Effects of social experience on the behaviour of male guinea pigs and rats

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EFFECTS OF SOCIAL EXPERIENCE ON THE BEHAVIOUR OF MALE GUINEA PIGS AND RATS.

by

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I declare that the work described in this thesis is all my own, and has not been submitted for any other degree.

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ABSTRACT.

Most animals have some social experience, and in non-solitary species social experiences may be frequent and various. Evolutionary theory predicts this experience should lead to changes in behaviour which maximise inclusive fitness. However, the effects of such experience on subsequent behaviour are largely unknown. Investigation of the effects of social experience on behaviour requires examination of the nature, causes and functions of social behaviour and organisation under natural and experimental conditions.

In a semi-natural colony of guinea pigs, a male dominance hierarchy was found. Comparison of dominance status with social behaviour suggested that agonistic experience determined subsequent agonism and (to a lesser extent) courtship. Both sexes apparently responded to males according to physical and behavioural cues indicative of resource holding power (Parker, 1974).

Early experience has often been studied in attempts to find critical periods for socialization. Isolation of rats during the post-weaning period of social play has long-term effects on some non-social and agonistic behaviours (Einon et al, 1981; Wahlstrand et al, 1983). Early isolation of non-playing rodents (including guinea pigs) has no long-term effects on non-social behaviour (Einon et al, 1981). This suggests that social play might be important in the socialisation of playing species.

The effects of both isolation and experience of females on male rat behaviour was examined. Early-isolated rats showed abnormalities in intra-group social behaviour, but no increase in aggressiveness. No group studied had a consistent social organisation.

Parallel experiments with guinea pigs showed increased intra-group aggressive intensity, but no other differences in social behaviour or organisation. Prolonged grouping increased individual differences in aggressiveness under all conditions, but dominance hierarchies were only formed when females were present. Reduced courtship by subordinates was apparently due to both direct and indirect effects of agonistic experience.

These findings are discussed in terms both of the causes and functions of behaviour, and of the social ecologies of the two species.

Chapter One.

INTRODUCTION. A REVIEW OF AGGRESSION AND DOMINANCE.

This thesis concerns the nature, causes and functions of the social structure and behaviour of male guinea pigs and rats, with a particular emphasis on the effects of different social experiences on these factors. The main aspects of social experience under investigation are a) agonistic experience within a cohabiting group; b) the presence of females; c) early isolation.

Intra-group agonistic experience and the presence of females are factors which are relevant to the reproductive success (and therefore to the inclusive fitness) of male animals. Thus it is thought that they must be important in determining male social behaviour and organisation. The importance of early social experience (as opposed to isolation) is less immediately apparent. Previous findings (e.g. Einon et al, 1981) have shown that social isolation during the postweaning/prepubescent period in rats has long term effects on aspects of their non-social behaviour. Similar isolation of non-playing rodents (e.g. hamsters, mice and guinea pigs) at this stage has no permanent effect on the non-social behaviours measured. Thus it was thought that postweaning social experience might also be critical for the long term development of social behaviours and social structure in rats, but not in guinea pigs.

Most of the social behaviours involved in the establishment and maintenance of social organisation in male rats and guinea pigs are apparently agonistic (e.g. Barnett, 1975; Rood, 1972), so these behaviours were of greatest interest in the present studies. A general review of the causes and functions of aggression and dominance is given in this chapter, as these findings are relevant both to the studies of a semi-natural colony of guinea pigs (reported in chapters Two to Five) and to the experiments on socially manipulated groups of guinea pigs and rats (reported in chapters Seven and Eight). The experiments described in chapters Seven and Eight are immediately preceded by a review of previous studies of the effects of early social experience on rodent agonistic and sexual behaviour.

1.1

Aggression

The concept of aggression and its relevance in animal behaviour has been the subject of considerable academic dispute (e.g Barnett, 1975; Lorenz, 1963; Scott, 1958). Aggression has been defined by Chambers (1977) as

> "..a first act of hostility or injury."

This definition has led to the loose use of the term 'aggressive behaviour' to include predation, defense against predation (fear-induced aggression), defense of young (maternal aggression), territorial defense, and fights between male conspecifics (e.g. Moyer, 1968). It is obvious that the causes of aggressive behaviour in these categories differ widely, both in terms of the stimuli which lead to its production and the physiological state of the animal performing it. It is equally obvious that the function of aggressive behaviour cannot be the same in all these cases. Thus, even if the behaviours classed as 'aggressive' in all these different categories were to appear alike (which they seldom do; Eibl-Eibesfeldt, 1963), it would still be incorrect to treat them as equivalent and classify them all under the same heading.

The aggressive behaviours I consider here are those which occur between male conspecifics. Such behaviour in the wild rarely leads to the severe injury or death of either of the animals involved, but rather culminates in flight or adoption of a submissive posture by one of the participants (Lorenz, 1964; Harrison Matthews, 1964; Ewer, 1968).

Intermale aggression can take place both between animals occupying separate territories and between animals occupying the same territory as part of a social group. Under natural conditions, territorial aggression is caused by the presence of a male on or near another male's territory, and its apparent function is to maintain the territorial spacing of the animals, and thus to regulate the allocation of resources between individuals (Davies, 1978). The cause of aggression in naturally-occurring groups is somewhat less clear-cut, but is generally thought to be related to intra-group competition for limited resources such as food, resting places and females. Its function, too, is presumably to optimise the allocation of these limited resources (Bertram, 1978).

So it appears that there is a major overlap between the causes and functions of territorial and intra-group intermale aggression. In the wild state, observation of the animals concerned may make the difference between these two types of aggression clear (though this may not be true in species which have overlapping home ranges rather than distinct territories). However, under artificial conditions, some considerable confusion between them may exist. If a strange male is placed in the home cage of one or more male conspecifics and fierce fighting results, then such fighting is most probably related to territoriality. Under these circumstances, it is not uncommon for the 'intruder' (who is unable to escape) to die, either as a result of injuries received or of the physiological effects of severe stress (Barnett, 1975). If, on the other hand, a group of males are reared together and kept together as adults in a confined space then it cannot be said that aggression occurring between them is necessarily of the normal intra-group type. It may be that these animals would normally disperse into separate territories or home ranges at maturity, and that they have only been prevented from doing so by captivity. Thus, aggression between these males may be due to their efforts to space themselves out and defend territories rather than to true non-territorial intra-group competition. This territorial aggression in a confined space might conceivably lead to the development of dominance hierarchies (Archer, 1970).

Many studies of intermale aggression in animals have been concerned with discovering more about its causes and functions i.e. under which precise circumstances it will occur, and what advantages in terms of fitness are associated with agonistic success. A review of these studies and those concerning the effects of social experience on aggression (with a focus on rodents in general and rats and guinea pigs in particular) is given below. The effects of isolation on aggression are reviewed in Chapter Six. Studies specifically concerned with dominance hierarchies as opposed to just aggression are considered in Section 1.2.

1.1.1

Causative factors in intermale aggression.

The causation of intermale aggression has received considerable attention. Factors which induce male conspecifics to fight one another have been investigated not only to discover what makes males in natural populations fight, but also in order to find a reliable method of causing aggression for experimental studies of its mechanisms and functions.

1.1.1.1

Pain-induced aggression.

Pain can be used to induce intermale fighting. The pain caused by foot-shock has been found to induce fighting in rats, hamsters, snakes, turtles, chickens, cats and squirrel monkeys (Ulrich and Azrin, 1962; Azrin and Hutchinson, 1963; Azrin et al, 1963; Ulrich et al, 1964; Ulrich et al, 1965). However, the true nature of this fighting is brought into question by Ulrich and Azrin's (1962) finding that rats fought each other much less when they were in a large chamber (usually quite a way apart) or when not facing each other at the time of the shock. Cahn (1966) discovered that if rats were given shocks via an electrode attached to their tails they responded by biting the electrode rather than by attacking another rat.

These findings suggest that pain-elicited aggression is really a defensive reaction to any aversive stimulus. In the case of foot-shock the animals fight each other simply because there is no other cause to which they can attribute the pain. Since pain usually occurs as a result of intra-specific aggression in natural populations rather then before such an experience, it seems unlikely that pain could be an important cause of naturally-occurring intermale aggression.

1.1.1.2

Territorial aggression.

Intermale aggression is undoubtedly closely linked with territoriality in many species. Mice, rats and guinea pigs have all been found to attack fiercely any strange male which is introduced to their cage, pen or natural territory (Brain, 1980; Luciano and Lore, 1975; Rood, 1972). As mentioned above, it has been recognised for a long time that territorial and intra-group intermale aggression may be parts of a continuum (Allee, 1949; Lorenz, 1963; Archer, 1970; Hausfater, 1975) depending on the ecological circumstances of natural populations, or on the experimentally manipulated housing conditions of laboratory animals. Thus, if a naturally territorial species is group-housed in a confined space from infancy, a system of intermale aggression may develop where one male is considerably more aggressive than any of the others, although he does not actually kill other males. In such a case, the 'dominant' male appears to be the holder of the territory and the 'subordinate' males would disperse to escape him if they were able to do so (e.g. house mice: Archer, 1970).

Apart from the despotic nature of this kind of social organisation, the types of intermale aggressive behaviours observed may closely resemble those seen within more naturally formed groups in similar species. Indeed, Deag (1980) has suggested that in wild populations of closely related species, their different social organisations may sometimes be related to environmental constraints rather than to an innate tendency to form a particular type of social structure. For example, common and sacred baboons (Papio cynocephalus and P. hamadryas) have multi-male and harem social organisations respectively, and live in rich and poor (semi-desert) habitats.

Owing to the apparent close relationship between territorial and intra-group intermale aggression, and the possibility of confusion between them, studies of both will be reviewed below. Experiments involving territorial aggression are commonly referred to as 'intruder' tests, as one or more intruder animals are put into another animal's (or a group's) home cage.

1.1.1.3

Hunger and aggression.

Hunger has not been found to induce spontaneous aggression, but does lead to fighting when food is presented in a form which requires the animals to compete for it. In mice, Fredericson (1950) found aggressive competition for the possession of a food pellet so long as the pellet was small enough to be carried and could be moved. He commented that the fighting he observed as a result of food competition was the same in females as in males, and was rarely serious. Seward (1945c) observed food competition in hungry rats and found that if only one pellet was available, then the rat with the pellet was more aggressive than the one without. This type of food competition is likely to arise in natural populations from time to time, though it is unlikely to lead specifically to intermale aggression, but rather to a generalised scramble competition among all members of a group (Seward,1945c). Its relationship with the social structure of an animal group will be considered later.

1.1.1.4

Aggression and the presence of females.

Taylor (1975) found that recent experience of an inaccessible oestrous female increased the aggressiveness of male rats to conspecific males. Van de Poll et al (1981) housed male rats with ovariectomised females and then tested them with other males and found increased levels of aggression. Hall and Klein (1942), on the other hand, found no change in aggressiveness following housing with a female, but in this case the rats had been isolated for five days after their experience of mixed housing before being tested.

In intruder tests, Barnett et al (1968), Barnett (1969) and Flannelly and Lore (1977a) found increased intensities of attack in wild and domestic male rats during and after housing with females. It seems likely that intra-group aggression in wild male rats may also be increased by the presence of females, as Barnett (1958b) found a higher death rate in wild males kept in mixed groups than in those kept singly or in all-male groups. He also found fewer alpha (i.e. socially high-ranking) males in mixed than in all-male groups, suggesting that more intense fighting may have occurred in mixed groups.

Barnett and Stoddart (1969), however, found no difference in the tendency to attack in sixth to ninth generation laboratory-bred male rats after mixed housing. Similarly, Brain et al (1980) claimed little improvement in male rat 'fighting capacity' in intruder tests when the males were housed with females. The difference between these findings and the previous ones might be attributable to the fact that two different measures were being made: intensity of attack and tendency to attack.

Thor and Flannelly (1976) also claimed to find no difference in territorial aggressiveness in laboratory male rats before and after housing with females, but their observation that intruders into mixed groups lost more weight than intruders into all-male groups suggests that there may have been an unmeasured change in intensity of attack, even if not in its frequency.

Similar effects have been found in mice. O'Donnell et al (1981) claimed that housing an adult male mouse with one or more females increased his aggressiveness towards another male in both home cage and neutral arena tests. Petrusewicz (1959) found a tendency for male mice housed with females to win fights with lone males when the partition separating their cages was removed.

These findings suggest that some aspects of the aggressiveness of male rats and mice may be increased by immediate experience of females, but that this effect may not last for long after the females have been removed.

There is no experimental evidence of changes in the aggressiveness of male guinea pigs as a result merely of experience of females, but it has been observed that considerable intermale fighting does occur during mating chases (Rood, 1972). Also, Riss and Goy (1957) found more aggression in a group of males during a group mating test (i.e. when a receptive female was present) than at other times. Thus the presence of female guinea pigs, particularly oestrous females, appears likely to increase intermale aggression.

In rats, however, Calhoun (1963), Barnett (1975) and Robitaille and Bovet (1976) have observed that wild males do not fight one another during a mating chase, though they may fight if they meet at the entrance to an oestrous female's burrow. These findings imply that any functional aspects of female-induced increases in intermale aggression in rats do not show themselves in aggressive competition at the time of mating, whereas those of guinea pigs do. However, such functional aspects may exist in a more subtle form.

1.1.1.5

Summary of causes of intermale aggression.

From the studies cited above it seems that territoriality and the presence of females are the main causes of intermale fighting in mice, rats and guinea pigs. However, it has not yet been agreed how the presence or absence of females affects the social structure and proportional aggressive behaviours of males in a group. The experiments described in chapters Seven and Eight of this thesis were designed to test the effect of the presence of females and of their subsequent removal on the aggressiveness of groups of male rats and guinea pigs.

Pain and hunger may also elicit fighting, but the evidence suggests that this is nonspecific and not limited to males, so these factors were not investigated in the present studies.

1.1.2

The effects of winning and losing experience on subsequent agonistic behaviour.

The type of winning or losing experience given to males in order to test its effect on their aggressiveness varies from the relatively 'natural' one of becoming the dominant or subordinate member of a pair of rats housed together, to inducing mice to attack helpless males which are dangled in the attacker's home cage. Using the latter method, Kahn (1951) found that after experience of attacking helpless, dangled males in their home cages, male mice would not only attack and kill other adult males in a neutral arena, but would also kill adult females and nonaggressive 21-day-old males. Brief exposure of other males to these 'winner' males was used to train them to consistent defeat. When these 'loser' males were tested with dangled males, they showed more defensive postures and were slower to attack than control animals who had had no winning or losing experience.

Van de Poll et al (1982b) trained rats of one strain to be either winners or losers by pairing them with rats of more or less aggressive strains. These 'winner' and 'loser' rats were then paired with each other in a neutral arena, and it was found that the 'winners' showed more approaches, initiation of aggression, and aggressive behaviours than did the 'losers'. Similarly, Flannelly and Lore (1975) gave intruder tests individually to the dominant members of pair-housed male rats and found that they showed more aggression than they had done in identical tests before their experience of dominance. From his observations of wild male rats, Barnett (1969) concluded that the experience of territorial attacking increased the tendency to make such attacks, whereas the experience of being attacked (i.e. being an intruder) reduced it.

This evidence shows that a male rat's or mouse's aggressiveness can be increased or reduced respectively by its experience of winning or losing fights with male conspecifics, though the effect of losing seems to be stronger. Controlled studies of the effects of winning and losing on male guinea pig aggression have not been made.

Males living in groups are likely to be subjected to repeated experiences of winning and/or losing, as long as intermale agonistic encounters occur. Changes in aggressiveness as a result of agonistic experience could have important effects on group structure by increasing the inter-individual differences within a group. Thus, if more aggression was found in a group containing females than in an all-male group, the effects of winning/losing might be accelerated, possibly resulting in the formation of a stronger dominance hierarchy, or stronger dominance relationships than are found in all-male groups.

1.1.3

Functional aspects of intermale aggression.

From an evolutionary viewpoint, intermale aggression of the kinds described above would not have developed unless it functioned to increase the fitness of the successful animals. Since the outcome of such aggression can sometimes be severe injury or even death (Wilson, 1975), it must be supposed that its functions, in terms of increased fitness of the winner, must be correspondingly important.

So it appears that intermale aggression might be a means of determining the allocation of such essential resources as territory, females and (to a lesser extent) food and water. In many strongly territorial or lek-breeding species, the acquisition of a favourable territory through aggressive interactions is often followed by the acquisition, with little further aggressive effort, of an attractive female or females (Davies, 1978). In these cases, intermale aggression functions immediately to allocate territory, but success in territorial fights leads to a considerable enhancement of reproductive potential i.e. fitness.

Many animals which do not occupy separate male territories live in groups whose size and composition may vary throughout the year. These groups may inhabit group territories or home ranges which are spatially or temporally defined (Wilson, 1975). Territorial intermale fighting within groups is minimal in these species, but fighting over females may be severe during the breeding season e.g. in most ungulates (Barash, 1977). In this type of social organisation, intermale fighting functions immediately to increase the reproductive potential of the successful male or males, as they are able to mate with the largest number of females.

Some multi-male group-living species maintain an almost constant group composition throughout the year, with few emigrations or immigrations and often no set breeding season e.g. brown rats (<u>Rattus norvegicus</u>: Calhoun, 1963; Telle, 1966) and common baboons (<u>Papio</u>

cynocephalus: Hausfater, 1975). It has been suggested (Bertram, 1976) that intermale fighting within this type of group should be limited, at least in severity, because of the high probability of the males being related to one another. Nevertheless, intermale aggression (often ritualised) is frequently observed in stable multi-male groups and is often said to have the immediate function of producing and maintaining a dominance hierarchy, which in turn determines the allocation of desired resources such as females, preferred resting sites and/or food.

The following sections of this chapter will investigate the meaning of the term 'dominance hierarchy' and the evidence for the existence and function of such systems, particularly in rats and guinea pigs.

1.2

Dominance hierarchies.

Since Schjelderup-Ebbe's (1922) observations of peck-right in chickens, the study of social (otherwise termed 'aggressive') dominance among animals has become very popular. Considerable disagreement has existed as to the true functional and structural meaning of a dominance hierarchy, however, and this has resulted in a wide variety of experimental approaches to the subject, as well as the use of many different behavioural measures in assessing it.

1.2.1

Studies of dominance hierarchies in non-cohabiting groups.

Interest in the formation and function of the dominance hierarchy has led some researchers to use suspect methods for the study of dominance, thereby devaluing their findings. A commonly used method of attempting to find linear dominance has been to house a 'group' of unfamiliar conspecifics separately and subject them to a round robin tournament of paired encounters in a neutral environment in order to measure aggressive interactions (Rats: Seward, 1945b; Ruskin and Corman, 1971. Guinea pigs: Bates et al, 1973), food competition (Rats: Bruce, 1941; Mezei and Rosen, 1960; Hoyenga and Lekan, 1970; Ruskin and Corman, 1971. Rhesus monkeys: Haude et al, 1976), or water competition (Rats: Bruce, 1941; Spigel et al, 1972; Robertson, 1982).

Another competitive means of measuring 'dominance' has involved the use of a runway or tunnel, in which two animals are made to run in opposite directions in order to obtain food or water (Rats: Schumsky and Jones, 1966; Ward and Gerall, 1968; Work et al, 1969; Howells and Kise, 1974). In these tests the runway or tunnel is only large enough for one animal to pass through at a time, so only the first animal through gets the reward.

The principle behind the use of food and water competition in these tests is that any dominance hierarchy formed will have the function of allocating these resources between the test animals. The function of a hierarchy produced from paired agonistic encounters, however, is less clear. In fact, these tests imply the assumption that the tested animals have an innate drive to form hierarchical relationships, such that relationships are formed in advance of their having any functional use.

The major criticism of these studies is that a dominance hierarchy can only have a real structure or function when formed in a cohabiting group of animals, preferably under natural conditions (Crook, 1970). The study of a dominance hierarchy through round robin paired competitions assumes that each animal has a predetermined immutable ability to dominate such that the results obtained would automatically reflect the structure that would develop if the same animals lived freely together as a group. (Another implication of this assumption is that the hierarchy formed would inevitably be linear or near-linear (Schjelderup-Ebbe, 1922).) King's (1965) experiment on hens yielded particularly interesting results with regard to this. The hierarchy calculated from the results of paired agonistic encounters before grouping bore no relation to the linear hierarchy formed when the hens were living in a group. Subsequent paired testing (while the hens were still living as a group), however, revealed a hierarchical order very close to that observed from spontaneous group interactions. Thus it seems that the formation of dominance relationships may be influenced by the presence of other group members. Also, once formed, these relationships may continue to hold even when the animals concerned are separated from their group for a short period. Similar results were found in male guinea pigs by Berryman (1978).

Probably the most interesting aspects of paired competitions or agonistic encounters between unfamiliar conspecifics are the data they yield with regard to the consistency of results in repeated comparisons, and the existence or absence of correlations between the results of different (e.g. food and water) tests. In paired agonistic encounters between male rats, Seward (1945b) did not find consistent pair relationships until the period from 75 to 100 days old. This may have been due to the fact that rats do not stop indulging in social play until about 60 days of age (Einon et al, 1981), so previously observed 'agonistic' behaviour may have actually been play. Alternatively, it is possible that Seward's rats did not spend sufficient time together (playing or otherwise) for dominance relations to develop. Meaney and Stewart (1981) have claimed to find evidence of dominance relations between young rats (in terms of the frequency and direction of on-top-of postures) from the age of about 45 days when the animals were housed together.

Hoyenga and Lekan (1970) found no consistency in terms of weight gain in the results of their food competition test, but Robertson (1982) did find consistent water competition 'dominance' as measured by the percentage of time spent at the water bottle. Significant positive correlations were found between repeated aggressive 'wins' ('aggressive posture'; Grant and Mackintosh, 1963) in water competition tests and food gain in food competition tests (Ruskin and Corman, 1971), and between time drinking in a water competition test and percentage time spent grooming the other rat in a neutral arena test (Spigel et al, 1972). Gage (1978) found a weak positive correlation between the amount of fighting initiated and possession of food in separate tests on unfamiliar pairs of male rats.

In runway/tunnel tests on rats, Schumsky and Jones (1966) found high positive correlations between repeated food competitions, but not between the results of food and water tests, nor between the results of repeated water tests. Howells and Kise (1974), on the other hand, found no correlation between the results of repeated food tests. However, since their tunnel was underwater, and the animals in each pair had had different previous social experience, the test is not really comparable to that of Schumsky and Jones.

A criticism of the validity of these food and water tests as indicators of pair dominance relationships has been levelled by Syme (1974). He pointed out that the different results obtained between the members of a pair could be due to different abilities in performing the required task rather than to dominance-related priorities of access to the resource. Thus he stated that priority of access can only be proved if the same results are obtained from (food or water) tests which require different performance skills. Masur (1975) specifically criticised runway/tunnel tests because they do not involve aggressive or submissive postures, nor have they been found to yield results which correlate with observed aggressive dominance or submission between the same pairs of rats.

In summary, it seems that paired agonistic encounters between unfamiliar animals have little to offer to the understanding of dominance hierarchies. King's (1965) study showed that the results of such encounters bear no relation to the hierarchy formed when the same animals are able to interact as a group. Thus it seems likely that an animal's dominance capacity is not entirely innate, and is affected by external environmental factors. Also, no information regarding the function of a dominance hierarchy can be gained from the results of paired fights. It seems, therefore, that it is necessary to investigate spontaneous agonistic behaviour in cohabiting groups of animals if it is desired to find out more about the functions of aggressive behaviour and dominance relationships in naturally group-living species.

The food and water competitions (in open cages and runways/tunnels) seem likely to test scramble competition rather than the priority of access to a resource which is assigned by relative dominance (contest competition; Barash, 1977). As such, it is very probable that the winner will be the animal which is more skilled at performing the required task (Masur, 1975). This would explain the consistency of results obtained from some repeated tests, and the absence of correlations between the results of food and water tests, which require different skills for success.

1.2.2

The measurement of dominance in cohabiting groups.

In the previous section, it was suggested that the only realistic way to study dominance in a naturally group-living species is to observe the formation of hierarchies (as determined by aggressive/submissive behaviours and priority of access to resources) in cohabiting groups (Syme, 1974). The problem then arises, however, of how to measure empirically the nature of group structure in terms of dominance relations. Criteria must be set with regard to the definition of 'dominant' and 'submissive' behaviours, and the means of ranking animals on these behaviours must also be decided.

The most important aspect of a dominance hierarchy is the direction of dominance between all the animals in the group, as this determines whether or not the hierarchy is linear, or approaches linearity. Without this information the term 'dominance hierarchy' can have no functional meaning. Despite this, several studies which professed to investigate dominance hierarchies have failed to use the direction of aggressive behaviours when ranking animals within a group. In these studies, rank was assigned according to such measures as total frequency of agonistic behaviours (<u>Rats</u>: Drews and Wulczyn, 1975; Drews and Dickey, 1977; Militzer and Reinhard, 1979, 1982. <u>Rhesus monkeys</u>: Kaufmann, 1967), percentage of animals dominated (<u>Cows</u>: Collis, 1976) and the ratio of total wins to total losses (assessed by aggressive and submissive postures: Grant and Mackintosh, 1963 in <u>rats</u>: Baenninger, 1966, 1970; Popova and Naumenko, 1972). In her 1966 report, Baenninger stated that the rank order obtained by this ratio measure correlated with the real directional rank order of the rats in the group, though no data were presented to support this claim. All of these measures are of interest when compared with directional rank order, but on their own they are not descriptive of dominance hierarchies, but merely of inter-animal variation in activity or aggressiveness.

Other studies have also shown a lack of directional specificity in their use of the term 'dominance'. Rohwer and Ewald (1981) assigned dominance ranks to Harris' sparrows according to the proportion of black feathers on their heads. This measure had previously been found to correlate with aggressiveness and territorial behaviour, but was not shown to be empirically related to directional dominance within a flock, except in gross terms. Telle (1966) attempted to rank wild male rats in terms of priority of access to food and females, but took no account of the direction of success in agonistic encounters. Harcourt (1979) ranked wild male gorillas according to whether they were silver- or black-backed, and by unspecified measures of group leadership and agonistic dominance. Samuels et al (1980) and Takahata (1982) referred respectively to the the ranks of bonnet macaques and Japanese monkeys without presenting any information as to how these ranks were assessed.

