in the nest box provided. Often the entrances to the box were sealed with the peat; the animals were sometimes seen re-sealing these entrances by pushing peat with their nose or throwing it up with their hind paws so as to cover the entrance holes with a small mound of peat and stones. The establishment of the nest on the days after their first introduction to the arena was also accompanied by a distinct change in behaviour. The pairs became very timid and retreated to their nest when disturbed. Their retreat was often accompanied by FOOT-THUMP from inside the nest box. This change in the behaviour of gerbils once a nest or burrow has been established has also been reported by Thiessen (1973). Pilot studies carried out prior to the experiments reported here also attempted to allow animals to establish a burrow system but the same problem was encountered and animals tended to remain in their nests and burrows almost continuously, only coming out from time to time to feed, although large stores of food were found in parts of the burrow system.

The changes in the activity and disposition of the gerbils were also reflected in the frequencies of VENTRAL-MARKING in both male and female (Table 3.1.) where the highest frequencies of marking in both sexes occurred on the first day.

MEAN FREQUENCIES OF VENTRAL MARKING / HALF HOUR PERIOD

	DAY	1*	2	3	4	5	6	7
MALE	$\bar{x}$	73.25	6.13	0.15	1.4	4.5	3.23	2.45
	SD	41.75	10.43	0.53	2.33	7.83	6.23	2.70
	N	22	8	13	10	12	13	11
FEMALE	$\bar{x}$	7.93	0.14	0	0.08	0	0.23	0
	SD	9.69	0.34	0	0.27	0	0.49	0
	N	22	14	15	12	13	13	12

Table 3.1. Mean total frequencies of VENTRAL-MARKING per day for male and female gerbils during their first seven days in the experimental arena.
N, the number of animals observed on each day is also given since animals were often inactive in their nest box during these observation periods.
* The frequencies of VENTRAL-MARKING on day 1 have been converted to frequency scores per 30 minutes in order to compare them to the scores on other days.

Table 3.1. also shows that on the days following their introduction (Days 2 - 7) often as many as half of the animals remained in their nests while those that were active marked very little in the half-hour. Female gerbils rarely marked at all after day 1. The difference in marking frequency was also apparent when the total frequencies of VENTRAL-MARKING over the seven days, for males and females, were compared using the Mann-Whitney "U" test. This showed that males marked more than females ($\bar{x}$ male = 154.95; S.D. male = 88.16; $\bar{x}$ female = 16.36; S.D. female = 19.16; M.W.U. $z = 4.19$; $p<0.0003$). The total frequency of VENTRAL-

MARKING during this period also correlated significantly with the initial weight of the animals in males only (Spearmans R = 0.61; N = 22, $p<0.05$); in females the Spearman Rank correlation coefficient was not significant (R = -0.058, N = 22; p NS).

The frequencies of the behaviours HIND-DIG and URINATE were too low for analysis but table 3.2. summarizes the data, where it is apparent that males perform these behaviours more than females.

TOTAL FREQUENCIES OVER SEVEN DAYS		
	HIND-DIG	URINATE
MALE	71	29
FEMALE	2	8

NUMBER OF ANIMALS OBSERVED PERFORMING BEHAVIOUR		
	HIND-DIG	URINATE
MALE	3	10
FEMALE	1	5

Table 3.2. Summary of data for behaviour patterns HIND-DIG and URINATE during the first seven days of the experiment. Both the total frequency of each behaviour for each sex and the number of animals observed performing these behaviours are given.

3.3.3. RESULTS OF THE TEN-DAY, SECOND PHASE

In the second phase of this experiment the trials involved removing the wooden partition between the two areas thus giving animals access to each other and the whole of the arena. On the first day that the partition was removed the pairs showed the same wariness that they had been showing during the previous six days and often a long time elapsed before a member of one or other pair began to move cautiously into the neighbouring area. If the animals or in some cases both animals of the pair did not come in contact with their neighbours immediately they began to explore and mark this neighbouring area but still behaved cautiously. The first contact between neighbours often resulted in a short fight but on two occasions this initial fight was long enough to have the bout terminated. The timing of the trial commenced when at least one animal had emerged from its box. These initial encounters produced a number of changes in the behaviour of the pairs after the trial had been terminated. After the first encounter it was clear that the animals had become more active and were less timid. An upsurge in digging behaviour throughout the arena was apparent during the 24 hour periods between each trial. This was obvious from the way in which the peat had been thrown into heaps, particularly in the middle of the areas and around the partition, leaving the concrete floor of the room exposed. The straw was also completely shredded. The animals' response to the experimenter also changed after the first few days of this second phase, rather than retreating to their nest boxes when disturbed the animals often came out, some actually waiting at the partition for the start of the trial.

During the first day of trials with the areas open to one another there was no significant upsurge in the rate of VENTRAL-MARKING (as expressed as number of marks/min.) over the rate observed on the final day of the seven day familiarisation period. None of the females marked on the seventh day and only one on the first day of the "open area" trials. The mean rate of VENTRAL-MARKING for males on the final day of familiarisation as opposed to the first day of the "open area" trials was not significantly different when individual rates were compared using the Wilcoxon Matched-Pair Signed-Ranks test (mean rate on day 7 = 0.082; S.D. = 0.09; mean rate on first "open area" trial = 0.34; S.D. = 0.64. N WILCOXON = 9, T = 14 p NS).

The trials themselves took a number of different forms after the first day. Some trials were characterized by a great deal of activity from two or more animals with long bouts of the behaviour sequence CHASE-FLEE interspersed with HIND-DIG and finally culminating in a long fight. In these types of trial it was not clear if one animal was dominant over the other or if one pair was dominant over the other. Other trials were characterized by long periods of exploration by members of both pairs in their neighbours' area similar to their behaviour when first introduced into their home areas. These periods of exploration were accompanied by marking behaviour and terminated when the members of the two pairs met. This resulted either in fights or chasing bouts. In one of the eleven experiments one pair became obviously dominant to the other and both members chased and attacked their neighbours relentlessly until they were totally submissive. Such behaviour was occasionally observed on single days with other pairs. In only two of the eleven experiments did the animals interact for a whole hour without serious fighting. These particular experiments will be discussed more fully in Chapter IV but it was clear in these cases that neither pair was dominant to the other in the hour-long interaction. The long periods of CHASE-FLEE and APPROACH-RETREAT that were observed in these experiments centred around the border areas and each animal tended to retreat rapidly into its own area if it had just chased the neighbour too far back into the neighbouring area.

Fighting occurred in 94 out of the 101 trials run. Of the seven trials that no fighting was observed two were terminated after the hour criterion period and five were terminated after fifteen minutes because of the complete dominance of one pair over the other. The time to the first fight between two animals from different pairs was calculated. A regression analysis was then carried out over the ten trials using a mean value of "time to first fight" as calculated for each trial. This showed that there was no significant increase or decrease in the latencies to the first fight in each trial over the ten days (b = 0.00074; t = 0.035; df = 8; p NS). The data is summarized in Table 3.3.

	DAYS									
	1	2	3	4	5	6	7	8	9	10
$\bar{x}$	837.00	619.09	236.72	210.00	252.01	255.00	184.29	410.00	522.86	934.29
S.D.	712.51	707.19	165.73	206.27	193.11	191.77	117.21	245.76	463.88	1101.71
N	10	11	11	11	10	10	7	9	7	7

Table 3.3. Mean latencies (in seconds) to the first fight between members of different pairs over the ten days of experimental trials.
N = the number of experiments used to calculate each mean value since two experiments were terminated before the tenth trial and some trials in others were stopped (see text)

Table 3.3. also clearly shows the large amount of variability in the time taken to the first fight in each trial. 43 of these "first fights" were also long enough to terminate the trial, which further highlighted the variable nature of this data from experiment to experiment.

The frequencies of the various behaviour patterns seen in the males and females during the trials were then analyzed separately.

The relationships between the various behaviours and a criterion of aggression was investigated for each sex. The criterion used was the frequency of the behaviour CHASE and its use as a criterion for identifying aggressive animals has been discussed before (Chapter II, Section 2.3.3.) where a high frequency of CHASE behaviour in an animal is indicative of high aggression (see also Section 3.1.0.)

The total frequencies of each behaviour over all the trials for each individual were compared to the individuals' total frequencies of the behaviour CHASE over all the trials using the Spearman Rank Correlation Coefficient. This comparison was done separately on the data for males and females. Table 3.4. summarizes the data.

	MALES	FEMALES
BEHAVIOUR	R	R
APPROACH	0.68**	0.50*
NOSE	0.41*	0.20
FLEE	-0.53**	-0.69**
RETREAT	0.14	0.15
ATTACK	0.48*	0.76**
FIGHT	0.23	0.51**
SIDEWAYS-OFFENSIVE	0.51**	0.65**
FOLLOW	0.65**	0.50*
INVESTIGATE	0.14	0.33
CHASE-BITE	0.71**	-
SNIFF	-0.29	0.01
HIND-DIG	0.48*	0.81**
VENTRAL-MARKING	0.04	0.66**
EXPLORE	0.55**	0.02
SIT	0.12	0.22
FREEZE	-0.01	-0.17
URINATE	0.07	-
SQUEAK	-	-0.48*
TAIL-RATTLE	0.31	0.48*
SELF-GROOM	0.23	-
FOOT-THUMP	-0.18	-

Table 3.4. Summary of the results of a Spearman Rank Correlation analysis comparing total frequencies of each behaviour in each animal with total frequencies of CHASE. N = 22; * = $p<0.05$; ** = $p<0.01$

The results of these analyses made it possible to classify the behaviour patterns according to their relationship with the frequency of "CHASE" criterion of aggression. Those that had significant positive correlations to the criterion were labelled as indicative of high aggression, while those with significant negative correlations to the criterion were labelled as indicative of low aggression. Other behaviours remained unclassified.

Table 3.5. lists the behaviours for male and female animals according to this classification scheme.

	HIGH AGGRESSION	LOW AGGRESSION	OTHERS
MALE	APPROACH	FLEE	RETREAT
	NOSE		FIGHT
	ATTACK		INVESTIGATE
	SIDEWAYS-OFFENSIVE		SNIFF
	FOLLOW		VENTRAL-MARKING
	CHASE-BITE		SIT
	HIND-DIG		FREEZE
	EXPLORE		URINATE
			TAIL-RATTLE
			SELF-GROOM
			FOOT-THUMP
FEMALE	APPROACH	FLEE	NOSE
	ATTACK	SQUEAK	RETREAT
	FIGHT		INVESTIGATE
	SIDEWAYS-OFFENSIVE		SNIFF
	FOLLOW		EXPLORE
	HIND-DIG		SIT
	VENTRAL-MARKING		FREEZE
	TAIL-RATTLE		

Table 3.5. Classification of behaviour patterns based on the results of the Spearman Rank Correlation analysis (see Tables 3.4.; 3.5.) for males and females. Those classified as indicative of high aggression had significant positive correlations with the CHASE criterion, those classified as indicative of low aggression had significant negative correlations with the criterion. The others showed no significant correlations.

A number of differences in the relationships of some of the behaviour patterns to the aggression criterion were evident between males and females. The behaviour pattern NOSE was indicative of high aggression in males only. In females the data for NOSE was insufficient for this type of analysis. The behaviour pattern FIGHT was indicative of high aggression in females only whereas the behaviour pattern CHASE-BITE correlated with aggression in males, but there was insufficient data for analysis in females. The frequency of the behaviour pattern EXPLORE was insufficient for analysis in the female but was indicative of high aggression in the male. VENTRAL-MARKING was only indicative of high aggression in females. Only the behaviour pattern FLEE was indicative of low aggression in both sexes, but in females low aggression was also indicated by the frequency of the behaviour pattern SQUEAK. Other behaviours were not related to the aggression shown by the animals and many did not provide sufficient data for analysis.

Table 3.6. provides a summary and comparison of the most frequent behavioural acts and postures seen during these ten-day trials for males and females. The comparison was carried out using a Mann-Whitney U test on the total frequencies of each behaviour for individual males with the total frequencies of each behaviour for individual females. The significance levels are given in the table and these reveal that males show a higher frequency than females in the behaviour patterns APPROACH; NOSE; FIGHT; FOLLOW; VENTRAL-MARKING; FREEZE and SQUEAK. Females show higher frequencies than males for only one behaviour pattern, FLEE.

	TOTALS (N = 22)				
BEHAVIOUR	MALE	RANGE	FEMALE	RANGE	P
APPROACH	666	2-84	278	1-44	<0.007
NOSE	260	1-24	118	1-12	<0.004
CHASE	346	0-59	128	0-25	NS
FLEE	209	0-39	250	0-42	<0.02
RETREAT	481	1-85	348	0-57	NS
ATTACK	85	0-15	27	0-6	NS
FIGHT	123	0-9	56	0-8	<0.005
SIDEWAYS-OFFENSIVE	62	0-17	42	0-6	NS
FOLLOW	162	0-31	40	0-14	<0.001
HIND-DIG	392	0-73	130	0-59	NS
VENTRAL-MARK	427	0-74	82	0-17	<0.007
EXPLORE	174	0-19	90	0-16	NS
SIT	78	0-14	38	0-27	NS
FREEZE	127	0-16	44	0-9	<0.02
URINATE	73	0-26	9	0-4	NS
SQUEAK	43	0-36	22	0-7	<0.03
TAIL-RATTLE	36	0-15	18	0-7	NS
FOOT-THUMP	30	0-18	4	0-3	NS

Table 3.6. Summary of total frequencies of behaviours seen in both sexes over the ten-day trials. Only those behaviours where the frequencies for each sex were sufficient to carry out a Mann-Whitney U test are given. The U test was carried out on individual totals for each sex over the ten trial days and the "P" values are given.

Further analyses were performed on those behaviour patterns previously classified as "Directed Behaviours" (see Section 3.3.1. a). The total frequencies with which animals performed each behaviour as the subject animal were calculated for each of the following interactions:

a) MALE as subject to MALE neighbour as object

b) MALE as subject to FEMALE neighbour as object

c) FEMALE as subject to MALE neighbour as object

d) FEMALE as subject to FEMALE neighbour as object

e) MALE as subject to FEMALE mate as object

f) FEMALE as subject to MALE mate as object

Comparisons, using the Wilcoxon Matched-Pairs Signed-Ranks test, were then carried out between the individual frequencies of conditions a) and b); c) and d) and e) and f) for each directed behaviour pattern where the data allowed. Table 3.7. gives the results of these comparisons for the male interactions with neighbouring males and females.

MALE AS SUBJECT	MEAN FREQUENCY TO NEIGHBOUR (N = 22)			
BEHAVIOUR	$\bar{x}$ MALE	S.D.	$\bar{x}$ FEMALE	S.D.
APPROACH	13.09	10.42	10.14	9.87
NOSE	5.41	5.76	3.36	5.02
CHASE	7.82	10.18	7.22	8.81
FLEE**	6.73	10.07	2.09	3.46
RETREAT*	13.86	16.34	7.18	8.82
ATTACK	2.32	2.96	1.41	1.61
FIGHT***	3.90	2.13	1.64	1.85
SIDEWAYS-OFFENSIVE	1.91	3.62	0.68	1.22
SQUINT	(2)	-	(3)	-
FOLLOW	3.77	6.05	2.55	4.13
INVESTIGATE	(23)	-	(6)	-
AVOID	(27)	-	(6)	-
CHASE-BITE	(9)	-	(7)	-
UPRIGHT-DEFENSIVE	(2)	-	(3)	-
CRAWL-UNDER	(0)	-	(1)	-
UPRIGHT-OFFENSIVE	(5)	-	(3)	-
ATTEMPT-MOUNT	(0)	-	(2)	-
SNIFF	(9)	-	(9)	-
AGGRESSIVE-GROOM	(1)	-	(0)	-
FULL-AGGRESSIVE	(0)	-	(0)	-

Table 3.7. Mean frequencies of male directed-behaviours toward male and female neighbours. Figures in brackets are total frequencies of each behaviour where the data was insufficient for analysis using the Wilcoxon Matched-Pairs Signed-Ranks test on individual frequencies for each behaviour.
Significance levels are for a one-tailed test, * = $p<0.025$; ** = $p<0.01$; *** = $p<0.005$.

There are few significant differences apparent in Table 3.7. Males APPROACH, NOSE, CHASE and ATTACK the neighbouring males and females with no apparent difference in frequency. However, males FLEE and RETREAT from the neighbouring males more frequently than they do from the neighbouring female. Males also FIGHT more with the neighbouring male than with the female but there are no differences in the frequencies with which males perform SIDEWAYS-OFFENSIVE and FOLLOW in interactions with the neighbouring male and female. Females APPROACH, NOSE, CHASE, FLEE, ATTACK, FIGHT and FOLLOW the neighbouring males and females with no apparent difference in frequency but RETREAT significantly more from the neighbouring males (Table 3.8.).

Table 3.9. summarizes the results of interactions between the members of mated pairs during the experiment. It is clear that the data is scanty indicating the low frequency of interactions within a pair, accounting for 11.85% of all male interactions and 11.44% of all female interactions (see also Table 3.10) and the only two behaviour patterns for which analysis was possible, APPROACH and NOSE indicate that males APPROACH and NOSE their female mates significantly more than females APPROACH and NOSE their male mates.

Table 3.10. summarizes the data for all interactions between animals involving directed behaviours, where the total frequency of all these behaviours for each animal have been calculated and a mean value for each sex has been given.

FEMALE AS SUBJECT	MEAN FREQUENCY TO NEIGHBOUR (N = 22)			
BEHAVIOUR	$\bar{x}$ MALE	S.D.	$\bar{x}$ FEMALE	S.D.
APPROACH	6.45	7.50	3.22	3.65
NOSE	3.00	3.16	1.45	2.10
CHASE	3.36	4.29	2.73	4.57
FLEE	6.36	9.02	2.82	5.50
RETREAT***	11.00	13.91	3.86	4.24
ATTACK	0.73	0.91	0.55	0.99
FIGHT	1.45	1.71	1.04	1.40
SIDEWAYS-OFFENSIVE	(23)	-	(16)	-
SQUINT	(1)	-	(0)	-
FOLLOW	1.00	2.92	0.32	0.69
INVESTIGATE	(5)	-	(1)	-
AVOID	(23)	-	(6)	-
CHASE-BITE	(3)	-	(8)	-
UPRIGHT-DEFENSIVE	(7)	-	(0)	-
CRAWL-UNDER	(0)	-	(0)	-
UPRIGHT-OFFENSIVE	(4)	-	(0)	-
ATTEMPT-MOUNT	(0)	-	(0)	-
SNIFF	(5)	-	(1)	-
AGGRESSIVE-GROOM	(0)	-	(0)	-
FULL-AGGRESSIVE	(3)	-	(0)	-

Table 3.8. Mean frequencies of female directed-behaviours towards male and female neighbours. Figures in brackets are total frequencies of each behaviour where the data was insufficient for analysis using the Wilcoxon Matched-Pairs Signed-Ranks test on the individual frequencies for each behaviour.
Significance levels are for a one-tailed test, *** = $p<0.005$.

MEAN FREQUENCY TO MATE (N = 22)

BEHAVIOUR	SUBJECT ANIMALS $\bar{x}$ MALE	S.D.	$\bar{x}$ FEMALE	S.D.
APPROACH*	5.68	5.46	2.91	2.79
NOSE***	4.95	5.22	2.18	2.42
CHASE	(14)	-	(2)	-
FLEE	(4)	-	(11)	-
RETREAT	(4)	-	(9)	-
ATTACK	(4)	-	(0)	-
FIGHT	(2)	-	(2)	-
SIDEWAYS-OFFENSIVE	(2)	-	(3)	-
SQUINT	(0)	-	(0)	-
FOLLOW	(8)	-	(10)	-
INVESTIGATE	(3)	-	(2)	-
AVOID	(0)	-	(1)	-
CHASE-BITE	(0)	-	(0)	-
UPRIGHT-DEFENSIVE	(0)	-	(0)	-
CRAWL-UNDER	(1)	-	(0)	-
UPRIGHT-OFFENSIVE	(0)	-	(0)	-
ATTEMPT-MOUNT	(0)	-	(0)	-
SNIFF	(18)	-	(11)	-
AGGRESSIVE-GROOM	(0)	-	(0)	-
FULL-AGGRESSIVE	(1)	-	(1)	-

Table 3.9. Mean frequencies of directed-behaviours toward the mate in the pairs. Columns show frequencies of males to female and female to male. Figures in brackets give the total frequencies of each behaviour where the data was insufficient for analysis by the Wilcoxon Matched-Pairs Signed-Ranks test on individual frequencies for each behaviour.
Significance levels are for a one-tailed test, * = $p<0.025$; *** = $p<0.005$.

MEAN FREQUENCIES FOR ALL DIRECTED BEHAVIOURS

INTERACTION	$\bar{x}$	S.D.	
MALE AS SUBJECT WITH MALE NEIGHBOUR	63.64	35.56	***
MALE AS SUBJECT WITH FEMALE NEIGHBOUR	37.05	27.55	
FEMALE AS SUBJECT WITH MALE NEIGHBOUR	37.68	32.40	***
FEMALE AS SUBJECT WITH FEMALE NEIGHBOUR	17.45	13.63	
MALE WITH FEMALE MATE	13.64	12.68	***
FEMALE WITH MALE MATE	7.05	5.56	

Table 3.10. Mean frequencies of all directed behaviours for all types of interaction between animals. Individual total frequencies for all directed behaviours were compared as shown by the brackets using the Wilcoxon Matched-Pairs Signed-Ranks test.
Significance level *** = $p<0.005$.

The results of the Wilcoxon analyses shown in Table 3.10 indicated that, in interactions with neighbours, both males and females had a significantly higher frequency of interaction with the neighbouring males. Within a pair, males showed significantly more directed behaviours towards the female mates than females showed towards male mates.