Boyd and Silk (1983) devised a method of assigning cardinal ranks (as opposed to ordinal ranks) to the members of a group so as to make quantitative comparisons between dominance ranks, or between different measures of dominance, possible. A severe drawback with the cardinal ranks obtained, however, is that they do not necessarily follow the directional pattern of dominance within the group.

Table 1.1 summarises some studies of dominance in animals (other than rats or guinea pigs) in which dominance ranks were assigned using the direction of aggressive/submissive behaviours between animals. All of these studies (except those made on chickens) were made on natural or semi-natural groups. It can be seen that only two of these studies showed no evidence of a linear hierarchy at all (Wolves: Lockwood, 1979. Bison: Lott, 1979) while most species had near-linear dominance structures. Near-linear means that the number of intransitive relationships in the group was quite small with respect to group size (e.g. two intransitive relationships in a group of eight animals), and that these non-linear relations occurred between closely ranked members of the group. It must be pointed out, however, that in most of these studies there were several pair relationships for which no data were obtained i.e. the animals were never observed to have an agonistic interaction. Thus most of the near-linear hierarchies have been assessed on the assumption that these missing relationships would follow the pattern of linearity. Appleby (1983) and Boyd and Silk (1983) have argued that, for mathematical reasons, it is essential that all relationships within a group (especially a small group) be known. Otherwise the probability of obtaining a linear hierarchy by chance is very high.

The behaviours used to assess dominance in these groups (Table 1.1) show considerable within species variation, especially in rhesus monkeys and baboons. Also, some researchers have used only one behaviour in order to rank their animals while others have used the summed totals of several aggressive and/or submissive actions (obviously the behaviours defined as aggressive and submissive were treated separately) between pairs of animals. The first method (using

Reference	Species	Sex ranked	Behavioural criteria	Hierarchy found
Schjelderup-Ebbe (1922)	Chickens	Females	Pecks	Near-linear
Allee et al (1939)	Chickens	Females	Pecks	Near-linear
Banks et al (1979)	Chickens	Males	Pecks, threats, avoids	Near-linear
	''	Females	''	''
Chase (1980)	Chickens	Females	Pecks	Mostly linear
(1982)	''	''	''	''
Schein and Fohrman (1955)	Dairy cattle	Females	Threats and fight 'wins'	Near-linear
Clutton-Brock et al (1976)	Highland cattle	Females	Threats	Near-linear
Lott (1979)	Bison	Males	Five agonistic behaviours	None
Clutton-Brock et al (1976)	Highland ponies	Females	Threats and displacements	Near-linear
Appleby (1982)	Red deer	Males	Threats and displacements	Near-linear
Hall (1983)	Red deer	Males	Threats	Near-linear

Table 1.1
Studies of dominance using directional behaviours in species other than rats or guinea pigs.

Reference	Species	Sex ranked	Behavioural criteria	Hierarchy found
Lockwood (1979)	Wolves	Males and females	Several agonistic behaviours	None
Sade (1967)	Rhesus monkeys	Males and females	Several agonistic behaviours	Near-linear
Richards (1974)	Rhesus monkeys	Male and females	Attacks and threats	Near linear
Bernstein and Gordon (1980)	Rhesus monkeys	Males	Several agonistic behaviours	Near-linear
Bernstein et al (1979)	Pigtail monkeys	Males	Attacks	Near-linear
DeVore (1965)	Baboons	Males	Threats and enlistment of help	Near-linear
Hausfater (1975)	Baboons	Males	Several agonistic behaviours	Near-linear
Packer (1979)	Baboons	Males	Displacement and avoidance	Near-linear
Bygott (1979)	Chimpanzees	Males	Threats and attacks	Subgroup linear

Table 1.1 (continued)
Studies of dominance using directional behaviours in species other than rats or guinea pigs.

one behaviour only) runs the risk that the behaviour chosen may not be the most appropriate for signalling dominance. The second method (summing several behaviours) is doubtful because it may include behaviours which have little or nothing to do with the formation or maintenance of dominance relationships within a group. These behaviours may considerably distort or dilute the results obtained. Hinde (1979) has suggested that dominance only has real 'group structural' meaning if it refers to consistent data across several correlated behaviours, not just to one behavioural measurement alone. None of the studies mentioned in this section conforms to these stringent specifications.

1.2.2.1

Measurement of dominance in cohabiting groups of guinea pigs.

The same criticisms with regard to the treatment of missing relationships and the use of summed agonistic behaviours may be levelled at the studies of dominance hierarchies in male guinea pigs (Table 1.2) as at studies of other species (see above). Nevertheless, it is notable that near-linear hierarchies have been reported in all cases in mixed groups containing from two to fifteen adult males. No evidence is available from previous studies concerning the formation of dominance hierarchies in all-male groups of guinea pigs. Riss and Goy (1957) found a correlation between the amount of spontaneous aggression shown by males in an all-male group and their aggressiveness during group mating tests. However, the direction of this aggression (which would have revealed whether or not a dominance hierarchy existed) was not reported. The formation of dominance hierarchies in all-male groups of guinea pigs is investigated in

Reference	No. of groups	Group size (adults)		Strain	Pre-group housing	Age at grouping (days)	Age at observation (days)	Behavioural criteria	Hierarchy found
		Males	Females						
Kunkel and Kunkel (1964)	?	?	?	Mixed	Mixed groups	?	?	Several agonistic behaviours	Mostly near-linear
Rood (1972)	2	?	?	C.aperea	Wild and mixed groups	?	?	Several agonistic behaviours	Near-linear
	1	?	?	Mixed	Mixed groups	?	?	''	Near-linear
Coulon (1975a)	2	4	3	?	None	0	60-150	Several agonistic behaviours	Near-linear
	1	3	3	?	''	0	60-150		''
Jacobs (1976)	6	2-15	2-13	Mixed	Mixed from 0-30 days then ?	Adult	? (2-12 months observation)	Displacement and running away	Near-linear
Berryman (1978)	1	8	8	Mixed	?	180	245-261	Several agonistic behaviours	Near-linear
Chivers (1979)	1	2	2	Mixed	Mixed groups	90	104-122 and 148-153	Several agonistic behaviours	Linear

Table 1.2
Studies of dominance using directional behaviours in groups of male guinea pigs.

chapter Seven of this thesis.

1.2.2.2

Measurement of dominance in cohabiting groups of rats.

In similar studies of dominance hierarchies in male rats (Table 1.3), the results are less consistent. Once again, missing relationships are largely ignored (i.e. treated as though they conformed with linearity). There is, however, some consensus of opinion as to the use of two particular behaviours (comprising one interaction between two animals) in order to determine dominance relationships. These are the 'aggressive' and 'submissive' postures described by Grant and Mackintosh (1963), whereby one animal stands with his forepaws on the belly of the other (who is lying motionless on his back). The use of these behaviours by Grant and Chance (1958) and Flannelly and Lore (1975, 1977b) makes the results obtained from these studies more readily comparable, though the criticism that this behaviour may not, after all, be that most relevant to dominance (although subjectively it appears so) is still relevant. It should also be pointed out that this aggression/submission interaction is by no means unidirectional in any relationship. In most cases, both animals were seen to take both roles at various times, so dominance in terms of this behaviour was determined according to the relative frequency of production of either posture by each animal in any pair.

Linear dominance hierarchies were found by Grant and Chance (1958) in all their groups of four male rats, but in none of their groups of six (though one group did show a near-linear hierarchy in the first period of observations). No females were present in these

Reference	No. of groups	Group size (adults)		Strain	Pre-group housing	Age at grouping (days)	Age at observation (days)	Behavioural criteria	Hierarchy found or % groups showing linearity.
		Males	Females						
Grant and Chance (1958)	4	2	0	Wistar	None	25	? (two 2-3 wk periods)	Submissive posture	25%
	12	4	0	''	''	''			100%
	4	6	0	''	''	''			0%
Barnett (1958b)	7	3-10	?	Wild	?	Adult	?	Unspecified	Alpha subgroup dominant to beta and omega subgroups. No linear dominance, but more alphas in mixed than in all-male groups.
	4	6-12	0	''	?	''	?	''	
Flannelly and Lore (1975)	10	2	0	Long-Evans	All-male groups then 3 weeks of isolation	100-120	100-120 and 114-134 (2 days)	No. and duration of aggressive/ submissive postures	100%
Flannelly and Lore (1977)	1	5	(2)	Long-Evans	?	75	290-365	(As above)	3 alpha males and 2 betas. One overall dominant.
Chivers (1979)	1	2	2	Hooded	All-male groups	90	104-122 and 148-153	Several agonistic behaviours	None
McClintock et al (1982a)	3	2	5	Sprague Dawley	Mixed and female groups	200 (M) 120 (F)	200-207 120-127	Several agonistic behaviours	100%

Table 1.3
Dominance studies using directional behaviours in groups of male rats.

groups.

Flannelly and Lore (1977b) found no evidence of a true linear hierarchy in their mixed group containing five males, though they claimed that there was a sub-group structure of alpha males dominating betas and omegas (as also found by Barnett, 1958b). In cohabiting pairs of male rats (with no females present) consistent dominance relationships were claimed by Flannelly and Lore (1975) in all their pairs, whereas only a quarter of Grant and Chance's (1958) pairs showed stable dominance. Further scrutiny of Flannelly and Lore's (1975) results, however, reveals that their animals only showed large differences in the duration for, rather than the frequency with, which they held aggressive/submissive postures. Also, these differences virtually disappeared after the first day of cohabitation.

These results suggest that groups of more than four male rats do not show simple linear (or near-linear) dominance hierarchies, but may have some kind of sub-group dominance. All-male groups of four males do show linear dominance, but there is no evidence as to whether this would be the case in a mixed group containing the same number of males. In cohabiting pairs of males (with no females) it seems that the establishment of long term consistent dominance relationships is rare. Studies of the relationship between two males cohabiting with females (Chivers, 1979; McClintock et al, 1982a) show conflicting evidence of intermale dominance. Chivers (1979) found no difference between the males in the number of aggressive behaviours shown in either of the two periods of observation, while McClintock et al (1982a) observed that one male was responsible for more than seventy percent of the 'dominant' behaviours in all three groups studied.

The experiment described in chapter Eight was designed to investigate the effect of the presence and subsequent removal of females on dominance relationships in groups of four male rats.

1.2.3

The formation and maintenance of linear dominance hierarchies.

The observation that many species exhibit something approaching a linear dominance hierarchy (Table 1.1) has led to attempts to discover more about the formation and maintenance, as well as the function, of these social structures. Much emphasis has been laid on the idea that relative dominance must be determined by individual differences in physical characteristics such as fighting ability, size, and pheromones (e.g. Darwin, 1859; Collias, 1943; Van Kreveld, 1970), though in investigating these physical factors, many people have omitted to consider the possibility that they may be caused by, rather than predictors of, dominance status. It has also been suggested that social factors such as experience, environment and individual recognition may be important in the formation and maintenance of dominance relationships (e.g. Allee, 1942; Christian, 1970; Bernstein et al, 1979; Bernstein and Gordon, 1980; Chase, 1982).

A currently popular approach to animal behaviour favours the theory that dominance ranks are assigned by a process of assessment whereby each individual assesses each other's aggressive competitive ability from one or more physical or behavioural cues (e.g. Dawkins and Krebs, 1978; Barnard and Burk, 1979). By some unspecified means (possibly involving past experience), the animal is able to compare its own competitive ability with that of the opponent, and will behave in a dominant or subordinate (aggressive or submissive) manner accordingly. This theory has the advantage that it is flexible enough to include both physical and social factors as influences on the formation of dominance relationships.

Landau (1951a) devised a mathematical formula for describing the linearity of any observed hierarchy using measures of dominance gained from each individual in the group. He then used this formula to test the theory that the observed probability of obtaining linear hierarchies could be explained by determination of dominance from the results of paired encounters within a group, the outcome being dependent on each individual's innate fighting ability (assuming a normal distribution of this ability). Landau found that this theory could only explain the observed frequency of linearity if unreasonably large differences in fighting ability existed between conspecifics.

Chase (1974) extended this mathematical investigation by looking at the problem in terms of the probability of the outcome of each pair encounter in a group (thus allowing for smaller individual differences in ability), rather than at a measure of the number of animals dominated. He, too, found that in order for this 'tournament' model of the formation of linear hierarchies to hold, the probability of each animal winning encounters with all lower-ranking animals had to be unreasonably high (greater than 0.9 in groups with more than five members). Since such high probabilities are not normally found (except in a few cases where dominance relations appear to be absolutely one-way), this model seemed no more useful than Landau's (1951a) for explaining the formation of linear hierarchies in terms of individual fighting ability.

Undeterred by his predecessors' failure, Fagan (1977) adapted Chase's (1974) formula so that it took account not only of the probability that each animal would win in encounters with lower-ranking individuals, but also of the number of such encounters that had previously taken place. Thus he found that quite low probabilities of winning (around 0.6) could explain the observed frequency of linearity if they were based on the results of a sufficiently large number of previous encounters. So it seems that the observed high frequency of occurrence of a linear (or near-linear) hierarchy in animal groups coupled with the commonly observed low probability of winning in each pair encounter can be explained in terms of individual differences in fighting ability if it is known that the data are based on a large number of previous agonistic interactions. Fagan (1977) suggests that in many naturally formed groups, this situation could arise through the frequent play interactions experienced during the juvenile period.

The mathematical rigidity of this and Chase's (1974) proofs differs from reality in that an equal probability of winning against all lower-ranking animals and an equal number of encounters with all other group members are assumed. Observations suggest that not only do animals have more frequent agonistic interactions with those close to themselves in rank, but they are also more likely to experience dominance reversals with these than with other group members (Van Kreveld, 1970; Hinde, 1979).

Having established that although it is possible to explain the observed frequency of occurrence of near-linear dominance hierarchies in terms of individual differences in fighting ability, it is unlikely (owing to the stringent conditions required) that this is the most important factor in most species, it is then necessary to investigate other possible explanations in a similar manner.

Landau (1951b) postulated that such social factors might exist as that a) an animal never challenges another whose dominance score (i.e. the number of animals dominated) exceeds his own by two or more, or b) if an animal makes such a challenge, he will never win the encounter. He tested these theories mathematically and found that both tend to cause group dominance structure to change in the direction of linearity. Since these and similar social factors related to agonistic interactions are commonly observed in animal groups (Van Kreveld, 1970; Hinde, 1979), it seems very likely that they may indeed be important in the formation of linear dominance hierarchies in many species. However, since it is improbable that many (if any) animals are capable of knowing the absolute ranks of the other members of their group, another theory must be developed to explain how a social inhibition against challenging higher-ranking animals (two or more ranks above) could exist. One possibility could be that animals are capable of remembering not only their own general experience of success or failure in fights (as required by a 'confidence hierarchy': Barnard and Burk, 1979), but also their specific experience in relation to their perception of their opponents' physical or behavioural cues.

Landau's (1951b) theory would not require individual recognition other than by means of a combination of 'confidence' and 'assessment' (Barnard and Burk, 1979), whereby the cue assessed may be the opponent's confidence. Thus if the disparity appears too great, the animal with less confidence will avoid an encounter with his superior. Barnard and Burk (1979) have claimed that it is not possible to distinguish between individual recognition and multiple cue assessment in such cases. Indeed, results such as Allee et al's (1939) in which hens treated with TP rose in rank (possibly through the effect of altered cues) and maintained their new ranks long after treatment had ended, could be explained in terms of assessment of multiple cues (including behavioural confidence) just as readily as by pure individual recognition.

An advantage of this 'assessment' theory of the formation of linear hierarchies is that it involves much smaller costs (for both formation and maintenance) in terms of time and energy to each individual than does the 'statistical' or 'tournament' theory outlined above (Barnard and Burk, 1979). If an animal can assess its chances of winning in a particular encounter before it actually expends energy on fighting, then it is able to avoid potentially damaging (i.e. costly) conflicts. The 'assessment' theory also allows for cues to take many different forms, both physical and behavioural, in different species.

Chase (1974) attempted to discover whether several possible physical cues (each treated separately) could be responsible for the observed frequency of formation of linear dominance hierarchies in chickens. He measured such factors as comb size and 'aggressiveness' (as had Collias (1943) in a previous study) and correlated these with the outcome of paired encounters between birds. The results yielded low correlations which, when substituted into Landau's dominance equation, gave a low measure of linearity. However, Chase himself admitted that his mathematical test of the predictive value of cues in determing linearity was inadequate, as the hierarchy had been obtained using the results of paired encounters between unfamiliar birds rather than of natural hierarchy formation in a group. Also, it was possible that the physical factors he had selected for investigation might not have been those used as cues by the birds e.g. olfactory factors or behavioural 'confidence', the latter of which would probably have altered over time according to the nature of the paired encounters each bird experienced during the round robin tests. Barnard and Burk (1979) have suggested that it is improbable that only one cue would be used to assess dominance ability. Thus Chase's (1974) mathematical model is also inadequate in that it does not allow for multiple cue assessment.

Wilson (1975: pp 292 and 293) has tabulated the results of dominance studies to show the physical and behavioural factors (i.e. potential assessment cues) which researchers have attempted to correlate with dominance rank. Size, age and previous agonistic experience occur frequently as investigated factors, though they do not always show strong positive correlations with rank. However, the frequency with which they are found to have at least a moderate correlation with rank order suggests that they are likely either to have some predictive value in determining dominance, or to be influenced by dominance status in a number of species. Either way, they may provide cues in the assessment of the outcome of interactions.

Two further investigations into the way in which linear dominance might arise in animal groups are worthy of mention. Landau (1965) investigated the theoretical effect of the successive addition of animals to a group, the structure of which was already established, though not necessarily linear. He found that this occurrence would maintain linearity if it already existed, and would tend to cause the group structure to move towards linearity if the current structure was non-linear. It has been observed (Rood, 1972; Bernstein and Gordon, 1980) that territoriality overrides other factors in determining dominance such that adults added successively from one group to another join the second group at the bottom of the dominance hierarchy, thus tending to make the enlarged group's structure more linear than before. However, Landau's (1965) theory shows that this would also be the case when individuals were added successively from inside the group i.e. not as territorial strangers. This, of course, occurs regularly in natural and semi-natural breeding groups.

Chase (1980 and 1982) observed the order in which stable dominance relationships were formed in groups of three and four chickens. The results showed that, for all possible triads, in over ninety percent of cases (as opposed to fifty percent by chance) the second relationship involved the first dominant dominating the initial bystander (74%), or the bystander dominating the initial subordinate (17%). Both of these processes guarantee linearity within the triad and so make overall linearity or near-linearity very probable even in larger groups. Indeed, in Chase's studies all the groups of four chickens formed linear hierarchies as opposed to a chance level of thirty-seven percent linear (Appleby, 1983). Such a social trend in the development of dominance relationships could be explained in terms of 'confidence' and/or 'assessment' (including assessment of confidence), but not of 'statistical' hierarchy formation (Barnard and

Burk, 1979).

1.2.4

Summary of dominance hierarchy measurement and formation.

In summary, it has been shown that a group can develop a linear structure through 'statistical', 'confidence' or 'assessment' methods (Barnard and Burk, 1979). However, the 'statistical' method of determining rank purely by the outcome of fights every time two animals meet is not only mathematically improbable but also very costly in terms of time and energy, and has been shown to carry little weight in the formation of natural hierarchies (e.g. Rood, 1972; Bernstein et al, 1979; Bernstein and Gordon, 1980). In particular, the 'statistical' theory of formation cannot account for the frequency of observation of directionally consistent displacement and avoidance behaviours in animal groups. It can be argued that a dominance hierarchy formed entirely by differences in fighting ability is not really a social hierarchy at all (Allee, 1942), as it involves nothing more complex than unbridled aggression and continuing fights. It would be difficult to imagine how such a system could be anything but detrimental to the animals living in a group, as they would probably suffer a higher risk of predation and reduced reproductive success than those in a group in which agonistic interactions were in some way restricted (Christian, 1970).

A 'confidence' hierarchy would involve a reduction in fighting compared to a 'statistical' hierarchy, and would result in the expected frequency of agonistic interactions between pairs of animals decreasing steadily as the sum of their ranks increased. There is some evidence for this pattern of behaviour (e.g. Coulon, 1975a), but other trends (e.g. more frequent agonistic interactions between closely ranked animals) are frequently found as well in natural groups (Van Kreveld, 1970; Hinde, 1979). This suggests that although 'confidence' may play a part in the formation of linear dominance hierarchies, it is not usually of primary importance.

The theory which best describes the observed frequency of linearity in dominance hierarchies and the observed social trends in dominance interactions is that of 'assessment', particularly when it is recognised that assessment can involve multiple physical and behavioural cues. (In fact, Barnard and Burk (1979) have suggested that assessment must involve multiple cues in order to minimise the feasibilty of the evolution of 'cheats'.) However, a system whereby each animal behaves aggressively/dominantly or submissively/subordinately to each other animal according to its assessment of the value of the other's cues must also involve some mechanism for estimating the relative value of its own and the opponent's cues (cf. comparison of 'resource holding power': Parker, 1974; Popp and DeVore, 1979). Certain physical factors e.g. body height, might easily be compared, but others might not e.g. olfactory cues.

To explain how these comparative assessments could be made, a mechanism similar to the idea of 'confidence' (Barnard and Burk, 1979) is required. Thus an animal may learn to compare his own competitive ability to the abilities and cues of the other group members through experience early in grouping. Alternatively, the mechanism could operate entirely, or largely, without learning, through hormonal or other physiological responses to agonistic experience. Such a mechanism has been suggested for male muroid rodents by Leshner (1975, 1980) and Brain (1980).

The formation and maintenance of dominance hierarchies through assessment, as described above, gives a possible explanation for the common finding of missing relationships in animal groups. If the group has been established for some time then the avoidance behaviour of subordinates may be so efficient that they may only rarely find themselves close enough to certain of their superiors for an agonistic interaction to occur. This type of avoidance behaviour may be so subtle that it remains undetected by the observer, so that no data is obtained on the nature of the relationship.

While this could explain missing relationships (more precisely termed 'missing data on relationships'), it does not solve the problem of how to deal mathematically with these situations. However, the realisation that there could be a valid social behavioural explanation of this phenomenon might justify the use of other measures than the strict mathematical ones described above for describing and comparing the dominance relationships and hierarchies within and between groups (e.g. flow diagrams of interaction direction and frequency instead of Landau's (1951a) equation).

It seems, therefore, that it is necessary to look for a pattern in the directionality of several agonistic behaviours between grouped males in order to establish whether there is sufficient evidence to warrant the conclusion that a linear dominance hierarchy exists. If missing relationships on any behaviour are found to render the mathematical measurement of linearity impossible (Landau, 1951a; Appleby, 1983), comparison of their pattern with directional evidence from other behaviours may nevertheless provide useful indications of the way in which the group's hierarchy is formed and maintained.

1.2.5

The function of dominance hierarchies.

It has already been observed that, in evolutionary terms, dominance hierarchies based on agonism would not be expected to exist unless they served one or more specific functions in allocating essential resources to the members of a group. Thus many studies of dominance have been concerned with attempting to find correlations between dominance rank and priority of access to resources (see Wilson, 1975, pp 292 and 293).

1.2.5.1

Priority of access to food and water.

Two resources which have often been investigated in relation to agonistic dominance are food and water. Both Allee (1942) and Banks et al (1979) have claimed that dominant hens in a group have priority of access to food, though Banks et al could find no similar priority with regard to water. Also, Schjelderup-Ebbe (1922) and Ruhwer and Ewald (1981) observed increased aggressive behaviour by birds (hens, and both sexes of Harris' sparrow) at cached food sources. DeVore (1965) found that the near-linear hierarchy in male baboons correlated with priority of access to food, while Bygott (1979) saw little evidence of regular hierarchical allocation of food in male chimpanzees, although he claimed that male chimps did use their status occasionally to obtain food from their subordinates (or to keep their subordinates away from food).

1.2.5.1.1

Food and water priority in guinea pigs.

In male guinea pigs, Berryman (1978) found only a slight correlation between dominance rank and success in water competition. However, Kunkel and Kunkel (1964) claimed that the alpha male in a semi-natural guinea pig colony tended to stay at the centre of the group near the preferred feeding sites.

1.2.5.1.2

Food and water priority in rats.

Candland and Bloomquist (1965) tested a cohabiting group of male rats in paired food competition tests, and found that no consistent rank order developed. No mention was made of the results of agonistic encounters in the group, so no comparison between food priority and agonistic dominance could be made. Telle (1966) observed no evidence of food priority in wild or captive male rats, and Lore and Flannelly (1977) found no correlation between male agonistic rank order and access to food or water.

No relationship between male agonistic dominance (as measured by aggression to colony intruders) and priority of access to water was found in Blanchard et al's (1984) mixed groups. However, Zook and Adams (1975) did observe that restricted access to food induced fighting in cohabiting, food deprived pairs of rats (both sexes).

1.2.5.1.3

A summary of the relationship between agonistic dominance and food and water priority.

The evidence for dominance hierarchies functioning to allocate priority of access to food and water is equivocal, particularly between species. However, it must again be remembered that the results obtained through experimental competition on deprived animals might be due to individual differences in ability to perform the required task (Syme, 1974), rather than to dominance priorities. Also, different results may be obtained when animals are tested as a group from when they are tested in pairs, due to different social strategies being adopted in the two situations. This is especially likely in primates (e.g. Anderson and Mason, 1978).

An additional problem is that many of these experimental tests measure success in food and water competition in different ways e.g. by total time spent eating/drinking; length or number of eating/drinking bouts; order of access to food/water; total amount eaten/drunk. The last of these measures must ultimately be the most relevant to the inclusive fitness of the animals tested (so long as it is related to their body weights and deprivation level), though it is, of course, probable that some of the other measures (especially total time spent eating/drinking) will be found to be highly correlated with the total amount of food/water obtained.

1.2.5.2

Reproductive priority.

The third factor commonly investigated with respect to dominance hierarchies is reproductive priority. Ultimately, reproductive priority means greater success in terms primarily of the number of offspring produced (i.e. successful fertilisation) and secondly of their survival rate (i.e. successful infant protection and feeding). Precise identification of paternity is very difficult, especially in natural groups, so most studies attempting to compare male agonistic dominance rank with reproductive success have been forced to compromise by measuring aspects of reproductive behaviour on the assumption that they predict fertilisation success.