3.3.4. RELATIVE AGGRESSION AND TEMPORAL PATTERNING OF BEHAVIOURS IN MALES AND FEMALES

In the analyses of the male-male paired encounter experiments reported in Section 2.3.3. of the previous chapter an important feature in describing and understanding the aggressive behaviour observed was an analysis of the changes in the frequencies of certain behaviour patterns over time (temporal patterning). It was clear that over time certain behaviour patterns decreased in frequency while others increased and it was suggested that the aggressive encounters became more ritualized over time. It was therefore important to consider the temporal patterning of the behaviours observed in the experiments reported here in order to provide more information on this aspect of the agonistic behaviour of the gerbil. The analysis was carried out separately for males and females as it was felt that this would allow some comparison with the previous results for males.

In the analysis of the male-male paired encounter experiments reported in the previous chapter it was possible to distinguish the "dominant" animal of the pair on the basis of its relatively higher frequencies of the behaviour pattern CHASE which was indicative of high aggression (Section 2.2.3.). The analysis of the temporal patterning was then carried out separately on the data for dominants and subordinates. In the experiments reported here, however, it has already been suggested that an analysis using the concept of dominance to distinguish between individuals would be inappropriate (see Section 3.1.0.). Nevertheless it was apparent, from an inspection of the data for the individual total frequencies of each behaviour pattern for males and females, that within each experiment there were possible differences between the two males and also between the two females in terms of their frequencies of those behaviour patterns positively correlated with aggressiveness (see Table 3.5.) and thus it was possible that there were differences in aggressiveness between individual males and between individual females in each experiment. A Chi-Square one-sample test was therefore carried out, using the data for the individual total frequencies of each of those behaviours positively correlated with aggressiveness in males, comparing the two males in each experiment for each behaviour. A similar analysis was carried out for females although some of the behaviours compared were different (see Table 3.5.). Where the frequencies of the behaviours were too low a Binomial test was used. As a result of these analyses it was clear that not all pairs showed significant differences in their frequencies of CHASE and often the significant differences in the other behaviours were not in the same direction. Nevertheless in each pair of males and females one animal showed significantly higher frequencies of performance of a majority of the behaviours and this animal was labelled as the "relatively high aggression" (R.H.A.) animal, the other being labelled as the "relatively low aggression"

(R.L.A.) animal. Thus over all the experiments males and females were divided into equal groups of R.H.A. and R.L.A. animals. The analysis of the temporal patterning of behaviours was then carried out separately for each of the four groups, Male (R.H.A.), Female (R.H.A.), Male (R.L.A.), Female (R.L.A.) by calculating Weighted Regression coefficients for each behaviour. These regression analyses were performed by computer and were carried out on the total frequencies of each behaviour pattern against time within a trial, where the total frequencies of each behaviour were calculated for each 30 sec. block (see Section 3.2.0.), and against trials, where the total frequencies of each behaviour pattern were calculated for each of the ten trials. Table 3.11. provides a digest of the results for significant changes in the frequencies of behaviours over time within trials. Overall it is particularly useful to examine those results with respect to the changes over time within trials in those behaviours related to aggressiveness (Table 3.5.) R.H.A. males showed significant decreases in the frequencies of APPROACH, NOSE, CHASE, FOLLOW, EXPLORE and SIDEWAYS-OFFENSIVE, while the frequencies of HIND-DIG and TAIL-RATTLE showed significant increases. R.L.A. males showed significant decreases in NOSE, CHASE and FOLLOW as well as FLEE, while the frequency of HIND-DIG increased. R.H.A. females showed significant decreases in APPROACH and CHASE, while the frequencies of HIND-DIG and VENTRAL-MARKING increased significantly. R.L.A. females showed significant decreases in APPROACH and FIGHT as well as SQUEAK and FLEE but did not show any significant increase in the frequencies of other behaviours related to aggressiveness. There therefore appeared to be a general decrease in the frequencies of those behaviours which were labelled "directed" (i.e. APPROACH, NOSE, CHASE, FOLLOW, FIGHT, SIDEWAYS-OFFENSIVE) and a corresponding increase in the "non-directed" elements TAIL-RATTLE, VENTRAL-MARKING and particularly HIND-DIG. This may indicate that during trials there is a tendency for animals to display their aggression in a more ritualized form which is not obviously directed at any specific animal. The less aggressive animals (R.L.A. males and females) also seemed to respond to this drop in "directed aggression" by showing decreases in the frequencies of FLEE, also SQUEAK and RETREAT in R.L.A. females.

WITHIN TRIALS

	MALE		FEMALE	
	R.H.A.	R.L.A.	R.H.A.	R.L.A.
INCREASES	HIND-DIG*	HIND-DIG***	HIND-DIG***	
	TAIL-RATTLE*	SELF-GROOM*	SIT*	
			VENTRAL-MARKING*	
DECREASES	APPROACH***		APPROACH***	APPROACH***
	NOSE***	NOSE**	NOSE*	NOSE***
	CHASE***	CHASE*	CHASE*	
	FIGHT*	FIGHT*		FIGHT*
	DIGS**		DIGS*	DIGS*
	INVESTIGATE***	INVESTIGATE***		
		AVOID**	AVOID*	
		FULL-AGGRESSIVE*	FULL-AGGRESSIVE*	
	FOLLOW***	FOLLOW***		
		SQUEAK**		SQUEAK***
	EXPLORE**			EXPLORE**
	SIT***			SIT**
		FLEE*		FLEE**
	FEED*		CHASE-BITE***	RETREAT***
	SNIFF**			
	SIDEWAYS-OFFENSIVE*			

Table 3.11. Summary of the results of regression analyses indicating changes in the frequencies of each behaviour pattern over time within trials. The table gives the names of these behaviours with significant increases or decreases in frequencies for "Relatively-high-aggression" (R.H.A.) and "Relatively-low-aggression" (R.L.A.) groups of males and females. The significance levels are given, * = p<0.05; ** = p<0.01; *** = p<0.001. Where there are changes in the same behaviour for two or more groups these are shown on the same line across the table.

The temporal patterns seen as a result of the regression analyses carried out on the total frequencies of each behaviour in each trial are summarized in Table 3.12. Again it is useful to examine these results with regard to changes in the frequencies of those behaviours related to aggressiveness (see Table 3.5.). Overall it is apparent that R.H.A. males showed increases in the frequencies of APPROACH, NOSE, CHASE and HIND-DIG, R.L.A. males showed increases in ATTACK and HIND-DIG, but the two female groups showed no increase in behaviours related to aggressiveness. This seems to indicate that, with repeated exposures of the pairs, the males, particularly R.H.A. males, showed an increasing level of aggression.

Although the behaviour pattern RETREAT was not found to be related to aggressiveness in either males or females it is interesting that there was an overall tendency for the frequency of this behaviour to increase in all the groups over trials. This seems to indicate that all animals showed an increased tendency to keep away from each other as a result of repeated exposure.

OVER TRIALS

	MALE		FEMALE	
	R.H.A.	R.L.A.	R.H.A.	R.L.A.
INCREASES	RETREAT*	RETREAT*	RETREAT***	RETREAT*
	HIND-DIG**	HIND-DIG**		
	APPROACH**	ATTACK***	SELF-GROOM**	AVOID*
	NOSE*	SQUEAK**	DIGS*	
	CHASE**			
	SIT**			
DECREASES	FOOT-THUMP**	FOLLOW**		
		SNIFF*		
		VENTRAL-MARKING*		
		DIGS*		

Table 3.12. Summary of the results of regression analyses indicating the changes in the frequencies of each behaviour pattern over trials. The table gives the names of those behaviours with significant increases or decreases in frequencies for "Relatively-high-aggression" (R.H.A.) and "Relatively-low-aggression" (R.L.A.) groups of males and females. The significance levels are given, * = $p<0.05$; ** = $p<0.01$; *** = $p<0.001$.
Where there are changes in the same behaviour for two or more groups these are shown on the same line across the table.

3.3.5. PREDICTORS OF RELATIVE AGGRESSION IN MALES AND FEMALES

In the previous chapter it was found that the frequency of male VENTRAL-MARKING on the day prior to a male-male encounter experiment was related to the subsequent dominance status of the animal, the highest markers becoming the dominants (Section 2.3.3.). In the experiments reported here it was felt that there may be similar predictors of the relative aggression of males and of females. Unfortunately the animals had done virtually no marking on the day prior to the second phase of experiments involving interactions with neighbouring pairs. Thus an attempt was made to identify predictors for R.H.A. animals from slightly different measures and behaviour pattern frequency scores recorded during the familiarization period. Accordingly the weights, individual VENTRAL-MARKING scores on the first day and individual total VENTRAL-MARKING scores for the whole seven day period for the animals identified as belonging to the R.H.A. and R.L.A. groups in the second phase of the experiment were compared for both sexes. The "t" text was used for the weight data whereas the Mann-Whitney "U" test was used for the data on VENTRAL-MARKING. The data for HIND-DIG and URINATE were insufficient for analysis. Table 3.13. summarizes the results for both sexes.

MALES

		VENTRAL-MARKING	
	WEIGHT	DAY I	TOTAL FOR 7 DAYS
RELATIVELY HIGH AGGRESSION	$\bar{x}$ 78.77	$\bar{x}$ 143.9	$\bar{x}$ 153.82
	S.E. 3.28	S.D. 87.27	S.D. 89.95
RELATIVELY LOW AGGRESSION	$\bar{x}$ 81.28	$\bar{x}$ 148.9	$\bar{x}$ 160.55
	S.E. 3.97	S.D. 79.49	S.D. 91.37
	t = 1.62	u = 59	u = 59
FEMALES			
RELATIVELY HIGH AGGRESSION	$\bar{x}$ 69.49	$\bar{x}$ 22	$\bar{x}$ 22.18
	S.E. 2.22	S.D. 22.79	S.D. 22.69
RELATIVELY LOW AGGRESSION	$\bar{x}$ 67.91	$\bar{x}$ 9.73	$\bar{x}$ 9.45
	S.E. 4.83	S.D. 12.49	S.D. 12.30
	t = 0.610	u = 34	u = 36

Table 3.13. Summary of mean weight, VENTRAL-MARKING scores on Day I, total VENTRAL-MARKING scores over all seven days for R.H.A. males and females and R.L.A. males and females. None of the comparisons was significant.
S.E. = Standard error; S.D. = Standard Deviation.
It can be seen that none of the measures taken prior to the second phase of the experiment was significantly related to the subsequent relative aggression of animals during encounters.

3.4.0. CHANGES IN THE BEHAVIOUR OF MALES AND FEMALES AS A RESULT OF ENCOUNTERS BETWEEN NEIGHBOURING PAIRS

At the conclusion of each trial, when the areas were open to each other, the animals were returned to their own half of the arena and the partition replaced. This was followed immediately by a fifteen minute observation period (see Section 3.2.0.) when it was clear that the pairs were now much more active in their own areas than they had been during the seven-day familiarization period. It was apparent that this activity centred around the partition between the two areas (see Chapter IV for further discussion) and that the increase in activity was reflected in the change in frequency of a number of behaviour patterns. No significant differences were found between the frequency scores of R.H.A. and R.L.A. males and females during this period using the Mann-Whitney "U" test and Table 3.14. summarizes these data.

MALES

	VENTRAL-MARKING DAY I	TOTAL VENTRAL-MARKING	TOTAL HIND-DIG	TOTAL URINATE
RELATIVELY HIGH AGGRESSION	$\bar{x}$ 9.18	$\bar{x}$ 42.90	$\bar{x}$ 14.42	$\bar{x}$ 8.86
	S.D. 8.49	S.D. 31.22	S.D. 4.86	S.D. 5.25
RELATIVELY LOW AGGRESSION	$\bar{x}$ 4.00	$\bar{x}$ 36.55	$\bar{x}$ 0.00	$\bar{x}$ 5.14
	S.D. 3.77	S.D. 27.19	S.D. 0.00	S.D. 4.19
	u = 34	u = 59	u = 15	u = 23.5
FEMALES				
RELATIVELY HIGH AGGRESSION	$\bar{x}$ 0.89	$\bar{x}$ 7	$\bar{x}$ 6.86	$\bar{x}$ 2.43
	S.D. 1.19	S.D. 3.39	S.D. 8.86	S.D. 2.87
RELATIVELY LOW AGGRESSION	$\bar{x}$ 0.00	$\bar{x}$ 3.56	$\bar{x}$ 3.29	$\bar{x}$ 2.57
	S.D. 0.00	S.D. 4.06	S.D. 5.09	S.D. 4.07
	INSUFFICIENT DATA	u = 34.5	INSUFFICIENT DATA	u = 23.5

Table 3.14. Mean frequencies during fifteen minute observation periods after areas reclosed. Means are shown for R.H.A. and R.L.A. groups separately for the total VENTRAL-MARKING frequencies on Day I of these observations (n = 11), total VENTRAL-MARKING frequencies over all the observation periods (n = 11), and total HIND-DIG and URINATE frequencies over all the observation periods (n = 7). Comparisons between R.H.A. and R.L.A. groups were carried out using the Mann-Whitney "U" test, none was significant.

The similarity between R.H.A. and R.L.A. groups for VENTRAL-MARKING, both on the days of the familiarization trials (see previous section 3.3.3.) and on Day I of the observation periods, made it possible to combine data for both categories for a comparison between VENTRAL-MARKING on the final day of the familiarization trials (see Chapter II, Section 2.4.2.) and Day I of the observation periods. Using the individual total frequencies in each case a score for the number of marks per minute was calculated, since the two observation periods were not equal. A comparison was then carried out using the Wilcoxon Matched-Pairs Signed-Ranks test. This was only possible on the male data since the female data were insufficient for analysis. In carrying out the analysis care was taken to eliminate scores for animals that had not been active during the final day of the familiarization period. Table 3.15. reviews the data.

MEAN MARKING RATES FOR MALES

DAY 7 OF FAMILIARIZATION TRIALS	DAY I OF OBSERVATION PERIODS
$\bar{x}$ 0.12	$\bar{x}$ 0.51
S.D. 0.10	S.D. 0.53
n = 11	n = 11

Table 3.15. Male mean marking rates (marks/minute) for the final day (Day 7) of the familiarization period and the first day (Day 1) of the observation periods after the reclosing of the areas. The results of a Wilcoxon test on the individual pairs was not significant (n = 9, T = 28, pNS). n = number of animals tested.

There was no significant difference between the rates of marking of animals that could be determined by this analysis (Table 3.15.) but it was clear that more males marked on day 1 of the observation periods (n = 16) than on the final day of the familiarization period (n = 8) although this was not a significant difference as tested with a Chi^2 one-sample test (df=1, Chi^2 = 2.67, p<0.2).

It was not possible to carry out a similar analysis on the frequency data of the behaviours HIND-DIG and URINATE as the frequencies were too low. It was possible, however, to combine data from the relatively high and low-aggression groups for each of these behaviours in each sex (see Table 3.14.) and further to total the individual frequencies over each day of the familiarization period and of each observation period after each "open-area" trial. The frequency per minute of each behaviour was then calculated, taking account of the trials in which certain animals had been inactive during the familiarization stage, and a score of each behaviour per minute for each individual obtained. Using a Wilcoxon test these scores were compared between the familiarization period and the fifteen minute observation periods. Table 3.16. summarizes the results.

MEAN RATES (BEHAVIOUR FREQUENCY/MIN)

	HIND-DIG I	HIND-DIG II	URINATE I	URINATE II
MALE	$\bar{x}$ 0.027	$\bar{x}$ 0.13	$\bar{x}$ 0.021	$\bar{x}$ 0.052
	S.D. 0.07	S.D. 0.125	S.D. 0.025	S.D. 0.034
	N=13 T=13*		N=14 T=18.5**	
FEMALE	$\bar{x}$ 0.00079	$\bar{x}$ 0.44	$\bar{x}$ 0.0026	$\bar{x}$ 0.018
	S.D. 0.003	S.D. 0.08	S.D. 0.0038	S.D. 0.026
	N=7 T=13*		N=9 T=3*	

Table 3.16. Means rate of HIND-DIG and URINATE, expressed as score/minute for total familiarization period (HIND-DIG I, URINATE I) and total of fifteen minute observation periods after "open-area" trials (HIND-DIG II, URINATE II). Wilcoxon comparisons between I and II for each behaviour were carried out and the results shown. * = $p<0.01$; ** = $p<0.005$.

It is clear from Table 3.16. that the rates of HIND-DIG and URINATE showed significant increases in the fifteen minute observation periods, immediately after the "open-area" trials, from the rates seen in the seven day familiarization periods in both sexes.

There were no significant differences in the final weights of the relatively high and low aggression groups of both sexes ($\bar{x}$ R.H.A. MALE = 71.63, S.E. = 1.49; $\bar{x}$ R.L.A. MALE = 74.73, S.E. = 2.03; t = 0.267, df = 20 p NS: $\bar{x}$ R.H.A. FEMALE = 67.84, S.E. = 1.78; $\bar{x}$ R.L.A. FEMALE = 56.49, S.E. = 2.86; t = 1.31, df = 20, p NS). However, males lost weight significantly during the experiment (mean weight loss = 6.89, S.E. 1.86, df = 21, t = 3.69, $p<0.01$), but females did not lose any significant amount of weight during the experiment (mean weight loss = 1.59; S.E. 1.64, t = 0.97, df = 21, p NS).

3.5.0. EFFECT OF THE PRESENCE OF LITTERS ON THE BEHAVIOUR OF THE MALES AND FEMALES

In five of the eleven replicates of this experiment one of the pairs gave birth to a litter before or during the familiarization period and thus litters were present during the ten days of trials, when the areas were opened and the animals were free to interact with each other,during these experiments. It was therefore possible to study the behaviour of the male and female pairs when the litter was present and the female lactating, and to compare it with pairs without litters. It was not possible to look at the effect of pregnancy on the female behaviour during the second-phase of the experiment since it was clear from the pattern of births for the pairs after the experiment that it was unlikely that any became pregnant during the experiment.

The most obvious effect on the behaviour of both animals when litters were present, particularly during the familiarization period, was indicated by the way in which the entrances to the nest-boxes were sealed with peat and stones. After each trial, when these nest-boxes were checked (see Section 3.2.0.) the disturbance caused animals to reseal the entrances immediately after by piling even more peat onto the mounds that surrounded the nest-boxes. In fact the increase in the size of peat mounds was a way of identifying if pairs had a litter or were about to have a litter. Both males and females maintained the nest, the female being more involved than the male, although on occasions the males were observed carrying nesting materials in their mouths to the nest.

Males were not generally excluded from the nest before or after the litters were born and it was noticeable that during the familiarization periods those pairs with litters were rarely seen. One exception to this was when a male was seen nesting alone at the alternative nest site (X) after a litter had been born. However, this only lasted for two days and on the third day the female had brought the litter to the male and both were nesting with the young at X.

In five of the eleven experiments one pair had a litter while the neighbouring pair did not and thus it was possible to compare the behaviour of pairs with litters directly with pairs without litters, in the same experiments.

Table 3.17 shows the result of a Mann-Whitney "U" test comparing total frequencies of VENTRAL-MARKING during the seven day familiarization period for males with litters and males without litters, and females with litters and females without litters.

MEAN MARKING FREQUENCIES

	MALES ($N_1=5$; $N_2=5$)			FEMALES ($N_1=5$; $N_2=5$)	
	WITH LITTER	WITHOUT LITTER		WITH LITTER	WITHOUT LITTER
$\bar{x}$	188.2	186.2	$\bar{x}$	31.00	3.4
S.D.	100.6	59.35	S.D.	30.84	2.42
u = 11			u = 7.5		

Table 3.17. Mean marking frequencies over the seven day familiarization period for males and females with and without litters. Mann-Whitney "U" comparisons were carried out on individual total frequencies but none was significant.

The results of the analysis shown in Table 3.17. indicate that no significant differences exist between the two groups for the males and although the mean marking frequencies of the females indicated a large difference between females with a litter and females without a litter, this was not significant. The data for HIND-DIG and URINATE during this period were insufficient for analysis.

Similar analyses were carried out on the data for the total frequencies of each behaviour pattern observed during the ten days of the second phase, when the areas were open to each other. The analysis of the Directed behaviours was carried out on the individual total frequencies of each behaviour between the animal and its neighbours, both male and female, and Table 3.18 summarizes the results.

MEAN FREQUENCIES OF EACH DIRECTED BEHAVIOUR

	MALES ($N_1=5$; $N_2=5$)				FEMALES ($N_1=5$; $N_2=5$)			
		WITH LITTER	WITHOUT LITTER			WITH LITTER	WITHOUT LITTER	
APPROACH	$\bar{x}$	25.00	17.20		$\bar{x}$	13.80	8.80	
	S.D.	14.10	8.61		S.D.	8.28	3.87	
NOSE	$\bar{x}$	10.20	8.20		$\bar{x}$	5.40	5.80	
	S.D.	11.53	8.76		S.D.	5.00	5.42	
CHASE	$\bar{x}$	15.2	1.80	**	$\bar{x}$	13.20	1.00	***
	S.D.	11.01	1.33		S.D.	9.83	1.55	
FLEE	$\bar{x}$	1.40	17.40	****	$\bar{x}$	1.20	18.60	****
	S.D.	1.02	11.83		S.D.	0.60	7.00	
RETREAT	$\bar{x}$	20.20	17.40		$\bar{x}$	13.40	18.00	
	S.D.	21.22	8.04		S.D.	16.57	15.34	
ATTACK	$\bar{x}$	6.60	3.00	*	$\bar{x}$	3.40	0.6	**
	S.D.	4.58	0.45		S.D.	1.85	0.8	
FIGHT	$\bar{x}$	6.40	7.00		$\bar{x}$	3.40	2.60	
	S.D.	2.42	1.79		S.D.	2.25	1.74	
SIDEWAYS-OFFENSIVE	$\bar{x}$	1.60	0.80		$\bar{x}$	4.40	0.20	****
	S.D.	1.85	0.98		S.D.	1.36	0.98	
FOLLOW	$\bar{x}$	3.00	2.20		$\bar{x}$	1.20	0.60	
	S.D.	1.67	0.98		S.D.	0.40	0.80	
CHASE-BITE	INSUFFICIENT DATA				$\bar{x}$	2.00	0.00	
					S.D.	1.00	0.00	
TOTAL FOR ALL DIRECTED BEHAVIOURS	$\bar{x}$	85.60	72.80		$\bar{x}$	59.20	55.20	
	S.D.	52.53	22.94		S.D.	29.94	23.58	

Table 3.18. Mean frequencies for each Directed behaviour during the 10-day second phase of the experiment for animals with litters and animals without litters. Comparisons between the two groups in both sexes were carried out using the Mann-Whitney "U" test, * = $p<0.05$, ** = $p<0.02$, *** = $p<0.008$; **** = $p<0.004$.

It can be seen that the males and females with litters showed higher frequencies of the behaviour patterns CHASE and ATTACK against their neighbours and significantly lower frequencies of the behaviour pattern FLEE. Females with litters also showed significantly higher frequencies of the behaviour pattern SIDEWAYS-OFFENSIVE. These results indicated that the pair with a litter were more aggressive than the pair without a litter. This type of analysis was not possible for the frequencies of the behaviour patterns SQUINT, INVESTIGATE, AVOID, UPRIGHT-DEFENSIVE, CRAWL-UNDER, UPRIGHT-OFFENSIVE, ATTEMPT-MOUNT, SNIFF, AGGRESSIVE-GROOM and FULL-AGGRESSIVE as the data were insufficient.

Table 3.19. shows the results of a similar analysis carried out on the total frequencies of some of the Non-directed behaviours for males with litters, males without litters, females with litters and females without litters during the ten-day second phase of the five experiments where litters were present. The data for the behaviour patterns SELF-GROOM, DIGS, URINATE, SQUEAK, FEED, FULL-SUBMISSIVE and SIT were insufficient to be included in this analysis.

MEAN FREQUENCIES OF EACH NON-DIRECTED BEHAVIOUR

		MALES ($N_1=5$; $N_2=5$)				FEMALES ($N_1=5$; $N_2=5$)		
		WITH LITTERS	WITHOUT LITTERS			WITH LITTERS	WITHOUT LITTERS	
HIND-DIG	$\bar{x}$	33.80	14.00		$\bar{x}$	11.40	4.20	*
	S.D.	27.35	12.44		S.D.	18.36	8.40	
FREEZE	$\bar{x}$	2.80	6.80		$\bar{x}$	1.40	2.20	
	S.D.	1.47	3.87		S.D.	1.96	1.33	
FOOT-THUMP	$\bar{x}$	0.00	4.20			INSUFFICIENT DATA		
	S.D.	0.00	6.94					
VENTRAL-MARKING	$\bar{x}$	39.20	18.40	*	$\bar{x}$	4.20	3.40	
	S.D.	20.77	19.64		S.D.	5.38	6.80	
TAIL-RATTLE	$\bar{x}$	4.20	0.40		$\bar{x}$	1.60	1.40	
	S.D.	5.72	0.49		S.D.	1.85	2.80	
EXPLORE	$\bar{x}$	6.60	6.60		$\bar{x}$	5.40	5.60	
	S.D.	5.16	4.22		S.D.	5.54	3.88	

Table 3.19. Mean frequencies for each Non-directed behaviour during the 10-day second phase of the experiment for animals with and without litters. Comparisons between the two groups in both sexes were carried out using the Mann-Whitney "U" test, * = $p<0.05$.

The results of this analysis showed that females with litters HIND-DIG more than females without litters, and males with litters show a higher frequency of VENTRAL-MARKING than males without litters (see Table 3.19.).

Finally a similar analysis was carried out on the data collected during the fifteen minute observation periods at the end of each of the "open-area" trials for these five experiments. The total frequencies for each group of each of the behaviours HIND-DIG, VENTRAL-MARKING and URINATE were calculated and the Mann-Whitney "U" analysis carried out as before. Table 3.20. summarizes the data and gives the results of the analyses.

MEAN FREQUENCIES OF EACH BEHAVIOUR

		MALES ($N_1=5$; $N_2=5$)			FEMALES ($N_1=5$; $N_2=5$)		
		WITH LITTERS	WITHOUT LITTERS		WITH LITTERS	WITHOUT LITTERS	
VENTRAL-MARKING	$\bar{x}$	51.20	29.30	$\bar{x}$	7.40	1.80	*
	S.D.	43.69	23.70	S.D.	5.46	3.60	
HIND-DIG	$\bar{x}$	17.60	13.00	$\bar{x}$	1.20	2.00	
	S.D.	15.45	6.48	S.D.	1.60	4.00	
URINATE	$\bar{x}$	6.40	5.20	INSUFFICIENT DATA			
	S.D.	5.04	4.26				

Table 3.20. Mean frequencies of behaviours, recorded during the fifteen minute observation periods after the "open-area" trials, for males and females with and without litters. Comparisons were made using the Mann-Whitney "U" test.
* = $p<0.03$.

From the results of the comparisons shown in Table 3.20. it is clear that females with litters showed a significantly higher frequency of VENTRAL-MARKING after the "open-area" trials. No other comparison revealed significant differences.

3.6.0. DISCUSSION

3.6.1. AGONISTIC BEHAVIOUR OF MALE AND FEMALE GERBILS

In this second study of the agonistic behaviour of the Mongolian gerbil, it was apparent that no changes in the form of the acts and postures resulted from the fact that they had been performed under very different conditions from the experiments reported in Chapter II, where these behaviours were originally identified. The form of each behaviour was also identical in both male and female gerbils and the main differences between the sexes were apparent only in the frequency of performance and temporal patterning of individual acts and postures. Similarly the differences between "relatively high aggression" and "relatively low aggression" groups of animals of both sexes appeared in the frequencies and temporal patterning of the individual behaviours rather than in their form.

High aggression in both sexes was indicated by high frequencies of the behaviour patterns CHASE (by definition), APPROACH, SIDEWAYS-OFFENSIVE, ATTACK, FOLLOW and HIND-DIG. The relationship between high aggression and the frequencies of APPROACH and SIDEWAYS-OFFENSIVE is in agreement with the findings reported in Chapter II for male gerbils. The fact that ATTACK occurs in these arena experiments when it was absent in the male-male encounter experiments reported in the previous Chapter, could be related to the availability of more space in these experiments. It was suggested that, like the hamster, ATTACK was replaced by an exaggeration of chasing behaviour in confined conditions (Chapter II), and thus its absence during the male-male encounter reported in Chapter II, was possibly an artifact of those experimental conditions.

The finding that FOLLOW is a behaviour pattern related to high aggression in both sexes is supported by the suggestion of Sadlier (1970) that, in groups of *Peromyscus maniculatus*, following behaviour had aggressive significance when the animals were establishing an aggressive rank order. This suggests that the male aggressive animals will FOLLOW other animals perhaps to fight or indulge in some form of agonistic display, in *Peromyscus* its function was obviously related to establishing some form of dominance, in gerbils the function of this following behaviour by an aggressive animal is unclear, although it may be related to territorial behaviour in these experiments (see Chapter IV).

The appearance of the behaviour pattern HIND-DIG during these experiments is probably related to the availability of the peat and straw on the floor of the arena (i.e. something to dig in) since it was not seen before when only a wooden floor was available to the gerbils during interactions (Chapter II). Its relationship to high aggression in both sexes makes it probable that this behaviour is either a threat or a sign of high arousal. Johst (1967) reported that the vole *Clethrionomys* displayed a similar behaviour and Clarke (1956) identified this agitated digging behaviour in *Microtus* and described it as a threat display. Ewer (1968) reported threat-digging behaviour, where earth was thrown at the opponent during an agonistic encounter, for a number of mammalian species. Allin and Banks (1968) reported that this behaviour in the Collared Lemming, *Dicrostonyx groenlandicus*, was associated with high arousal. In the gerbil Dunn (1971) observed it in *Meriones unguiculatus* and identified it as a threat behaviour. It has also been reported as a threat behaviour in *M. hurrianae* (Fitzwater and Prakash, 1969) where it was suggested that dirt was "thrown" at the opponent by one gerbil using its hind feet. The significant increases in the frequency of this behaviour during and after trials in the R.H.A. groups of males and females, as well as the significant increases in its frequency in R.L.A. males, and its significant increases for both groups of males over trials, make it probable that it is related to the high arousal of animals as time within a trial progresses and as the trials continue over the days.

High aggression in the two sexes was also associated with higher frequencies of different behaviours in each sex. Males in the high aggression group could also be identified by their higher frequencies of the behaviours NOSE, CHASE-BITE and EXPLORE. The correlation of CHASE-BITE with high aggression in males has been reported before, but the correlation of the behaviour pattern NOSE with high aggression shows a complete reversal of the results reported before for male gerbils (Chapter II). No explanation for this difference can be offered although the association of NOSE with aggressive males seems likely to relate to the higher frequency of interactions initiated by males (see Table 3.10) and the fact that aggressive males are probably more likely to initiate interactions with other animals. In doing so these males are more likely to perform the behaviour pattern NOSE in the initial identification of other individuals (Chapter II). It is interesting to note that during trials the frequency of NOSE declines in all types of males and females, which supports the suggestion that this behaviour is important in olfactory identification of individuals and it thus occurs more frequently at the beginning of every trial when animals are re-establishing their identities (see Chapter II). The increases in the frequency of this behaviour over trials in R.H.A. males may be related to the increased arousal and "directed" aggressive activity seen in this group (Section 3.3.4. Table 3.12.).

A similar explanation can be invoked for the association of high frequencies of the behaviour pattern EXPLORE with high aggression in males; that is the aggressive males are less likely to be restricted in their freedom of movement throughout the whole arena. Poole and Morgan (1976) observed that it was the most aggressive and dominant animals in hierarchically organized groups of mice who occupied new areas when the size of their environment was increased.

In the females high aggression was also associated with high frequencies of the behaviour patterns FIGHT, VENTRAL-MARKING and TAIL-RATTLE. It would seem obvious that the frequency of the behaviour pattern FIGHT should be correlated with aggression, however its relationship to high aggression in females and not males is interesting. Males FIGHT more than females and also FIGHT with other males more frequently than with females. This is in agreement with the findings of Norris and Adams (1972) reported in Section 3.1.0. Females fight less and show no significant difference in the frequency with which they FIGHT both sexes. However, it is probable that only very aggressive females engage in fights at all and thus FIGHT becomes related to high aggression. In males the relatively high and low-aggression groups show little distinction in their frequency of FIGHT and this may be related to the influence of other factors, such as the possession of a territory (see Chapter IV).

The association of the behaviour pattern TAIL-RATTLE with high aggression in females could also be the result of its low frequency of occurrence and appearance only in very aggressive females. In males the R.H.A. group showed a significant increase in this behaviour during trials which may indicate that it relates to the high arousal of animals as the trial progresses.

The data for the behaviour pattern VENTRAL-MARKING will be discussed separately.

There is little need to discuss the behaviour patterns related to low aggression in both sexes as both FLEE and SQUEAK are generally regarded as indicative of less aggressive animals. Majundar et al (1974) list SQUEAK (or squealing) as a normal part of the FIGHT element during aggressive interactions between Mongolian gerbils, although in these experiments it appeared to be related to persistent aggression by other animals on females.

A more interesting finding was the absence of further associations between behaviour patterns and low aggression. In part this was undoubtedly due to the low frequency of occurrence of some of the postures, particularly the UPRIGHT and SIDEWAYS DEFENSIVE postures. Whether these low frequencies were as a result of the difficulties of observation under these experimental conditions or a direct effect of the conditions on the behaviour of the animals is unclear. Nevertheless it seems likely that the methods adopted for restricting the formation of a dominance hierarchy (Section 3.2.0.) would have influenced the behaviour of the animals, particularly by preventing long bouts of fighting behaviour where dominance could be established. This is discussed more fully in Chapter IV but it was clear, from the way in which the behaviour pattern RETREAT showed no significant associations with low-aggression (as was implied in the findings reported in Chapter II), that even animals from the high aggression groups of males and females had a tendency to RETREAT, particularly from other males. This indicates that dominance-subordinate relationships had not been completely formed or that their behaviour was related to where it occurred in the arena (see Chapter IV). The changes in behaviour with time during these experiments indicated a general decrease in the frequency of aggressive interactions during trials, as evidenced by the significant decreases in the behaviour patterns CHASE, FIGHT, APPROACH and FOLLOW for all groups. However, in all but the female low-aggression group, the non-directed element HIND-DIG, which was associated with high aggression, showed significant increases. Animals also tended to contact each other less during trials, as indicated by the decreases in the frequencies of: INVESTIGATE, NOSE and SNIFF in the male high-aggression group; INVESTIGATE and NOSE in the male low-aggression group; NOSE in the female high and low aggression groups. Similar changes in the frequencies of aggressive behaviours and behaviours associated with individual identification and recognition were previously reported for male gerbils (Chapter II). Like these previously reported changes, where very aggressive acts were replaced by ritualized offensive-defensive postures during trials, there was a gradual replacement of directed aggressive acts and postures by a non-directed aggressive display, HIND-DIG. It is probable that the offensive postures are used at close-quarters when little space is available, as in the confined conditions of the previous male-male encounter experiments, and that the agitated dirt throwing display is used when the dirt is available and animals have more space. The HIND-DIG display under such conditions may serve therefore as a visual threat to other conspecifics.

The pattern of behavioural changes over trials is less clear and may further reflect the results of the attempts by the experimenter to prevent the formation of hierarchies. Thus in males there were increases over trials in behaviours related to high aggression in both groups, males in the high aggression group showed increases in CHASE, FLEE, APPROACH and HIND-DIG, and males in the low aggression group showed increases in ATTACK and HIND-DIG. Both showed increases in the behaviour pattern RETREAT. In females the increases in the behaviour pattern RETREAT in both groups has been discussed before in relation to the effect of the experimental conditions. In this respect the absence of any significant decline in the latency to the first FIGHT in each trial is of interest. In the previous Chapter the decline in latency to the first FIGHT between males in paired encounters was probably the result of the dominant animal re-establishing his status at the start of each trial more and more quickly. In the experiments reported here the absence of such a significant decline may be further evidence in support of the suggestion that stable dominance relationships were never completely formed.

The relative aggressiveness of male and female gerbils has been discussed by Swanson (1974) where she suggested that, on the evidence of female attacks on males and inter-female aggression during paired encounter experiments, that "the generally held view that the male is the more aggressive sex may have to be qualified". From the results of the experiments reported here it appears that such a qualification is necessary. Male animals tended to FLEE and RETREAT from male neighbours more frequently than from female neighbours. Males fought more frequently with male neighbours than they did with female neighbours, and approached and nosed their female mates more than females approached and nosed their male mates. Females tended to

RETREAT more from neighbouring males than females. Males also showed significantly greater frequencies than females in certain behaviours associated with aggression, i.e. APPROACH, NOSE, FIGHT and FOLLOW, whereas females showed a greater frequency of the behaviour FLEE. However there were no apparent significant differences in the frequencies and direction of other behaviour patterns associated with aggression e.g. ATTACK, CHASE, CHASE-BITE, SIDEWAYS-OFFENSIVE and HIND-DIG. Thus females were equally as aggressive as males when certain behaviours were considered. The overall involvement of males in a significantly higher frequency of interactions with neighbouring animals cannot be ignored and is probably related to the relative status of the male in the male-female pair relationship. Alberts and Galef (1973) found that in pairs of rats one animal was often stronger and showed more aggression towards intruders. Flannelly and Lore (1975) demonstrated that this was related to the dominance status of that rat, the male in a hetero-sexual pair being more aggressive and dominant over the female. It is likely therefore that, in a mated pair of gerbils, the aggressiveness of the female is subdued as a result of her relationship to her male mate, although not completely. The full range and intensity of female aggression is likely to appear when this relationship to a male mate is removed and this could account for the high levels of female aggression observed in the experiments reported by Swanson (1974) where her animals were maintained in single sex groups. The significant weight loss during the experiment in males and not females (see Section 3.4.0.) can also be regarded as a reflection of the higher frequencies of interaction between males. This loss in weight may have been the result simply of a higher rate of activity in males or may have been a manifestation of the physiological effects of increased stress in males as a result of their higher frequencies of agonistic interactions (Christian, 1961).

While there is evidence to suggest that intersex fights were less frequent (Table 3.7) and on the whole males tended to interact more with neighbouring males than females, it was also apparent that the frequency of ATTACK by a male on a female was not significantly different to attacks by males on males. Thus it is not clear if, as in other rodents, males were inhibited from attacking or behaving aggressively towards females. The results indicated that females showed a greater tendency to flee than males (Table 3.6.) and also tended to retreat more from males (Table 3.9.). This suggests that the less frequent interactions with males were the result of female behaviour rather than any inhibiting effect on males. This is in general disagreement with the findings reported in other rodents and indicates the need for further research in this area. In mice, males are inhibited from attacking females even when they are intruders in established colonies (Poole and Morgan, 1976a). In rats too, males are similarly inhibited from attacking females (Ewer, 1971), and similar inhibition exists in hamsters (Dieterlen, 1959, Payne and

Swanson, 1970, 1973). Lee and Brake (1971) suggested that the inhibition of attack in male mice was mediated by odour cues from the females. Dixon and Mackintosh (1971) found that these odour cues were present in the urine of the female. In the hamster Payne (1974 b) suggested that the attack-inhibiting cues were probably not localised in the urine but present also in the animals' flank glands. As yet there is no evidence of attack-inhibiting odours in the female gerbil and the results of the experiments reported here are not clear enough to provide any evidence of their presence.

The most interesting aspect of the aggression observed during these experiments was shown in the experiments where one of the pairs had a litter. Here it was quite obvious that both males and females showed greater amounts of aggression in the form of CHASE and ATTACK over their male and female neighbours. The pair with a litter also showed less of the behaviour pattern FLEE and the lactating females showed higher frequencies of the aggressive posture SIDEWAYS-OFFENSIVE and the display HIND-DIG. This lends support to the suggestion that females become more aggressive when lactating (Gandleman, 1972). Moyer (1969) also suggested that maternal aggression was one of the seven basic functions of aggression in both animals and man. It also appears that males are influenced by the presence of litters or a lactating female and are significantly more aggressive towards their neighbours. Barrett et al (1968) found that male rats were more aggressive when a female was present and Taylor (1976) reported that submissive male rats became more aggressive after exposure to an oestrus female. Whether this increase in aggression can be elicited by a lactating female is unclear but certainly in the gerbil the male's behaviour can be significantly altered by the presence of a pregnant female (Elwood, 1977) and male gerbils are capable of performing parental activities in looking after the young (Elwood, 1975). On the evidence of the observations made during these experiments it would seem that males, like females, respond to the presence of a litter or the hormonal state of the female by increased aggression over their neighbours; it may be that this is in defence of the nest and litter in both sexes and that, like the mongoose (Rood, 1974), male gerbils actually guard their young.

In relation to the aggression shown during interactions with neighbours it was clear from the data that the initial weight of the animal, in both sexes, was not correlated with the level of aggression. This supports the findings reported in Chapter II. The final weight of the animal was also unrelated to the level of aggression shown during the "open-area" trials.

3.6.2. SCENT MARKING BEHAVIOUR

During these experiments two behaviour patterns were recorded which were associated with the deposition of odourous material in the arena, VENTRAL-MARKING and URINATE. The function of these behaviours will be more fully discussed in Chapter IV, however the data presented here on these behaviours provided some useful results.

The frequency of VENTRAL-MARKING in male gerbils was found to be significantly greater than marking of female gerbils. This has been shown before (Thiessen et al, 1969 a) and it is a common feature among many species of animals to find sexual dimorphism in relation to scent-marking behaviours (Chapter I). This dimorphism was not apparent in the data for the behaviour URINATE. VENTRAL-MARKING was also correlated to the initial weight in males but not females. This finding has been reported before for males (Chapter II) and it is probable that the low frequencies of marking in the female were responsible for the lack of a significant correlation with initial weight.

The temporal changes, indicating a decrease in the frequency of VENTRAL-MARKING, during the first seven days of the experiment (the familiarization period), in both sexes, are similar to the findings reported in Chapter II and relate more closely to the observations of low marking rates by gerbils in a thoroughly familiar home cage (Higgins et al, 1967). However, the familiarization period after day 1 was characterised by the timidity of the gerbils once they had established a nest and it is likely that this exaggerated the decrease in the frequency of VENTRAL-MARKING seen in both sexes. The highest marking rates were seen on day 1 and this relates to the findings reported in ChapterII where the highest marking rates were also found in the most novel environments. The absence of any significant changes in the rate of VENTRAL-MARKING in males from the final day of the familiarization period and over the periods during and after the first day of the "open-area" trials do not agree with the findings reported in Chapter II where the dominant males showed significant decreases in the rate of marking during encounters, and significant increases after encounters with other males. Although these previous findings supported the observations of Nyby et al (1970) the results here suggest that this is not always the case. In Chapter II the increase in the marking frequency of the dominant animals after encounter could have been the result of the novel olfactory stimuli deposited in the dominant's area by the subordinate during the first encounters. In these experiments, where the area available was much larger, it is possible that during the first encounter there was little chance for animals to deposit large amounts of odorous substances in the neighbouring areas, either because they were quickly challenged by the neighbours or because of their initial reluctance to explore the neighbour's area. Thus when animals returned to their own areas after the "open-area" trials on the first day there were little in the way of novel olfactory stimuli from the neighbours to provoke marking. The lack of any clear dominance-subordinate relationships during these experiments may have masked further any increases related to the status of the animal after an encounter, since Nyby et al (op. cit) also suggest that status is an important factor in determining who marks after an encounter. However, there was evidence of a significant decrease in the marking rate per trial of low aggression animals over trials (Table 3.11.) which supports the findings of Nyby et al (op. cit.) where the level of marking in subordinates dropped gradually as a result of aggressive encounters.