The simplest measures of reproduction made in these studies are the frequencies of courtship and mating behaviours produced by the males in a mixed group. Scott (1941) observed that in sage grouse leks only one percent of the cocks carried out seventy-four percent of the matings, and a further one percent carried out thirteen percent of the matings. The successful cocks were those which had achieved high dominance status and therefore gained the most favoured territories on the lek. Allee (1942) found that the dominant male chicken in a mixed group did nearly all the mating, and spent a considerable amount of time preventing the other cocks from approaching oestrous hens. If the cocks were separated and put into different flocks of hens, however, they all showed equal amounts of mating activity. This emphasises the fact that the difference in male mating success was due to the influence of agonistic dominance rather than to differences in mating capacity.

In red deer, Appleby (1982) found that rank order established in winter groups of males correlated with copulation frequency the following autumn. Kaufmann (1967) and Bernstein and Gordon (1980) observed that there was a positive correlation between male Rhesus monkey rank and amount of mating activity in the breeding season. Bernstein and Gordon also found that the removal of the first and second ranking males for one day resulted in a corresponding temporary increase in the frequencies of sexual behaviour shown by the third and fourth ranking males. Takahata (1982) observed that dominance rank correlated with the number of mounts and ejaculations shown by male Japanese monkeys, and Packer (1979) found a high correlation between male baboon dominance rank and the amount of consorting activity with oestrous females.

More complex measures of reproduction which have been made in order to find out if rank order functions to determine reproductive success have involved the study of mating strategies. In baboon troops with a system of central and peripheral males (central males dominant to peripheral males) as well as an individual near-linear hierarchy, DeVore (1965) observed that the central males copulated most at the time of female ovulation, while the peripheral males copulated at other times when fertilisation was less likely to occur. Similarly, Hausfater (1975) observed that the alpha male baboon in his troop mated most around the time of ovulation, while the second and third ranking males did most of the mating seen during other stages of oestrus. In both of these cases, the actual number of copulations by the dominant male/s was often smaller than that of lower ranking males, but because of their strategy of copulating at the optimal time, the dominant males probably fathered considerably more offspring than their subordinates.

Harcourt (1979) observed a different mating strategy in gorilla groups. Here only the silverback (dominant) males mated with primi- and multiparous females, though all the males mated with nulliparous and adolescent females. This system may considerably enhance the reproductive fitness of the silverbacks, as they are the only males to copulate with females whose fecundity has already been proved.

Two studies indicate that the mating strategy of animals in a group may be changeable, depending on environmental or group structural factors. Bygott (1979) found that, in general, the rank order of male chimpanzees seemed not to be used to determine access to females, though under certain (unspecified) conditions it could be used in this way.

Samuels et al (1980) observed a group of bonnet macaques during two breeding seasons in the first of which the males had a stable dominance hierarchy, while in the second many reversals occurred and no stable structure was apparent. While the structure was stable, the alpha male consorted most often and for long periods with the highest ranking females (and was presumed to have fathered the offspring of at least three of the eight females in the group), while the lower ranking males formed only brief associations with low ranking females. There is some evidence (Wilson, 1981) that, in Rhesus monkeys at least, high ranking females have a better young survival rate than others. Thus the alpha male bonnet macaque's strategy might have made sure not only that he fathered a large proportion of the young in the group, but also that those young would have a better chance of surviving than most.

During the season of instability in the bonnet macaque male hierarchy, however, all the group males associated briefly with females, none showing consistent consortship. Indeed, Samuels et al estimated that the former alpha male probably fathered one infant that year, while the new alpha male fathered none. It seems probable that the overall mating success of the group at such an unstable time may be lowered, as females are less likely to be fertilised when males associate with them briefly than when one male consorts with them through all, or a large part of oestrus. Also, infants and pregnant females could well have been damaged during the fights over group leadership which occurred at that time.

As mentioned above, studies which are able to compare actual paternity with agonistic rank are very rare. DeFries and McClearn (1970) set up experimental colonies of two or three male (of different strains) and three female mice, and observed that the dominant male in each cage fathered over ninety percent of the litters produced. It must be remembered, though, that mice under these conditions show a despotic type of dominance (suggesting attempted individual territory ownership) such that the subordinates are extremely restricted in their general activity.

Another way in which the reproductive success of males can correlate with their dominance rank is by active female preference for the higher ranking males. Hoffmeyer (1982) discovered that oestrous female bank voles would show a preference (in terms of proximity time) for the smell of an unfamiliar dominant male (from a stable group of males) over that of an unfamiliar subordinate male. When the females were tested with just the urine from the males (as opposed to the smell of cardboard tubes previously inhabited by them), they still showed a general preference for the dominant male, though it was necessary to test the females for a longer time before this difference became significant. Thus different pheromones released in male urine according to agonistic dominance status could be responsible for preferential mate choice by female bank voles, so increasing a high ranking male's chances of reproductive success.

1.2.5.2.1

Reproductive priority in male guinea pigs.

Male guinea pigs do not only show sexual behaviours to females in oestrus, but also (in the form of courtship, which may include attempted mounting) to immature, anoestrous and pregnant females (Louttit, 1927; Jacobs et al, 1971; Rood, 1972; Jacobs, 1976; Berryman, 1978). Although male guinea pig courtship behaviour is not directly related to reproduction, its existence has led researchers to suppose that it must be related to agonistic dominance and/or reproductive priority during oestrus. Such priority could operate through female preference for the male which had courted her most. Alternatively, frequent courtship of a female might ensure proximity to that female when she came into oestrus. Thus studies of the relationship between agonistic dominance and reproductive priority in the male guinea pig have frequently investigated courtship interactions in addition to actual mating behaviours.

King (1956) observed that the two oldest (founder) males in a semi-natural group apparently did all the mating and sired all the litters born during the year of observation. Any young males which attempted to court females were immediately chased or attacked by the dominant males (King, 1956; Coulon, 1975a).

Rood (1972) and Berryman (1978) both found a correlation between male dominance rank, aggressiveness, and frequency of courtship (including purring) to females, especially to adult females. Riss and Goy (1957), Rood (1972), Coulon (1975a) and Martan and Shepherd (1976) further observed that the alpha male guinea pig usually copulated first when a female came into oestrus, though a mating chase often ensued in which the alpha male would try (frequently unsuccessfully) to keep the other males away from the female. Kunkel and Kunkel (1964) suggested that the alpha male spent so much time chasing other males at this time that he was actually less successful than they in copulation. It seems likely, however, that this observation may have been due to extremely overcrowded housing conditions such that the males were in closer proximity to one another than would normally be the case.

Jacobs et al (1971) and Jacobs (1976) claimed to find a more complicated reproductive strategy in guinea pigs whereby a male formed an association with a female during her pregnancy, and had copulation priority (and alpha male dominance status) on the day of parturition (i.e. at post partum oestrus). Each female associated with (i.e. was courted much more frequently by) one male, but one male could associate with more than one female over the same period. Jacobs et al observed that in small groups, the associating male was almost always the normal alpha male, but in larger groups (containing ten to fifteen males) other males were able to form associations, though the alpha males still associated the most. Thus there appeared to be a correlation between rank order and number of associations with females. It is possible that this phenomenon might be due simply to the less complicated correlation between rank order and courtship/mating activity mentioned above, with the apparent complexity of 'associations' being caused by an unnaturally large number of animals (both males and females) in the large groups.

It seems from these studies that the dominant male in any group of guinea pigs usually mates first when a female comes into oestrus and also usually shows the largest amount of courtship to anoestrous females. For these factors to have functional meaning, it must be shown that primacy in mating leads to reproductive priority in terms of production of young.

Ishii (1920) and Young et al (1935) claimed that oestrus in the guinea pig usually lasts for about eight or nine hours (range one to eighteen). Tresidder (1922) found that, under laboratory conditions, postpartum oestrous females would only permit copulation during the first six hours after parturition, while in Rood's (1972) outdoor colonies of guinea pigs and guinea pig x <u>C.aperea</u> hybrids, mating only occurred between thirty and one hundred and fifty minutes post partum. This short period of mating should not be surprising, as Young and Grunt (1951) and Grunt and Young (1952a) have observed that male guinea pigs rarely copulate to ejaculation more than once with any oestrous female. Thus unless a very large number of males were present, it would not take long for all the males to mate.

Martan and Shepherd (1976) found that the copulatory plug formed in a female's vagina after her first copulation successfully blocked sperm transport from a subsequent copulation. They also found that this plug remained in the vagina, gradually diminishing in size, for up to eighteen hours. Since ovulation usually occurs around six hours after the first copulation (Stockard and Papanicolaou, 1919; Young et al, 1935), and all mating is completed within this period, it seems likely that the first male to copulate will sire all, or nearly all, of the young born to the female. These observations contradict Ishii's (1920) claim that copulation early in oestrus is less likely to lead to pregnancy than later copulation. However, the weakness of Ishii's claim (which is not substantiated by data) suggests that it can be ignored in the light of more powerful evidence to the contrary.

Thus it appears that the dominant male guinea pig's strategy of mating first with an oestrous female gives him a distinct reproductive advantage, even if subordinate males in the group do succeed in copulating with the female during the subsequent mating chase.

In the present studies, actual copulation in male guinea pigs was not measured, but their courtship behaviour was extensively investigated and compared with present and future dominance status (chapters Three, Four and Seven).

1.2.5.2.2

Reproductive priority in male rats.

Little direct evidence is available concerning possible relationships between reproductive priority and agonistic dominance in rats. Telle (1966) could find no evidence of hierarchical priority of access to females in his observations of wild rats. However, occasions when one male monopolised an oestrous female by blocking access to her burrow have been observed (Robitaille and Bovet, 1976). The social status (in agonistic terms) of these successful rats was not known.

Flannelly and Lore (1977b) observed that the dominant male in their group of five captive males did most of the copulating with and ano-genital sniffing of the two females in the group. When this male died, the remaining four males showed equal frequencies of these behaviours, thus suggesting that rats, too, may be subject to changes in reproductive behaviour according to the current social structure, or more specifically to the stability of the current social structure of their group. The dominant male rats (as measured by aggressiveness in colony intruder tests) in Blanchard et al's (1984) mixed groups showed more copulatory behaviour in 30 min. mating tests than did the other males. These dominant males did not monopolise the test females, however.

There are very few observations of a direct relationship between dominance and gross reproductive behaviour (e.g. monopoly or attempted monopoly of oestrous females by the dominant male) in male rats. This does not, however, necessarily mean that dominant males do not achieve reproductive advantage over their subordinates. There are other ways in which they could potentially improve their probability of siring the majority of an oestrous female's litter. It has been shown that female rats require about ten intromissions before receiving their first ejaculation in order for full sperm transport to occur, and for the induction of the hormonal response (especially progesterone production) necessary for successful implantation (Adler, 1969; Adler et al, 1970; Chester and Zucker, 1970; Edmonds et al, 1972). Sperm transport is also increased by the tight positioning of the vaginal plug in the female's vaginal-cervical junction. Such positioning is most often achieved if the male maintains pelvic contact with the female for at least one second after ejaculation (Matthews and Adler, 1977, 1978).

Inhibition of sperm transport can occur, however, if a male intromits a female within about fifteen minutes after an ejaculation (intromission within four minutes causes almost total inhibition) (Adler and Zoloth, 1970; Matthews and Adler, 1977; Lanier et al, 1979). Male rats show a postejaculatory interval (PEI) such that they are very unlikely to inhibit their own sperm transport (Matthews and Adler, 1977; McClintock et al, 1982a, 1982b). Females also show a PEI which is, in a multimale situation, usually slightly shorter than that of a male (in McClintock et al's 1982 study of mating in a multimale/multifemale group it was estimated that the PEI would result in an average seventy percent of sperm being transported after each ejaculation). Thus it is in the male's reproductive interest to cause the female to extend her PEI after he has ejaculated in her.

In addition to these factors, it has been found that the proportion of sperm deposited in a female by a particular male is directly related (unless sperm transport is inhibited by early postejaculatory intromissions) to the proportion of the litter sired by him (Lanier et al, 1979; Dewsbury and Hartung, 1980). Neither recency nor primacy was found to affect this result. So the more ejaculations a male has with any oestrous female, the better are his chances of siring a large proportion of her litter.

These findings suggest that a male rat in a group mating test (or a cohabiting mixed group) could improve his relative reproductive success by a) intromitting more frequently than the others before ejaculating (especially before his first ejaculation in a series); b) maintaining pelvic contact with a female for longer than one second after each ejaculation; c) causing the female to extend her PEI for a longer time after his than after other males' ejaculations; d) ejaculating more often in a series than other males. If more than one oestrous female were present then it would also be advantageous to have a shorter PEI than other males, provided there was a mechanism preventing the male from starting his next copulation by intromitting the female in which he had just ejaculated. This would increase his chances of inhibiting other males' sperm transport whilst maximising his own.

Gärtner et al (1981) compared the number of intromissions in a copulation test (two or four males to one female) with relative paternity success in pairs of males (two males housed with four females). They found a positive correlation between intromission frequency and paternity success in sixty-six percent of pairs tested. They also found that in ninety-four percent of pairs of males, one male sired significantly more of the offspring (around eighty-four percent), so obviously behaving in a manner which greatly increased his reproductive success. In cases of superfecundation, the reproductively superior males fathered an average seventy percent of the litter. It is a great pity that Gärtner et al (1981) did not even attempt to assess agonistic dominance in their rats, so enabling a comparison to be made between their relative paternity results and the results of intermale agonistic encounters.

A somewhat conflicting result concerning relative paternity success was found by Price (1980). In his study, half of the pairs of males investigated did not sire significantly different proportions of the litter produced in two male to one female mating tests, i.e. neither male in a pair sired significantly more or less than fifty percent of the litter. Since there was no overall difference in fertilisation between the wild type and Long Evans males used in this study, it appears that these results must have been due to the males showing equally successful mating strategies in half of the pairings. It is possible that the difference between these results and those of Gärtner et al (1981) may have been due to the fact that Gärtner et al's rats lived together for about four weeks with females, whereas Price's were only together for the duration of the test (maximum 150 minutes). Thus Gärtner et al's animals potentially had more time to develop a social dominance relationship than Price's. Another possible explanation could lie in the fact that all Gärtner et al's rats were able to copulate to satiation, which was not the case in Price's study. Thus some significant behavioural differences producing differential reproductive success (e.g. number of ejaculations in a series) may not have been able to be put to effect by Price's males.

McClintock et al (1982a) compared male agonistic dominance with mating behaviour in groups containing two males and five females (not all of which came into oestrus during the observation period). They found that the dominant males intromitted more before ejaculating than did the subordinates. The dominant males also tended to ejaculate more often than the subordinate males and the females were quiescent for a longer period after receiving a dominant's than a subordinate male's ejaculation. Dominant males were seen to have shorter PEIs than subordinates in groups where more than one female was in oestrus at the same time. Since all males initiated mating with a different female after ejaculation in these groups, there was little risk that a dominant male would inhibit his own sperm transport by reducing the length of his PEI. These factors would be expected to give the dominant males a distinct reproductive advantage over the subordinates in terms of the relative number of offspring produced (see above).

These results are very interesting as they suggest that male rats can and do show reproductive dominance. This dominance tends to be mediated by subtle behavioural differences rather than by the actual or attempted monopoly of oestrous females that is seen in many other species including guinea pigs (see above). An exception to this may sometimes be found when only two male rats compete for one female, as aggression has been seen under these conditions (Thor and Carr, 1979).

In chapter Eight an attempt is made to find out whether there was a relationship between dominance status and some of the behavioural aspects of copulation in male rats which might indicate reproductive priority. Actual paternity of resulting litters was not examined.

1.2.5.2.3

Correlations between priorities of access in guinea pigs.

No correlation between three measures of priority of access to water and amount of courtship (purring) to females was found by Berryman (1978) in the males of her mixed colony. No other comparisons have been made between priorities of access in guinea pigs.

1.2.5.2.4

Correlations between priorities of access in rats.

A few studies have looked at the relationship between priorities of access (or rather attempted measures of priority of access) for different resources in rats. Baenninger (1970) found some correlations between the results of paired water and food competition tests conducted using male rats from a cohabiting group. These results might have been more interesting if the tests had been made on the group as a whole, rather than on pairs taken from it. Gärtner et al (1981) found no correlation between drinking rank (measured by total drinking time) and copulation rank (measured by frequency of intromission) in groups of two and four male rats.

1.2.5.3

A summary of the relationship between agonistic dominance and priority of access to resources.

From the evidence cited above, it seems that many species show a close relationship between their agonistic dominance hierarchy and aspects of reproduction, while few show a clear correlation between dominance and food or water priorities. A possible explanation of this could be that species which live in close proximity as a group (especially species which are mainly herbivorous) are probably only able to do so because their food and water supply is not normally restricted, so competition for these resources is rarely necessary. The fact that one male can mate with more than one female, however, combined with the fact that many species have a limited breeding season, or females which only come into oestrus occasionally and/or produce small litters, means that intermale competition for reproductive priority is almost inevitable. The prevalence of this situation might have led to the evolution of a tendency for males to develop dominance relationships even in the absence of females. Controlled experiments are needed to establish whether or not this is the case.

1.3

Dominance and submission.

Much debate has taken place regarding the validity and usefulness of the concept of 'dominance' in describing and explaining animal behaviour (e.g. Schneirla, 1946; Van Kreveld, 1970; Crook, 1970; Rowell, 1974; Parker, 1974; Hinde, 1979; Popp and DeVore, 1979; Bernstein, 1981). Although it must be admitted that the ways of assessing dominance relationships are far from perfect, it has been shown that the results of the measures used do have an apparent functional connection with reproductive behaviour in many species. This functional connection cannot satisfactorily be explained by coincidence. Thus it seems that the current approaches to measuring agonistic relationships between animals are sensitive enough (although open to considerable improvement) to reveal a behavioural mechanism which has an important function in determining fitness in group-living species.

Parker (1974) and Popp and DeVore (1979) explain this mechanism in terms of resource holding power (RHP). They suggest that animals fight over a resource (e.g. reproductive priority) only if they assess each other's ability and desire to win as being almost equal. Thus submission or subordination occur when one of the animals assesses the potential costs of conflict as outweighing its benefits. Ritualised display is seen as a low-cost way of facilitating assessment before conflict begins, and subordination as a means of avoiding conflict altogether. Thus agonistic behaviour (especially of a serious kind) in the group as a whole is reduced by each individual's minimisation of his own conflict costs.

This theory suggests that the submitting animal is more important than the dominant animal in reducing aggression and determining the nature of the agonistic relationship between the two. This idea has been supported by many other writers (e.g. Crook, 1970; Rowell, 1974; Bekoff, 1977; Ferguson, 1978; Hinde, 1979), some of whom have placed even more emphasis on the importance of submission, to the extent of suggesting the use of the term 'submission' rather than 'dominance' hierarchy. In itself, this change in nomenclature has little use. After all, the structure under observation is essentially the same. But the idea that the directionality of agonistic relationships should be determined by using the frequency of submissive and avoidance behaviours as well as attacking and threatening behaviours is valid.

The existence of submissive behaviours and subordination in groups of animals has been the cause of considerable dispute amongst sociobiologists, who have found it difficult to explain how such behaviours could evolve unless there were some advantage to be gained from being subordinate. These theorists see dominance in a strictly functional light, whereby to be dominant means to have greater inclusive fitness (chiefly in terms of reproductive advantage). If dominants have greater inclusive fitness it follows that subordinates must have lesser inclusive fitness. Thus subordination should not be selected for. The argument that subordination should not be selected for ignores the fact that, for animals to be found living as a group, there must be advantages to all members in group life as opposed to a solitary existence. In many species a male which found himself unable to win in agonistic encounters with the other males in his group and so left the group would be subject to immediate predation. Such emigratory behaviour would be highly maladaptive and would be selected against. If the same animal were to adopt a subordinate role and remain in the group, he would have a much greater chance of personal survival which would be likely, in turn, to give him occasional opportunities for copulation while the dominant males were temporarily distracted. This type of behaviour by subordinates has been observed in several species (Kunkel and Kunkel, 1964; Rood, 1972; Hausfater, 1975). Also, by remaining in the group, the subordinate male may later have the chance to improve his status, since dominance is relative rather than absolute.

At this point, it is worth mentioning that although subordinate animals may show much less reproductive behaviour or less efficient reproductive behaviour than their superiors due to behavioural inhibition, they are not expected to be any less capable of successful copulation than dominants (in terms of the ability to ejaculate viable sperm). Even though there is evidence that testosterone level may be linked with aggressiveness and dominance (Beach, 1961; Rose et al, 1971, 1972; Leshner, 1975, 1980; Brain, 1980), all non-castrated males should have considerably more testosterone than the minimum necessary for the production of sexual behaviour and ejaculation (Damassa et al, 1977; Sachs and Meisel, 1979).

In some studies (e.g. in red deer stags; Appleby, 1982) a longitudinal pattern of dominance status has been observed, such that dominance rank (and concomitant yearly reproductive success) is closely related to age. Some people have argued that this type of structure renders the concept of dominance meaningless (Rowell, 1974), as it means that the lifetime reproductive success and mean dominance rank of all males would theoretically be equal. However, since no animal could be certain (in evolutionary terms) of surviving for the full span required to achieve maximal fitness, it is not surprising that agonistic dominance for reproductive priority is still strongly contested especially within each peer group. After all, in any group of animals it is relative rather than absolute reproductive success that counts, so even if the advantages to be gained by dominance are small in real terms, they are still very important in relation to each individual's relative inclusive fitness.

The concept of the dominance hierarchy has received further theoretical criticism by researchers who say that it is only useful if the animals under observation are aware of its existence i.e. are aware of the transitivity of dominance relationships (Altmann, 1981) or more particularly of the actual rank they hold in a group (Bernstein, 1981), and behave accordingly. Such criticisms tend only to be made by primatologists, whose subjects show a complexity of social behaviour not known in other vertebrate orders. Researchers into dominance behaviour in other vertebrates do not have the same expectations, and regard the term 'dominance hierarchy' as being of useful descriptive value to the observer, but not to the animals concerned. Each animal is only thought to be aware of its status relative to each other member of the group individually, so that a linear dominance hierarchy is formed only when the system of dominance relationships within a group happens to fulfil the criteria for linearity. If the animals in the group all use similar cues in order to develop these relationships, then linearity or near-linearity would tend to be found in the observed dominance hierarchy.

1.4

The present studies.

The aim of the studies reported here was to investigate the nature, causes and functions of social behaviour and structure in male guinea pigs and rats, with particular reference to the effects of social experience on these factors.

Chapters 2 to 5 concern studies of the social structure of a semi-natural colony of guinea pigs (Cavia porcellus). In particular, the avoidance or association shown between animals and the relationship between aggressive and sexual behaviours were investigated and related to the dominance hierarchy found in the group.

Chapter 2 describes the life history and environment of the semi-natural colony of guinea pigs. These guinea pigs lived outdoors in the courtyard of Durham University Psychology Department under conditions similar to those in King's (1956) and Rood's (1972) observational studies.

Chapter 3 reports an investigation of preferences for resting sites (hut preferences) and affiliation with other colony members at these sites (associations) in order to find out whether pairs of animals showed a tendency to avoid or associate with each other independently of their hut preference. This study was intended to replicate and extend King's (1956) and Jacobs' (1976) investigations of the relationship between male dominance status, avoidance and association in mixed groups of guinea pigs.

The two studies described in chapter 4 examine the evidence for the existence of a linear dominance hierarchy based on agonistic interactions between the colony males. This was related to the frequency and nature of the recorded agonistic and courtship behaviours. It was hoped in this way to increase the knowledge of the nature and function of the dominance structure in male guinea pigs. In particular, it was hoped to find out more about the relationship between agonistic experience and dominance status, and between both these factors and sexual behaviour. Similar investigations had been carried out by Kunkel and Kunkel (1964) and Berryman (1978).

Chapter 5 summarises the results obtained from the guinea pig colony studies and relates them to previous findings and to theories of the causes and functions of agonistic and dominance behaviour.

Chapter 6 contains a review of previous findings regarding the effects of early social experience on rodent social behaviours, focussing especially on the results of studies of male rats (Rattus norvegicus) and guinea pigs (C. porcellus).

Chapters 7 and 8 report experiments which investigate the effects of different social experiences at two periods (post-weaning and post-puberty) during their life on the social behaviours of male guinea pigs and rats. Three types of social housing (isolation, all-male and mixed) were established.

Early isolation has previously been found to have permanent effects on the non-social behaviour of the rat (which plays during the postweaning period), but not on the guinea pig (a non-playing species) (e.g.Einon et al, 1981). Some evidence suggests that it may also permanently affect male rat agonistic behaviour (Wahlstrand et al, 1983). The present studies were designed to investigate the social behaviour and group social structure of early-isolated male rats and guinea pigs in order to see whether early isolation differentially affects adult social organisation in a playing and a non-playing species.

The effect of the experience of being housed with females early or late in life was also examined with respect to the patterns of male social behaviours and social structures. In particular, it was hoped that the results might give some indication of the importance of the presence of females in the formation of dominance relationships/hierarchies in these species. Such relationships appear to function to determine reproductive priority. However, it is not known whether they are formed in anticipation or as a result of reproductive competition.

The thesis is concluded in chapter 9 with a discussion of the effects of social experience on male guinea pig and rat social behaviour and structure. The results obtained are interpreted in terms of the causes and functions of social behaviour and structure, and of their possible implications in the social ecology of these species. Further studies and experiments to improve on the present knowledge of these aspects of guinea pig and rat behaviour are suggested.

Chapter Two.

THE GUINEA PIG COLONY.

The guinea pig colony was set up during the summer of 1979 when ten adult outbred animals (five males and five females) of mixed coat type and colour were released into Durham Psychology Department courtyard.

The colony was established in order to replicate and extend previous studies of guinea pig social behaviour (King, 1956; Kunkel and Kunkel, 1964; Jacobs et al, 1971; Rood, 1972; Jacobs, 1976; Berryman, 1978) with a particular focus on the evidence for and functions of the male dominance hierarchy.

2.1

Habitat.

The courtyard measures 21 x 14m (i.e. 294 square m.) and is overlooked by two floors of offices and corridors. The area consists mainly of grass (197 square m.), but there are also areas of deciduous and evergreen shrubs planted in beds of soil (36 square m.), and paving stones (61 square m.). Additional shelter in the form of one large hut (floor, 130 x 94.5 cm: centre height, 43 cm sloping to 24 cm on two sides) raised 13 cm above the ground, two small huts (floor, 76 x 44.5 cm: height, 19.5 cm sloping to 15 cm) and two pieces of plastic tube (217 x 31 cm and 92 x 33 cm) was provided. Access to the raised hut was via ramps to each of its four entrances (one in the middle of each side). The huts were made of wood and the large hut and one of the small ones were heated by electric coils during the winter months (approx. November to March). This heating kept the inside of the huts above freezing point, but was not sufficient to cause snow on their roofs to melt. The layout of the courtyard and the positions of the tubes and huts are shown in Figure 2.1.

2.2

Maintenance.

The grass and other plants were sufficient to constitute a major part of the animals' diet in summer, with only a small amount of laboratory guinea pig food being required to supplement them. In winter, however, the animals relied almost entirely on laboratory food and occasional extra greens. Water (to which ascorbic acid was added in winter) was continuously available from two hoppers. Hay was put inside the huts and tubes about once a week to provide extra food and bedding.

When the colony was founded, it was decided to attempt to maintain it at a maximum size of ten adults (no more than five of either sex) and their young aged up to one or two months. Thus, whenever the number of young animals exceeded the number required to replace adults that had died, the excess animals were captured and removed from the colony.

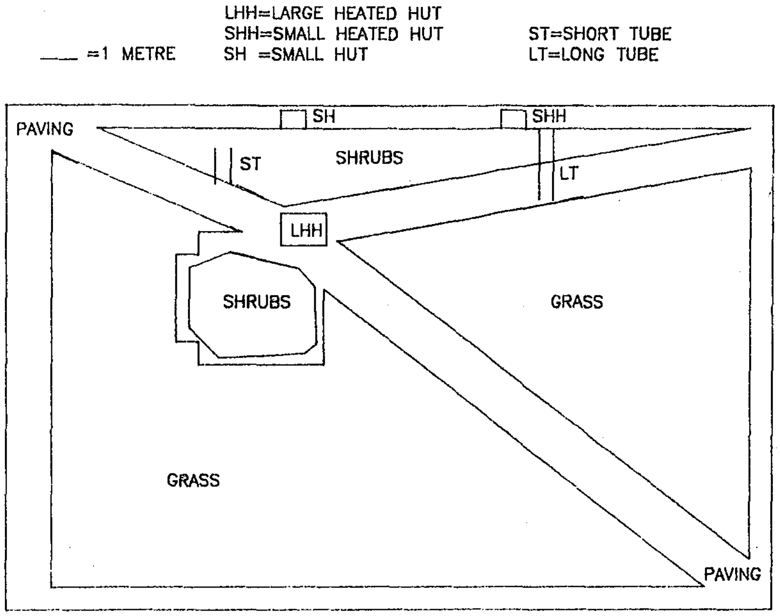

Figure 2.1
Plan of guinea pig colony enclosure.

2.3

Population records.

The colony was checked daily for dead animals and new litters from October 1979 until the end of 1981. During this time, a record of maternal identity (where known) and dates of birth and death was kept for all the colony adults (Tables 2.1 and 2.2). The date and place of birth of all litters, their mother's identity, the number of young born and the number which survived until at least two months old were also recorded (Table 2.3). Adult animals were individually identified by their fur type and colour and were referred to by names, the first letter of each name being unique for that animal's life span. Thus, when recording and analysing behavioural and other data from the colony, only the first letter of each name was used.

Figure 2.2 shows a time profile of the number of adults in the colony and also the number of young born and surviving for each three month period during the twenty seven months of the colony study. In both 1980 and 1981 the largest numbers of young were born between July and September, but these peaks did not correspond with the peaks for the numbers of young surviving. Highest survival rates were found in the spring. This might suggest that the colony females were at their most fertile during the early summer when the largest amount of natural food was available. Owing to their long gestation (about 68 days), the young conceived at this time of year were not born until the autumn when supplies of natural food were diminishing and the weather was becoming colder.

The number of adult females present in the colony fluctuated more

Name	Mother	Date of birth	Date of death	Age at death (days)
Buster	?	20.9.78	14.3.80	541
Humbug	?	27.3.79	15.6.81	811
Cuthbert	?	26.4.79	18.6.80	419
Adam	?	15.8.79	5.1.81	509
Rupert	Emma	3.8.79	12.3.80	222
Isambard	Ferocious	4.3.80	2.11.81 *	608
Marmaduke	Lizzie	10.4.80	?	(>630)
Nelson	Dinah	29.6.80	?	(>550)
Sylvester	Queenie	10.12.80	18.5.81	159
				Mean=467
				SD =225

* Animals eaten by owls.

Table 2.1
Colony adult males from 1.10.79 to 31.12.81.

Name	Mother	Date of birth	Date of death	Age at death (days)
Emma	?	15.7.78	10.3.80	604
Dinah	?	20.9.78	28.9.80	739
Ferocious	?	15.1.79	29.9.80	621
Jane	?	17.6.79	31.3.80	288
Lizzie	Emma	3.8.79	29.9.80	423
Gloria	Ferocious	4.3.80	29.9.80	209
Katie	Lizzie	10.4.80	28.10.80	201
Queenie	Dinah	29.6.80	24.10.81 *	483
Ruby	Lizzie	16.8.80	?	(>502)
Thelma	Ruby	8.1.81	?	(>357)
Ursula	Ruby	8.1.81	?	(>357)
Violet	Ruby	15.1.81	?	(>291)
				Mean=446
				SD =202

* Animals eaten by owls.

Table 2.2
Colony adult females from 1.10.79 to 31.12.81.

Mother	Date of conception*	Number born	Number survived	Date of birth	Birth place
Dinah	1. 8.79	4	2	8.10.79	?
Ferocious	8. 8.79	3	2	15.10.79	?
Emma	29. 8.79	4	4	6.11.79	?
Dinah	8.10.79	2	1	12.12.79	LHH
Ferocious	19.10.79	6	4	26.12.79	SHH
Jane	22.11.79	3	1	29. 1.80	SHH
Lizzie	23.11.79	3	2	30. 1.80	LHH
Dinah	12.12.79	1	0	18. 2.80	Out
Emma	14.12.79	4	0	20. 2.80	SHH
Ferocious	26.12.79	3	3	4. 3.80	LHH
Jane	(Premature)	3	0	17. 3.80	SHH
Lizzie	1. 2.80	3	3	10. 4.80	SH
Dinah	18. 2.80	2	2	25. 4.80	SH
Ferocious	4. 3.80	6	4	11. 5.80	LT
Lizzie	10. 4.80	2	2	11. 6.80	LHH
Dinah	25. 4.80	3	3	29. 6.80	Out
Ferocious	12. 5.80	5	4	19. 7.80	LT
Katie	5. 6.80	2	0	12. 8.80	LHH
Lizzie	11. 6.80	7	2	16. 8.80	Out
Dinah	29. 6.80	3	0	3. 9.80	LHH
Gloria	9. 7.80	3	0	15. 9.80	Out
Ferocious	19. 7.80	5	0	25. 9.80	Out
Queenie	3.10.80	1	1	10.12.80	SHH
Ruby	1.11.80	2	2	8. 1.81	SHH
Queenie	10.12.80	2	2	10. 2.81	SHH
Ruby	8. 1.81	3	2	15. 3.81	LHH
Queenie	10. 2.81	1	0	19. 4.81	Out
Ruby	15. 3.81	3	1	19. 5.81	LHH
Queenie	23. 4.81	2	0	30. 6.81	LHH
Thelma	24. 4.81	1	0	1. 7.81	SHH
Ruby	19. 5.81	4	0	23. 7.81	LHH
Ursula	16. 6.81	2	0	23. 8.81	Out
Queenie	30. 6.81	4	0	30. 8.81	Out
Violet	9. 7.81	4	0	15. 9.81	SHH
Ruby	25. 8.81	2	0	1.10.81	LHH
Queenie	30. 8.81	2	0	24.10.81	ST
Thelma	4. 9.81	3	1	11.11.81	Out

LHH=Large (heated) hut.
SHH=Small (heated) hut.
Out=Outside.
SH =Small (unheated) hut.
LT =Long tube.
ST =Small tube.

* Estimated from mean gestation period of 68 days, unless this preceded birth of previous litter, when the latter date was taken.

Table 2.3
Guinea pig colony breeding data from October 1979 to December 1981.

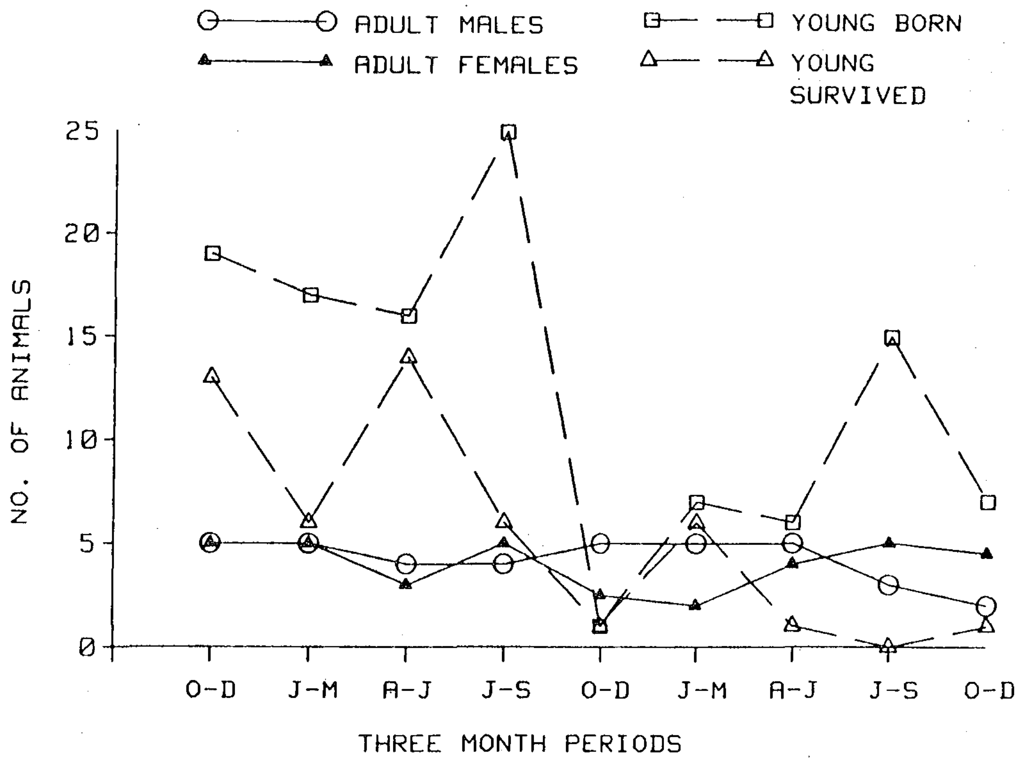

Figure 2.2

Guinea pig colony members from October 1979 to December 1981.

than the number of males, chiefly because of their tendency to die either at the beginning or end of winter when insufficient replacement animals were available. The number of adult males present did not fall below four until late summer in 1981. After this time the colony went into a decline and the study was ended. There were two main reasons for the onset of this decline. Firstly, having suffered no predation for the first two years of its existence, the colony suddenly started to lose animals to the local tawny owl population. This predation chiefly affected young animals around one to two months old, thus reducing the number of surviving young to a smaller number than was required to replace adults that had died. Two adults (Isambard and Queenie) were also taken by the owls, but this was probably because they were old and out of condition.

The second factor contributing to the colony's decline was the severity of the winter of 1981-1982. The temperature remained below zero degrees centigrade for two weeks during January 1982 (falling as low as minus seventeen degrees centigrade) and by the end of the winter only three animals (one male and two females) remained alive. These animals failed to breed for the whole of 1982, despite plentiful natural food and a warm summer, and the last guinea pig finally died in January 1983.

2.4

Population size and density comparison with other outdoor guinea pig colonies.

Previous studies of guinea pigs in outdoor semi-natural colonies have been reported by King (1956), Jacobs et al (1971), Rood (1972) and Jacobs (1976). Table 2.4 shows how the field size, population size and population density of the present colony compares with the others. It can be seen that the present colony enclosure is most similar in area to that of King (1956). King's population density was also closest to that of the colony investigated in this thesis.

None of the outdoor colonies inhabited areas as large as the estimated home range (1173-2475 square m) of the guinea pig's closest wild relative, C.aperea (Rood, 1972). The density of animals in Rood's wild study area was not precisely known, but by dividing the study area (12150 square m.) by the number of adults captured on it (forty-three), estimated maximum densities of one adult per 282.56 square m. (one adult male per 486 m.) were found.

Reference	Field area (square m.)	No. of adult males	Min. field area per adult (square m.)	Min.-Max. field area per adult male (square m.)
Jacobs et al (1971)	13.31	10-15	?	0.89-1.33
Jacobs (1976)	11.70	4- 5	0.65	2.34-2.93
	53.00	3- 4	7.57	13.30-17.70
	53.00	1- 2	8.83	26.50-53.00
Rood (1972)	25.00	2- 4	1.50	6.25-12.50
This study (Chivers, 1984)	294.00	4- 5	29.40	58.80-73.50
King (1956)	216.09	2- 3	24.01	72.03-108.05

Table 2.4
Population sizes and densities in guinea pig outdoor colony studies.

Chapter Three.

COLONY STUDY 1.

AN INVESTIGATION OF ASSOCIATION AND HUT PREFERENCE IN A SEMI-NATURAL COLONY OF GUINEA PIGS.

3.1

Introduction.

In his study of a semi-natural colony of guinea pigs living in a field of similar area to that of the present colony, King (1956) recorded the resting sites of the three male and four female adults daily for a month. The resting sites investigated were four huts positioned in the four corners of the field. King observed that the grouping of the animals in the huts showed no particular pattern, though some individuals were never found together. He claimed that the animals went to the huts irrespective of the social contacts they made there. No statistical analyses were performed on the data to substantiate these claims, nor was any mention made of whether individuals showed any preference for particular huts.

Jacobs et al (1971) and Jacobs (1976) reported the finding that each anoestrous (usually pregnant) female was courted more by one male than by the others, and that this 'associating' male had copulation priority and alpha male status on the day of oestrus. They also found that these male-female associations were shown by greater 'social affinity' at resting sites. In this respect, King's (1956) data showed only one male to associate noticeably more frequently with a particular female when resting than with others. In groups with less than five males, Jacobs et al (1971) and Jacobs (1976) observed that the alpha male was responsible for almost all of the associations at any time.

The present study was undertaken in order to extend and quantify King's (1956), Jacobs et al's (1971) and Jacobs' (1976) findings by establishing a) whether or not guinea pigs rested preferentially in particular huts and b) whether they appeared to associate randomly with other animals in these huts or actively to avoid or seek out certain individuals. With respect to the second question, it was thought that certain male-female associations might occur more frequently than others, while certain male-male associations might be found less often than chance due to the possibility of the existence of intermale dominance relationships causing males (especially high-ranking non-alpha males) to avoid proximity with their superiors.

3.2

Method.

Subjects

The animals studied were all members of the courtyard guinea pig colony described above. All the adults present in the colony during the study period were recorded individually and young animals (less than two months) were identified according to their mother. Ten adults (five males and five females) were present throughout the first three months of this period, but four of these died and were replaced by young animals born in the colony, when such became available.

Procedure

This study was made between January and June 1980. Recordings of the positions of all the guinea pigs in the courtyard were made nearly every day between 1200 and 1500 hours. Since guinea pigs are crepuscular in their habits this was a quiet time of day when little activity took place in the colony and most animals were resting. The position of each adult was marked (using the first letter of its name) on a plan of the courtyard. Young animals were noted by their mother's initial followed by a '+'. The presence of animals in each hut was noted on the plan. The date and time of day were recorded, together with comments on any unusual weather conditions e.g. snow.

Treatment of results

Ninety-two records of the positions of the colony guinea pigs were made between 3.1.80 and 17.6.80. Four adults died between 10.3.80 and 17.4.80 so it was decided to leave this period out of the data analysis. The remaining recordings were divided up into four periods: 3.1.80-5.2.80 (18 records); 6.2.80-7.3.80 (19 records); 21.4.80-12.5.80 (15 records); 13.5.80-17.6.80 (23 records). For the third of these periods only eight adults were present, as opposed to ten in each of the other periods.

The data in each time period were analysed as a block. Chi-squared tests were performed on the observed and expected frequencies of occurrence of each animal in each hut and outside. Further chi-squared tests were performed for each possible pair of animals to compare their observed and expected frequencies of being found together and apart. The expected frequencies in the latter tests were calculated using each individual's probability of being found in each hut. Thus the expected frequency of finding animal A in hut LHH with animal L was obtained from the product of A's and L's probabilities of occurrence in hut LHH, multiplied by the total number of recordings in that time period. Yate's correction for continuity was applied in all these Chi-squared tests, as the expected scores were often smaller than five (Ferguson, 1976).

3.3

Results.

No animals were recorded in the small unheated hut (SH) until April, so the analyses of the first two periods only involved frequencies of occurrence in the large heated hut (LHH), small heated hut (SHH) and outside(OUT). For the third and fourth periods, analyses included frequencies of occurrence in all three huts and outside. Tables 3.1a-d show the observed number of times each animal was recorded in the huts and outside for each time period. The results of Chi-squared tests on these data are also given.

In three of the four tests the null hypothesis that the animals were all found as often as each other in the different huts and outside was rejected. This implied that the animals may have had preferences for resting in particular huts, though it does not differentiate between entirely voluntary preferences and the possibility that animals may have had their preferences forced upon them i.e. a dominant animal might not have allowed a subordinate into the most desirable hut when he himself was in residence. If the

Site	Animal ID									
	A*	L	D	F	C*	H*	E	J	B*	R*
LHH	5	6	8	1	7	5	0	1	6	7
SHH	0	1	0	6	3	4	9	9	7	4
OUT	13	11	10	11	8	9	9	8	5	7

Total no. of records=18

Chi-squared=37.43
df=18
p<.01

Table 3.1a
Time period: 3.1.80-5.2.80

Site	Animal ID									
	A*	L	D	F	C*	H*	E	J	B*	R*
LHH	4	12	15	9	10	1	1	0	0	1
SHH	0	1	0	5	1	7	15	14	14	17
OUT	15	6	4	5	8	11	3	5	5	1

Total no. of records=19

Chi-squared=119.05
df=18
p<.001

Table 3.1b
Time period: 6.2.80-7.3.80

Site	Animal ID							
	A*	L	D	F	C*	H*	G	I*
LHH	3	7	0	0	4	3	0	6
SHH	0	0	2	0	0	0	0	0
SH	0	0	3	2	2	0	1	0
OUT	12	8	10	13	9	12	14	9

Total no. of records=15

Chi-squared=27.40
df=21
p>.1

Table 3.1c
Time period: 21.4.80-12.5.80

Site	Animal ID									
	A*	L	D	F	C*	H*	G	I*	M*	K
LHH	0	12	10	0	3	8	0	1	5	7
SHH	2	0	0	0	0	0	0	0	1	0
SH	0	0	0	0	2	0	0	0	0	0
OUT	21	11	13	23	18	15	23	22	17	16

Total no. of records=23

Chi-squared=57.28
df=27
p<.001

Table 3.1d
Time period: 13.5.80-17.6.80

* =Male
LHH=Large (heated) hut.
SHH=Small (heated) hut.
SH =Small (unheated) hut.
OUT=Outside.

Tables 3.1a-d
Colony study 1. Frequencies of recording of guinea pig colony members in huts and outside.

dominant individual spent a lot of time in this hut, the subordinate may have been forced to show an apparent preference for a less desirable hut.

The Chi-squared tests comparing observed and expected frequencies with which each pair of animals was found together and apart yielded only two results significant at the five percent level (see Tables 3.2a to 3.2d). Since one hundred and sixty-three such tests were carried out, these two significant results were most probably due to chance. Thus it appears that the guinea pigs showed preferences for huts rather than for each other, and did not actively avoid or seek one another's company regardless of hut.

3.4

Discussion.

The results obtained in this study give a strong indication of the existence of individual guinea pig preferences for resting in particular places in the colony enclosure. No statistical evidence for preferential avoidance of or association with individuals was found, however. This finding agrees with King's unsubstantiated observation that hut groupings appeared to be random. It also suggests that male-female associations of the kind claimed by Jacobs et al (1971) and Jacobs (1976) did not exist in this colony. However, there was still a possibility that such associations might have been shown by the frequency of courtship activity (a factor unmeasured in this study) rather than by association ('social affinity') while resting. Dominance relationships between males did not make themselves evident by active avoidance of male pairings at resting

Animal ID

L	D	F	C	H	E	J	B	R	
.44	.32	.59	.49	2.7	.10	.45	.72	.00	A
	.57	1.2	1.5	2.4	.54	.90	.23	1.0	L
		.72	1.2	.36	.23	1.5	.03	.35	D
			2.1	0.1	.54	1.1	1.2	.34	F
				1.1	.28	.36	.25	.27	C
					.57	4.0*	0.4	1.4	H
						1.0	.04	.10	E
							.05	1.1	J
								2.0	B

Table 3.2a
Time period: 3.1-5.2.80

Animal ID

L	D	F	C	H	E	J	B	R	
.27	.01	1.5	.19	.36	.20	.00	.00	.29	A
	.78	.23	1.5	1.5	1.3	.85	.85	1.5	L
		.00	.88	.80	.81	.00	.13	1.1	D
			.43	.08	.51	.12	.16	.12	F
				2.1	1.4	.80	.78	1.6	C
					1.5	.90	.76	1.3	H
						.76	.76	1.7	E
							.01	.78	J
								.78	B

Table 3.2b
Time period: 6.2-7.3.80

Animal ID

L	D	F	C	H	G	I	
.09	1.0	.45	1.2	.60	.15	1.2	A
	.02	.90	.90	.31	.45	.25	L
		.75	.92	.00	.30	.00	D
			3.1	.45	.15	.75	F
				1.2	.45	.33	C
					.15	.03	H
						0	G

Table 3.2c
Time period: 21.4-12.5.80

*=p<.05 (df=1)

Tables 3.2a-d
Colony study 1. Results of chi-squared tests on the frequencies with which all pairs of guinea pigs were found together and apart.

Animal ID

L	D	F	C	H	G	I	M	K	
.62	.00	0	.23	.69	0	.09	.70	.69	A
	.17	0	.11	.00	0	.46	.57	.12	L
		0	.11	.08	0	.46	.46	1.3	D
			0	0	0	0	0	0	F
				.70	0	.20	8.4*	1.6	C
					0	.23	.61	.85	H
						0	0	0	G
							.27	.23	I
								.23	M

Table 3.2d
Time period: 13.5-17.6.80

*=p<.05 (df=1)

Tables 3.2a-d (continued)
Colony study 1. Results of chi-squared tests on the frequencies with which all pairs of guinea pigs were found together and apart.

sites.

In addition to the above findings that colony guinea pigs showed preferences for particular huts but not for particular individuals, one observation from the data is of interest with respect to the reasons for one hut being consistently chosen as opposed to another. From the beginning of this study, the most unhealthy-looking animals in the colony were females E and J, and males B and R. (After their deaths, these animals were found to be emaciated and suffering from scabby skin and loss of hair.) During the lifetime of these animals (i.e. for the first two periods of this study), E and J were consistently found in the small heated hut (SHH). B and R switched apparent preference from the large heated hut (LHH) to the small one half way through the first period of recordings. In the observer's opinion, the small heated hut was a less desirable resting place than the large heated hut, as it had a concrete base offering little protection from the damp (as opposed to the raised wooden floor of the large heated hut).

No more than six animals were ever found resting in the large heated hut at one time, which suggests that this may have been the largest number the hut could contain before aggression caused by extreme proximity led to the weaker animals being made to leave. Thus it seems possible that E,J,B and R were forced through ill health to rest in the less desirable hut. The conditions of this hut probably accentuated their poor health, leading to their deaths.

Thus there is a possibility that the tendency for hut preferences to be found in the colony may have been due, at least in part, to differences in hut quality and individual guinea pig health (i.e. competitive ability). So it might be supposed that all the animals seeking a hut to rest in (at least during the winter months) would have preferred the large heated hut in terms of its comfort. However, some were forced by weakness to shelter in the small heated hut.

Chapter Four

COLONY STUDIES 2 AND 3.

INVESTIGATIONS OF THE MALE DOMINANCE HIERARCHY, COURTSHIP AND AGONISTIC BEHAVIOUR IN A SEMI-NATURAL COLONY OF GUINEA PIGS.

4a

General Introduction.

Studies of guinea pig behaviour in mixed groups have been carried out by King (1956), Kunkel and Kunkel (1964), Jacobs et al (1971), Rood (1972), Coulon (1975a), Jacobs (1976) and Berryman (1978). All except King (1956) claim to have found a linear or near-linear dominance hierarchy based on agonistic behaviours among the males in the groups. For most of King's (1956) study, only two adult males were present in a very large enclosure. He found no evidence of a dominance relationship between these two males, although they fought each other quite often. He did observe, however, that the adult males dominated younger males in the colony so that the young males seemed to be prevented from copulating with oestrous females.

Kunkel and Kunkel (1964) put more emphasis on the discovery of some triangular (i.e. intransitive) relationships than did the other researchers. Triangular relationships were defined as cases when male A dominated B and B dominated C, but C nevertheless dominated A.

In the studies cited above, all dominance rankings were determined using the direction of intermale agonistic behaviours.

However, only in Berryman's (1978) study was any distinction made as to the ranks obtained from data on different behaviours, as opposed to those gained from generalised observation of agonistic actions. Berryman was also the only experimenter to test the linearity, or the significance of the linearity, of her data statistically. She tested the data obtained from her eight colony males using Landau's (1951a) equation and binomial tests. These gave strong indication of the existence of a linear hierarchy from attack (bite), flee and combined attack and flee scores.

The small number of males (four) in the present colony studies meant that the probability of obtaining a linear hierarchy (using any one directional measure) by chance was very high at $p=0.375$ (Appleby, 1983). This was also true in Rood's (1972), Coulon's (1975a) and some of Jacob's (1976) colonies. Thus only perfect linearity could even be considered as evidence of a linear dominance hierarchy. Even so, if the evidence for a dominance hierarchy was to be at all convincing, another way of testing whether observed linearity was likely to be representative of a functional linear dominance hierarchy had to be found. To this end, it was decided to follow Berryman's (1978) example, and Hinde's (1979) recommendation by looking for linear dominance in each agonistic behaviour separately, rather than in a single behaviour or in a totalled score. The probability of the same linear rank order being found by chance for more than one behaviour in a group of four animals is very small ($p=.375 \times .0156 = .006$ for two behaviours), so if similar hierarchies were found for each agonistic behaviour this would provide strong evidence for the hierarchy having been formed in a non-accidental way.