In the light of the evidence that suggested animals were unable to establish dominance relationships (Section 3.4.3.) it is perhaps not surprising that VENTRAL-MARKING was not significantly related to the level of aggression in the male, either before, during or after opportunities to interact with neighbours. The association of VENTRAL-MARKING with the level of aggression in the female, however, may suggest that the neural stimuli involved in a social interaction are key regulatory factors in the control of marking in females. Thiessen et al (1971 b) suggested that because of the apparent low degree of hormonal control in the female marking behaviour, neural stimuli were more important although females were low markers anyway and it was difficult to make any specific proposals. There was evidence, however, of the increased marking frequencies in lactating females as previously reported by Wallace et al (1973). Lactating females marked more than other females in periods after interactions and it was also clear that, although the data was too variable to be significant, lactating females showed a much greater frequency of marking during the familiarization trials than other females.

The effect of the presence of a litter and/or a lactating female on the marking behaviour of the male is also clear during the "open-area" trials in these experiments where males that had litters marked significantly more than those without. The possible function of this behaviour is probably better understood in the light of the data reported in Chapter IV. Scent-marking in the male, however, particularly in the presence of litters may assist in identification of pups. Wallace et al (op. cit) reported that the scent marks of the female assists in the retrieval of pups. The effect of paternal scent marks is not mentioned, although it was observed in the experiments reported here that a male will mark a pup from its litter. It was not clear, however, if this behaviour would also assist the female in retrieving the pup later.

The overall increase in the frequency of the behaviour URINATE after interaction may be related to the physiological state of animals after aggressive interactions, that is stress or heightened arousal. Its possible significance as a territorial scent mark is discussed in Chapter IV.

3.7.0. CONCLUSIONS

Male and female Mongolian gerbils exhibited agonistic behaviour patterns that were indistinguishable in form but varied, often quite markedly, in their frequencies of performance and temporal patterning. In both sexes it was possible to identify clusters of behaviours which were associated with high aggression and low aggression. Within each experiment it was also possible to distinguish animals exhibiting different levels of aggression relative to the neighbouring animal of the same sex. Thus each animal could be classified as showing relatively high or relatively low aggression for each experiment.

These two groups of animals in each sex also revealed differences in the temporal patterning of their behaviours, although there was a general tendency for aggression in all groups to become more ritualized in the short term during a trial. This ritualization of aggression took the form of increasing frequencies of the display HIND-DIG, which probably serves as a threat behaviour in the gerbil.

The effect of the experimental conditions on the behavioural interactions between neighbouring animals appeared to prevent the formation of clearly defined dominance-subordination relationships between members of the two pairs and thus affected the way in which certain behaviours were related to each other. In particular a number of behaviours, previously identified as being associated with low aggression and subordination, did not appear to be associated with the level of aggression in either sex. In general females were involved less frequently in interactions with neighbouring animals; however it was clear that, for certain behaviour patterns associated with aggression, they were as aggressive as the male. It was probable that the females' lower frequency of interaction with neighbours was in part a result of the relatively higher status of the males in the pairs and a probable avoidance of interactions by females.

Pairs with litters were found to be generally more aggressive over their neighbours, who did not have litters. In females this was thought to be related to her hormonal state while lactating. In males it was unclear whether the greater frequencies of certain aggressive behaviours, when compared to the neighbouring males, was due to the effect of the hormonal state of the female or in defence of the young.

The frequencies of VENTRAL-MARKING behaviour in males was not related to the level of aggression shown in the interactions with neighbouring animals, but was related in the female. It was suggested that the lack of correlation in the male was a symptom of the experimental conditions which mediated against the formation of dominance relationships. In the female the correlation was probably related to the relative importance of social interactions in controlling the rate of marking.

Evidence was also presented that suggested lactating females exhibited higher marking frequencies than nonlactating females particularly after interactions. The finding that males with litters marked more than males without litters and a discussion of the function of marking behaviours in this experiment is probably best carried out in Chapter IV where the data reported in this Chapter are reviewed in the light of data relating the performance of behaviours to location within the experimental arena.

CHAPTER IV

THE EXPERIMENTAL INDUCTION OF TERRITORIAL BEHAVIOUR IN THE MONGOLIAN GERBIL

4.0.0. THE EXPERIMENTAL INDUCTION OF TERRITORIAL BEHAVIOUR IN THE MONGOLIAN GERBIL

4.1.0. INTRODUCTION

Studies of populations of several species of gerbil in their natural habitats have so far failed to yield anything more than a hypothetical description of the true nature of their social organization, particularly in relation to their spatial organization. For the species Meriones unguiculatus, the dearth of relevant data from field studies of wild populations make it even more difficult to suggest the nature of its social organization (Chapter I). Many authors claim that the Mongolian gerbil is a territorial species, which actively defends a home area and excludes intruders (Thiessen, 1973), although the evidence for this is questionable (Section 1.4.2.). The belief that this species of gerbil is territorial has meant that the scent-marking behaviours, particularly marking with the ventral gland, have been assumed to be territorial behaviours, which function as a means of labelling the animal's territory and assisting in its maintenance. There is virtually no evidence to support this and Johnson (1973) has pointed out that in many other species, that are known to have a territorial organization and a means of scent-marking, there is no case where the communication value of a scent-mark with respect to its territorial organization has been determined.

In Chapter I (Section 1.3.3.) the concept of a territory was discussed in relation to the social organization of mammalian societies. It was shown that, although the use of a strict definition of the term was open to question, in order to avoid confusion when using the term territory or territorial behaviour, many authors had used these terms to describe the social organization of different species where animals were seen to occupy a more or less exclusive area and maintained its exclusivity through the repulsion of other conspecifics by means of overt aggression or advertisement (Wilson, 1975). It was felt that this type of definition was also in the minds of the authors who had originally labelled the Mongolian gerbil a territorial species (Thiessen, 1973), and this definition will be used here to examine the behaviour of pairs of gerbils.

It was felt that three questions, relating to the spatial organization of the Mongolian gerbil, therefore needed to be asked:

a) Can territorial behaviour, as defined above, be demonstrated in the Mongolian gerbil under laboratory conditions?

b) If this species does show territorial behaviour, what role does scent-marking play?

c) If territorial behaviour cannot be induced under laboratory conditions what role does scent-marking play in the social organization observed?

Thus an experiment was designed in an attempt to seek answers to these questions using mated pairs of gerbils, which were felt to be the type of groupings that would exist in the wild (Chapter I, Section 1.4.1.). Territorial behaviour, the occupation and maintenance of an exclusive area, has been demonstrated previously in mice (Crowcroft and Rowe, 1963; Anderson and Hill, 1965; Mackintosh, 1970; Poole and Morgan, 1976) and rats (Calhoun, 1961). In the gerbil, however, many of the results of previously reported studies of their social organization under laboratory conditions may have depended on the pathological effects of densities of animals that were artificially high, and this may have accounted for the formation of a dominance hierarchy and high mortality rate observed in the study by Gallup and Waite (1970) (see Chapter I, Section 1.4.2.). However it is obvious that, unless unlimited space is available, the density of animals (i.e. number of animals per unit space) will always be higher in the laboratory than in the wild, particularly when the densities of gerbils in the wild are probably of the order of 55-100 animals per hectare (Chapter I, Section 1.4.1.). These higher densities would seem to favour the formation of a dominance hierarchy and not allow for the possibility of territory formation. In the limited space available during these experiments it was therefore necessary to try to reduce the apparent density of animals using procedural manipulation. Davis (1971) highlighted the important signals that would increase as density increased and suggested that the effects of high density could be reduced if the number of these signals were decreased rather than allowing animals to adapt to these high densities by changing their social organization. The important signals are probably acoustic, olfactory, visual and social such that an increase in density would increase the number of sounds and smells as well as increasing the probability of seeing other animals and interacting with them. It was felt to be unrealistic to attempt to control the number of sounds and smells during the experiments and, in any case, as the study was conceived to examine the relationship between olfactory cues and spatial organization, any control of olfactory cues would seem undesirable. However sight of and interactions with other animals could be realistically controlled by keeping the animals separated by an opaque, unclimbable barrier, and by limiting the animals' access to each other. In this respect a complex environment, with frequent opaque screens preventing uninterrupted surveillance of the environment, was found to enhance territory formation in mice (Anderson and Hill, 1965) which may have been due, at least in part, to the reduction of the visual signals indicating the density of animals. It is doubtful, in any case, that territorial mammals would be in a position to survey even the whole of their territory all the time (Leyhausen, 1965). However the use of complex areas with screens and barriers was rejected for the experiments reported here as it made observations very difficult and sometimes impossible.

Although it was possible to limit the interaction and visual contact between animals and thereby possibly reduce the number of signals indicating the higher density, it was clear that once animals had access to each other and the whole arena the limited space would have an effect on their behaviour. In particular animals could only retreat or flee so far and could not totally escape persistent chases by another animal. In Chapter I (Section 1.4.1.) it was shown that the size of an area that an animal could actively defend was related to the density of the population and relative aggressiveness of the animal to its neighbours. In these experiments no attempt was made to match animals on the basis of their aggressiveness, thus an animal that was far more aggressive than its neighbour could, in effect, take over the neighbour's area. Since the less aggressive neighbour could not be driven out it was likely that an hierarchical dominance-subordination relationship would develop between the animals, or the less aggressive animal would be killed. Accordingly it was necessary to attempt to reduce this by preventing one animal from persistently defeating its neighbour in fights or other forms of aggressive behaviour. It was hoped that, by curtailing trials in which one animal was persistently dominated by the other, and by imposing a limitation on the length of fighting behaviour which may have lead to one animal becoming dominant, the likelihood of dominance-hierarchies forming would be reduced.

Finally, in an experiment attempting to induce territorial behaviour, it was necessary to have some criteria which would enable the formation of territories to be recognised. Anderson and Hill (1965) suggested that one indicator, that territories had been formed in colonies of mice, was the cessation of fighting behaviour. However, it has been found that among populations of rodents in the wild there is a very low incidence of fighting, regardless of the social organization that exists, and that even within groups of strangers some form of social organization develops and fighting behaviour is reduced (Wolfe and Summerlin, 1968). Thus in order to use the cessation of fighting as a criterion of territory formation, it was also necessary to ensure that the animals were at least not showing signs of a dominance-hierarchy when the criterion was reached and were also showing signs of maintaining exclusive use of their area.

4.2.0. MATERIALS AND METHODS

The experimental apparatus and the procedures used have been described before (Chapter III, Section 3.2.0.), however the results of the experiments presented in this Chapter are based on behavioural data collected in respect of the specific locations in the arena (see Chapter III, Fig. IV). In making the recordings of the behaviours during all phases of the experiment a note was made of where each behaviour occurred.

During the first seven days of seven of the experiments (Nos. 5-11), that is during their familiarization periods, a record was made in particular of the location of each performance of the behaviour patterns VENTRAL-MARKING, HIND-DIG and URINATE, in the animals' home area. During the second phase of all eleven experiments, that is the ten consecutive days of trials when the partition between the two areas was removed, a record was made of all the changes of location for each animal throughout the whole arena. At the start of each trial the position of each animal was recorded just before the partition was lifted and subsequently only changes from one specified location to another were noted. These data were then analysed by computer to give values for the amount of time individual animals spent at each location during a trial. This was achieved by totalling the number of 30 second blocks, the time base used during the recording of all behaviours during the second phase of the experiment, where an animal had remained in one place. If an animal had changed its location during a 30 second time period it was assumed, for the purposes of the calculations, that it had spent an equal amount of time at each location during this period. The time at each location during a 30 second block was thus easily calculated by dividing the 30 seconds by the number of locations, this was then added to the running total for each location. At the end of each trial, during the fifteen minute observation periods after the partition had been replaced and the animals returned to their own halves of the arena, the location for each performance of the behaviours VENTRAL-MARKING, HIND-DIG and URINATE were also recorded in seven of the experiments (Nos. 5-11).

The criteria used for terminating each trial have been discussed before (Chapter III, Section 3.2.0.), however it is important to discuss the criteria used to terminate trials, and each experiment before the end of ten days, here.

The termination of trials when a fighting bout lasted for more than 30 seconds was both an attempt to limit the formation of dominance-subordination relationships between animals, as discussed in Section 4.1.0., and to prevent serious wounding to the experimental animals. Similarly the curtailment of trials where one animal was being persistently harassed by a more aggressive animal also aimed at preventing the formation of a dominance relationship and serious injury to the less aggressive animal.

The experiments could be terminated before the end of the ten day period, if animals interacted without any serious fighting (i.e. bouts of less than 30 seconds) and without the formation of any apparent dominance hierarchy, for a period of one hour. The choice of these criteria,or indeed any criteria at all, was based on the findings of other authors (see previous section) that fighting between animals stopped once the population became organized in some way. However, the results of pilot studies carried out prior to the final setting up of this experiment suggested that any social organization adopted by animals under these laboratory conditions was unlikely to be stable and that fighting persisted even after the establishment of dominance-hierarchies when two pairs of animals were allowed unrestricted access to each other. Similar observations were reported by Gallup and Waite (1970). It was probable that the high densities of animals, estimated at 3,500 per hectare, under these laboratory conditions were too great to allow the formation of a stable social organization. Similarly it was felt to be unrealistic to expect that a stable territorial organization would be established for any length of time during these experiments, even though the strict controls were introduced in an effort to lessen the effects of high densities. Accordingly it was decided that, at most, only indications that the gerbils were capable of behaving in a territorial manner would be seen during these experiments, and these were laid down in the criteria for the termination of experiments. It was felt that this would be sufficient to enable a study of the aggressive behaviour and scent-marking in relation to the establishment of a territory to be carried out.

4.3.0. RESULTS

4.3.1. USE OF SPACE BY ANIMALS

It was clear during the experiments that in no case did pairs of gerbils maintain exclusive control over their own half of the arena throughout the experiment. After the initial trials, intrusions by neighbours were frequent and in the majority of cases no behaviour patterns that could be obviously construed as territorial were seen. Nevertheless in two of the eleven replicates of the experiment the criteria indicating possible territorial behaviour were reached. These will be discussed more fully in Section 4.3.3. However in order to look generally at the spatial organization of the gerbils under these conditions the data from all eleven experiments were pooled. This enabled analyses to be carried out on the data relating to the time spent at each location during the second phase of the experiment when animals were allowed to interact. Male and female data were analyzed separately.

Although animals did not maintain an exclusive area during these experiments it was possible to discover how much time they actually spent in each half of the arena. From the individual totals of time spent at each location in the arena it was possible to calculate individual grand totals for time spent in each half of the arena in each experiment. The individual totals for the true border area (B in Fig. IV) were not included in these calculations as animals were neither in one area nor the other when they were at this location. Since each of the experiments was of different duration these grand totals were expressed as a percentage of the total duration of the second phase of each experiment and a mean value for all the eleven experiments for each sex in each half of the arena was calculated. A Wilcoxon Matched-Pairs Signed-Ranks test was performed on the individual scores comparing the total percentage time spent in the home half with the total percentage time spent in the neighbour's half of the arena. Table 4.1. summarizes the data and gives the results of the analysis where it can be seen that both sexes spent significantly more time in their home halves of the arena when the partition was removed.

PERCENTAGE TIME IN ARENA

	MALE (N=22)		FEMALE (N=22)	
	HOME HALF	NEIGHBOURS' HALF	HOME HALF	NEIGHBOURS' HALF
$\bar{x}$	71.05	25.56	80.92	15.91
S.D.	23.031	21.10	16.02	15.18
WILCOXON	T = 26		T = 3	

Table 4.1. Mean percentage time spent in "home" and "neighbours'" halves of the arena by males and females during the second phase of the experiment. The individual total percentage times spent in each half were compared for both sexes using the Wilcoxon test; both were significant at $p<0.005$ (one-tailed test).

A further analysis comparing individual total percentage times in each half across the sexes was carried out using the Mann-Whitney "U" test and this revealed that there were no significant differences between males and females in the amount of time spent in each half of the arena (HOME HALF (MALE VS FEMALE) N_1=22, N_2=22, Z=1.49 pNS: NEIGHBOURS' HALF (MALE VS FEMALE) N_1=22, N_2=22, Z=1.37 pNS). Thus there appears to be some attachment to the home area even though animals have access to the whole arena. An analysis of the data for the total percentage of time spent at each of the specified locations in the animals' home half of the arena was then carried out in order to discover if the animals' attachment to the home area was centred around any particular location. Table 4.2. summarizes the findings and gives the result of a Friedman Two-Way Analysis of Variance carried out on the individual percentage time scores for each location in the home area for males and females. As in the previous analysis the data for the true border ("B" in Fig. IV) have been omitted. In respect of locations W and F (see Fig. IV) there were insufficient data to include these scores in the analysis. Individual totals for each location were also compared across the sexes using the Mann-Whitney "U" test (see Table 4.2.).

MEAN PERCENTAGE TIME SPENT AT LOCATIONS IN HOME AREA

LOCATIONS		E	N.B.	X	B(1,2)	FRIEDMANS x^2_R (df=3)
MALE (N=22)	$\bar{x}$	18.88	32.34	7.95	11.27	396
	S.D.	11.29	22.45	14.25	9.46	
FEMALE (N=22)	$\bar{x}$	18.82	40.29	9.00	9.10	338
	S.D.	13.51	47.87	6.79	10.37	
U test		z=0.25	z=0.95	z=0.76	z=0.52	

Table 4.2. Mean percentage times spent at each location in the home area for males and females. The results of the Friedmans Two-Way Analysis of Variance performed separately on the individual totals for each location for males and females were both significant, $p<0.001$. The results of the Mann-Whitney U tests comparing the individual totals for each location for males and females were not significant.

The results shown in Table 4.2. revealed that both males and females spend significantly different amounts of time at each location in their home area. The two sexes do not show any significant differences between them in percentage time spent at each location and it appears that both spend most time in and around their nest (NB), during the time when the two halves of the arena were open to each other.

A similar analysis can be carried out on the data for percentage time spent at each location in the neighbours' half of the arena. Data for areas W and F were omitted from this analysis again because they were insufficient. Table 4.3. summarizes the results of the "Friedmans" analysis carried out separately on the individual total percentage times spent at each location in the neighbours' area for males and females. The data for males and females were also compared using the Mann-Whitney U test and the results are also presented in Table 4.3.

MEAN PERCENTAGE TIME SPENT AT LOCATIONS IN NEIGHBOURS' AREA

LOCATIONS		E	N.B.	X	B(1,2)	FRIEDMANS x^2_R (df=3)
MALE	$\bar{x}$	9.17	4.59	2.91	6.75	336
	S.D.	7.59	5.69	3.66	4.97	
FEMALE	$\bar{x}$	6.40	4.15	2.03	4.65	335.3
	S.D.	5.97	4.64	2.72	3.57	
U test		z=1.38	z=0.328	z=0.633	z=1.67*	

Table 4.3. Mean percentage times spent at each location in the neighbours' area for males and females. The results of the Friedmans Two-Way Analysis of Variance performed separately on the individual totals for each location for males and females were both significant, $p<0.001$. The results of the Mann-Whitney U test comparing the individual totals for each location for males and females are shown where * = $p<0.05$.

The results shown in Table 4.3. indicated that both males and females spent significantly different amounts of time at the different locations in their neighbours' area, spending most time at locations E and B(1,2). Males and females showed no significant differences in total percentage time spent at locations E, NB and X in their neighbours' area but females spent significantly less time at location B(1,2).

So far the analyses of the time data has revealed significant preferences for animals to spend a higher percentage of their time in their home area particularly at their nesting site and less time overall in their neighbours' half of the arena, although when they are in their neighbours' area they tend to spend more time in the largest location, E. If this attachment to the home site is as a result of aggressive encounters with their neighbours (i.e. animals showing defence of their home area) the time spent at locations within the neighbours' area might be expected to decline, and the time spent at locations within the animals' home area might be expected to increase over the ten trial days. Individual totals for percentage time spent at each location in home and neighbours' areas for each trial, with the exception of location B, the true border, were therefore submitted to regression analyses wherever possible. The regressions were carried out for each experiment on transformed data, the individual percentage totals being converted to "arc-sin" values, which normalized the data making it more amenable to this type of analysis (Rohlf and Sokal, 1969). The results of this analysis are shown in Table 4.4. where male and female data were analyzed separately and a summary of the significant values is given. Each experiment was treated separately and thus the summary of the significant values has been constructed from the results.

NUMBER OF SIGNIFICANT REGRESSIONS (i.e. $p<0.05$)

	HOME AREA		NEIGHBOURS' AREA	
LOCATION	MALE	FEMALE	MALE	FEMALE
E	1(+)	1(+) 1(-)	1(-) 1(+)	0
B(1,2)	0	2(+)	1(-)	0
NB	1(+) 2(-)	2(+) 1(-)	1(-)	1(+)
X	0	0	1(+)	0
W	1(-)	0	0	0
F	0	0	0	0

Table 4.4. Summary of the significant values for regression slopes from the analyses carried out on the transformed data of total percentage time spent at each location during each trial for each individual male and female. The results are shown as total numbers of significant slopes where the significance levels were at least $p<0.05$. The direction of the slopes, either increases (+) or decreases (-) over trials are shown in brackets. Total N for males and females = 44.

It is clear from the results of the regression analyses shown in Table 4.4. that there was no conclusive evidence to suggest that animals spent less time in their neighbours' area and more time in their own as the experiments progressed over the ten days.

4.3.2. FREQUENCY OF BEHAVIOUR PATTERNS AND LOCATION

Although animals showed significant attachment to their home area during these experiments, it did not appear to be a consequence of previous encounters with neighbours, since there were no indications that any overall increases or decreases in time spent at various locations in the arena had occurred over the experimental days. Nevertheless there may be distinct differences in the behaviour of animals depending on whether they are in their home area or in their neighbours' area.

Wilson (1975) discussed the concept of an "invincible centre" in connection with territory in birds. Unless an adult male bird is grossly over-matched or ill he is usually undefeatable by conspecific birds at the centre of his territory (Nice, 1941; Tinbergen, 1939). In studies of mammalian societies this concept has been used in terms of the reversal of dominance when animals cross from their own home range to a neighbours' (Chapter I, Section 1.3.3.) In effect this suggests that a territorial individual has an area in its home range where it is dominant (i.e. has the right of way to obtaining food and other limited resources) to all other conspecifics. This also implies that a resident will be more aggressive than an intruder, who will tend to be more submissive (Dunford, 1970).

If this phenomenon is occurring during the second-phase of the experiments reported here it would be expected that the frequencies of behaviours shown by individual animals, particularly those associated with aggression and submission towards the neighbours, should show marked differences depending on whether the animal was a resident or an intruder in the area. Thus the resident animal should be expected to show higher frequencies of aggressive behaviour in its home area and higher frequencies of submissive behaviour in its neighbours' area where it will be an intruder. These differences may become more marked towards the "centre" of each home area (Krebs, 1971). The "centres" of the areas here are probably those locations where the animal spends most time (the core-area, [Kaufman, 1962]), which were shown to be the nesting sites (NB) in the previous section.

The total frequencies of each behaviour pattern for each animal over the whole experiment were therefore calculated for each location in the animals' home and neighbours' areas. This was done using a computer. For those behaviours that were classified as directed behaviours (Chapter III, Section 3.3.1.a) the frequencies used were those between an animal and its neighbour. The data for males and females were collected separately. A Wilcoxon Matched-Pairs Signed-Ranks test was then carried out comparing the individual total frequencies of each behaviour for each location in the home-area with its equivalent in the neighbours' area. A further analysis was also carried for each behaviour comparing the individual grand total frequencies in the home area with the neighbours' area. Males and females were tested separately.

Table 4.5. summarizes the data and gives the results of the analysis for the directed behaviours in males. Insufficient data were available for the separate analysis of the frequencies of the behaviours at locations F and W in both areas, although they were included in the calculation of the grand totals. There were also insufficient data for any analysis of the behaviour patterns SIDEWAYS-DEFENSIVE, SQUINT, UPRIGHT-DEFENSIVE, CRAWL-UNDER, SNIFF, AGGRESSIVE-GROOM, AVOID, FULL-AGGRESSIVE and ATTEMPT-MOUNT. Where the data were amenable to analysis it was clear that males CHASE neighbours more in the neighbours' area X, FLEE more from neighbours when at their own home nest box (NB) and perform more SIDEWAYS-OFFENSIVE towards their neighbours when at the neighbours' nest box (NB).

MEAN FREQUENCIES OF DIRECTED BEHAVIOURS (MALES; N = 22)

	LOCATIONS	E		$B_{1,2}$		NB		X		W		TOTALS	
	AREA	$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.
APPROACH	HOME	6.45	6.12	5.23	5.74	2.60	3.21	0.91	1.38	-		15.45	13.03
	NEIGHBOUR	4.56	6.28	3.23	2.57	2.36	4.19	1.73	3.63			12.00	14.26
NOSE	HOME	-		-		-		-		-		5.86	5.68
	NEIGHBOUR											4.64	5.04
CHASE	HOME	2.55	3.11	1.64	2.32	1.09	1.76	0.23	0.52	-		5.36	6.01
	NEIGHBOUR	3.59	6.56	1.68	2.36	2.59	5.54	1.45	3.13 *			9.68	16.28
FLEE	HOME	4.00	7.94	0.50	1.82	1.82	3.26	0.91	1.47	-		7.45	11.96
	NEIGHBOUR	1.45	2.57	0.55	0.94	0.27	** 0.54	0.27	0.54			3.86	5.45
RETREAT	HOME	2.45	3.17	2.27	3.15	0.82	1.11	0.36	0.64	-		5.86	4.56
	NEIGHBOUR	3.41	5.77	6.09	8.28 **	1.23	2.59	0.77	2.02			11.14	16.74
FIGHT	HOME	0.95	0.006	0.91	1.04	0.73	0.91	-		-		2.64	2.14
	NEIGHBOUR	0.72	0.86	0.45	0.72	1.05	1.64					2.73	2.39
SIDEWAYS-OFFENSIVE	HOME	0.50	0.99	-		0.05	0.21	-		-		0.68	1.10
	NEIGHBOUR	0.45	1.07			0.77	1.31 **					1.95	3.54
FOLLOW	HOME	-		-		-		-		-		3.45	3.99
	NEIGHBOUR											3.45	4.82
INVESTIGATE	HOME	-		-		-		-		-		0.68	1.89
	NEIGHBOUR											0.59	1.55
CHASE-BITE	HOME	-		-		-		-		-		0.45	0.89
	NEIGHBOUR											0.27	0.62
UPRIGHT-OFFENSIVE	HOME	-		-		-		-		-		0.14	0.46
	NEIGHBOUR											0.23	0.52
ATTACK	HOME	0.41	1.07	0.86	1.42	0.32	0.70	-		-		1.68	2.24
	NEIGHBOUR	0.64	1.17	0.50	1.12	0.50	1.31					1.86	2.74

Table 4.5. Summary of mean frequencies of directed behaviours performed by males with neighbours at each location in his home area and his neighbours' area. The results of a Wilcoxon test comparing total frequencies for individual males at home locations and at neighbours' locations are given, where * = $p<0.05$, ** = $p<0.02$, *** = $p<0.01$.
Where the comparisons were not possible because of insufficient data no figures have been entered.

The data and analyses for females are summarized in Table 4.6. Insufficient data were available for the separate analyses of the frequencies of behaviour at locations F and W in both areas. There were also insufficient data for analysis of the frequencies of the behaviour patterns CHASE-BITE, SIDEWAYS-DEFENSIVE, SQUINT, UPRIGHT-OFFENSIVE, UPRIGHT-DEFENSIVE, CRAWL-UNDER, SNIFF, AGGRESSIVE-GROOM, AVOID, FULL-AGGRESSIVE and ATTEMPT-MOUNT. Where the data were amenable for analysis it was clear that females APPROACH neighbours more when they were in their home location E but FLEE more from neighbours when they were at their home location X. Females also FIGHT neighbours more when they were at their home location F and generally FOLLOW neighbouring animals more in their own home area.

Thus there is very little evidence to indicate any obvious effect of location on the frequencies of the directed behaviours towards neighbours.

MEAN FREQUENCIES OF DIRECTED BEHAVIOURS (FEMALES; N = 22)

	LOCATIONS	E		$B_{1,2}$		NB		X		W		TOTALS	
	AREA	$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.
APPROACH	HOME	2.91	3.69	1.91	1.83	1.5	2.51	0.77	1.5	-		7.09	7.67
	NEIGHBOUR	1.00	** 1.62	2.23	2.31	0.86	1.10	0.65	1.5			4.95	5.03
NOSE	HOME	-		-		-		-		-		2.82	2.69
	NEIGHBOUR											2.23	2.37
CHASE	HOME	1.18	1.83	0.32	0.63	0.73	1.30	-		-		2.32	3.40
	NEIGHBOUR	0.91	1.73	0.59	1.07	0.86	1.54					3.09	5.66
FLEE	HOME	2.73	5.31	0.86	1.22	2.09	3.18	1.27	2.07	-		7.36	10.58
	NEIGHBOUR	1.55	2.08	0.86	1.52	0.86	1.32	0.14	** 0.35			3.82	3.72
RETREAT	HOME	2.50	6.00	2.14	2.88	1.14	2.38	0.36	0.64	-		6.36	10.82
	NEIGHBOUR	1.45	2.55	4.41	6.28	1.41	2.59	0.27	0.86			7.64	9.87
FIGHT	HOME	0.68	1.33	0.41	1.07	0.36	0.71	-		-		1.32	1.89
	NEIGHBOUR	0.09	* 0.29	0.32	0.63	0.36	0.83					1.14	1.71
SIDEWAYS-OFFENSIVE	HOME	-		-		-		-		-		1.00	2.47
	NEIGHBOUR											0.82	1.56
FOLLOW	HOME	-		-		-		-		-		1.18	1.82
	NEIGHBOUR											0.36	*** 0.57
INVESTIGATE	HOME	-		-		-		-		-		0.18	0.38
	NEIGHBOUR											0.18	0.49
ATTACK	HOME	-		-		-		-		-		0.55	1.12
	NEIGHBOUR											0.68	1.06

Table 4.6. Summary of mean frequencies of directed behaviours performed by females with neighbours at each location in her home area and her neighbours' area. The results of a Wilcoxon test comparing total frequencies for individual females at home locations and at neighbours' locations are given, where * = $p<0.05$, ** = $p<0.02$, *** = $p<0.01$.
Where comparisons were not possible because of insufficient data no figures have been entered.

The data and analyses for the non-directed behaviour patterns for males are summarized in Table 4.7. Insufficient data were available for the separate analyses of the frequencies of these behaviours at location F in both areas. There were also insufficient data for analysis of the frequencies of the behaviours DIGS, FEED, FULL-SUBMISSIVE and SQUEAK. In the analyses of the remaining behaviours it was apparent that most VENTRAL-MARKING by males occurred in their neighbours' areas particularly at locations B, X and W, where there were significantly higher frequencies of marking than in the males' home area. Not surprisingly males performed higher frequencies of the behaviour pattern EXPLORE at all locations (except W and F) in their neighbours' area and generally explored the neighbours' area more than their own. Males also performed higher frequencies of the behaviour pattern URINATE in their neighbours' area than in their own, and showed higher frequencies of the behaviour pattern FOOT-THUMP in their home areas than in their neighbours' areas.

MEAN FREQUENCIES OF NON-DIRECTED BEHAVIOURS (MALES; N = 22)

	LOCATIONS	E		$B_{1,2}$		NB		X		W		TOTALS	
	AREA	$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.
VENTRAL-MARKING	HOME	1.18	2.84	0.32	0.70	0.64	1.36	0.09	0.27	0.27	1.25	2.95	5.31
					*				***		*		**
	NEIGHBOUR	3.14	5.40	1.64	2.72	3.18	3.91	4.09	7.42	2.05	3.70	13.27	20.77
FREEZE	HOME	2.00	4.67	1.00	1.95							3.27	5.27
						-		-		-			
	NEIGHBOUR	1.23	2.13	0.68	1.06							2.09	2.50
TAIL-RATTLE	HOME											0.77	2.40
		-		-		-		-		-			
	NEIGHBOUR											0.77	2.08
SELF-GROOM	HOME											0.77	1.16
		-		-		-		-		-			
	NEIGHBOUR											0.32	0.82
FOOT-THUMP	HOME											1.14	3.12
		-		-		-		-		-			**
	NEIGHBOUR											0.32	1.06
HIND-DIG	HOME	5.73	10.60	3.59	11.17	0.32	0.76					9.68	17.90
	NEIGHBOUR	4.50	6.83	0.86	2.16	1.82	5.35					8.14	15.24
EXPLORE	HOME	0.00	0.00	0.13	0.34	0.00	0.00	0.00	0.00			0.14	0.35
			***		***		**		*	-			***
	NEIGHBOUR	2.82	2.82	2.18	1.68	0.50	0.89	0.45	1.08			6.09	5.08
URINATE	HOME	0.55	1.90									0.64	2.10
				-		-		-		-			***
	NEIGHBOUR	1.45	3.30									2.32	4.17
SIT	HOME			0.73	0.73							1.09	1.35
		-				-		-		-			
	NEIGHBOUR			0.82	1.34							1.36	2.03

Table 4.7. Summary of mean frequencies of non-directed behaviours performed by males at each location in his home area and his neighbours' area. The results of a Wilcoxon test comparing total frequencies for individual males at home locations and at neighbours' locations are given, where * = $p<0.05$, ** = $p<0.02$, *** = $p<0.01$.
Where the comparisons were not possible because of insufficient data no figures have been entered.

The female data and analyses of the non-directed behaviour patterns can be seen in Table 4.8. Insufficient data were available for separate analyses of the frequencies of behaviours at locations W and F in both areas. There were insufficient data for analysis for the behaviour patterns SELF-GROOM, FOOT-THUMP, DIGS, URINATE, FEED and FULL-SUBMISSIVE. In the analysis of the remaining data there were only significant differences in the frequencies of the behaviour pattern EXPLORE when it was clear that females explored the neighbours' area more than their own, in particular exploring the locations E and B to a greater extent in their neighbours' area.

MEAN FREQUENCIES OF NON-DIRECTED BEHAVIOURS (FEMALES; N = 22)

	LOCATIONS	E		$B_{1,2}$		NB		X		W		TOTALS	
	AREA	$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.
VENTRAL-MARKING	HOME	0.68	2.55	-		-		0.09	0.29	-		1.41	4.48
	NEIGHBOUR	0.36	0.83					0.59	1.50			2.23	4.39
FREEZE	HOME	0.55	1.23	0.27	0.62	-		-		-		1.09	1.99
	NEIGHBOUR	0.09	0.30	0.18	0.49							0.50	0.78
TAIL-RATTLE	HOME	-		-		-		-		-		0.23	1.04
	NEIGHBOUR											0.55	1.16
HIND-DIG	HOME	1.86	4.61	-		-		-		-		4.18	9.94
	NEIGHBOUR	0.50	1.27									1.18	2.42
EXPLORE	HOME	0.045	0.21	0.13	0.34							0.18	0.38
			***		***								***
	NEIGHBOUR	1.64	1.37	1.77	2.86							3.77	3.66
SIT	HOME	-		-		-		-		-		0.64	1.90
	NEIGHBOUR											0.64	1.94
SQUEAK	HOME	-		-		-		-		-		0.82	1.75
	NEIGHBOUR											0.05	0.21

Table 4.8. Summary of mean frequencies of non-directed behaviours performed by females at each location in her home area and her neighbour's area. The results of a Wilcoxon test comparing total frequencies for individual females at home locations and at neighbours' locations are given, where * = p<0.05, ** = p<0.02, *** = p<0.01.
Where the comparisons were not possible because of insufficient data no figures have been entered.

4.3.3. THE EFFECTS OF THE PRESENCE OF LITTERS ON THE USE OF SPACE

In the previous Chapter it was shown that a lactating female with a litter and her mate were generally more aggressive than their neighbours during the second phase of the experiment (Section 3.3.5.). It was suggested that this aggression was in defence of the litter, however the aggression may have been also in defence of a space or "territory" in which the female could successfully raise the litter. Ahroon and Fidura (1976) maintained, on the basis of their observations of the behaviour of females with litters either with or without their mates, that the female gerbil "may demand some increase in territorial space following the birth of a litter, a change necessary for the development of appropriate maternal behaviour" (p. 374). Similarly, in other rodent species, the presence of a litter may cause females to establish a territory and defend their nest (Chapter I, Section 1.3.2.). In the general analysis of these experiments no significant indications of territorial behaviour, apart from the demonstration of site attachment, were found. However, a separate examination of the data for those experiments where one pair had had a litter might have revealed significant indications of territorial behaviour, which were masked in the general analysis but may have been clearer in these experiments.

Perhaps the most obvious effect that the presence of litters had, was shown in two experiments where the criterion laid down to indicate that a temporary social organization, possibly territorial, was reached. It was clear that, during the course of the hour-long trials where no fighting occurred, the animals were behaving in a way which kept them apart although not necessarily confined to their own areas.

For the most part animals did intrude into each others areas during these hour-long sessions. However, the intruding animals often retreated when approached by the resident and often avoided the neighbour if they had made only visual contact. The intruders were chased and would flee if they got too far into the neighbours' area but on several occasions the chasing animal retreated rapidly if it had entered the neighbours' area during this CHASE-FLEE bout. These bouts were not continuous and there were long periods where animals seemed to tolerate each other and remained in their own halves of the arena. However, they would make frequent visits to the border locations ($B_{1,2}$) and, if the neighbour was not visible, often intruded as far as the border location in the neighbours' area. Most of the activity during the hour stemmed from the locations around the borders. Where neighbours met they would often start CHASE-FLEE bouts or both would retreat into their home areas. Occasionally these neighbours would remain in visual contact with each other while performing the behaviour pattern HIND-DIG which thus appeared to be a form of mutual threat display, but the highest frequencies of this behaviour appeared to occur after an APPROACH-

RETREAT or CHASE-FLEE bout.

The overall impression gained from observations of these trials in these two experiments was that animals were reluctant to fight, although frequently very agitated and aroused. They were also very prone to retreating from neighbours, particularly at the areas around the partition. Thus the behaviour of the pairs during these two experiments was somewhat similar to the behaviour of other animals that have been shown to be territorial, particularly with respect to the animals' tendency to retreat when in the neighbours' area (Mykytowycz, 1965; 1968). It seemed, however, that this tendency arose more out of the animals' avoidance of each other than any defence of a home area. Again, as in the general analysis of these experiments, there was no evidence of any significant changes in percentage time spent in the neighbours' area during these two experiments, when the results of the regression analyses carried out on each experiment (Table 4.4.) were examined individually. Thus the apparent low percentage time spent in the neighbours' area was a feature of these experiments from the start.

Unfortunately, as only two experiments had reached the criterion chosen to indicate possible territorial behaviour, it was not possible to carry out any further statistical analyses. However an overall analysis of the five experiments where litters were present, was carried out and thus these two experiments were analyzed in the context of the effect of litters on the behaviour of the pairs.

An analysis of the individual total percentage times spent in the home area and nest boxes during these experiments was carried out comparing animals with litters to those without for males and females. This comparison was done using the Mann-Whitney U test when it was found that pairs with litters did not spend any more time in their home area or nest than those without litters. Table 4.9. summarizes these results.

Nevertheless when pairs with litters left the nest it was always sealed with peat before they left it and, although they did not appear to stay close to the nest, it was frequently checked by one or other of the pair during the time the second-phase trials were running.

MEAN PERCENTAGE TIME SPENT AT EACH LOCATION

		MALE		FEMALE	
LOCATION		WITH LITTER	WITHOUT LITTER	WITH LITTER	WITHOUT LITTER
HOME AREA	$\bar{x}$	83.78	67.04	84.04	78.44
	S.D.	14.15	21.56	12.31	9.91
NEST BOX	$\bar{x}$	47.88	32.32	49.48	44.54
	S.D.	26.81	16.04	24.10	29.43

Table 4.9. Mean percentage total time spent in home areas and at own nest boxes for animals with and without litters. None of the differences were significant when the individual mean frequencies of time for animals with and without litters were compared using the "U" test.

The final analysis of the data in these five experiments was carried out on the total frequencies of each directed and non-directed behaviour pattern for each individual at each location in the arena. Comparisons between the same locations in the animals' home and neighbours' area were then carried out using the Wilcoxon Matched-Pairs Signed-Ranks test as before (Section 4.3.2.). In totalling the frequencies of each directed behaviour only the frequencies of the behaviours involving neighbouring animals were used. A comparison of the individual grand-total frequencies of each behaviour pattern for all the locations in the home area versus all the locations in the neighbours' area was also carried out using the Wilcoxon test.

In carrying out these analyses it was found that there were insufficient data for comparisons to be made of locations F, X and W. These were therefore omitted from the analysis but were included in the analyses of the grand-total frequencies for home and neighbours' areas. Tables 4.10, 4.11 and 4.12. give a complete summary of the data and analyses, but where the data were insufficient for analysis, no figures were entered.

Few significant differences in these data were evident. Males APPROACH neighbours more frequently at E and B in their home area and also FOLLOW neighbours more frequently in their home area. Males and females EXPLORE more frequently in their neighbours' area, in particular at E and B. Beyond these significant differences the data from the experiments where litters were present showed no conclusive evidence that the frequencies of behaviours, particularly those associated with aggression, alter as a function of the location of the animal in relation to its home area.

MEAN FREQUENCIES OF DIRECTED BEHAVIOURS (MALES; N = 10)

	LOCATIONS	E		$B_{1,2}$		NB		TOTAL	
	AREA	$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.
APPROACH	HOME	6.80	4.85	6.30	5.78	3.10	2.74	16.6	10.56
	NEIGHBOUR	3.50	* 3.92	2.60	* 1.43	1.80	3.46	8.60	6.77
NOSE	HOME	-		-		-		4.80	1.94
	NEIGHBOUR							3.70	3.90
CHASE	HOME	1.40	1.96	1.60	2.42	1.50	2.16	4.60	5.26
	NEIGHBOUR	1.90	3.21	0.60	1.18	0.60	1.02	3.50	5.43
FLEE	HOME	2.40	3.80	-		1.20	1.66	4.80	6.68
	NEIGHBOUR	2.30	3.40			0.40	0.66	3.80	5.53
RETREAT	HOME	1.80	2.40	2.60	2.54	1.10	1.37	5.80	4.98
	NEIGHBOUR	2.20	2.14	4.90	6.16	1.00	2.05	8.50	8.51
FIGHT	HOME	1.30	1.10	1.30	1.19	0.70	0.90	2.90	2.34
	NEIGHBOUR	1.20	0.98	0.70	0.78	1.20	1.78	3.70	2.37
FOLLOW	HOME	-		-		-		2.40	1.50
	NEIGHBOUR							1.10	* 0.94
ATTACK	HOME	0.90	1.44	1.20	1.40	-		2.50	2.54
	NEIGHBOUR	0.90	1.30	0.30	0.64			1.90	1.97

Table 4.10. Summary of mean frequencies of directed behaviours performed by males with neighbours at each location in his home area and his neighbours' area, for the five experiments where litters were present. The results of a Wilcoxon test comparing total frequencies for individual females at home locations and at neighbours' locations are given, where * = $p<0.05$.