Both Rood (1972) and Coulon (1975a) observed a more or less linear relationship between male guinea pig dominance rank and the frequency of initiation and reception of aggressive behaviours such that the highest ranking animal initiated the most and received the least. Kunkel and Kunkel (1964), Rood (1972), Coulon (1975a) and Martan and Shepherd (1976) observed that the male guinea pig hierarchy apparently had the function of allocating reproductive priority such that the alpha male had the greatest reproductive success (i.e. was either the first or the only male to mate with each oestrous female). Also, Rood (1972), Jacobs et al (1971), Jacobs (1976) and Berryman (1978) observed a correlation between rank and frequency of courtship behaviour (though Jacobs et al, 1971 and Jacobs, 1976 reported that this relationship was complicated by the formation of male-female associations).

In the present studies it was intended to investigate the relationships between dominance, agonistic, and courtship behaviours further in an attempt to find out which factors apparently caused differences in aggressiveness and courtship activity. Also, since no evidence of male-female associations (Jacobs et al, 1971; Jacobs, 1976) shown by 'social affinity' had been found in Colony study 1 (chapter Three), it was thought that the present studies would reveal whether such associations existed in this colony in the form of preferential courtship.

4.1

COLONY STUDY 2.

4.1.1

Introduction.

In this study, the frequency and direction of intermale agonistic and male-female courtship behaviours were observed over a period of three months in order to establish a) whether there was evidence for a linear dominance hierarchy among the males b) what relationship, if any, existed between this hierarchy and the frequency and nature of male agonistic and courtship behaviours and c) if there was any evidence of male-female associations (in terms of courtship) of the kind reported by Jacobs et al (1971) and Jacobs (1976).

4.1.2

Method.

Subjects.

The animals of the colony were observed between 19.5.80 and 28.8.80. Four adult males (H, A, I and M) and five adult females (D, F, L, G and) and their offspring were present during this period. Twenty-five guinea pigs were born during and immediately before this time, of which fifteen survived to maturity. Of the twenty guinea pigs conceived during this period, however, only two survived to maturity (see Table 2.3).

Procedure.

Observations of the sexual and aggressive behaviours of the guinea pig colony were made on 31 evenings from 19.5.80 to 28.8.80 (total observation time: 1300 minutes). The experimenter watched the colony from a first floor window in the south corner of the courtyard. This position afforded a good view of almost all the grass and a large area of the shrubs and paving. Observation periods took place between 1700 and 2000 hours and were never shorter than 10 mins or longer than one hour. At this time of day the animals were usually out grazing and showing frequent social activity. They were also less prone to disturbance from noises or movements inside the building than at earlier hours.

The frequency and length of observation periods during the summer of 1980 depended on the weather conditions and the natural activity levels of the colony. If all the guinea pigs went out of sight (usually to rest or shelter in the huts or bushes) for more than 5 mins, the observation period was ended. Extreme dampness and rain usually deterred the animals from their normal evening activities so that they would remain in their huts. Since this summer was very wet, observations could only be made on an opportunistic rather than a regular basis.

The aggressive and sexual behaviours recorded were based on those described in Table 4.1, with the following exceptions. For this study, 'displacements' were not distinguished from 'threats', and 'run away' was not scored as it was almost never seen in the uncrowded conditions of the courtyard. A category of 'sexual approach' incorporated both 'rumba' and 'circle', and 'following' was not recorded.

BEHAVIOUR CATEGORY	EQUIVALENT TERMS USED BY: Experimenter	Rood (1972)	DESCRIPTION
Defensive	Displace		One animal moves away when another approaches it. In this behaviour the recipient is the active animal and the initiator pays no attention to the animal it has displaced.
	Run away		One animal runs away from another, usually after being threatened by the second animal.
Aggressive	Threat	Head-thrust	The agent jabs its head at the recipient while standing in close proximity. The initiator's head does not normally touch the recipient.
	Chase	Chase	The agent chases the recipient at a running speed over a distance of at least one metre.
	Bite		The agent lunges, mouth open, at the recipient and bites it. Blood is usually drawn, and the recipient squeals with pain.

Table 4.1
Description of guinea pig behaviours recorded in chapters 4 and 7.

BEHAVIOUR CATEGORY	EQUIVALENT TERMS USED BY: Experimenter	Rood (1972)	DESCRIPTION
Sexual	Rumba	Rumba	Male approaches female slowly, rhythmically swaying his hindquarters from side to side.
	Circle	Chin-rump follow	Male circles slowly around female between rumbas or attempted mounts.
	Ano-genital sniff/lick	Naso-anal	Male sniffs or licks female's perineal region.
	Follow		Male follows female, or female follows male over a distance of several metres at a proximity of of less than one metre. The leader's movements e.g. running and stopping, are closely copied by the follower.
	Attempted mount	Attempted mount	Male approaches female from behind and places his forepaws in front of her hind legs. He may thrust his hips rapidly. Female does not respond with lordosis, and no intromission occurs.
	Mount	Mount	As attempted mount with hip-thrusting, but female responds with lordosis and intromission may take place.

Table 4.1 (continued)
Description of guinea pig behaviours recorded in chapters 4 and 7.

The aggressive behaviours seen during each observation session were scored on predrawn matrices according to initiator and recipient identities. Thus no sequential or temporal data on these behaviours were available for analysis.

Sexual behaviours and the identities of their initiators and recipients were recorded in note form on the same sheet of paper. Sexual interactions between adult males and juveniles (of either sex) were categorised according to the identity of the adult male and the general term 'Young', as no distinction was made between the unnamed young guinea pigs.

Treatment of results.

The total numbers of intermale aggressive acts initiated and received by each adult male were plotted as histograms. Flow diagrams of each of the three aggressive behaviours (threat, chase and bite) were drawn to show the number of times each male directed these behaviours at each other male.

The total numbers of sexual acts directed at adult females and at juveniles by each adult male were plotted as a histogram. Frequencies with which each male showed sexual behaviours to each adult female were tabulated. Chi-squared analyses of these data were performed in order to discover whether or not there was a difference between the males in their relative frequencies of showing sexual behaviour to the different females.

4.1.3

Results.

The histogram of initiated male-male aggressive behaviours (Figure 4.1) shows perfect rank correlations between all three behaviours performed by the four males. In all cases, the order of frequency of initiation of the behaviours was as follows; H (who showed most male-male aggression), A, M, I. I never chased or bit another male, and H showed considerably more chasing and biting than any of the others.

The histogram of received male-male aggressive behaviours (Figure 4.2) shows that although H received the smallest number of aggressions from the other males, a perfect negative rank correlation between aggressive behaviours initiated and received only existed for threats and not for chases or bites. A received the largest number of bites, and M was chased more often than the others.

The flow diagrams of intermale aggression (Figures 4.3a-c) suggest the existence of a dominance hierarchy in this group of male guinea pigs, the rank order of which correlated exactly with the rank order of the number of aggressive acts initiated. There are no missing relationships for either threats or chases, so it is possible to calculate the probability of the same linear rank order occurring by chance in both these behaviours. Sixty-four possible hierarchies, of which twenty-four are linear, can be found in a group of four animals (Appleby, 1983). Thus the probability of finding the same linear hierarchy in two behaviour measures in this group is 0.375 x 0.0156, i.e. p=.006. So the linear hierarchy observed in

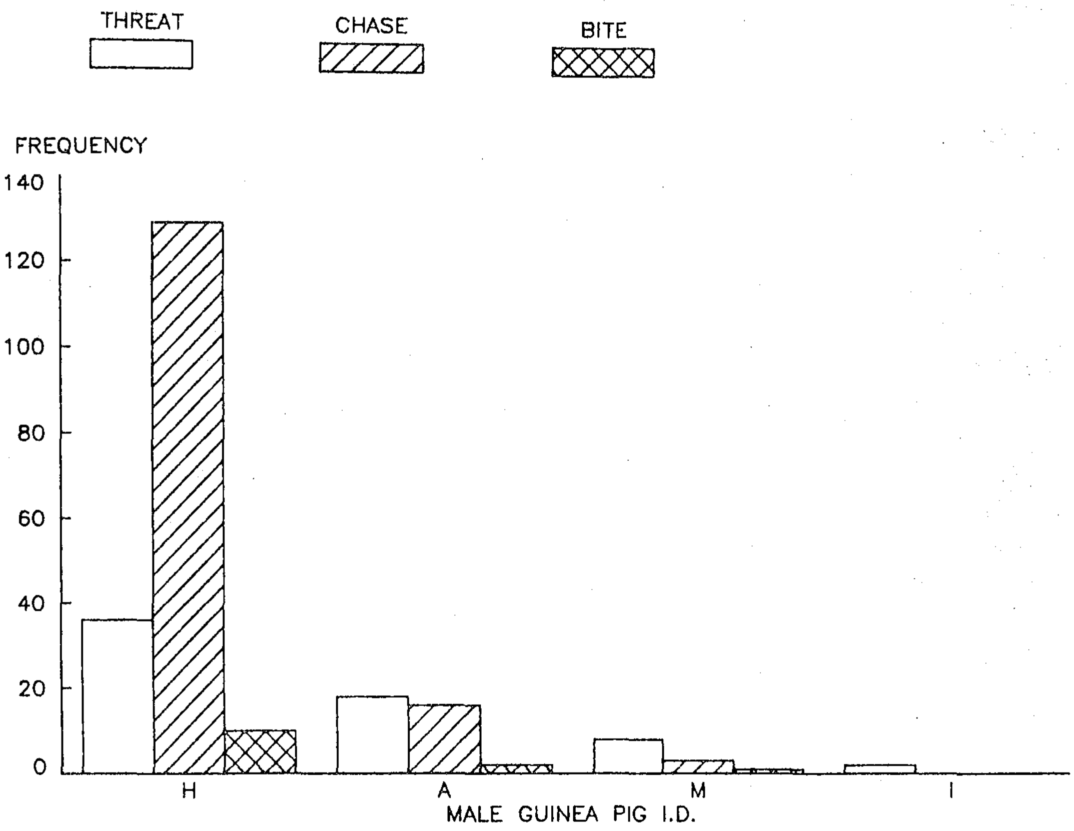

Figure 4.1

Colony study 2. Initiated intermale agonistic behaviour.

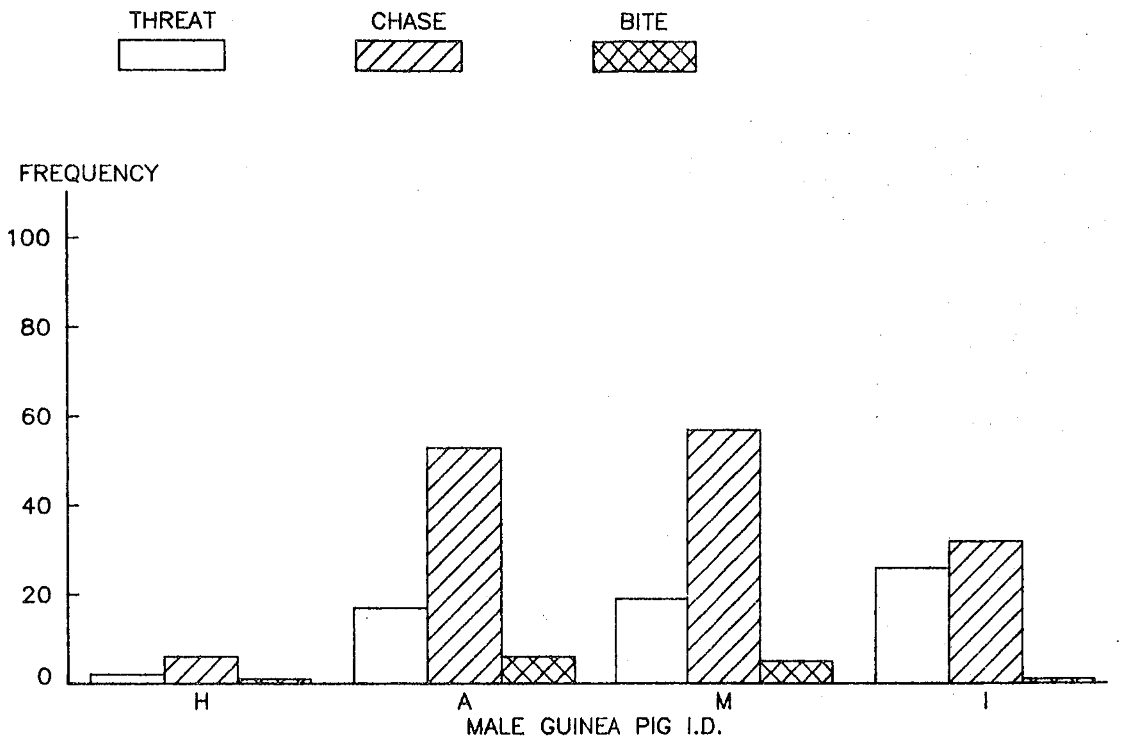

Figure 4.2
Colony study 2. Received intermale agonistic behaviour.

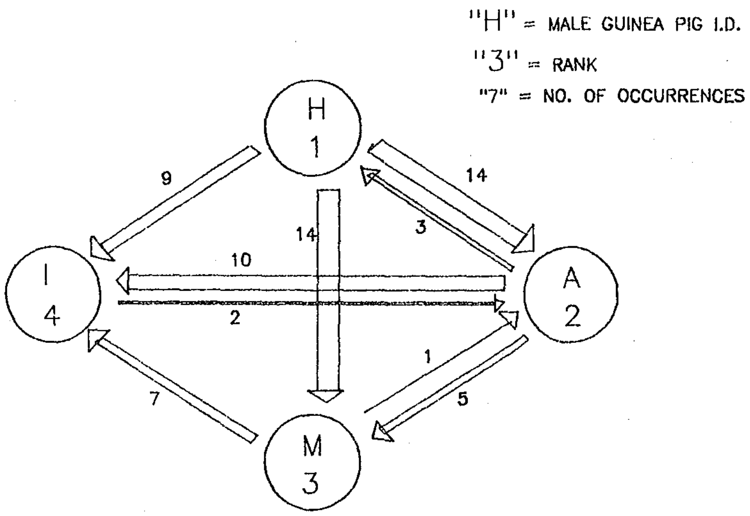

Figure 4.3a.
Colony study 2. Flow diagram of intermale threats.

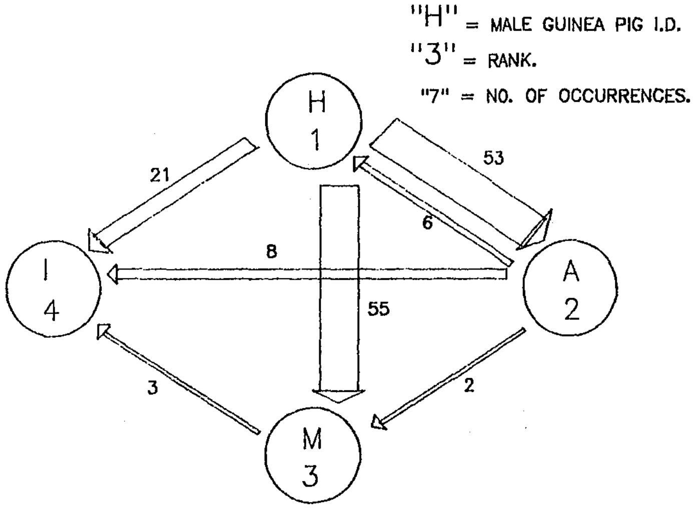

Figure 4.3b.
Colony study 2. Flow diagram of intermale chases.

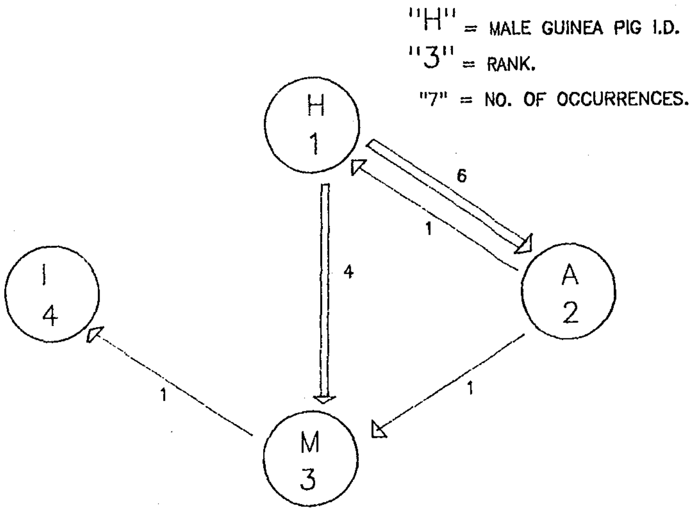

Figure 4.3c.
Colony study 2. Flow diagram of intermale bites.

this group is unlikely to have occurred by chance. The fact that the data available for bites between males follows the same pattern further strengthens this observation.

Inspection of the flow diagrams reveals that, for all three aggressive behaviours, H (the alpha male) showed most aggression to A and M and much less to the omega male, I. A, ranking second, showed almost equal amounts of aggression to all three other males, but received a great deal more from H than from M or I. M, ranking third, was most aggressive to I and only threatened A once. Neither M nor I ever showed aggressive behaviour towards H. The omega male, I, threatened A twice and was never seen to threaten either H or M.

Thus it appears that in this dominance hierarchy, each male directed most aggressive behaviour to the two males immediately below and the male immediately above him in rank. The aggressive behaviours directed to an animal two ranks above the initiator were threats. Also, the only animal which chased or bit the male one rank higher than himself was A, the second ranking male.

It is particularly notable that the alpha male was responsible for nearly all the chasing and biting which occurred between the colony males, while the number of threats shown by each male decreased more steadily down the ranks. Thus, from this study, it seems that a male guinea pig's dominance status is indicated not only by the direction of his aggressive behaviour towards other males, but also by its nature and overall quantity.

From Figures 4.4 and 4.1 it can be seen that the total numbers of

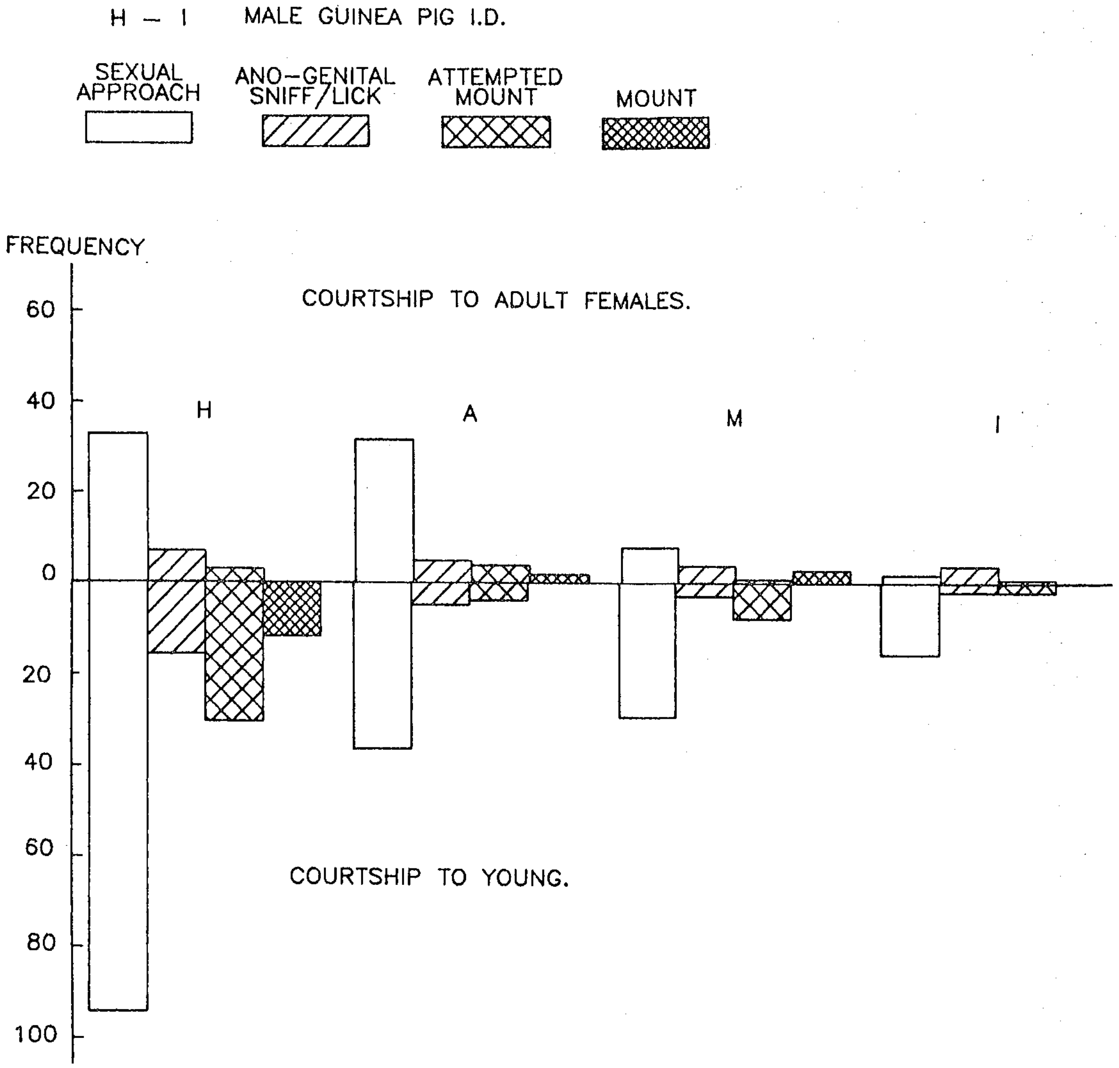

Figure 4.4
Colony study 2. Male courtship behaviour.

sexual approaches and ano-genital sniff/licks by each male are perfectly rank correlated with their respective numbers of aggressive acts and their dominance hierarchy. The largest numbers of attempted mounts and mounts were shown by the alpha male, H, and the smallest numbers by the omega male, I, but in both these measures M was slightly more sexually active than A.

The numbers of sexual approaches shown to adult females by both the alpha- and second-ranking males (H and A) are very similar, and considerably greater than the numbers of sexual approaches to adult females by the lower ranking males (M and I). Juveniles, however, were sexually approached by the alpha male much more often than by the lower ranking males. The alpha male also ano-genital sniff/licked, attempted to mount and mounted juveniles more often than did any of the others. Overall, the frequency of courtship behaviours shown by the males to juvenile guinea pigs was closer to perfect rank correlation with dominance status than was that shown to adult females.

Tables 4.2a-c show the frequencies with which each male sexually approached, ano-genital sniff/licked and attempted to mount each adult female. The results of chi-squared tests (with Yates' correction for continuity) on these data are given beneath each table. The null hypothesis that there was no difference between the males in their relative frequencies of sexual behaviour to the different females was accepted for all three behaviours. These data gave no indication of the existence of associations between male and female guinea pigs, as described by Jacobs et al (1971) and Jacobs (1976).

Female recipient	Male initiator			
	H	A	M	I
D	4	4	1	0
F	0	4	0	0
L	1	7	2	0
G	12	7	3	1
K	16	10	2	1

Chi-squared=8.64, df=12, p>.7

Table 4.2a: Sexual approach.

Female recipient	Male initiator			
	H	A	M	I
D	1	1	2	2
F	1	0	1	1
L	1	3	0	1
G	2	0	0	0
K	2	1	1	0

Chi-squared=3.58, df=12, p>.98

Table4.2b: Ano-genital sniff/lick.

Female recipient	Male initiator			
	H	A	M	I
D	0	3	1	1
F	0	0	0	0
L	0	0	0	0
G	3	1	0	0
K	0	0	0	0

Chi-squared=2.13, df=12, p>.99

Table 4.2c: Attempted mount.

Tables 4.2a-c
Colony study 2. Frequencies of male guinea pig courtship behaviours to adult females.

Data on mounting behaviour are not included in the above tables as M's three and A's two mounts were all on D. There must be some doubt as to the true nature of these recorded mounts as they all occurred between 12 and 2 days before and 2 and 11 days after the birth of D's litter on 29.6.80. Since the date of birth of D's next litter suggests that she conceived on 29.6.80, these apparent mounts were probably attempted mounts from which she did not run away as quickly as usual. The absence of recorded mounts within two days either side of 29.6.80, when D may have been in oestrus, is explained by the fact that no observations were made on these days.

Tables 4.3a-d show the number of sexual approaches per hour per week (starting from 19.5.80) that each adult male made to each adult female. The trend for the number of sexual approaches to a female to increase before parturition was very slight and inconsistent. The results of Chi-squared tests on these data (given below each table) indicate that the null hypothesis that there was no interactive effect of weeks on the number of sexual approaches given to each female must be accepted for all four males.

4.1.4

Discussion.

The consistent direction of intermale aggressive behaviours strongly indicates the existence of a male dominance hierarchy in the guinea pig colony. The frequencies of threats, chases and bites were correlated with this hierarchy such that the alpha male did most of the threatening, and nearly all of the chasing and biting of other males. It appears that aggressive acts were almost always directed at

Female I.D.	Week No.														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
K	1.8	3.0	0	0	0	0	0	0	*	0	2.0	0	*	0	0.8
G	0.9	2.0	0	0	0	0	0	3.0	*	0	0	0	*	0.4	0
L	0	0.5	0	0	0	0	0	0	*	0	0	0	*	0	0
F	0	0	0	0	0	0	0	0	*	0	0	0	*	0	0
D	0	0	0	0	0	0	0	0	*	0	0	0	*	0	0
			(K)	(L)		(D)		(G)					(K+L)		

Chi-squared=10.57, df=48, p>.99

Table 4.3a: Sexual approaches by male H.

Female I.D.	Week No.														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
K	0.5	1.5	0	0	0	0	1.8	0	*	0	1.5	4.0	*	0.4	0
G	0	1.0	0.6	0	0	0	1.8	0	*	0	0	0	*	0.4	0.1
L	0.9	1.0	0.3	0	0	0	0	0	*	0	0.5	0	*	0.4	0.4
F	0	0.5	0	0	0	0	0	0.7	*	0	0	0	*	0	0.4
D	0	0	0	0	0.6	0	1.8	0.7	*	0	0	0	*	0.4	0
			(K)	(L)		(D)		(G)					(K+L)		

Chi-squared=7.21, df=48, p>.99

Table 4.3b: Sexual approaches by male A.