MEAN FREQUENCIES OF DIRECTED BEHAVIOURS (FEMALES; N = 10)

	LOCATION	E		B1,2		NB		TOTAL	
	AREA	$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.
APPROACH	HOME	2.80	2.27	2.80	2.09	1.50	1.02	7.90	5.26
	NEIGHBOUR	1.50	1.91	3.00	2.68	1.20	1.40	6.80	5.65
NOSE	HOME	-		-		-		3.10	2.17
	NEIGHBOUR							2.80	2.79
CHASE	HOME	1.00	1.48	-		-		2.30	2.86
	NEIGHBOUR	1.20	2.18					4.30	7.20
FLEE	HOME	1.70	2.76	0.70	1.27	1.20	1.54	4.70	6.40
	NEIGHBOUR	1.50	2.62	1.30	2.05	1.30	1.62	4.40	4.74
RETREAT	HOME	0.60	0.80	2.30	1.85	0.60	1.02	3.60	2.62
	NEIGHBOUR	1.40	2.42	5.80	7.89	2.20	3.52	9.70	12.30
FIGHT	HOME	-		0.70	1.49	-		1.30	1.42
	NEIGHBOUR			0.60	0.80			1.70	2.05
FOLLOW	HOME	-		-		-		1.00	0.77
	NEIGHBOUR							0.40	0.49
ATTACK	HOME	-		-		-		1.00	1.48
	NEIGHBOUR							1.00	1.18

Table 4.11. Summary of mean frequencies of directed behaviours performed by females with neighbours at each location in her home area and her neighbours' area, for the five experiments where litters were present. The results of a Wilcoxon test comparing total frequencies for individual females at home locations and at neighbours' locations were not significant.

MEAN FREQUENCIES OF NON-DIRECTED BEHAVIOURS FOR MALES (N=10) AND FEMALES (N=10)

		LOCATION	E		$B_{1,2}$		NB		TOTALS	
		AREA	$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.
MALE	VENTRAL-MARKING	HOME	2.50	3.80	0.60	0.80	1.20	1.83	6.00	6.68
		NEIGHBOUR	3.80	4.90	2.10	3.21	3.20	4.64	17.6	24.57
	FREEZE	HOME	-		-		-		2.40	1.96
		NEIGHBOUR							2.10	2.74
	HIND-DIG	HOME	10.70	13.74	-		-		17.10	23.13
		NEIGHBOUR	3.10	6.83					7.00	15.82
		HOME	0.00	0.00	0.10	0.30			0.10	0.30
	EXPLORE			**		**	-			***
		NEIGHBOUR	1.70	1.41	1.90	1.75			4.20	3.03
		HOME	0.00	0.00	0.10	0.30			0.10	0.30
FEMALE	EXPLORE			***		*	-			***
		NEIGHBOUR	1.80	1.33	2.70	3.93			4.90	4.48

Table 4.12. Summary of the mean frequencies of non-directed behaviours for males and females at each location in their home area and their neighbours' area, for the five experiments where litters were present. The results of a Wilcoxon test comparing total frequencies for individuals at their home location and at neighbours' locations are given, where * = $p<0.05$, ** = $p<0.02$, *** = $p<0.01$.

4.3.4. THE EFFECT OF THE SECOND-PHASE TRIALS ON THE LOCATION OF SCENT-MARKING BEHAVIOUR

On the seven days before the second phase of the experiment, when the two halves of the arena were opened to each other, the frequencies of the behaviour patterns VENTRAL-MARKING, HIND-DIG and URINATE were recorded and the location of each performance of these behaviours also noted during experiments 5 to 11. At the end of each trial of the second phase of these experiments the same records were made of the three behaviours. Thus it was possible to examine the effect that interactions between neighbours had on the location of these behaviours, particularly the scent-marking behaviour VENTRAL-MARKING. In Chapter I (Section 1.5.2.) the function of scent-marks as a means of territorial defence was discussed. In particular it was shown that if scent marks are to act as a means of territorial defence it might be expected that they would occur most frequently at the territorial boundaries (Hediger, 1949). It might therefore be expected that in these experiments if the animals were responding to the conditions of the second-phase by forming territories, of some sort, the distribution of scent-marks would be altered and animals might show a tendency to mark at the border between the two areas. This tendency would be more readily revealed by a consideration of the distributions of marks in the seven days prior to the "open area" trials, and in the periods immediately after the "open-area" trials, since the partition provided an ideal reference point as an artificial boundary, once the neighbourshad had the chance to interact and had been returned to their respective halves of the arena. This was possible in seven of the experiments (Nos. 5 - 11).

The distribution of the scent-marks, during the seven day familiarization period and during the fifteen minute observation periods after the areas had been reclosed, were examined statistically by first providing a measure of what proportion of marks occurred near the partition during the familiarization period and after the "open-area" trials. This was done by calculating individual values for the ratio of marks performed in the areas B(1,2) to marks performed in the rest of the home area, during the two relevant periods. In calculating the ratios for the familiarization period it was clear that in all cases the highest frequencies of marking behaviour occurred on the first day of introduction (see Chapter III, Section 3.3.2., Table 3.1.) and it was also the time when the animals were most active and exhibited a great deal of exploratory behaviour throughout the whole arena. Thereafter their behaviour became localised around the nest site; this may have had the effect of localising their marking behaviour around the nest which was quite close to the border areas $B_{1,2}$ (see Fig. IV); however the marking frequencies were too low after the first day to establish that any localisation of scent-marking at $B_{1,2}$ had occurred. The ratios for the familiarization period were thus calculated from the frequency data for the whole period. The ratios for males and females were calculated separately (Table 4.13).

In calculating the values for this ratio from the data recorded during the fifteen minute observation periods individual values were also calculated from a combined frequency score for all the observation periods. Males and females were treated separately.

The ratios for each individual during the two periods were then compared separately for males and females using the t-test for related samples (Morris , 1974). The data are summarized and the results of this analysis given in Table 4.13.

MEAN RATIO FOR NO. OF MARKS: BORDER AREAS/REST OF HOME AREA

	MALES (N=14)		FEMALES (N=14)	
FAMILIARIZATION PERIOD	$\bar{x}$ 0.14	S.E. 0.02	$\bar{x}$ 0.13	S.E. 0.07
15 MINUTE OBSERVATION PERIODS	$\bar{x}$ 0.55	S.E. 0.02^*	$\bar{x}$ 0.25	S.E. 0.14

Tab;e 4.13. Mean values for ratio of number of marks in border areas ($B_{1,2}$) to number of marks in the rest of the home area for males and females during 7 day familiarization period and the 15 minute observation periods, after "open-area" trials. The results of the t-test carried out on the differences between individual ratios are given. df=13, * = $p<0.01$ (one-tailed test).

It is clear from Table 4.13. that the ratio of number of marks at the border locations to number of marks throughout the rest of the home area alters significantly for males from about 1:7 during the familiarization period to 1:2 during the fifteen minute observation periods. This indicates that there is a shift in the distribution of scent-marks deposited by males towards the border after the second-phase of trials. For females the ratio of marks does change from the familiarization period to the observation periods from 1:8 to 1:4 but this change is not significant since many females did not mark during the observation periods.

This tendency to localise marks at the border after the "open-area" trials was also reflected partially in the data for the frequencies of the behaviour patterns HIND-DIG and URINATE.

It was not possible to carry out the same comparison for these behaviours as had been carried out on the VENTRAL-MARKING data since there were insufficient data available from the familiarization period. However comparisons between the frequencies of these behaviours at the border areas and the frequencies throughout the rest of the home areas for each animal were possible from the data recorded during the fifteen minute observation periods. The total frequencies of each behaviour performed by each animal at the border areas and in the rest of the home areas were calculated for males and females. A Wilcoxon Matched-Pairs Signed-Ranks test was then performed on the individual frequencies of each behaviour comparing the totals for the border areas and the rest of the home areas for the behaviour patterns HIND-DIG and URINATE in males and females separately. Table 4.14. summarizes the data and the results of the analysis.

MEAN FREQUENCIES AT EACH LOCATION

		HIND-DIG		URINATE	
		BORDER LOCATIONS	REST OF AREAS	BORDER LOCATIONS	REST OF AREAS
MALE	$\bar{x}$	5.65	12.50	3.15	4.46
			*		
	S.D.	8.27	9.62	2.71	3.89
FEMALE	$\bar{x}$	1.22	5.67	2.00	3.29
			*		
	S.D.	1.03	5.49	1.85	2.37

Table 4.14. Mean frequencies of HIND-DIG and URINATE at the border areas and the rest of the home areas during the 15 minute observation periods for males and females. Comparison of the individual frequencies at each location was carried out using the Wilcoxon test where * = $p<0.025$ (one-tailed test).

Table 4.14. shows that both males and females perform significantly lower frequencies of the behaviour pattern HIND-DIG at the border during the 15 minute observation periods which is to be expected since the border locations in each half only accounted for approximately one thirteenth

of the total area of each half. It is all the more surprising that, given this disparity in the size of the areas compared, there were no significant differences in the frequencies of the behaviour pattern URINATE between these two areas in males and females. This would suggest that like VENTRAL-MARKING the performance of the behaviour URINATE and deposition of urine is directed towards the area around the partition, the artificial border between the two areas.

4.4.0. DISCUSSION

This study was carried out in an attempt to induce territorial behaviour in pairs of gerbils, maintained under laboratory conditions, in an effort to examine the role of their scent-marking behaviours. The results of these experiments, however, cast doubt on the suggestion that these animals are strictly territorial.

During the trials, where animals had access to the home areas of the neighbouring pairs, it was clear that these home areas were not maintained as exclusive areas by their occupiers, although, overall, animals spent significantly less time as intruders in the adjacent area than they did in their home area (Table 4.1.). As intruders, animals were not restricted from moving throughout the neighbours' area and the proportion of time spent at the various locations seemed to be related to the relative sizes of the area at each location, thus animals spent most time at location E, by far the largest location (Table 4.3.). There was also no evidence overall that previous aggressive encounters with the resident animals had any effect on the time that animals spent in the adjacent area (Table 4.4.). Defeat by a male in its home area has been reported as being sufficient to cause avoidance of that area by the defeated animal, in mice (Anderson and Hill, 1965) and in gerbils, where even the odours from the area will cause avoidance (Nyby et al, 1970). In the experiments reported here the lower percentage times spent at locations in the neighbouring area are evident on the first day of the trials and persist throughout the ten days at the same level in practically all cases regardless of the aggressive encounters. These findings are related to the discovery that animals exhibit very few changes in the frequencies of aggressive behaviours depending on whether they are in their home area or are intruding in a neighbours' area (Section 4.3.2.). In Chapter III (Table 3.6.) clusters of behaviours related to the aggressiveness of males and females were found. Here there was little evidence to suggest that animals showed consistently higher frequencies of those behaviours related to high aggression in their home locations, and higher frequencies of those behaviours related to low aggression in their neighbours' locations. Thus there was no evidence that resident animals were in any way more likely to defeat an intruder, as would be expected of a territorial species. The dominance of a resident in an encounter with an intruder is one way in which an animal might successfully maintain exclusive use of an area and it has been stressed before (Chapter I, Section 1.3.3.). Changes in dominance across a territorial border should therefore be generally noticed when neighbouring animals interact, where the social organization is stable, and any absence of this dominance-reversal could mean that either the social organization is not stable or the animals are not territorial. Bronson (1964) concluded that Woodchucks were not territorial when he failed to get evidence of any site-related dominance phenomenon. However in the experiments reported here it is possible that one of the reasons for the lack of any indication of site-related dominance was related to the lack of a stable social organization between the pairs. Thus the aggression shown at the locations in the arena was more likely to be related to the overall aggressiveness of the animal. It is surprising, nevertheless, that the nesting sites did not seem to influence the frequency of aggressive behaviours shown, particularly by residents with litters (Section 4.3.3.). It was certainly the location where animals spent the most time during the trials, when the areas were open and this has been found before in *M. unguiculatus* (Thiessen, 1973) and in wild populations of *M. hurriannae* (Fitzwater and Prakash, 1969). It was therefore most likely to be the location that would provoke the most aggression by residents in its defence if it was in some way functioning as the centre of their territory (Krebs, 1971), that this was not the case may mean that it was simply the undefended "core-area" of the animals home area (Kaufman, 1962).

The evidence presented so far has not given any indication of the reasons why the animals tended to remain to a large extent in their own areas when they had free access to the neighbouring area, and also were apparently undeterred by the aggression from its residents and generally as aggressive in this neighbours' area as they were in their own. It was certainly clear that these animals were not territorial according to the commonly accepted definition of territorial behaviours (see Chapter I, Section 1.3.2.) and Young et al (1950) reported a similar localisation of activity in their indoor populations of mice although they did not observe any territorial behaviour. Ginsburgh and Braud (1970) also reported that gerbils showed a significant preference for their own home environment when given a daily choice between their own area and a similar but novel environment. This preference gradually decreased over six days but returned when given aversive stimulation. In the experiments reported here, even where the behaviour of the pairs reached a stage where it resembled territorial behaviour in two experiments (see Section 4.3.3.), it seemed that it was not so much the result of defence of the home area by the resident but more a result of mutual avoidance. Mutual avoidance could in fact account for the results presented here and it was seen in its clearest form in these two experiments.

Hill (1977), discussing the findings of his work on the utilization of space by <u>Peromyscus</u>, suggested that:

> "the dispersion patterns observed in natural populations of <u>Peromyscus</u> appear to result more from mutual avoidance than from aggressive defence of specific areas". (p. 386)

His study looked at several factors affecting the utilization of space in two species of <u>Peromyscus</u> and he found that the initial reaction of two individuals was active avoidance which persisted for several days. These findings support the results of the experiments reported here where there were no significant changes in the way animals use the arena although there were persistent and unchanging indications of the overall avoidance of the area occupied by another pair of gerbils. This avoidance was not influenced significantly by previous aggressive encounters with resident animals and King (1957) also reported that aggression in Peromyscus had no significant effect on mutual avoidance. It is interesting to note that in the analysis of the behaviour patterns carried out in the previous Chapter, the frequency of the behaviour pattern RETREAT was not related to high aggression or low aggression groups of males or females (Table 3.6.); it was suggested that this was in some way the result of the experimental conditions. In the light of the evidence presented here it is probable that the behaviour pattern RETREAT was a reflection of the animals' mutual avoidance, whether an animal was highly aggressive or not. Thus the apparent attachment to the home area was in fact a manifestation of a mutual avoidance phenomenon occurring between the two pairs and it becomes clear why animals were generally as aggressive in encounters with neighbours in both their home area and the neighbours' area. Since animals were not defending a specific area but perhaps maintaining a social distance, aggression would not be dependent on location but on the proximity of another animal. The concept of social distance has been discussed before (Chapter I, Section 1.4.1.) and it has been described for wild populations of M. hurriannae (Fitzwater and Prakash, 1969) where animals maintained an individual distance of about 2-4 metres and chased animals who came closer. These animals also indulged in dirt throwing behaviour when this individual distance was violated and the authors suggested that, although in general the home ranges of this species of gerbil overlapped, the chasing and dirt throwing were territorial behaviours related to the defence of the burrow, which they use more frequently than any other part of the range. Both these behaviours were observed in the experiments reported here but there was no evidence that they were in any way used more frequently to defend their home nest area (Sections 4.3.2., 4.3.3.). It is far more likely that they served to maintain an individual distance in these Mongolian gerbils since, although the patterns of these behaviours was similar to the patterns reported for *M. hurrianae* they were not significantly related to any specific site.

It is therefore apparent that the behaviour of the pairs of gerbils involved in these experiments is best described as the result of mutual avoidance rather than territorial behaviour. The scent-marking behaviours, particularly VENTRAL-MARKING, cannot therefore function as territorial behaviours although they may have some significance in the spacing of individuals.

During these experiments scent-marking in the form of the frequency of VENTRAL-MARKING was clearly affected by the location and in particular the novelty of the location. Its decline to low frequencies during the seven day familiarization period has been discussed before as an aspect of the declining novelty value of the home area (Chapter III). However once the two areas were open to each other animals had access to a novel area and, although the marking rate did not increase significantly as a consequence of having the new area to mark (Chapter III, Section 3.3.3. and Tables 3.11, 3.13.), there was a significant tendency for males to mark more in this neighbouring area. This has been found before (Chapter II and Thiessen et al, 1971 b).

More remarkable was the shift in the distribution of marks towards the border (the partition) between the two areas in males, as a result of interactions with the neighbours (Section 4.3.4.) and there was evidence that this was not only for the behaviour pattern VENTRAL-MARKING but also for the behaviour pattern URINATE. This significant shift in the location of these two behaviours in the animals' home area is all the more interesting when it is clear that the threat behaviour HIND-DIG does not show this shift (Table 4.14.). Thus it is not merely localisation of activity immediately after an aggressive encounter but a preferential shift in behaviour in order to deposit odourous substances, sebum and urine, at the partition (border) between the two areas. Hinde (1970) suggested that animals actively seek aggressive encounters by going to the place where they last fought and concluded:

> "a wide range of species can show appetitive behaviour for aggression in the laboratory, and strongly support the plentiful and highly suggestive field data indicating that the same occurs in nature" (p. 344)

It was observed during these experiments that some animals would come to the partition just before the start of an "open area" trial which may have been a manifestation of this phenomenon in the gerbil. This could mean that these behaviours are functioning as some sort of threat aimed at the animals' neighbours (Johnson, 1973) but the absence of any similar shift in the others threat behaviour HIND-DIG makes this unlikely. It is far more likely that the VENTRAL-MARKING at least might be significantly localised at the border because there would be more likelihood of novel scent marks from the neighbours at this point. Inspection of Table 4.7. shows that locations $B_{1,2}$, X and W all receive a significantly higher frequency of marks from intruding males, which could account, at least in part, for the proportional increase in VENTRAL-MARKING by resident males at $B_{1,2}$ when the partition was replaced. Similarly, disproportionately high frequencies of the behaviour URINATE at $B_{1,2}$ as a result of encounters may also indicate that this behaviour pattern is a scent-marking behaviour, although its relationship to novelty is unclear in the gerbil. Other authors have suggested that the deposition of urine can constitute a scent-marking behaviour (Ewer, 1968; Ralls, 1971; Kleiman, 1966; Johnson, 1973). Maruniak (1974) has reported that urinary marking in male mice is increased in a novel environment, but there has, so far, been no evidence of its function as a scent-mark in the gerbil until now.

Nevertheless the novelty of the border in terms of olfactory stimuli cannot fully account for the proportional shift in the frequencies of the scent-marking behaviour since, as can be seen from Table 4.7. other locations in the animals' home area are marked by intruders with more or less the same frequency. Thus male gerbils seem to be actively going to the border to deposit scent-marks after encounters. Its purpose seems therefore to be to place scent-marks as near to a neighbour as possible and it appears that, in the light of the avoidance animals showed towards each other during the experiments, the scent-marks may serve as an olfactory signal which could act to assist this mutual avoidance. Leyhausen and Wolff (1959) suggested that scent-marks might act like "railway signals" which minimize encounters between individuals by signalling an animal's presence and how recently it passed. There is some evidence that this occurs in the cheetah, Acinonyx jubatus, where animals have no fixed territories but avoid encountering each other (Eaton, 1970). The scent-marks of the otter may also have this sort of effect (Erlinge, 1968) where intrusions, even to the centre of a neighbouring territory, are common. However there is virtually no evidence of animals withdrawing on encountering an alien mark (Johnson, 1973). It is more likely that these marks may signal that an animal is either in a foreign territory or that another conspecific is nearby and thus predispose withdrawal in the presence of that resident or conspecific animal. However it is reasonable to suppose that such marks only acquire aversive properties or will only affect the behaviour of another animal through a learning process as a result of repeated aggressive encounters with the resident or conspecific animal. Nyby et al (1970) have reported that defeated gerbils will avoid the odours from the area where they received their defeat, which supports this suggestion.

In these experiments there was certainly no evidence of any aversive property in the marks deposited at the border by neighbours after each "open area" trial since there was no apparent drop in the amount of time spent in neighbours' areas. However this does not rule out the possibility that the marks could have obtained some value as a signal which predisposed animals to retreat, and that this was as a result of the previous encounters between neighbouring pairs. In two experiments it was clear that animals showed a predisposition to retreat from their neighbours' area during their hour-long trials, which may have been mediated, at least in part, by olfactory cues. It is significant that this behaviour minimised contact between the neighbours but that it took a number of trials for it to be clearly seen, which points to the operation of a learning process taking place over a number of repeated aggressive encounters.

The possible signalling function of the scent-marking behaviour in the gerbil will be investigated further in the next chapter.

4.5.0. CONCLUSIONS

Pairs of male and female Mongolian gerbils showed significant attachment to their home area when they had access to an adjacent, but occupied area. Neighbouring pairs, however, did intrude regularly into each others areas even to their centres. During this time no obvious defence of the home area was seen and although animals were very aggressive towards neighbouring pairs this did not alter the percentage time animals spent in the neighbouring areas. The Mongolian gerbil was therefore not behaving in a manner that was in accordance with the definition of territory adopted previously by many authors, that is "a defended area". It was suggested that the relationship between neighbours and the attachment to the home area was a result of the mutual avoidance between the pairs.

Scent-marking behaviour, and in particular VENTRAL-MARKING, cannot therefore be considered as a territorial behaviour in this species in the sense that it is a behaviour carried out in defence of an area. Its frequency appears to be partly a function of the relative novelty value of environments but it was suggested, on the basis of the shift in the proportion of marking done at the border of the two areas after the "open-area" trials, that it could function as a signal which could assist in minimising meetings between animals in adjacent areas. This suggestion will be investigated in the following Chapter.

CHAPTER V

THE MODIFICATION OF BEHAVIOUR IN MALE GERBILS THROUGH OLFACTORY CUES

5.0.0. THE MODIFICATION OF BEHAVIOUR IN MALE GERBILS THROUGH OLFACTORY CUES

5.1.0. INTRODUCTION

In the previous chapter the possible signalling function of scent-marks, in particular the scent deposited during the behaviour VENTRAL-MARKING, was briefly discussed. It was suggested that these marks might act as signals which assisted in minimising encounters between conspecifics. The effect of the marks would be to predispose animals to retreat from or avoid each other when they met. The signalling function of these marks could have been a consequence of the repeated aggressive encounters between animals, when the scent-marks associated with each animal acquired some aversive properties through a learning process. There was, however, no direct evidence of this from the results of the experiment reported in the previous chapter.

Generally, the scent-marks of a strange male are attractive to other male conspecifics in a number of species, and are therefore approached readily (Johnson, 1973). In male Mongolian gerbils there is evidence that strange male sebum is also attractive (Baran and Glickman, 1970; Thiessen et al, 1970 c), but that when male animals were given the choice between strange male sebum and strange female sebum in a Y-tube apparatus there was no evidence that male sebum was preferred over the female sebum (Thiessen et al, 1970 a) which may indicate that it is the unfamiliarity of the scent-mark which is attractive, rather than its "sex".

It is therefore clear that any properties of a scent-mark that might cause a modification of the approach behaviour in males must be learned. Baran and Glickman (op. cit., p. 243) suggested that ".... one might expect that the association of any .... odour types with aversive situations (e.g. defeat) in the mutual habitat could lead to their acquisition of aversive or deterrent properties". Halpin (1974) also suggested that the odours produced by gerbils were for individual identification and found that male Mongolian gerbils could detect differences in ventral gland and urine odours from 31 intact male conspecifics. She hypothesized that approach-avoidance responses to these odours may have to be learned and depended on previous positive or negative experiences with the individual producing any one odour. There is evidence that these negative experiences with individuals appeared to be connected with defeat during aggressive encounters, which, according to Nyby et al (1970), resulted in the defeated individuals avoiding the odours from their opponents in preference tests run in a Y-tube after a series of aggressive encounters. It was not clear, however, from the study by Nyby et al (1970), what specific role the scent marks from the ventral-gland played in mediating the avoidance behaviour observed.

So far there have been no studies that have looked specifically at the role of ventral-gland secretions in modifying the behaviour of other gerbils (Johnson, 1973), but it is clear from the work of Halpin (1974) that there could be a differential response to individual ventral-marks which might be related to the degree of negative and positive experiences associated with it. Thus a strange mark would elicit an approach response, but a familiar mark, i.e. one that is associated with a conspecific with whom the animal had interacted, might elicit differing degrees of approach depending on the degree of aversiveness of the previous experience. However, in order to study the overall effect of scent-marks in a sample of animals it would be necessary to control for the degree of aversiveness. In the experiments reported by Nyby et al (op. cit.) the avoidance response to odours from other animals was the result of being defeated by these animals in highly aggressive encounters. In each case the experimental animal was attacked by four animals in a very confined box, had no way of escape and was often mobbed. Although the procedure ensured that the experimental animals received very aversive experience with other animals, it was a very unnatural situation. On the basis of the experiments previously reported in Chapter IV it was clear that, when conditions were designed to mimic more closely the supposed natural situation, the avoidance shown by animals was less clearly a result of aggressive encounters, although there was evidence that animals were sometimes relucant to fight (Chapter IV, Section 4.3.3.). However there was no way of detecting what effect these aggressive encounters had on the animals' responses to odours from neighbours as many other cues were available to the animals which could have been used in maintaining the avoidance behaviour throughout the trials. Yahr (1977) reported that visual cues significantly affected the marking behaviour of subordinate gerbils particularly if these cues were similar to the visual cues associated with an area in which it was defeated. Thus in order to study the possible signal value of ventral gland secretions it was necessary to design an experiment which controlled for a number of variables that might affect the use of this olfactory cue as a means of communication.

When two animals fight there are a number of odours that could become associated with the aversive nature of the aggression. In close contact with each other they would be able to smell the odour of the fur which may be impregnated by the odour of the ventral-gland sebum from nesting material. There may also be residual odours from urine and faeces in the fur possibly transferred from nesting material. It has been suggested that the behaviour pattern NOSE enables individuals to identify other animals by means of a pheromone produced by the Harderian glands (Thiessen et al, 1976 a). This behaviour is a feature of introductory behaviour between gerbils (Chapters II and III) and unfamiliar animals sniff the face and genital region as a prelude to further interaction (Halpin, 1976). There would therefore be a good deal of olfactory information available to a pair of animals prior to an aggressive encounter between them, particularly if the aggressive encounter took place in one animal's home area, which would be saturated with its own odours (Ewer, 1968). It is possible that the aversive properties of the whole spectrum of odours, indicated in the results reported by Nyby et al (1970) could apply to each one of the specific odourous substances produced by a gerbil. In this way the sebaceous material from the ventral gland might become less attractive to other gerbils. It was decided to use an escape-response paradigm modelled on this hypothesis of the possible way in which a response to a scent-mark might be learned. Animals would be trained first to avoid the odours produced by another animal using a mild electric shock as the unconditioned stimulus (U.C.S.). The use of mildly aversive shock instead of allowing animals to undergo a series of aggressive encounters was chosen in order to avoid the intrusion of visual cues as variables which may have been attended to in preference to olfactory cues (see Yahr, 1977). It also allowed the possibility of animals escaping from the aversive situation, the unconditioned response (U.C.R.) being fleeing or retreating from the shock. This procedure was chosen since Bolles (1970) suggested that learning was better in animals if the U.C.R. was already the normal response of the animal to a shock. Walters and Abel (1971) showed that Mongolian gerbils were very poor at learning a passive avoidance task, and Walters et al (1963) demonstrated that gerbils responded to a mild shock by trying to run away. Gerbils also attempt to flee or retreat from a more aggressive animal after they have been defeated (see Chapter II), but under laboratory conditions it has been rarely possible to provide enough space for them to escape totally from such an animal, as they would do in the wild (Chapter IV, Section 4.1.0.). Using an escape-training procedure with a mild shock as the U.C.S. it was possible to design a procedure that would allow the experimental animals to escape.

Once trained to avoid odours from an animal it would then be possible to test how much of the response could be elicited only by the sebum from the ventral gland of the stimulus animal.

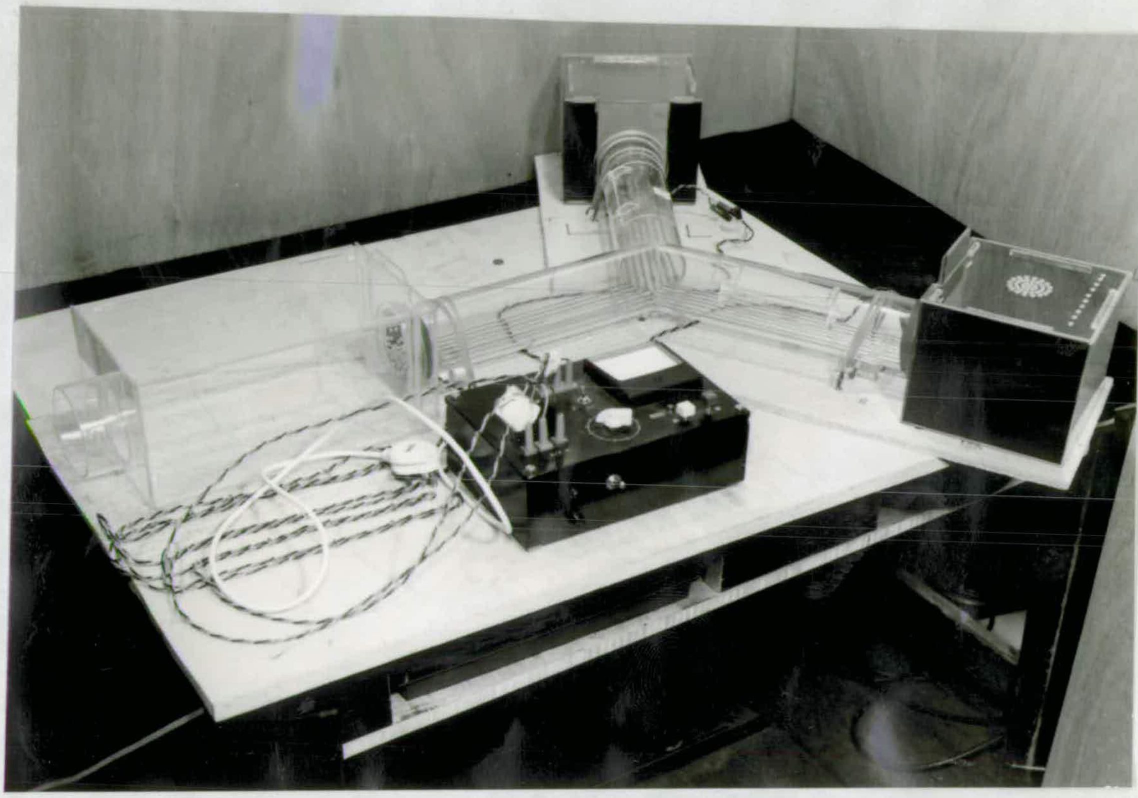


PLATE III

Apparatus used in the experiment reported in Chapter V. The goal boxes can be seen at the ends of the arms of the perspex "Y" tube with their sides masked with black tape. The opaque guillotine doors can also be seen. The larger transparent goal box can also be seen at the base of the "Y" although the extractor fan is not shown. The shock generator is shown in the fore-ground.

5.2.0. APPARATUS

The apparatus used is shown in Plate No.III and was based on the design described by Thiessen et al (1970 a). It consisted of a transparent perspex "Y" tube with arms 30 cm. in length with an internal diameter of 7 cm. At each top end of the "Y" perspex "goal" boxes, 13.5 x 15.5 x 15.5 cm. were linked to the tube using an air-tight rubber sealing-ring. These boxes were rendered opaque by covering their outside walls with black masking tape. At the base of the "Y" a larger transparent "start" box, 28 x 18 x 13.5 cm., was linked to the tube using an air-tight rubber sealing-ring. The tops of each of these boxes were removable and the tops of the "goal" boxes were drilled with a series of small holes to allow air to enter. The boxes were connected to the tube by three guillotine doors which had been perforated to allow the circulation of the air through the tube arms. However the guillotine doors of the "goal" boxes were designed such that no visual contact could be made through them. This was simply achieved by making these doors of two layers of Formica material with a small space between, and the holes drilled in each sheet slightly off-set. This also allowed a filter-paper to be inserted in the space, which was used later to provide the test stimulus when smeared with the secretions of the ventral gland from stimulus animals (see next section).

Air was drawn through the apparatus by a small extractor fan connected to the rear of the "start" box. The fan was baffled and insulated, with foam rubber, from the main body of the apparatus in order to eliminate noise and vibration which had previously been found to disturb the animals (Thiessen et al, 1970 a). When tested this fan provided an even air-flow drawn through the two "goal" boxes and down the arms of the "Y" tube. The noise of the fan itself did not have any apparent effect on the animals.

In each arm of the "Y" tube, a "floor" consisting of seven stainless-steel bars running lengthways along it provided three independent "shock-grids". Each of these grids was separately connected to a shock-generator, based on the design of shock-generators described by Thompson and Higbee (1970). This provided a variable 0 - 10 ma shock of 210 volts. The intensity could be pre-set manually and was shown on a milliameter set in the shock-generator. The generator also provided a means of "scrambling" the shock between the bars of the grid, which meant that polarity of the bars, during the time the shock was on, was changing randomly such that animals could not learn to avoid the shock by standing on bars of the same polarity, which is a common occurrence using an "unscrambled" shock grid (Thompson and Higbee, op. cit.). The shock could be administered to each grid using press-button switches, the duration of the shock being dependent on how long the switch was depressed. During these experiments the intensity of the shock administered was set at 0.9 ma. which was a figure based on reports of previous work (Thompson and

Higbee, 1970; Powell, 1971; Powell and Peck, 1969).

Further refinements to the apparatus, made after pilot trials, included the provision of hinged regions in the top of the two "goal" arms of the tube to facilitate access to the inside of the tube for cleaning and drying.

Because of the possibility that the live stimulus animals, used in the training trials, were producing auditory stimuli, such as scratching, the sound from one box was "matched" with the other, empty box. This was achieved by placing a sensitive microphone over the lid of the "goal" box containing the animal. The sound was fed through an amplifier and into a speaker placed in a similar position over the empty "goal" box. A series of holes were drilled in the lids of the "goal" boxes for this purpose. As far as possible the level of the noise from the animal was reproduced by the speaker at the empty goal box in an attempt to prevent the animals using auditory cues. However this apparatus was not sensitive enough to pick up and reproduce ultrasonic sounds which may have been produced by the stimulus animal (see Sales, 1968, 1972) and constant checks were made using an ultrasonic detector to discover if the stimulus animals were regularly producing this type of acoustic cue. There was no evidence of any ultrasound being produced by the stimulus animals or the experimental animals during these experiments.

5.3.0. MATERIALS AND METHODS

Thirty adult male Mongolian gerbils from the main colony were assigned to four different treatment groups. None had been used in any other experiments. There were 12 animals in a control group (C); 6 animals in an experimental group (E); 6 in an experimental group where the auditory matching apparatus was used (E.A.M.) and 6 in a further control group run after they had had experienced the training procedure (P.T.C.). Prior to these experiments all animals had spent at least one half-hour in the apparatus to habituate them to the fan. During this time the amount of time animals spent in each of the "goal" arms was recorded to test if there was any significant side preference over all the experimental and control animals. None was found. All training and testing was done under a Home Office Licence (No. ED 2018) in a special test room. All testing and training was carried out in the dark phase of the animals' light-dark cycle and the test room was illuminated by a diffused, 40 watt, red light.

The stimulus animals, used to provide sources of olfactory stimuli during the training trials, were single adult males that had been kept individually isolated from the main colony for at least a month before this experiment. This ensured that the olfactory stimuli they provided were solely male odours and contaminating stimuli from females and litters were absent.

Testing and training were carried out as follows:

CONTROL GROUP (C):- A single filter paper that had been very recently smeared with the ventral gland sebum from one of the stimulus males was placed in the door of one "goal" box. A clean filter paper was placed in the door of the other "goal" box. An animal from the control-group was then placed in the "start" box, the door lifted and the animal allowed to go into the "Y" tube. Once the animal had left the "start" box the guillotine door was closed behind it to prevent return. When the animal entered one of the "goal" arms and its head and forepaws remained beyond half-way along the tube for five seconds it was removed and scored as having shown a preference for that side. It was then replaced in the "start" box and after a 30 second delay then allowed to enter the tube and run again. This procedure was repeated for ten consecutive trials, after which the animal was returned to the colony and its cage. The apparatus was then cleaned thoroughly with a soap solution which was rinsed off with clean hot water and the tube and boxes dried in a stream of warm air from a hair-dryer. During each set of ten trials the position of the sebum-smeared filter paper was varied according to a special random table produced by a computer such that no more than two consecutive trials occurred with the stimulus in the same arm. Each of the twelve animals in this group were tested in the same way. When an animal had completed ten trials it was possible to calculate the number of times it had shown a preference for the scented arm and the clean arm and then calculate a ratio of visits to a scented arm versus visits to a clean arm.

EXPERIMENTAL GROUP (E); EXPERIMENTAL GROUP WITH AUDITORY MATCHING (E.A.M.); POST-TRAINING CONTROL GROUP (P.T.C.) :- These groups all had the same training procedure. Each animal was trained for ten trials per day. At the start of each trial a stimulus animal was placed in one of the "goal" boxes and the fan turned on. The animal under training was then placed in the "start" box and after a delay of 30 seconds the guillotine door to the tube opened. The animal was then gently coaxed into the "start" arm and the door closed. After fifteen seconds in which to make a choice of a "goal" arm, a one-second shock of 0.9 ma was administered in the "start" arm. Having made a choiceof an arm the animal was then given five seconds in which to change its choice. If it chose the arm containing the stimulus animal in the "goal" box it was given a shock of 0.9 ma which remained on for three seconds and scored as having made an incorrect response. If the animal was obviously leaving the arm no shock was given. If the animal chose the arm without the stimulus male after they had made an incorrect response they were immediately allowed out of the "Y" tube via the "goal" box. If the animal chose to return to the "start" arm they were given a one second 0.9 ma shock after fifteen seconds but allowed out of the apparatus via the "start" box if they chose to run that way. Any subsequent return to the arm containing the stimulus male resulted in a three second 0.9 ma shock after five seconds. Animals that received more than five shocks in one run were removed from the apparatus. If an animal first went to, and remained in, the arm without the stimulus male for five seconds it was not shocked but was removed via the "goal" box. These were scored as having made a correct response, thus a correct or an incorrect response was only scored on the result of its first choice. After each trial the animal was returned to the "start" box on its removal from the apparatus. The position of the "goal" box was then changed, according to the random tables that were used for the control group (C), and after a 30 second delay the animal was allowed into the "Y" tube again. Ten trials per day were run consecutively up to a maximum of ten days or until each animal had achieved a criterion level of nine correct responses out of the ten trials per day. Each animal was trained with the same stimulus animal each day.

During the training trials of the E.A.M. group the apparatus described in the previous section, for matching the sounds from the empty "goal" box to the sounds coming from the stimulus animal in its "goal" box, was used.

Once each animal had attained the criterion level of correct responses it was put through a test procedure on the following day. An animal in the E or E.A.M. group was given a further ten trials in the tube. This time no shocks were administered and the stimulus animal was absent. Instead a filter paper, which was smeared with the ventral gland sebum from the male stimulus animal on which it had been trained was used as the olfactory cue. Each animal was tested in the same way as the control group (C) and consequently a ratio of visits to the scented arm versus the clean arm could be calculated for each animal. An animal in the P.T.C. group was given a further ten trials in the tube but no shocks were given although the stimulus animal remained to provide the olfactory cues.

5.4.0. RESULTS

5.4.1. CONTROL GROUP (C) (N = 12)

The individual values for the ratio of visits to scented arm versus clean arm were tested, to see if the differences between individuals were greater than chance, using the Chi square test for heterogeneity. This was not found to be significant (Chi square heterogeneity = 7.3; df = 11; p NS). The individual results were therefore combined and a further Chi square test was carried out to discover if there was a significant preference for the arm which contained the goal box with the male sebum. The mean ratio of visits to scented arm versus visits to clean arm for the control group was 2:1 and this ratio was significantly different from chance (Chi square = 22.00, df = 12; $p<0.05$) indicating that males showed a significant preference for the ventral gland sebum from a strange male.

5.4.2. EXPERIMENTAL GROUPS (E, E.A.M. and P.T.C.) (N = 6 per group)

All these groups received the same training to the criterion level and all but one animal attained the level after only six days of training. The animal that failed to reach the criterion within six days received further training until the tenth day but still failed to reach the criterion level and was removed from the sample used in the analyses of the E.A.M. data.

It was clear on the first day of training that animals showed a distinct preference for the arm which contained the "goal" box with the stimulus animal. An analysis was performed on the individual ratios of correct responses versus incorrect responses during the first days training using the Chi square test for heterogeneity. It was found that there were no individual differences in the ratios that were significantly greater than chance (Chi square heterogeneity = 15.91; df = 16; p NS). The mean ratio of correct responses versus incorrect responses was 1:2 and this value was significantly different from chance (Chi square = 41.6; df = 17; $p<0.01$). This showed that animals were showing a significant preference for the arm which contained the odours from the stimulus male in his "goal" box.

After this first day animals learned quickly to avoid the shock and soon made rapid choices without being shocked in the "start" arm. Many animals achieved a level of 100% avoidance of the arm containing the stimulus male.

In the test trials that followed the attainment of the criterion level in training the E group and E.A.M. did not show any significant differences in their ratios of visits to the arm containing the stimulus male sebum versus visits to the clean arm on the basis of a Chi square test for heterogeneity. (Chi square heterogeneity = 15.56, df = 10, p NS). Thus the data from both groups were combined, this gave a mean ratio of visits to the arm containing sebum versus visits to the clean arm of 1:1 which was not significantly different from chance on a Chi square test (Chi square = 15.6, df = 11, p NS). However the expected ratio of visits to the arm containing male sebum versus the clean arm should have been significantly different from chance as shown by the Control group (C) i.e. 2:1 (Section 5.4.1.) and thus a further Chi square test was carried out comparing the ratios after training to the ratio before training. This revealed that there had been a significant change in the ratio of visits to the arm containing male sebum versus visits to the clean arm (Chi square = 31.34, df = 11, $p<0.001$). This was as a result of the training procedure.

Finally an analysis of the data from the test trials in the P.T.C. group was carried out. These animals had been given further trials without shock, after reaching the criterion in the training trials, where the olfactory cues were the same as for their training trials i.e. odours from a stimulus animal. In all but one case did the animals perform at criterion levels. A Chi square test of heterogeneity carried out on individual data was not significant (Chi square heterogeneity = 1.13, df = 5, p NS) and the mean ratio of visits to the arm containing the stimulus animal versus visits to the clean arm was 1:9 and significantly different from chance (Chi square = 42.8, df = 6, $p<0.001$).