Female I.D.	Week No.														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
K	0	0	0	0	0	0	0	0	*	0	0	0	*	0.4	0
G	0	0	0	0	0	0	3.4	1.5	*	0	0	0	*	0	0
L	0	0.5	0.3	0	0	0	0	0	*	0	0	0	*	0	0
F	0	0	0	0	0	0	0	0	*	0	0	0	*	0	0
D	0	0	0	0	0.6	0	0	0	*	0	0	0	*	0	0
			(K)	(L)		(D)		(G)					(K+L)		

Chi-squared=2.01, df=48, p>.99

Table 4.3c: Sexual approaches by male M.

(X) = X bore a litter during this week.
* = No observations were made in these weeks.

Tables 4.3a-d
Colony Study 2. Number of sexual approaches per hour per week by each male guinea pig to each adult female.

Female I.D.	Week No.														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
K	0	0	0	0	0	0	0	0	*	0	0	0	*	0	0.4
G	0	0	0	0	0	0	0	0.8	*	0	0	0	*	0	0
L	0	0	0	0	0	0	0	0	*	0	0	0	*	0	0
F	0	0	0	0	0	0	0	0	*	0	0	0	*	0	0
D	0	0	0	0	0	0	0	0	*	0	0	0	*	0	0
			(K)	(L)		(D)		(G)					(K+L)		

Chi-squared=0.09, df=48, p>.99

Table 4.3d: Sexual approaches by male I.

(X) = X bore a litter during this week.
* = No observations were made in these weeks.

Tables 4.3a-d (continued)
Colony Study 2. Number of sexual approaches per hour per week by each male guinea pig to each adult female.

animals one or two ranks below the actor, and only occasionally at higher-ranking animals (usually of the next rank up) or at an animal three ranks below. As a result of this tendency, only received threats showed a perfect negative correlation with dominance rank.

Total frequencies of sexual approaches and ano-genital sniff/licks were perfectly correlated with dominance rank, and attempted mounts and mounts only varied slightly from this pattern. The overall relationship between dominance rank and courtship behaviour by the males appeared to be largely due to the differences in the amount of courtship behaviours they showed to young guinea pigs. Courtship behaviours to adult females were performed almost equally often by the top two ranking males. This finding differs from that of Rood (1972), where the alpha males usually directed all their courtship at adult females, while the subordinates directed most at juveniles.

The results of this study show no evidence of preferential courtship of particular females by males i.e. no male-female associations of the kind described by Jacobs et al (1971) and Jacobs (1976). Also, courtship of females did not increase significantly throughout pregnancy to a peak just before parturition, as claimed by these authors. The present results cannot be explained in terms of the alpha male being the only associating male in the group, as the difference between him and the second ranking male in frequency of production of courtship behaviours to any adult female was proportionally quite small, and certainly nothing like so great as the difference found by Jacobs (1976) between associating and non-associating males.

4.2

COLONY STUDY 3.

4.2.1

Introduction.

This study was carried out in a similar manner, and essentially for the same reasons, as the preceding one. On this occasion, the categories of threats and sexual approach used in the previous study were subdivided into threats, displacements, rumbas and circles (see Table 4.1) so as to provide more detailed information on the agonistic and courtship behaviour of the colony males. Also, following behaviour by males and females was recorded. It was thought that examination of the results obtained for females following males might indicate whether or not the females showed any preference for the alpha male, or recognition of his status.

In the previous study, it was found that the frequency and nature of aggressive behaviours performed by males were closely related to their dominance rank, as also were (to a lesser extent) their courtship behaviours. However, no information was available to indicate whether the reduction in overall courtship activity with decreasing rank was due to a general behavioural inhibition (possibly caused by the effects of win/loss experience) or whether it was due to an aggressive reaction of the dominant male whenever a subordinate male showed signs of courting a female. The latter possibility was suggested by King (1956) who observed anecdotally that his adult males chased and bit younger males whenever the younger males attempted to court females.

In this study, a more sophisticated behaviour recording technique was used to make the sequential aspects of the data available for analysis. In this way, the behaviour of subordinate males immediately before being chased by their superiors could be determined. The sequential information was also used to find out whether any particular behaviour was performed by the colony males in order to induce females to follow them.

4.2.2

Method.

Subjects.

The animals observed during this study were those comprising the courtyard guinea pig colony between 12.5.81 and 10.6.81. Four adult males (H, M, I and N) and five adult females (Q, R, T, U and V) and their offspring were present during this period. Only three guinea pigs were born at this time and only one of these survived to maturity (see Table 2.3). Also, no young animals born before 12.5.81 were present. Four guinea pigs were conceived during this period, of which none survived to maturity.

Towards the end of this series of colony observations H, the oldest male, started to look very emaciated and ill. His death on 15.6.81 made continuation of this study impossible.

Procedure.

Observations of the sexual and aggressive behaviours of the guinea pig colony were made on 18 evenings from 12.5.81 to 10.6.81 (total observation time: 1100 minutes). The experimenter watched the colony in the manner described in Colony Study 2 (section 4.1). Observation periods took place between 1700 and 2100 hours and were never shorter than 25 or longer than 95 minutes. The frequency and length of observation periods were determined by the same factors as described for Colony Study 2 (section 4.1.2).

The aggressive and sexual behaviour patterns recorded in this study were those described in Table 4.1, with the exception of 'run away', which was not scored. Recordings were made directly onto an Apple II micromputer. For each observed behavioural interaction, the experimenter recorded the identities of the agent (initiator), behaviour and recipient. The current reading of the computer's clock was also stored alongside each interaction. This temporal data meant that interactions occurring in quick succession could be analysed as a sequence of behaviours. Computer hardware errors caused the loss of data from several observation sessions. These sessions are not included in the number of sessions and total observation times given above. As in Colony Study 2, sexual behaviour by adult males to young guinea pigs was categorised according to the identity of the adult male and the general term 'Young', as no distinction was made between the unnamed juveniles.

Treatment of Results.

The total numbers of intermale aggressive acts initiated and received by each adult male were plotted as histograms. Flow diagrams of each of the four aggressive behaviours (displace, threat, chase and bite) were drawn to show the number of times each male directed these behaviours at each other male.

The total numbers of sexual acts directed at adult females and at juveniles by each male were plotted as a histogram. Following behaviour was plotted separately to show both the number of times each adult male followed adult females and juveniles, and also the number of times each adult male was followed by adult females and juveniles.

Frequencies with which each male showed rumba, circle and ano-genital sniff/lick behaviours to each adult female were tabulated. Chi-squared analyses were performed on these data in order to determine whether or not a significant difference existed between the males in their relative frequencies of sexual behaviour to each female.

In order to investigate the order in which male guinea pigs perform aggressive behaviours to one another and sexual behaviours to females, the data were organised into sequences in which the same initiator interacted with the same recipient at least twice within 10 seconds. Tables and flow diagrams of behaviour sequence pairs were drawn up for both male-male aggressive behaviours and male-female sexual behaviours. Chi-squared tests (with Yates' correction for continuity) were performed on these data to find out whether the distribution of occurrence of behaviour sequence pairs differed from that expected by chance.

4.2.3

Results.

The histogram of initiated male-male aggressive behaviours (Figure 4.5) shows a perfect rank correlation between all four behaviours performed by the four males. Neither N nor H ever chased or bit any of the others, nor did H ever threaten another male. The order of frequency of initiation of aggressive behaviours was; M (who showed most male-male aggression), I, N and H.

The histogram of received male-male aggression (Figure 4.6) reveals that M received the smallest number of aggressive behaviours from other males. Only received displacement, however, was perfectly negatively rank correlated with the initiated aggressive behaviour scores. I received the largest number of threats, followed by H, N and M. N was chased the most, followed by I and H. M was never chased at all. Only I and N were ever bitten, N receiving slightly more bites than I.

As in Colony Study 2, the flow diagrams of inter-male aggression (Figures 4.7a-d) suggest the existence of a dominance hierarchy in this group of male guinea pigs, the rank order of which correlated perfectly with the rank order of the number of aggressive acts initiated. There are no missing relationships in the data for displacements and threats and both these behaviours show the same linear hierarchy. The probability of this occurring by chance is .006

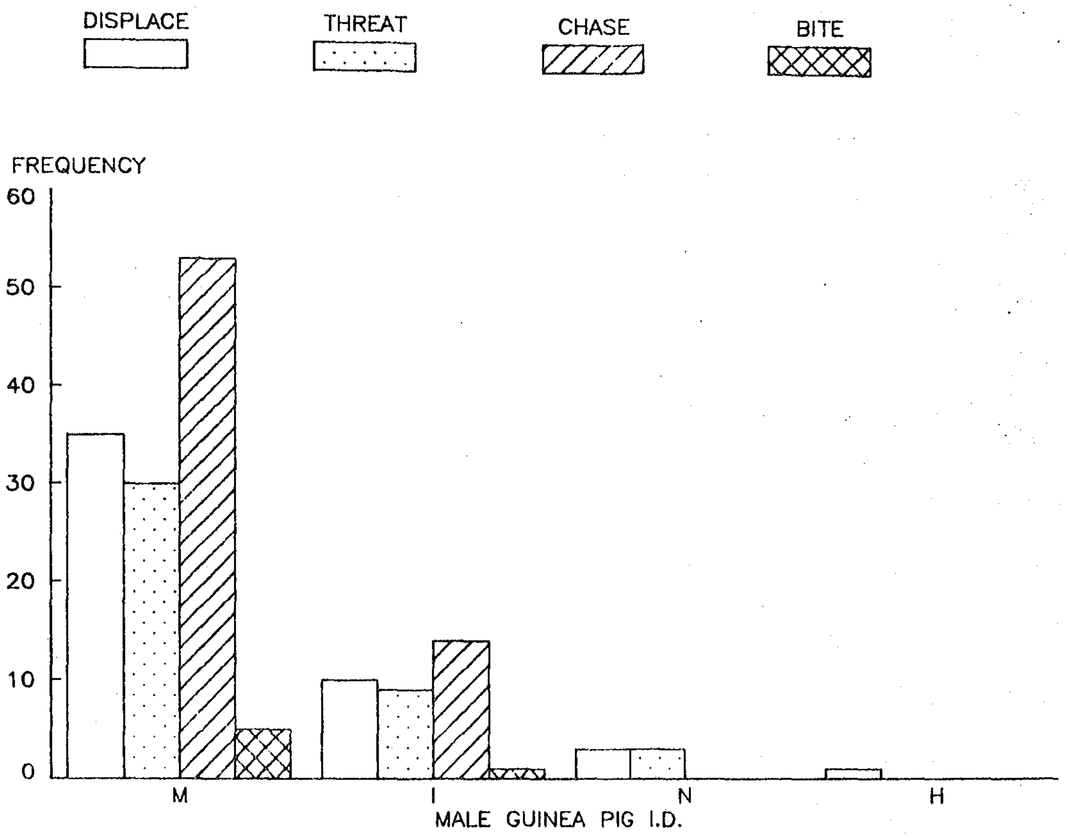

Figure 4.5
Colony study 3. Initiated intermale agonistic behaviour.

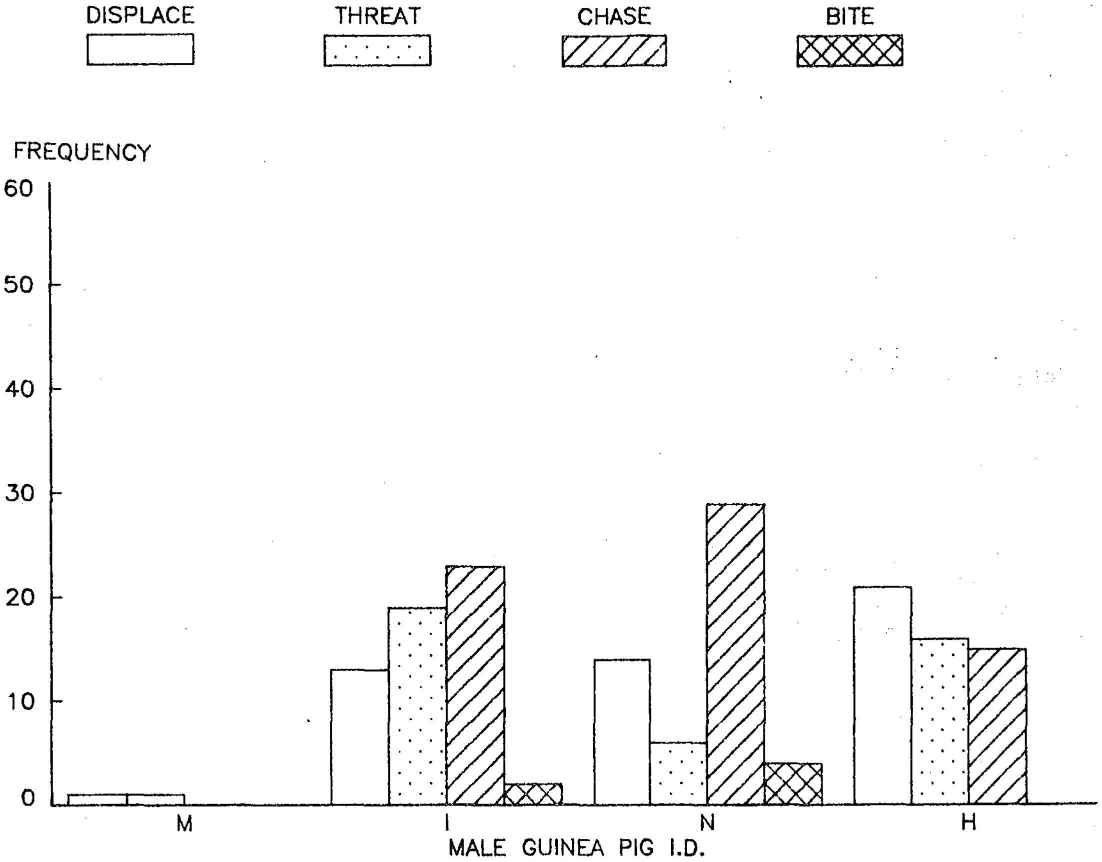

Figure 4.6
Colony study 3. Received intermale agonistic behaviour.

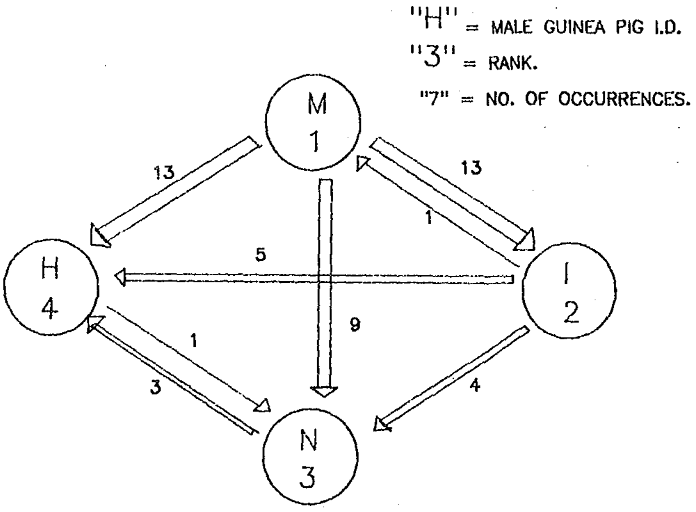

Figure 4.7a.
Colony study 3. Flow diagram of intermale displacements.

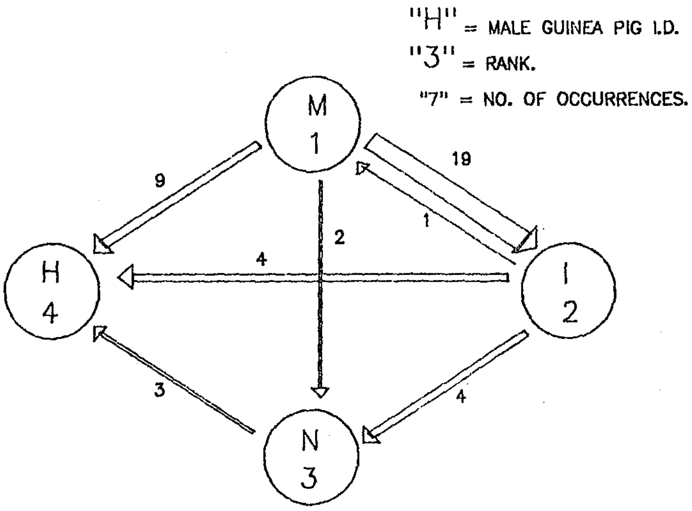

Figure 4.7b.
Colony study 3. Flow diagram of intermale threats.

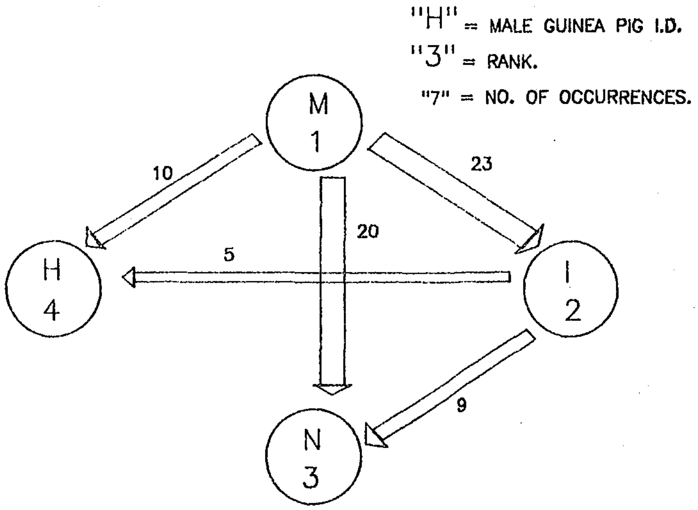

Figure 4.7c.
Colony study 3. Flow diagram of intermale chases.

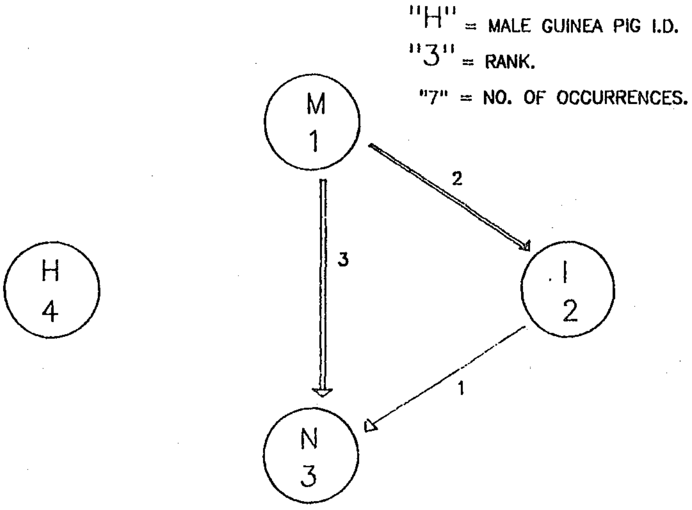

Figure 4.7d.
Colony study 3. Flow diagram of interrnale bites.

(see colony study 2). The observation that the data for chases and bites follow the same pattern (although there are missing relationships) further strengthens the evidence for the existence of a linear dominance hierarchy.

M, the alpha male, displaced and threatened all three lower ranking males, though he directed more of these behaviours at I and H than at N. I, the second most dominant, also displaced and threatened all three other males, but he only displaced and threatened the higher-ranking M once. N, ranking third, only displaced and threatened the omega male, H. H threatened no other male and only displaced N once. Thus no male displaced or threatened another male who was more than one rank higher than him in the hierarchy.

The pattern of dominance is shown particularly clearly in the flow diagram of chase behaviours (Figure 4.7c). M chased I most often, N next most often, and H least often. I chased N more often then he chased H and never chased M. The pattern for bites is similar, but in this case neither M nor I ever bit H.

Thus the alpha male was responsible for nearly all the chasing and biting between the colony males, and only the top two males in the hierarchy chased or bit other males at all. The second ranking male, I, never chased or bit the alpha male, M. As in Colony Study 2, it seems that a male guinea pig's dominance status is shown not only by the direction of his aggressive behaviour towards other males, but also by its nature and overall quantity.

During the observation periods, the experimenter gained the impression that chasing between males often occurred shortly after the chased male had shown courtship behaviour towards a female. In order to test whether this impression was borne out by the facts, the total number of non-alpha courtships preceding chases by the alpha male was scored in the following manner. If the (to be) chased male showed courtship towards a female in either of the two interactions (i.e. within 20 seconds) preceding the chase, then this was counted as a positive score.

Only the top two males in the hierarchy, M and I, chased other males so data were compared between these two animals only. Taking into account the fact that no sexual behaviour was ever initiated by females and that no attempted or actual mounting was scored for males during this study, the expected frequencies of these situations were calculated as follows:

$$\text{Expected frequency} = \frac{g}{((a \times b)+(c \times d))} \times f$$

where
No. of females (a) =5
No. of males (c) =4
No. of non-sexual behaviours (b) =5
No. of behaviours (excluding mounts and attempted mounts) (d) =8
Observed no. of chases (f) =53 (for male M)
=14 (for male I)
No. of sexual behaviours (g) (excluding mounts and attempted mounts) =3

The observed and expected results obtained are shown below.

	Observed	Expected
Male M	20	2.86
Male I	2	0.76

Chi-squared (with Yates' correction) =82.84, df=1, $p<.001$.

Thus it seems that the alpha male (M) chased males who had just shown courtship behaviour significantly more often than would have been expected by chance. The second-ranking male (I), on the other hand, showed such chasing behaviour only slightly more often than the chance level.

Figure 4.8 shows that the omega male, H, exhibited hardly any sexual behaviour at all, but the alpha male, M, rather than showing more sexual behaviour than any of the others, only exceeded I's and N's sexual behaviour scores in the number of times he circled adult females. Both I and N rumba-ed and ano-genital sniff/licked adult females and young more often than did M. No attempted mounts or mounts were observed during the entire observation period. It is notable that, although both I and N were quite sexually active towards the juveniles, M directed almost no sexual behaviour to them. H, as the omega male, might not have been expected to show much sexual behaviour. His almost total lack of interest in females, however, was probably due to illness rather than rank.

Tables 4.4a-c show the frequencies with which each male rumba-ed, circled and ano-genital sniff/licked each adult female. (No attempted mounts or mounts were recorded.) The results of chi-squared tests (with Yates' correction for continuity) on these data are given beneath the tables. The null hypothesis that there was no difference between the males in their relative frequencies of showing sexual behaviour to the different females was accepted for all three behaviours. This suggests that no associations between males and females existed.

Tables 4.5a-d show the number of rumbas per hour per week

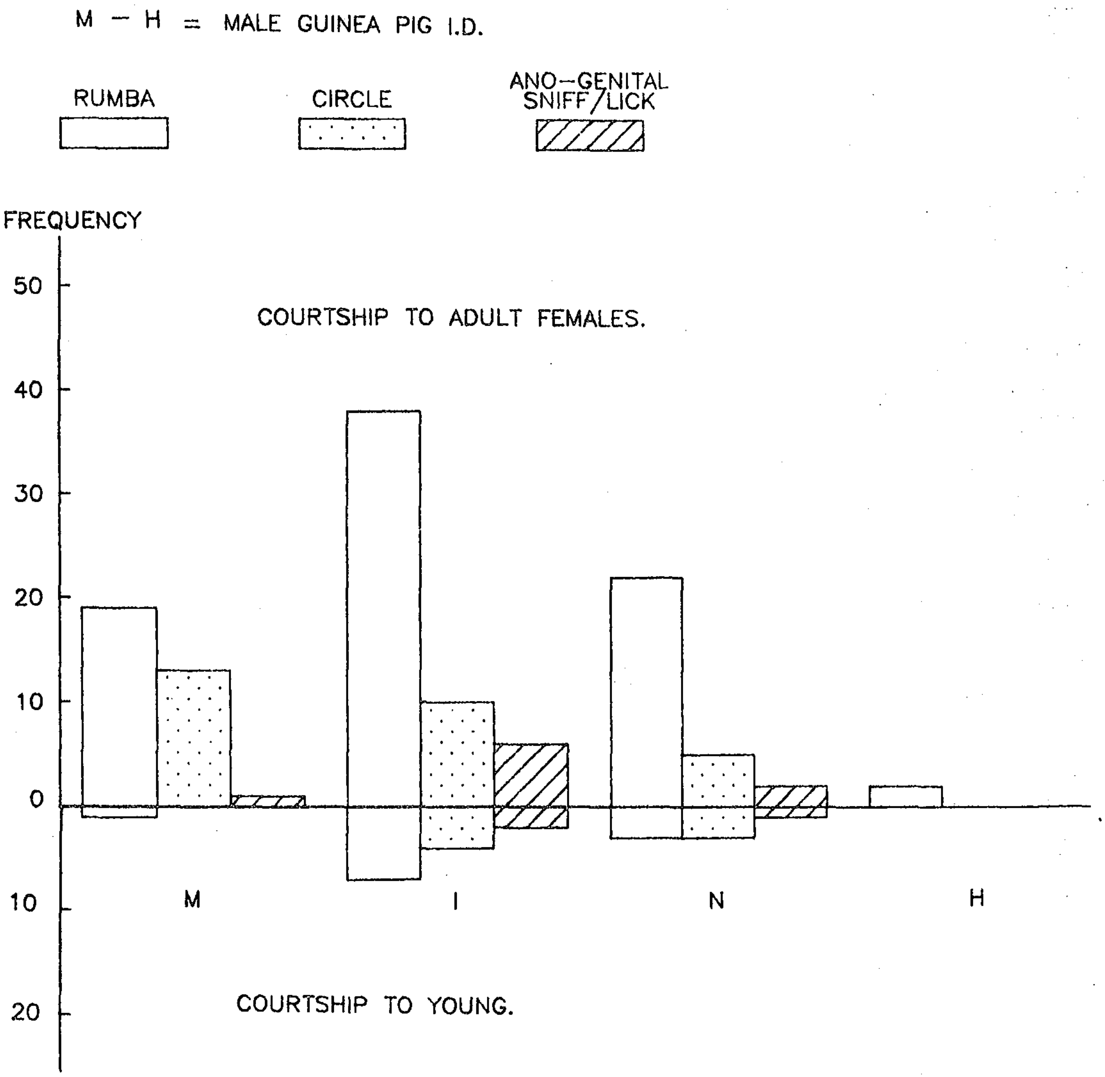

Figure 4.8
Colony study 3. Male courtship behaviour.