5.5.0. DISCUSSION

Thiessen et al (1970 a) demonstrated that the sebum from the ventral gland of a strange male gerbil was attractive to another male gerbil, and the results reported here for the control group of animals (Section 5.4.1.) supported his findings. It was also clear from the results of the first day of training trials (Section 5.4.2.) that the odours from a strange male were also attractive, even when the animals were probably under some stress due to the shocks administered during this first day of training. This may, in fact, indicate how attractive strange male odours are.

It was clear, however, that gerbils could quickly learn to avoid odours from another male using this training procedure which seems to indicate that avoidance learning of this type as a result of the aversive nature of aggression between two animals may be possible, as suggested by a number of authors (Section 5.1.0.). The persistence of this avoidance behaviour was also demonstrated in this experiment when animals maintained their learned avoidance even when the aversive stimulus was absent in the P.T.C. group (Section 5.4.2.).

It was also apparent that conspecific odours are likely to be used in preference to other cues, like auditory cues, since there was no significant effect on the behaviour of animals when the control for auditory cues was employed. This did not rule out the possibility that animals were using ultrasonic calls, produced by the stimulus animal, but there was no evidence that the stimulus animals were in fact producing any during the trials. Nigrosh et al (1975) showed that rats attended preferentially to olfactory cues rather than sound or visual cues in discrimination experiments and this was probably true for the male gerbil in this experiment.

The effect of the training procedure employed in this experiment on the subsequent behaviour of animals towards the sebum from the ventral gland of their stimulus animals was marked. It was clear that the learned avoidance of odours from a male gerbil was transferred to some extent to the ventral gland secretion, such that these secretions became significantly less attractive. Thus the odour of a ventral mark can be used as a signal whereby an animal can modify its behaviour on the basis of its previous experience.

A number of authors have suggested that the change in behaviour observed in some animals when they enter alien territory is mediated by scent marks. Mykytowycz (1965, 1968) has described how a rabbit, on entering alien territory will become alert, move with an altered posture, cease to feed and readily flee from an occupant. Thiessen et al (1970) have reported that animals appear to become more cautious and hesitant when in the presence of scent marks from other gerbils. Thus the altered behaviour with regard to ventral marks, seen in this experiment as a change in the number of approaches or visits to the arm of a "Y" tube containing the odour of a ventral mark from a male, may manifest itself in the cautious behaviour suggested by these other authors, when translated into behavioural terms for animals in the wild. Baran and Glickman (1970), Johnson (1973) and Halpin (1974) have emphasized the possible role of previous experience in suggesting that scent-marks may have some function as a behavioural modifier but it has not been experimentally demonstrated prior to the results presented here.

5.6.0. CONCLUSION

Using the method of escape-training, it has been demonstrated that the normally significant preference of a male gerbil for the sebum from the ventral-gland of a strange male gerbil can be clearly modified if the olfactory cues emanating from that strange male become associated with an aversive stimulus. This suggests that ventral marks may play the role of a behaviour modifier in natural populations, its role being dependent on previous experience.

CHAPTER VI

DISCUSSION AND SUMMARY

6.0.0. DISCUSSION AND SUMMARY

6.1.0. AGONISTIC BEHAVIOUR IN THE MONGOLIAN GERBIL

The agonistic behaviour of the Mongolian gerbil has been examined here under two very different conditions. In the experiments reported in Chapter II the analysis of these behaviours was from the results of male-male encounters carried out in a small cage, whereas in the experiments reported in Chapter III the agonistic behaviours were recorded in a larger arena between pairs of males and females. Thus it was possible to obtain a much broader picture of the agonistic behaviour of this species than has previously been reported (Chapter II, Section 2.1.0.).

The behaviours observed under the two conditions were identical in form in both males and females. It was clear, however, that a number of postures seen in males under the more confined conditions reported in Chapter II occurred less frequently in the larger arena (Chapter III). Although there is no doubt that the use of a video-film analysis technique in the first instance had made identification of the postures reported in Chapter II much easier, where in the larger arena the observations were made directly into a tape recorder, it is unlikely that this alone could account for the different character of the encounters observed in the two experiments. Under the more confined conditions a number of postures associated with dominance and subordination were observed particularly SIDEWAYS and UPRIGHT postures, in the larger arena only the SIDEWAYS-

OFFENSIVE posture occurred frequently enough to allow some interpretation of its significance. It was apparent that the SIDEWAYS-OFFENSIVE posture was indicative of high aggression in both cases. Dunn (1971) described this behaviour as "hipping" where she reported it as being characteristic of an attacking animal. She also observed that this behaviour was accompanied by a narrowing of the eyes, described here as SQUINT, along with a great deal of movement of the hind quarters, which pushed against the opponent. Swanson (1974) maintained that the UPRIGHT-OFFENSIVE posture was the most common threat posture to another animal of the same sex and that in mixed sex encounters the female adopted this posture while the male adopted a SIDEWAYS-DEFENSIVE posture. This was not apparent from the observations reported here, in fact both male and female appeared to use the SIDEWAYS-OFFENSIVE posture as the predominant threat at close quarters and males appeared to threaten male and female opponents in this manner with equal frequency (Chapter III, Section 3.3.3.). The UPRIGHT-OFFENSIVE posture did not appear very frequently as a threat posture in either sex and the SIDEWAYS-DEFENSIVE posture was only seen in subordinate animals during the male-male encounters reported in Chapter II.

The relative aggressiveness of males and females was discussed in Chapter III (Section 3.6.1.) and it was revealed that males tended to interact with neighbouring animals more frequently than females. Nevertheless, females were equally as aggressive during encounters with neighbours in respect of the behaviours ATTACK, CHASE, CHASE-BITE, SIDEWAYS-OFFENSIVE and HIND-DIG, although males exhibited higher frequencies in what might be described as "Introductory acts", APPROACH, FOLLOW and NOSE,as well as being involved in more fights than females. This would seem to suggest that female gerbils are equally as aggressive as males when involved in fights with conspecifics (Swanson, 1974), but that when paired with a male tend to be less involved in encounters. Females also seemed to be more aggressive when lactating with a litter (Chapter III, Section 3.5.0.), chasing and attacking and threatening neighbouring animals more frequently than other females without litters. Wise (1974) reported that pregnant and especially lactating female Golden hamsters were more aggressive than other females in pseudo-pregnancy or various stages of oestrus. He suggested that this was facilitated by increased levels of prolactin and the suppression of ovarian hormones. This is probably similar in the lactating female gerbil where their higher frequencies of aggressive behaviour observed in the experiments reported in Chapter III support the idea of maternal aggression as one function for aggressive behaviour proposed by Mayer (1968). The higher levels of aggression reported for the male gerbil in these experiments also suggest that males play a part in rearing the young and that, like the mongoose, males may actually play a role in defending the litter (Rood, 1974).

The absence of any clear indication that males were inhibited from attacking females during the experiments reported in Chapter III disagree with the findings reported by Swanson (1974). Odour cues in the urine or sebaceous glands of other rodents have been found to be responsible for the inhibition of attack by males or females (Dixon and Mackintosh, 1971; Payne, 1974 b), and thus the findings reported in this thesis suggest that either such cues are lacking in the female gerbil or that their effects were masked by cues from the male partner. Lee and Brake (1971) suggested that in mice androgens might produce a pheromone to evoke the aggression of other males. Thus in a pair of animals nesting together, as was the case in the experiments reported in Chapter III, the female may have become scented with the male pheromone, if such a thing exists in the gerbil. Other researchers have found that female mouse urine can inhibit male aggression when rubbed onto other males (Dixon and Mackintosh, 1971) and thus it is likely that the reverse might occur. Certainly the results reported by Swanson (op. cit.) were based on interactions between males and females that had been reared in single sex groups, thus enhancing the effect of any female pheromonal cues inhibiting male aggression.

Overall the agonistic behavioural acts and postures observed in males and females in the two experimental conditions were identical in form. However, where more space was available (Chapter III) the relative frequencies of "offensive" and "defensive" postures was much lower in the males. Lorenz (1966) believes that animals have developed various behavioural mechanisms for preventing injury and death during aggressive encounters between members of the same species. Thus in confined conditions where animals are unable to escape from each other, ritualized postures and acts take the place of the more overtly aggressive acts CHASE, ATTACK and FIGHT. This was clearly demonstrated in these experiments by the results of the analysis of the temporal patterning of the various behaviours. In both experiments the changes in the male behaviour with time showed a tendency to an increase in the ritualized threat behaviours e.g. SIDEWAYS-OFFENSIVE (Chapter II). In the more confined conditions the more overtly aggressive behaviour CHASE and to a certain extent fighting tended to occur more frequently at the beginning of each trial and thereafter declined. It was suggested that this was the way in which the dominant animal reasserted its status at the start of each trial and subsequently maintained it in a more ritualized manner, probably by threat (SIDEWAYS-OFFENSIVE) (Section 2.4.0.). It is interesting to compare the results of this analysis with the analysis of the temporal patterning of behaviours when the animals were in the larger arena. Although in general there was the same tendency to an increase in ritualized aggression in both males and females it was more apparent that the animals threatened using a "non-directed" behaviour pattern, HIND-DIG. This "dirt" throwing display was violent enough to act as an effective threat behaviour at a distance and thus the encounter could continue in the form of a more ritualized display. Maynard-Smith (1974) proposed that from the standpoint of individual selection it was possible to divide fights into "displays" and "tournaments". Tournaments involved contact, a test of "strength" and possible damage, whereas displays involved no physical contact and the winner was the contestant which continued displaying the longest. From the results of the experiments performed here it appears that in general the aggressive behaviour between gerbils tended to start as tournaments (e.g. the dominant male re-establishing his status (Chapter II, Section 2.4.1.)) and then moved into a phase where agonistic displays became more frequent. Certainly in the encounters observed in the larger arena there was strong evidence of less contact between neighbours as trials continued (Chapter III, Section 3.6.1.). It thus appears that in the short-term the pattern of aggressive behaviour between gerbils of the same and opposite sexes lends support to the idea of ritualization proposed by Lorenz (op. cit.).

6.2.0. TERRITORIAL BEHAVIOUR IN THE MONGOLIAN GERBIL

Chapter I, Section 1.3.2. concluded that the concept of territory was better described in its various forms, than rigidly defined. However, it was clear that many researchers into the behaviour of the Mongolian gerbil had assumed that it was a territorial species where territory was strictly defined as an exclusive area actively defended by the owners (Section 1.4.2.). However, the results of the attempts to induce territorial behaviour in pairs of *Meriones unguiculatus* (Chapter IV) clearly demonstrated that any territorial behaviour exhibited by these gerbils did not appear to be in the form of defence of an exclusive area.

There was strong evidence that pairs of gerbils showed site-attachment to their home areas particularly around their nesting site and spent very much less time in their neighbours' areas. Thus there appears to be some of the elements of territoriality in the behaviour of this species, i.e. those of site-attachment (Allee, 1949) and exclusivity (Pitelka, 1959). However there was no evidence that the aggressive behaviour observed throughout these experiments had any effect on the movement of the animals at all. It was also obvious that animals were no more aggressive in their home area than in their neighbours' area and thus there was no evidence of a resident's dominance over an intruder or of any dominance-reversal as a result of entering an alien territory (see Chapter I, Section 1.3.3.).

The maintenance of a constant amount of time spent in each area is therefore very interesting. Chapter IV (Section 4.4.0.) concluded that it was likely that this relative exclusivity of the home area was maintained by the mutual avoidance between the pairs. This was supported by the finding that the frequency of the behaviour RETREAT had increased significantly over trials in all animals, independently of sex or relative aggressive status (Chapter III, Section 3.3.4.). This increasing tendency to RETREAT from neighbours, which was seen most clearly in two experiments described in Section 4.3.3., thus had the effect of maintaining the two home areas but without any obvious effective defence by the residents. The aggression seen during these experiments is probably best considered as a manifestation of an individual distance phenomenon described by Fitzwater and Prakash (1969) for Meriones hurriannae (see Section 4.4.0.). As the arena in which the experiments took place was probably too small to allow animals to maintain this distance there was a constant level of aggression, often violent and prolonged (see Chapter III, Section 3.2.2.), which occurred throughout a number of the experiments and which were found to be independent of the location in the arena. It is probable that the threat display HIND-DIG was an important visual signal which may have assisted the animals' mutual avoidance and maintenance of individual distances. It is also possible that olfactory cues also may have played a role in the maintenance of this individual distance and this will be discussed later (Section 6.4.0.).

From the limited behavioural data available from studies of related gerbillid species in the wild, there has been little evidence of territorial defence (Section 1.4.0.). The densities of gerbils in the wild are generally considerably lower than the densities used in these experiments and on the whole wild individual gerbils appear to inhabit large overlapping home ranges which are largely undefended. This is in general agreement with the findings reported here. Similarly the finding in these experiments that the aggression shown between individuals was largely independent of location was in broad agreement with Daly and Daly (1974) who reported that the outcomes of aggressive interactions between individuals of Psammonys obesus were independent of location.

In the light of the results of the experiments reported in Chapter IV it would seem useful to settle for a more descriptive approach to studying the social behaviour of the gerbil rather than using the blanket term territory which has been open to so much criticism in the past. Hill (1977) suggested that researchers should not be so concerned about whether a species is territorial or not but whether the species exhibits some form of social behaviour that restricts the space utilization of individuals. He further suggests that

> "The overriding biological consideration for a species is to possess some mechanism to spread out members or groups within the population at least during the part of the annual cycle when spatially organized resources may be limiting".

6.3.0. OLFACTORY COMMUNICATION IN THE MONGOLIAN GERBIL

The Mongolian gerbil has a variety of channels through which olfactory communication could occur - faeces, urine, ventral-gland secretions and the secretions from the facial Harderian glands being the most probable. It is likely that the use of the ventral sebaceous pad in object marking is ideally suited for desert species which must conserve body water and therefore would avoid responses such as urination, defaecation or salivation (Thiessen and Rice, 1976); although there was tentative evidence to suggest that urination might also function as a scent-marking behaviour (Chapter IV, Section 4.4.0.).

It was concluded, from the decreases over time in the frequency of the behaviour pattern NOSE, seen in the experiments reported in Chapters II and III, that this behaviour was probably important in individual recognition probably through the pheromone released from the Harderian glands (Halpin, 1976; Thiessen et al, 1976). However, this series of experiments was particularly directed at investigating the communicatory properties of the scent-marks from the ventral gland.

The results generally supported the findings of previous workers. The novelty of the environment was found to affect the frequency of marking. Marking frequency in males waned as a result of repeated exposure to the same test area until the response reached a minimum level (Chapter II, Section 2.3.2.). Males were found to exhibit very low marking rates in an area that was their home and females showed virtually no marking at all under these conditions (Chapter III, Section 3.3.2.). Sexual dimorphism was also found in the marking behaviour, males marking significantly more than females (Chapter III, Section 3.3.3.) and this has been reported previously for the majority of mammals (Chapter I, Section 1.5.1.). Dominant males were also found to mark more than their subordinate opponents in paired encounter experiments (Chapter II). In fact it was possible to predict the status of an animal from the results of marking tests carried out in familiar areas prior to encounters and it was proposed that these frequencies were directly related to the levels of circulating androgens in the male, as has been suggested before (see Chapter I, Section 1.6.1.).

The frequency of marking behaviour was also seen to be affected by agonistic encounters. This was particularly evident in the results of the paired encounter experiments (Chapter II, Section 2.3.0.) where the dominant males marked more after initial encounters. It was suggested that this may have been the result of the presence of the novel olfactory stimuli deposited by the subordinates during the encounters. This was supported by the observation that dominants marked more frequently in the subordinates home area during encounters, that is where the novel olfactory stimuli were greatest. Dominance and novelty therefore interact to give this result: dominant rank resulting in more frequent marking in areas of olfactory novelty.

In the experiments reported in Chapter III the encounters did not result in subsequently higher marking frequencies in either males or females. It was suggested that this was partly a result of insufficient quantities of novel olfactory stimuli from the neighbouring animals deposited in the animals' home area during a trial. It was also felt that the experimental conditions, which were designed to avoid the formation of dominance hierarchies, may have further masked any increase in marking related to dominance status (Section 3.6.2.). Certainly in males there was also no significant correlation of VENTRAL-MARKING frequencies with the criterion of high aggression (Section 3.3.3.), whereas in the previous male-male encounter experiments marking frequency was significantly positively correlated with dominance status. There was however, evidence that animals were unable to form dominance relationships during these experiments (Section 3.4.3.) and thus the lack of any relationship with high aggression and marking was perhaps not surprising. In females the picture is less clear although there was a positive relationship between marking frequency and high aggression. This, it was suggested, indicated that the stimuli involved in social interactions were more important factors in controlling the marking frequencies of females than males. There was also evidence in support of the findings of Wallace et al (1973) that lactating females marked more frequently than other females.

6.4.0. FUNCTIONS OF SCENT-MARKING IN THE MONGOLIAN GERBIL

In Chapter I, Section 1.6.2. the possible functions so far proposed for scent-marking in the Mongolian gerbil were reviewed. The experiments reported in this study have attempted to clarify some of these functions particularly in relation to the animal's "territorial" behaviour. Already, however, it has been made clear that the territorial behaviour observed during these experiments was not of the classic "defence of an exclusive area" type (Section 6.2.0.). Thus in this sense scent-marking with the ventral sebaceous pad in the Mongolian gerbil is not strictly a territorial behaviour.

Some of the results of these experiments, however, give an indication of the function of this behaviour. In the experiments reported in Chapter IV the results of interactions with neighbours significantly altered the distribution of marking behaviour such that the border areas received more marks after encounters than they did before (Section 4.3.2.). Two explanations can be proposed for this. Swanson (1974) suggested that the marking of male gerbils in the presence of females was a means of attempting to assert dominance while they were inhibited from fighting with them. Ralls (1971) and Thiessen and Rice (1976) also support the theory that marking is an expression of dominance. How far the VENTRAL-MARKING of the gerbil can be said to be a threat however is difficult to determine. Certainly in the case of behaviours like SIDEWAYS-OFFENSIVE, ATTACK and HIND-DIG there are visual signs of agitation (pilo-erection etc.) which are absent in the performance of VENTRAL-MARKING. The fact that in these experiments the threat behaviour HIND-DIG did not show the same shift towards the border areas after encounters also casts doubt on the interpretation that animals moved to the border to threaten their opponents using VENTRAL-MARKING.

It is more likely that the main stimulus for VENTRAL-MARKING is olfactory novelty and thus marking after encounters occurred at the borders where the novelty was likely to be greatest. However it is possible that this marking behaviour could also serve to maintain the relative exclusivity of the animal's home area. In Chapter V it was shown that male gerbils could be trained to avoid the general olfactory cues produced by another male and that this training significantly altered subsequent responses to the stimulus male's ventral mark. Scent marks from strange males are normally attractive to other male gerbils but it is clear that learning plays an important part in this response. Nyby et al (1970) reported that, as a result of aggressive encounters with dominant males in their home cage, this was aversive enough to cause subordinates to avoid the odours from the dominants' home cage. Similarly the avoidance of the odours from a male gerbil was brought about by their association with the aversive stimulus, electric shock. This, it was suggested, was comparable to being constantly beaten by a dominant male during aggressive encounters; the odour of that male being fairly prominent during the encounter and subsequently becoming associated with the aversive stimuli of aggression. However the experiments reported in Chapter V revealed that this avoidance response could also directly influence the normal approach response of the trained animal to scent marks from the stimulus male. Although further experiments should be carried out to test the specificity of this response it is still obvious that the effect of a ventral-mark on another animal is related to the past learning of that animal, possibly in the same way that dominance status or territorial boundaries may be learned (see Hinde, 1956). The association of the boundary areas (see Chapter IV) with increased amounts of marking after interactions with neighbouring animals may have the effect of assisting the use of this olfactory stimulus as a means of distributing animals in their habitat by mediating avoidance of familiar conspecifics. In his study of territory in mice Mackintosh (1973) concluded that it was visual cues, i.e. landmarks in the environment, rather than olfactory cues which lead to the observance of territorial boundaries. Nevertheless Jones and Nowell (1975) argued that although other cues were involved olfactory cues were more important than Mackintosh suggested. Visual cues alone may not account for the regulation of territory boundaries.

It is apparent therefore that the ventral-marking behaviour of the male Mongolian gerbil may have communicatory properties which assist in the maintenance of spacing between individuals or groups of individuals. Such marks may act as cues, the response to which is dependent on the previous experience with the owner of the mark. Thus if the previous experience with the owner was aversive (i.e. defeat) the probability of approach to that mark, or areas saturated with the marks, would be significantly decreased. (It would be interesting to carry out further experiments to investigate the effect of "winning" on the responses to scent-marks since it may be the actual aggression and not the outcome which constitutes the aversive stimulus.) In the long term it can be seen that such a mechanism, which could be called "sign-posting" (Leyhausen and Wolff, 1959), would have the effect of limiting aggressive encounters between familiar animals and could perhaps confer some selective advantage on those individuals utilizing the cues from scent-marks. Avoidance of frequent aggressive encounters would certainly lessen the chances of serious injuries due to fighting and leave more time and energy for foraging, reproductive and "maternal" activities.

However there is still the need for continued investigation both in the field and the laboratory before the extent of the function of functions of VENTRAL-MARKING are clearly understood. Hopefully the work presented here has helped to clarify some issues in relation to scent-marking and territorial behaviour in the Mongolian gerbil but neither the time nor the resources were available to continue. It would seem, nevertheless, that the Mongolian gerbil presents an ideal animal with which to continue research into the olfactory communication in rodents.

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