Female recipient	Male initiator M	I	N	H
Q	0	5	4	2
R	10	14	9	0
T	2	4	2	0
U	3	9	4	0
V	4	6	3	0

Chi-squared=6.11, df=12, p>.9

Table 4.4a: Rumba.

Female recipient	Male initiator M	I	N	H
Q	4	2	3	0
R	3	3	0	0
T	3	2	1	0
U	1	2	1	0
V	2	1	0	0

Chi-squared=1.43, df=12, p>.99

Table 4.4b: Circle.

Female recipient	Male initiator M	I	N	H
Q	1	1	0	0
R	0	4	1	0
T	0	0	0	0
U	0	1	0	0
V	0	0	1	0

Chi-squared=1.03, df=12, p>.99

Table 4.4c: Ano-genital sniff/lick.

Tables 4.4a-c
Colony study 3. Frequencies of male courtship behaviours to adult females.

Female I.D.			Week No.			
	1	2	3	4	5	6
Q	0	0	0	0	0	*
R	0.9	0.8	0	0.8	0	*
T	0	0	0	0.5	0	*
U	0.6	0.2	0	0.3	0	*
V	0	0	0	0.5	0	*
		(R)				(U)

Chi-squared=0.96, df=16, p>.99

Table 4.5a: Rumbas by male M.

Female I.D.			Week No.			
	1	2	3	4	5	6
Q	0.3	0.5	0.2	0.3	0	*
R	0	1.5	1.1	0.5	0	*
T	0	0.5	0.2	0.3	0	*
U	0	0.6	0.5	0.5	1.4	*
V	0	0.5	0	0.5	0	*
		(R)				(U)

Chi-squared=1.64, df=16, p>.99

Table 4.5b: Rumbas by male I.

Female I.D.			Week No.			
	1	2	3	4	5	6
Q	0	0.4	0.2	0.3	0	*
R	0.3	1.8	0	0	0	*
T	0	0	0	0.5	0	*
U	0	0	0	1.1	0	*
V	0.7	0	0	0.3	0	*
		(R)				(U)

Chi-squared=2.66, df=16, p>.99

Table 4.5c: Rumbas by male N.

* = No observations were made in this week.
(X) = X bore a litter during this week.

Tables 4.5a-d
Colony Study 3. Number of rumbas per hour per week to adult females.

Female I.D.	Week No.					
	1	2	3	4	5	6
Q	0	0	0.5	0	0	*
R	0	0	0	0	0	*
T	0	0	0	0	0	*
U	0	0	0	0	0	*
V	0	0	0	0	0	*
		(R)				(U)

A Chi-squared test cannot be performed on this data.

<u>Table 4.5d</u>: Rumbas by male H.

* = No observations were made in this week.
(X) = X bore a litter during this week.

<u>Tables 4.5a-d</u> (continued)
Colony Study 3. Number of rumbas per hour per week to adult females.

(starting from 12.5.81) that each adult male made to each adult female. As in Colony Study 2, the Chi-squared tests on these data (see below tables) revealed no interactive effect between weeks and females on the number of rumbas given by any of the males. Once again it seems that there is no significant increase in rumba-ing to females around parturition.

From Figure 4.9 it can be seen that I was not only the most sexually active of the four male guinea pigs, but the one who followed adult females and young most often. M and N showed equal amounts of following behaviour, but in M's case most of it was directed at adult females, whereas N followed adult females and young almost equally often. H never followed another animal.

The pattern of results for males being followed was different, however (Figure 4.10). Young animals were never observed to follow the males, and the adult females never followed H, and rarely I or N. The alpha male, M, was quite frequently followed by the females. These frequencies of being followed are significantly different from those that would be expected by chance (Chi-squared=28.26, df=3, p<.001).

Both circling to and being followed by adult females showed positive rank correlations with aggressive behaviour scores and with each other. These findings suggest that the adult females in the colony actively followed the alpha male in preference to the other males. It would appear, from the data collected, that this judgement by the females cannot have been made on the basis of the amount of sexual, or at least courtship (i.e. outside oestrus) behaviour

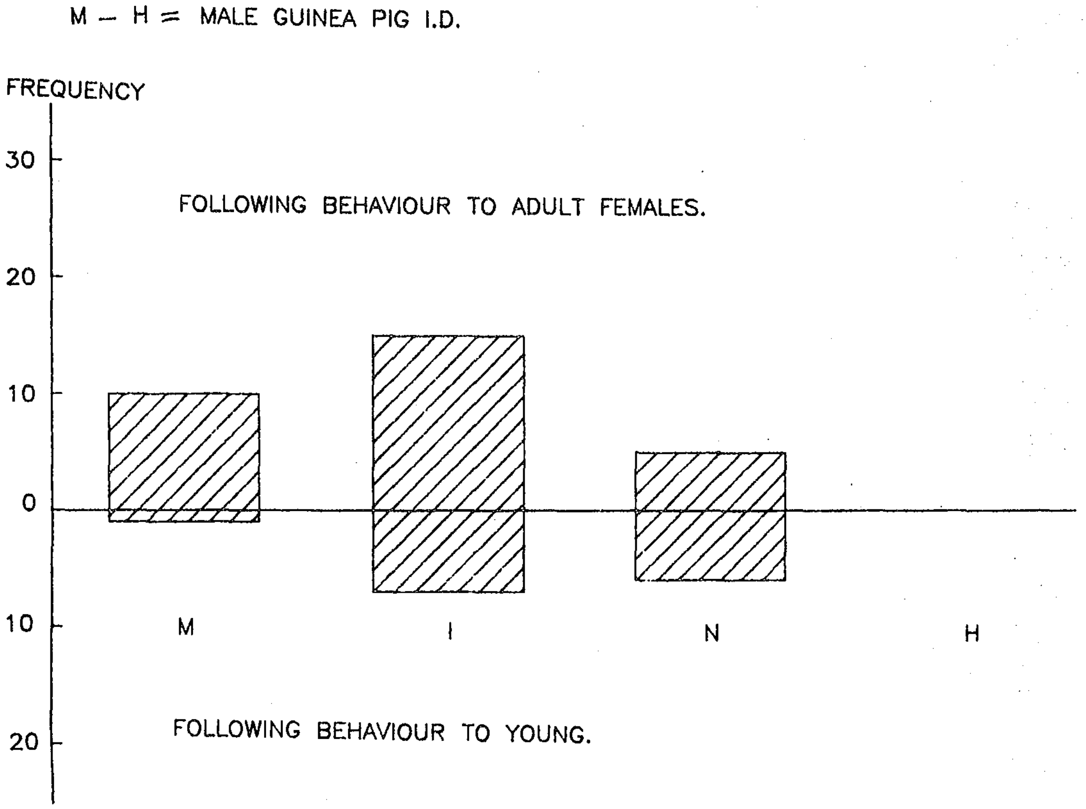

Figure 4.9
Colony study 3. Following behaviour by males.

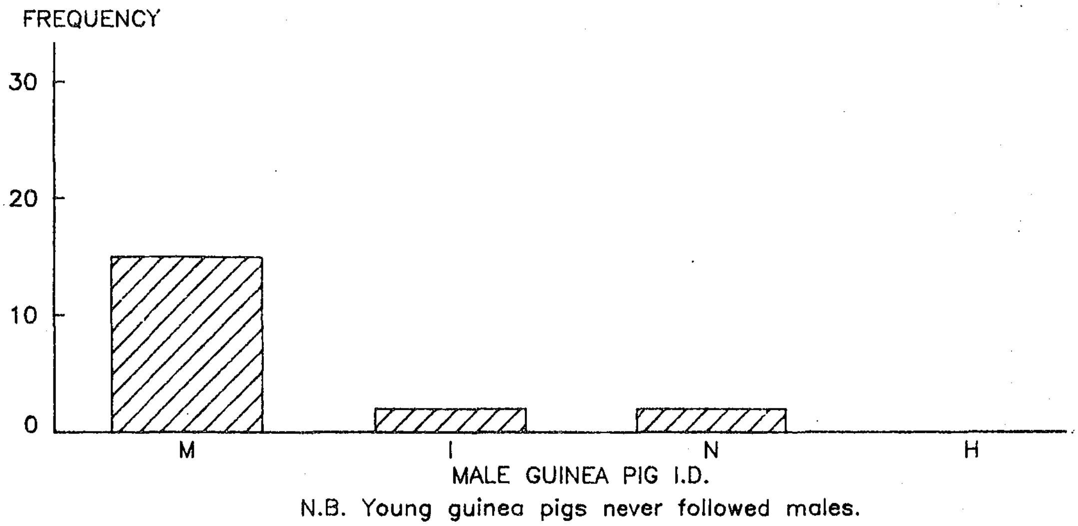

Figure 4.10
Colony study 3. Following behaviour by adult females to males.

they received from each of these males. Table 4.6 shows the type of behaviour (if any) that each male had initiated or received immediately before being followed by an adult female. No male had received aggression from a male or a female before being followed, but with this negative exception, there seems to be no particular preceding behaviour which encouraged a female to follow a male.

The frequencies of male-male aggressive and male-female sexual behaviour sequence pairs are given in Tables 4.7 and 4.8 and the flow diagrams of these sequence pairs in Figures 4.11 and 4.12. The Chi-squared test on aggressive behaviour sequence pairs showed that the distribution of occurrence of these paired behaviours was significantly different from that expected by chance. The Chi-squared test on sexual behaviour sequence pairs, on the other hand, showed that their frequency distribution did not differ significantly from the chance level. Thus it seems that the order in which a male guinea pig performs aggressive behaviours to another male may be more rigidly predetermined than the order in which he performs sexual behaviours to females.

4.2.4

Discussion.

The same strong evidence for the existence of a male agonistic dominance hierarchy in the colony was found in this study as in Colony Study 2. This study also showed the same relationship between dominance rank and nature and frequency of performance of aggressive behaviours. As in the previous study there was a trend for most aggressive behaviours to be directed at the two animals immediately

Preceding behaviour	Male ID M	 I	 N	 H
Aggression to a male		T		
Aggression to same female	T			
Aggression to another female	VT			
Courtship behaviour to same female	Q	V	Q	
Courtship behaviour to another female	Q			
Following same female	VT			
Following other female	V			
Followed by same female	T			
None	VVTTQ	V	V	

n.b. Letters in table represent female IDs.
Each letter depicts one occurrence.

Table 4.6
Colony study 3. Behaviour initiated or received by each male guinea pig immediately before being followed by an adult female.

First behaviour	Second behaviour			
	Displace	Threat	Chase	Bite
Displace	1	0	3	0
Threat	13	0	5	0
Chase	0	0	5	4
Bite	0	0	1	0

Chi-squared=48.60, df=9, p<.001

Table 4.7
Colony study 3. Frequency of male-male guinea pig agonistic behaviour sequence pairs.

First behaviour	Second behaviour			
	Rumba	Circle	Follow	Ano-genital sniff/lick
Rumba	3	2	8	5
Circle	0	2	3	0
Follow	0	1	0	2
Ano-genital	0	0	2	0

Chi-squared=3.63, df=9, p>.9

Table 4.8
Colony study 3. Frequency of male-female courtship behaviour sequence pairs in guinea pigs.

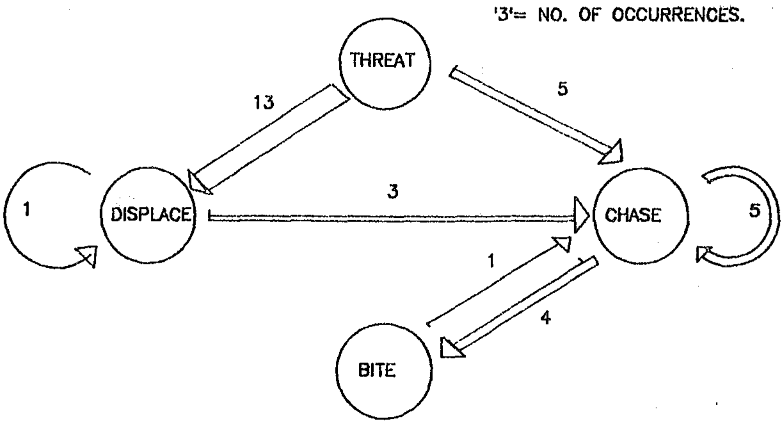

Figure 4.11
Colony study 3. Flow diagram of intermale agonistic behaviour sequence pairs.

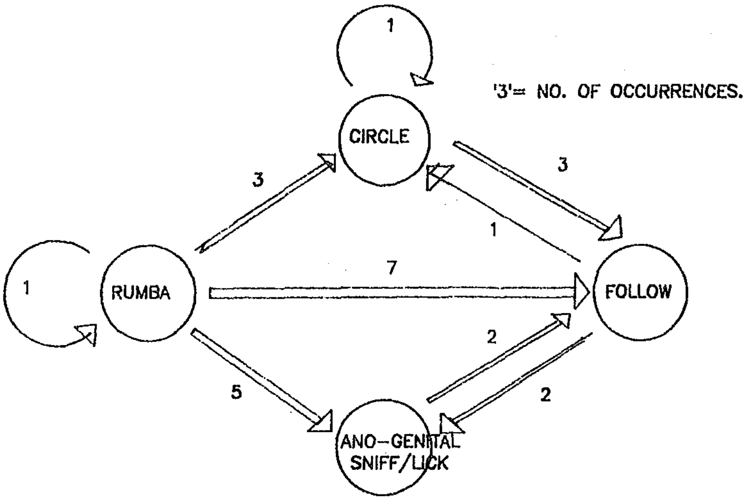

Figure 4.12
Colony study 3. Flow diagram of male to female courtship behaviour sequence pairs.

subordinate to the actor. The only received behaviour which correlated perfectly (negatively) with dominance rank was displacement. This finding was reminiscent of the negative correlation between rank and 'threats' found in the previous study. Thus it appears that the negative correlation between rank and 'threats' in colony study 2 was probably caused by the inclusion of displacement in this category at that time.

The relationship observed between dominance rank and courtship behaviours in colony study 2 was not found in the present study. Very few young animals were in the colony during the present study, so very little courtship to young was seen. The only aspect of courtship behaviour which correlated with rank was circling to adult females. Both the second and third ranking males had higher frequencies of rumba and ano-genital sniff/lick than did the alpha male. These results are very different from those reported by Rood (1972). As in Colony Study 2, the omega male was the least sexually active as far as courtship behaviours were concerned, though in this study he was very old and weak. His limited courtship behaviour could have been due to his illness rather than to aspects of his rank. It is possible, considering his former alpha male status (see Colony Study 2), that H's low rank was due to his illness. Alternatively, he might have become ill after being deposed from his alpha position (Rood, 1972).

Despite these observations regarding the lack of correlation between dominance rank and courtship in this study, it was neverthless found that the adult females followed the alpha male significantly more often than they followed any of the other males. No observable incitation to follow on the part of the male preceded this behaviour.

The results of the sequential analysis of behaviours preceding chases show that courtship behaviour by subordinate males was a significant factor in inciting aggression by the alpha male and, to a lesser extent, by the second ranking male. However, while this might have partially explained the pattern of results obtained for courtship in Colony Study 2, it does not seem to have prevented the second and third ranking males from showing more courtship than the alpha male in this study. Also, the omega male showed almost no courtship and yet was chased quite frequently. In this case, however, it must be remembered that the omega male was a deposed alpha. In colony study 2, the omega male was a young animal who had not yet risen in rank. These two situations could lead to somewhat different behaviour towards the omega by the other males. If the deposition was recent (an unknown factor in colony study 3), the omega male might still have been chased considerably by the former second-ranking male (now alpha) as a result of the latter's recent experiences of severe fighting with the deposed animal.

Thus it appears that the relationship between male guinea pig aggressive behaviours/dominance rank and courtship behaviour may be more complicated than that suggested by Rood (1972) and Berryman (1978). Once again, the results of this study showed no evidence of male-female associations (Jacobs et al, 1971; Jacobs, 1976). However, females were observed to follow the alpha male in preference to other males.

4b

General Summary.

A male dominance hierarchy was found in both these studies of the semi-natural colony of guinea pigs. This hierarchy was shown by the predominant direction of all the intermale agonistic behaviours recorded.

A perfect correlation between male dominance rank and frequency of all the agonistic behaviours was observed. Of the agonistic behaviours received, however, only frequency of displacement correlated negatively with rank. Most aggressive actions were directed at the two males ranking immediately below the actor (especially at the next rank down), with considerably fewer directed at the rank above. Aggression to an animal more than one rank higher up the hierarchy than the actor was very rare. The aggressive acts performed by the two highest ranking males (especially the alpha male) were more often of a serious nature than were those of the lower ranking males.

When agonistic acts were performed in a sequence, they showed a very definite pattern of progression. Thus a threat always led either to a displacement or to a chase, and was never preceded by a chase or a bite. Similarly, a displacement was never preceded by a chase or a bite, and always led to chasing or repeated displacement. Bites were only preceded by chases.

In Colony study 3, it was found that a high proportion (37%) of chases by the alpha male were preceded by courtship behaviour to a female by the (to be) chased male. The same was true, to a lesser extent, of chases performed by the second ranking male.

The frequency of overall male courtship was correlated with male dominance rank in Colony study 2, but not in Colony study 3. In Colony study 2, this appeared to be largely due to the high frequency of courtship of young animals, especially by the alpha male. Very few young animals were present in the colony during Colony study 3, so little courtship to juveniles was seen at this time. The only aspect of courtship to adult females which was apparently closely correlated with male dominance rank in both studies was circling.

The sequential order with which courtship behaviours were performed was not as rigidly patterned as that observed for agonistic behaviours. However, it was notable that a rumba was never preceded by any courtship behaviour other than itself.

In Colony study 3, it was found that the alpha male guinea pig was followed significantly more often by adult females than were any of the other males. Young animals were never observed to follow adult males. Males sometimes followed females while courting them, though the frequency of performance of this behaviour was not found to be correlated with male dominance rank.

Chapter Five

DISCUSSION OF THE COLONY STUDIES.

The guinea pigs were found to have a male dominance hierarchy, thus replicating the results of Kunkel and Kunkel (1964), Jacobs et al (1971), Rood (1972), Coulon (1975a), Jacobs (1976) and Berryman (1978) in this respect. This hierarchy fulfilled Hinde's (1979) criterion of having 'structural meaning' by being consistent across several correlated behaviours. Indeed, it appeared to be consistent across all the agonistic behaviours recorded.

The observation that the frequencies of both initiated and received displacement correlated perfectly with the male dominance rank order strongly suggests that the animals were able to assess each other's relative dominance without a fight. Thus displacement occurred very often when a dominant male approached a subordinate or simply walked near him. That some kind of cue assessment of relative dominance ('resource holding power'; Parker, 1974) was taking place is further suggested by the observation that most aggression was observed between closely ranked males. This would be expected according to Parker's (1974) and Barnard and Burk's (1979) theories of cue assessment, whereby aggression only occurs if the perceived disparity between the animals is small. Thus a male (B) ranking immediately below another male (A) may be expected to hold his ground rather than run away (i.e. be displaced) when A approaches him. In this situation, a threat given by A to B might represent a sufficient increase in A's RHP cues (as perceived by B) for B to leave, or otherwise submit, at that point. Alternatively, B may continue to hold his ground (or even threaten A back), so that escalated conflict (i.e. chasing and biting) might result before the disparity in cue quality between the two animals (as perceived by B) becomes great enough for the fight to end. Thus the subordinate animal is normally expected to be the one to end an agonistic encounter, so supporting Rowell's (1974) and Bekoff's (1977) suggestion that submission is more important than dominance in the formation and maintenance of hierarchies.

Occasions when the result of a fight is contrary to the normally observed dominance relationship between two animals could be explained as being due to a temporary change in cue quality (perceived RHP) caused by such factors as an animal's waking/sleeping state, minor illness or fatigue. It could even be due, sometimes, to a temporary misperception of cues by one or both animals.

The exact nature of cues used by male guinea pigs in their assessment of relative dominance is not known, though it would appear from this study that they may be at least partly behavioural. Thus a threat is seen as a ritualised aggressive behaviour constituting a behavioural cue and also reducing the likelihood of a damaging escalated fight occurring between unevenly matched individuals (Parker, 1974). The observed sequential order of agonistic behaviours also generally supports the above theory. The occasional occurrence of a chase immediately after a displacement could be due to the displaced animal not having moved sufficiently far enough away from his superior to have ceased to be an aggression-inducing stimulus to him.

In these studies, it was observed that the aggressive acts performed by the two top ranking males, and especially the alpha male, were more often of a serious nature (i.e. chases or bites) than were those performed by the third and fourth ranking males. A possible explanation of this phenomenon could be that of 'confidence' (Barnard and Burk, 1979), whereby a male's behaviour is affected by his relative experience of winning and losing in previous agonistic encounters (see section 1.1.2). Since the two top ranking males in the present colony had had more recent experience of winning relative to losing in agonistic encounters than had the lower ranking males, they would be expected to have greater agonistic confidence i.e. to be more willing to allow fights to escalate, than would the other males.

The above 'confidence' hypothesis implies that the fiercest fights would be expected to occur between the alpha and beta males, as was indeed the case in the present colony. Such behaviour can be justified in functional terms since the benefit of winning a fight between the two top ranking males is much greater (assuming that the alpha male has a considerable reproductive advantage) than that of winning a fight between two low ranking males. Thus, in terms of Parker's (1974) theory that fights should be avoided or escalated depending on the perceived relative value of the potential resource to each animal, the value of the resource to be gained is very great when the top males fight and so is worthy of the risk of injury in escalated fighting.

The observation that male guinea pigs frequently court anoestrous females (Kunkel and Kunkel, 1964; Jacobs et al, 1971; Rood, 1972;

Jacobs, 1976; Berryman, 1978) has led to the belief that this behaviour must have some advantageous function, probably with respect to male reproductive priority. One possible explanation for such a relationship between courtship and reproductive priority could be that male courtship of a female leads to the female spending more time close to the male (or vice versa) so making it more likely that he will be close to her and thus first to copulate when she comes into oestrus.

From their observations of several densely populated guinea pig colonies, Jacobs et al (1971) and Jacobs (1976) claimed that this was indeed the case. They found that associations appeared to be formed such that each female was courted most by one male, and this male had reproductive priority on the day of oestrus.

The relationship between courtship and reproductive priority observed by Rood (1972) was more straightforward. He noticed that in his colony the two top ranking males in the dominance hierarchy rumba-ed the most to females, and the alpha male usually copulated first when a female came into oestrus (thus making it probable that he would sire all or most of her litter; see section 1.2.5.2.1). The alpha male not only showed most overall courtship (as measured by rumbas), but he also directed most of this at adult females, whereas subordinate males usually courted juveniles. Berryman (1978) similarly observed that the amount of purring (an aspect of the rumba) by males in her colony was closely related to their dominance rank.

In the light of the above observations, it was perhaps surprising that a similar relationship was not immediately apparent in the present colony. No evidence to support Jacobs et al's (1971) and Jacobs' (1976) theory of associations between males and females was found either in terms of social affinity at resting places or of preferential courtship relations. It may be significant that Jacobs and his co-workers found their most compelling evidence for associations in colonies of guinea pigs that were not only densely populated, but also contained large numbers of males (10-15) and females. Such conditions would be unlikely to occur in the wild (Rood, 1972) and so may have led to a state of affairs whereby the alpha male could no longer maintain his normal functional role in the group.

The results of the present studies show a closer approximation to those of Rood (1972) and Berryman (1978) than to Jacobs et al's (1971) and Jacobs' (1976) as far as courtship is concerned. The relationship found between dominance rank and courtship was, however, weak and variable, being more consistent at the bottom of the hierarchy than at the top. In Colony study 2, the two top ranking males courted adult females much more often than did the two lower ranking males, but they also courted young animals a great deal. In Colony study 3, the second and third ranking males were both more active than the alpha male in courting adult females in all respects bar that of circling.

The consistent observation that very low ranking males do not court females very often could indicate that win/loss experience influences courtship as well as agonistic behaviour. Functionally, this would seem quite reasonable, as courtship incites potentially damaging attack by the top ranking males (especially the alpha male). Also, there is no evidence to suggest that a paucity of courtship behaviour prevents a low ranking male from taking part in a mating chase, even though his chances of copulatory success may be small. The effect of win/loss experience on courtship behaviour does not appear to be overriding, however, as the frequency of courtship by middle ranking males is still quite high in all the studies.

The observation in the present colony that the adult females showed a definite tendency to follow the alpha male in preference to the other males is a strong indication that they could distinguish the alpha male's dominance status, despite the fact that the only courtship behaviour they received more often from him than from the other males was circling. This suggests that the female guinea pigs in a colony may be able to assess a male's dominance status by using the same physical and behavioural cues that the males use to assess each other's relative status. It is possible that courtship behaviour (especially circling ?) may provide additional cues in this process, but that these are not necessarily the most important. The advantage in reproductive terms to the alpha male of being followed by females is obvious, as it increases his chances of proximity to them during oestrus. This would be particularly important under more natural, less densely populated conditions (Rood, 1972). It is also possible to suggest a functional advantage to the female in this behaviour. Closer proximity to the alpha male than to the other males would a) increase her chances of being impregnated by a healthy male early in oestrus, and b) reduce the possibility of failure of fertilisation during oestrus through involvement in an aggressive mating chase before any complete copulations had taken place.

The observation that females did not show preferential resting association with the alpha male in the colony huts does not necessarily contradict the above hypothesis because of the limitation of availability of comfortable resting sites (especially during the winter). This may have forced the animals to rest together with little regard for other factors (except that the weakest individuals ended up in the less desirable hut). In such a confined space as a hut, any courtship by a subordinate male while the alpha male was present would be expected to have resulted in immediate fierce attack. Thus subordinate males probably had to act very submissively in this situation in order to avoid either injury or having to relinquish their protection from the weather.

In conclusion, the present studies have confirmed previous reports of male guinea pig dominance hierarchies, but have failed to show the consistent very close relationship between dominance rank and courtship behaviour that has previously been claimed (Rood, 1972; Berryman, 1978). It has been suggested from the current studies that male and female guinea pigs are able to assess male status using a variety of cues, some at least of which appear to be behavioural. Courtship behaviours may constitute some of the cues used by females (and also possibly by males) in this process, though they do not seem likely to be of overriding importance in determining reproductive advantage, as has been suggested by Jacobs et al(1971) and Jacobs (1976).

The present studies also indicated that a male guinea pig's agonistic behaviour is affected by his previous experience in agonistic encounters such that his willingness to avoid or escalate future encounters is altered. This type of experience might also have some effect on his future frequency of courtship behaviour, thus reducing a subordinate's risk of being attacked by the alpha (or other high ranking) male.

The colony of guinea pigs established in the Psychology department courtyard had the advantage of not being very densely populated, with areas of land per animal being about as large as in any previous enclosed colony. However, it also had the disadvantage of containing quite a small number of animals, thus reducing the amount of data available on interactions between different pairs of individuals. Ideally, a future semi-natural study would involve more animals housed in an even bigger enclosure so that population density was not significantly increased. This would, of course, bring about greater observation problems, though these would not be insurmountable.

A major criticism of the present studies must be that no data were obtained regarding the paternity of litters, or even of copulation priority at oestrus. Thus the dominance hierarchy is assumed to function to allocate reproductive priority, though this function has not actually been proved in genetic terms. Instead, it was assumed that the animals in this colony behaved in the same way as had been observed in previous studies such that the alpha male copulated first and so probably sired all, or most of, the young.

During informal observations of the colony (outside the observation periods), only one mating chase was briefly witnessed, and this involved the males running in and out of one of the huts in which the oestrous female had obviously just given birth. Since no observation could be made of behaviour inside the huts, it was impossible to record details of mating behaviour. Thus, if such behaviour were to be observed in a future colony, it would be necessary to ensure that all the favoured resting places were clearly visible. Another problem with observing mating behaviour was that most births took place at night (as revealed by the discovery of newborn young during the routine colony check the following morning). To overcome this, all-night watches of the colony would be required, with arrangements made for subdued red lighting of the enclosure.

No precise information was available from the present colony studies as to what causes male guinea pigs to form a dominance hierarchy, nor whether or not innate factors are involved in determining an animal's potential rank. The close link between the alpha male's chasing behaviour and courtship by other males suggests that the presence of females may be of some importance in causing dominance relationships to be developed. Also, the observation that rank is not constant but changes over time (cf. comparison of the ranks of individual males in Colony studies 2 and 3) suggests that innate qualities are not of paramount importance. However, it is possible that some animals are more sexually and/or aggressively active than others from an early age, and so tend to rise higher or more quickly up the hierarchy. It is noticeable that male M, although very young (1-4 months old) during Colony study 2, had already succeeded in dominating I, who was one month older than him. M subsequently rose to alpha status by Colony study 3.

This study raises the following questions with regard to the cause and function of male guinea pig dominance. a) Is the presence of females necessary for the formation of a dominance hierarchy among male guinea pigs? b) If a hierarchy is formed in the absence of females, does it differ qualitatively from that found when females are present? c) How does the addition or removal of females affect the social structure of an established group of males?

Chapter 7 attempts to answer these questions, and also investigates the effect of early social isolation on subsequent intermale behaviour. In addition it examines whether aspects of pre- and post-grouping courtship (with and without the other members of the group being present) has any predictive value in determining future dominance rank, and/or whether it is at all representative of present dominance rank. It was thought that the results obtained might shed more light on the question of whether low ranking males are inhibited from showing much courtship by being attacked by high ranking males, or whether their 'confidence' from win/loss experience is of greater importance in the reduction of courtship behaviour.

Riss and Goy (1957) had previously found that copulatory performance in an individual mating test (as opposed to courtship behaviour in a courtship test) did not show any correlation with intermale aggressiveness within their all-male group. However, mating performance in a group test was closely correlated to intermale aggression. Thus, if the results of the present study showed a similar trend, it could be said that the observed variability of sexual behaviour (in terms of both courtship and copulation) in grouped male guinea pigs is not internally controlled by a measure related to 'confidence', but rather is due to active inhibition of the behaviour of low-ranking males by their superiors. Alternatively, it might be found that courtship does appear to be controlled internally, while copulation is not.

Chapter Six.

A REVIEW OF EARLY EXPERIENCE STUDIES ON RODENTS.

The discovery of critical periods for the action of hormones in the physiological development of embryos and neonates led to the suggestion earlier this century that similar critical periods may exist with regard to the development of behaviour (see Scott, 1962 and King, 1968 for reviews of the early literature). In embryology, critical periods for hormonal effects on a system or organ were found to coincide with the time at which that structure was developing most rapidly. Thus, it is generally thought that any critical periods for effects of experience on behaviour are likely to be found during periods of rapid behavioural development i.e. early in life.

Both social and non-social early experiences have been investigated in the search for critical periods in the development of behaviour in animals. Non-social experiences have included handling (Denenberg, 1968; Schaefer, 1968), shock (e.g. Denenberg, 1968), unfamiliar environment (Levine and Lewis, 1959), enriched versus impoverished environments (Morgan, 1973; Will et al, 1979; Roeder et al, 1980), and tunnel versus open caging (Catlin, 1981).

The present studies are only concerned with the effects of social experiences on social behaviour. Most of the previous work on the effects of social experience has concerned isolation, though single-sex versus mixed housing, the pre-weaning presence or absence of the mother (Harper, 1966; Eibl-Eibesfeldt, 1956), and the presence or absence of adult males during early life (Levinson et al, 1979) have also been investigated.

Many of the earlier studies of isolation have looked at its effects on non-social rather than social behaviour. Despite this, these studies are reviewed below, as it is thought that their results may be pertinent to social as well as non-social behaviour.

Experiments on the non-social behavioural effects of isolation have yielded a variety of interesting results. The continuous isolation of rats from an early age has been found to slow down reversal learning (Morgan, 1973), alter incentive motivation and behavioural inhibition (Morgan et al, 1975; Morgan and Einon, 1976), slow down approach to novel food (Einon et al, 1981), increase behavioural variability in a learning task (Watson and Livesey, 1982) and increase gregariousness (Latané et al, 1970; Monroe and Milner, 1977). Similar experience slowed down the approach to novel food in mice (Einon et al, 1981), reduced gregariousness in guinea pigs (Nagy and Misanin, 1970), and increased open field activity and object investigation in ferrets (Chivers and Einon, 1982).

A further line of study has investigated whether or not isolation effects can be reversed by subsequent social experience. Einon and Morgan (1977) found that isolation of rats at any age would increase the latency of emergence into an open field, but that later housing in social groups would restore emergence latency to normal (i.e. to that of animals with no isolation experience). However, rats isolated from 25 to 45 days of age were found to show persistent increases in open field activity and object contact, even after 135 days of social housing (Einon and Morgan, 1977; Einon and Morgan, 1978; Einon et al, 1981). Partial isolation (one hour of social contact per day) during the same early period did not have this effect. Changes in the activity of early isolated mice (22 to 45 days), gerbils (22 to 45 days) and guinea pigs (12 to 35 days) did not persist after subsequent social housing (Einon et al, 1981).

The period between 22 and 45 days of age coincides with the peak period for social play in rats (Baenninger, 1967; Panksepp, 1981; Einon et al, 1981; Humphreys, 1982). Mice, gerbils and guinea pigs, on the other hand, have not been observed to indulge in social play during their early life (Einon et al, 1981). These findings have led Einon and her co-workers (Einon et al, 1978 and 1981) to suggest that the experience of social play between the ages of about 25 and 45 days is critical to a rat's future behaviour in terms of its activity and object contact.

The experiments reported in chapters Seven and Eight are concerned with the effects (both short and long term) of early social experience on the social (especially aggressive and sexual) behaviour of male rats and guinea pigs. Many people have suggested that, because of its social nature, social play is likely to be important in the development of adult social behaviour patterns and relationships (Bolles and Woods, 1964; Bekoff, 1978; Olioff and Stewart, 1978; Meaney and Stewart, 1981; Panksepp, 1981; Smith, 1982). If this were the case, it might be expected that early isolation would have a permanent effect on the social behaviour of rats, but possibly not on the social behaviour of guinea pigs.

Previous research on the effects of social experience on aggression and sexual behaviour, chiefly in male rats and guinea pigs, is reviewed below.

6.1

The effects of social experience on intermale aggression.

6.1.1

Social isolation and intermale aggression.

The effects of social isolation on intermale aggression have been investigated in few non-primate species. In this section, only experiments on rodents (chiefly mice, guinea pigs and rats) are reviewed.

Studies by Benton and Brain (1979) and O'Donnell et al (1981) have shown that isolated laboratory mice are at least as aggressive to intruder males or males in a neutral arena as are dominant males from groups. Bronson (1967) found that male mice isolated during the post-weaning period were slower to fight strange males than were group reared males, but that they fought them for longer. King and Eleftheriou (1957) released mice of the Peromyscus genus into the field after either group or isolation rearing, and found that the isolation reared mice dispersed more rapidly than the others.

All these findings on mice suggest that social isolation has a similar effect to that of the experience of dominating other mice in a group i.e. it increases aggressiveness and reduces social tolerance (see section 1.1.2). Brain (1980) pointed out that this should not be unexpected, since observations of wild mice have shown the males to be strongly territorial. Thus the dominant mouse in a group is probably the one which holds the cage as his territory in the same way as an isolated mouse does. Isolation from the age of weaning is probably a near-normal state for a mouse, rather than one of social deprivation.

6.1.1.1

Social isolation and intermale aggression in male guinea pigs.

Few experiments have been made on the effects of social isolation on guinea pig intermale aggression. Hull et al (1973) found that early isolated (21-100 days old) males were more aggressive to others in neutral arena tests than were males which had been kept in single sex groups for the same period. Pairs of group reared males showed no aggression to one another and less aggression was seen when an early isolate was paired with a group reared male than when two isolates were put together. A similar pattern was found in the frequency of occurrence of non-aggressive (sniffing and contact) interactions.

Late isolates (isolated for three months during adulthood) and late-grouped males were similarly tested (Hull et al,1973). Aggressive interactions were extremely rare in any of these pairings, but late isolates interacted non-aggressively with one another much more frequently than any other experimental pairing. No details of the previous housing conditions of the late isolated/grouped males were given, but it is assumed (since they were acquired from a breeder as adults) that they had probably been kept in single sex groups until the experiment was begun.

Conversely, Fara and Catlett (1971) had found that male guinea pigs aged six months (which had been housed in single sex groups since weaning) showed aggressive interactions in 20-40% of paired neutral arena encounters after a one week period of isolation. In this experiment, however, one of the animals in each pair was wired up to a cardiogram at the time of testing, and it is possible that this interference may have affected both animals' tendencies to respond aggressively to one another.

These results suggest that early isolation may increase the aggressiveness of a male guinea pig slightly, whereas late isolation does not. They also indicate that isolation at any age appears to increase the number of non-aggressive (especially sniffing) interactions between two unfamiliar males.

In mice, isolation would appear to be a closer approximation to their natural social preferences than is social grouping. For guinea pigs, the increased aggression in early isolated males might indicate a similar preference for dispersal. However, the concomitant increase in nonaggressive behaviours suggests that the increased aggression could be due to a general rise in social activity after early isolation. Also the lack of increased aggression in late isolated animals suggests a greater degree of social tolerance in male guinea pigs than is found in mice.

The experiments cited above reported behaviours observed in brief neutral encounters between pairs of males. None of them has shown whether or not the increased aggressiveness of early isolated males can be removed by subsequent all-male or mixed housing. Also, they give no information as to the effects of early social isolation on agonistic behaviour between the members of a cohabiting group of guinea pigs. Nor do they show whether early isolation affects the structure of such a group. In the experiment described in chapter Seven, the effect of early social isolation (from weaning to maturity) on the subsequent agonistic behaviour and structure of groups of four male guinea pigs, with and without females present, was investigated.

6.1.1.2

Social isolation and intermale aggression in male rats.

Experiments involving the social isolation of rats have been rather more diverse than those on mice or guinea pigs. Eibl-Eibesfeldt (1961) observed the reaction of isolation reared (17 days to five months) males to intruders, and concluded that they showed all the normal aggressive behaviours to the strange males. From this finding he surmised that there could be no critical period between these ages for the learning of aggressive behaviours, and indeed that the behaviours were probably innate. However, this finding that early isolated animals produced the normal aggressive behaviour patterns did not indicate whether these behaviours were used in the normal proportions or in the normal response contexts.

Barnett and Stoddart (1969) compared the reaction of isolation housed sixth to ninth generation laboratory bred wild male rats to strange males with the reaction of isolation housed wild-trapped males, and found that the latter were more aggressive than the former. There were many unknown factors in this experiment, such as age and previous experience, so the results may not necessarily prove that laboratory breeding reduces aggressiveness of wild-type rats. Also, since no comparison was made with the reactions of group housed males to strangers, the results do not show whether any interactive effects of isolation and laboratory/wild breeding exist.

Price (1977) investigated the effects of post-weaning isolation or group housing (in all-male groups) on intruder tests in both domestic and first generation laboratory-bred wild male rats. In this study, all the experimental animals were isolated between two and three months old, regardless of their previous postweaning experience, so that they would face the intruders (anosmic, wild/domestic hybrid males) alone. Price found no real differences in the amount or intensity of aggression shown to an intruder by any of the experimental animals, though there were some differences in the frequency of certain behaviours. Isolation and group reared domestic males differed significantly in the number of 'broadsides' they used. The group reared domestic males exhibited 'broadside' behaviour more often than the isolated males. Also, domestic males showed more 'broadsides', ano-genital sniffing and conspecific grooming (aggressive grooming) than did the wild-type males.

In comparison, Price field-trapped some wild male rats and subjected them to the same intruder test. These animals were considerably more aggressive towards intruders than were any of the wild or domestic laboratory-bred males, which led Price to conclude that territorial intermale aggression may increase with experience of strange animals, but does not increase simply as a result of early isolation. The wild-bred males had undoubtedly met and probably fought many strange males before, whereas neither the isolation reared nor the group reared laboratory-bred rats had had any such encounters before testing.

Luciano and Lore (1975) reared male and female rats in isolation or in single sex groups from weaning (22 days) to adulthood (180 to 300 days). They then formed groups of two males and two females, each one comprised of either isolation reared or unfamiliar group reared animals. Casual observations of these groups immediately after formation and over the next twelve days showed little intra-group fighting at all, and even less in the isolation reared than in the group reared groups, though the isolation reared males lost more weight than did the group reared males during colony housing. This finding can be seen to be very different from that for mice, and may reflect a difference in the natural sociability of mice and rats.

In the same experiment, Luciano and Lore (1975) introduced isolation reared and group reared male intruders individually into their two categories of social groups. They found that no fighting occurred during the first hour when group reared intruders were put into group reared colonies, and little fighting took place in the other conditions at this time. Isolation-reared intruders were observed to be more active when initially placed into the colonies than were group reared intruders.

After 21 hours, the intruders were removed and examined for physical signs of fighting and stress. It was found that isolation reared intruders into group reared colonies had the most wounds, had lost the most weight and were most likely to have developed gastric ulcers. None of the group reared intruders had developed gastric ulcers, and only one isolation reared intruder into an isolation reared colony had one ulcer. It seems, therefore, that isolation reared male intruders in group reared colonies elicited the most attack from resident males. It is possible that these results may be due to isolation reared males having an inappropriate smell, or behaving (or vocalising) in a manner which failed to inhibit or reduce the territorial aggression of group reared males.

Another interesting observation from this experiment was that the isolation reared colony males showed very little aggression to intruders, and seemed to accept them quite readily into their group. This could reflect some abnormality in the social structure of these colonies such that members were unable to distinguish an intruder from other members of the group. In considering this possibility, it is important to bear in mind that these colonies had only been established for a few days before they were subjected to intruder tests. This meant that the isolation reared animals had had very little social experience after a very long period of social isolation before these tests. Another explanation of these findings could be that the low levels of aggression shown by isolation reared colony members to intruders were simply an extension of the previously observed low levels of aggression within these groups.

An effect of isolation rearing apparently contradictory to that of Luciano and Lore (1975) was found by Day et al (1982). They reared some male rats in social isolation from 21 to 70 days old, while others were housed in all-male groups for this period. All but one of the grouped rats were removed from each group cage and two male and two female group reared rats were added to each isolate's and single group reared male's cage. It was observed that the isolation reared males showed more dominating ('on top of' or 'aggressive posture'; Grant and Mackintosh, 1963), fighting (wrestling) and boxing behaviours than did the group reared resident males. Also, the isolation reared males boxed more often with the introduced males than with the introduced females, whereas the group reared males boxed equally with both sexes of intruder.

Day et al's conclusion that isolation reared male rats are more aggressive than group reared males in an intruder test is rather sweeping, as no record of the initiator of the bouts of fighting was kept. So it is possible that the isolates presented a different social stimulus to group reared intruders than did the group reared residents, and thus may have elicited more aggressive behaviour from the intruders. The observed greater amount of aggressive behaviour of isolation reared residents may have actually been due to their response to increased attack by the male intruders, or to their inability to inhibit the attack of intruders, or both. If either of these possible explanations were found to be true, then the results of this study would show more agreement than disagreement with those of Luciano and Lore (1975). It is perhaps worth noting that Day et al's intruder study was rather different from most in that the intruders outnumbered the residents.

The most recent study of the effects of early and late social isolation on male rat agonistic behaviour was performed by Wahlstrand et al (1983). They found a significant increase in aggressive behaviour (as measured by 'kick and bite' and 'dominant' actions) observed between 69 and 91 days of age in groups of male rats which had been isolated from 16 to 41 days old, as compared to animals which had lived in all-male groups for the same period. Isolation or all-male grouping from 42 to 68 days of age did not alter this effect. Thus Wahlstrand et al concluded that early isolation had a long-term global effect on agonistic behaviour (i.e. it increased such behaviour) in male rats, whereas late isolation (from puberty onwards) did not.

The studies mentioned above suggest that the effects of social isolation on the male rat may be rather more complex than on the male mouse. In rats, early isolation appears to have a long-term effect on their agonistic behaviour towards each other when later grouped with similar males in single sex groups (Wahlstrand et al, 1983). It is possible that the same effect is not found in mixed groups containing early isolated males (Luciano and Lore, 1975), though the difference in duration of isolation between this and the previous study make such a conclusion rather dubious. Early social isolation also affects the behaviour a male elicits when presented as a stranger to a group of socially reared males (Luciano and Lore,1975; Day et al, 1982). Late isolation (around puberty or later) does not seem to increase intermale aggression.

None of these studies looked at the effects of early or late social isolation on the direction of interactions between male rats (i.e. on group structure) or on individual differences in production of aggressive behaviours. Also, little evidence is available as to which agonistic behaviours are most affected by isolation. It is possible that there may be proportional as well as absolute changes in the agonistic behaviour of early isolated male rats.

No controlled study of the possible difference between subsequent all-male and mixed housing on previously isolated male rats has yet been reported. The experiment described in chapter Eight investigated the behaviour (agonistic and otherwise) of early isolated male rats which were subsequently grouped either in single sex groups of four, or in groups of four males housed with two (socially reared) females.

6.1.2

Other social experience effects on intermale aggression.

Most of the experiments cited above which investigated the effects of social isolation on agonistic behaviour used all-male groups as their controls, while a few used mixed groups. No research has been reported, however, to show whether the social interactions of a group of male rats or guinea pigs are affected by having females living with them, either before or after puberty. One might expect an effect on social behaviour, especially agonistic behaviour, or social structure. Results of investigations into this are reported in chapters Seven and Eight.

6.2

The effects of social experience on male sexual behaviour.

6.2.1

Social experience and sexual behaviour in male guinea pigs.

6.2.1.1

Copulation.

The results of previous experiments on the effects of different social experiences on male guinea pig copulation are summarised in Table 6.1.

The results obtained in mating tests after isolation rearing are very variable between studies. In some cases, only a small proportion of males ejaculated on test, whereas in others nearly all animals ejaculated. It appears that early-isolated Strain 2 guinea pigs are more likely to fail to copulate during a series of ten minute tests than are similarly-reared outbred males. This difference (which is also found in socially-reared males) could well be due to a strain difference in reaction to novel stimuli. A Strain 2 male may 'freeze' for longer than an outbred male when confronted with an oestrous female. Since the tests only lasted for a maximum of ten minutes, prolonged 'freezing' could mean that a male never had the chance to initiate copulation on test. The observation that 47% of the isolation-reared Strain 2 males mounted and 14% intromitted on test (Riss et al, 1955) supports the hypothesis that they were simply slower to initiate, rather than less capable of, copulation.

In general, it seems that early isolation does not harm

Reference	Strain	Period of experimental housing (days of age).			Age at mating tests (days).	Maximum no. of tests.	Duration of each test (mins).	Percentage of animals in each condition ejaculating by last test.		
		Isolate	All-male	Mixed				Isolate	All-male	Mixed
Webster and Young (1951)	?	25-			(22-50) -96	16	?	100		
Riss et al (1955)	Outbred	25- +		0-	7-119	17	10	70		100
	Strain 2	25- +		0-	7-119	17	10	0		100
Valenstein and Young (1955)	Strain 2	25- +		0-73 *	77-119	7	10	6		84
Valenstein et al (1955)	Outbred	25- +	25-73 *	0-73 *	77-119	7	10	71	80	100
Valenstein and Goy (1957)	?	W-			77-119	7	10	0		
	?		W-73 *	25-73 *	77-126	7	10		80	80
	?			0-73 *	77-405	7	10			100
Gerall A.A and Dunning (1958)	?	10- +		0-	60- ?	5	10	50		75
Gerall A.A (1963)	Outbred	W- +			60- ?	5	10	50		
Gerall H.D (1965)	Outbred	2-	2-		60- 74	3	10 ++	40	80	
Harper (1968)	?	0-	45-		100-105	3	10	20	44	

\+ = Siblings removed at birth. * = Subsequently isolated. W = Weaning.
++ = Or until ejaculation, if mounting began within 10 minutes.

Table 6.1
Summary of social experience effects on male guinea pig ejaculation in mating tests.

postpubertal copulation much, and that this harm is only temporary; subsequent housing with females led to full copulation in nearly all cases (Riss and Young, 1953; Valenstein and Goy, 1957; Harper, 1968).

Rearing in all-male groups apparently only slightly reduces the proportion of male guinea pigs ejaculating on test as compared with rearing in mixed groups (Table 6.1). Harper (1968) rehoused all-male non-copulators with females and found that this led to full copulation by all animals. Thus the copulatory deficit caused by all-male rearing is also only temporary.

Although quite a large proportion of isolation-reared male guinea pigs failed to copulate fully in mating tests, they generally showed great interest in the oestrous females presented to them (Riss et al, 1955; Valenstein and Young, 1955; Valenstein et al, 1955; Gerall,A.A and Dunning, 1958; Gerall,A.A, 1963; Harper, 1968). This interest manifested itself in circling and ano-genital sniffing (Gerall and Dunning, 1958; Gerall, 1963) and also in poorly-oriented mounts (Valenstein and Young, 1955; Valenstein et al, 1955; Gerall, 1963; Harper, 1968).

No quantitative differences in pre-ejaculatory mounts or intromissions have been recorded between isolation- and socially-reared male guinea pigs. However, Gerall (1963) observed that isolates ano-genital sniff/licked oestrous females less frequently than did socially-reared males in mating tests.

Riss and Goy (1957) found that sexually experienced all-male reared (0-120 days) guinea pigs were less sexually active (i.e. showed fewer pre-copulatory behaviours or ejaculations) in mating tests during periods of late isolation than during a period of all-male grouping. Unfortunately, no precise data on this effect are given with regard to the behaviours affected.

The differences in copulatory behaviours and in ejaculation between isolation-reared and socially-reared males seem to be due to poor organisation of sexual behaviours in the isolated animals rather than to copulatory inability. All isolates which intromitted on a test were subsequently observed to ejaculate (Riss et al, 1955; Valenstein and Young, 1955). Thus once they had learned to mount in the correct posterior position (and so intromit), the isolates all copulated normally.

It appears that early experience of other males (with no females present) is almost as good as experience of females in allowing male guinea pigs to organise their copulatory behaviours normally. Post-isolation housing with other males has been shown to lead to a considerable improvement in subsequent copulation in guinea pigs (Valenstein and Goy, 1957), though housing with females has a more rapid remedial effect (Riss and Young, 1953; Valenstein and Goy, 1957; Harper, 1968). However, whether or not the observed reduction in ano-genital sniff/licking by early isolates is removed by later mixed housing has yet to be tested.

In general, it appears that male guinea pig copulatory ability is not dependent on a critical period of early social experience. However, it is possible that there is an early optimal period in which social experience will lead to the most rapid development of copulatory behaviours (Moltz, 1973).

6.2.1.2

Courtship.

No studies of the effects of social experience on the courtship of anoestrous females by male guinea pigs have been reported. The behaviours observed during courtship are essentially the same as those observed during copulation, except that the female does not permit intromission (Rood, 1972). Thus it is possible that male guinea pigs are attracted to oestrous and anoestrous females in a similar way, and that it is the female who determines when copulation takes place. If so, then the effects of social experience on copulatory behaviours should be replicated in courtship i.e. isolation-reared males would be expected to ano-genital sniff/lick females less than socially-reared males, and currently isolated males of any age would be expected to show less courtship behaviour than currently group-housed males.

In chapter Seven, an experiment is described in which the courtship behaviour of male guinea pigs was measured in both individual and group tests during and after isolation, all-male or mixed rearing and subsequent housing. In this way, it was hoped to discover whether any effects of early isolation on courtship behaviour would persist after subsequent experience of group housing.

6.2.2

Social experience and mating behaviour in male rats.

6.2.2.1

Copulation.

Table 6.2 summarises the results of experiments on the effects of different social experience on male rats with respect to the achievement of full copulation (i.e. copulation to ejaculation) in mating tests. In reading this table, it should be remembered that in all the experiments except those marked otherwise, copulation was allowed to proceed to ejaculation so long as a male started mounting within the minimum duration of each mating test. This meant that no distinction could be made between animals that were slow to initiate copulatory activity and those that might not have copulated at all in each test.

From Table 6.2 it can be seen that neither early (from 10 days old) nor late (post-pubertal) isolation destroyed the ability to copulate to ejaculation with a female, though many of the isolated animals did require quite a large number of tests before initiating copulation within the allotted time period.

While the above findings are true of animals after at least 10 days of age they may not, however, be so true of perinatally isolated animals. Gruendel and Arnold (1969) completely isolated some albino rats from 24 hours of age by removing their siblings and their mothers. Other males just had their mothers removed at this age, but were subsequently completely isolated at 30 days. All these rats were

Reference	Strain	Period of experimental housing (days of age).			Age at mating tests (days).	Maximum no. of tests.	Minimum duration of each test (mins).	Percentage of animals in each condition ejaculating by last test.		
		Isolate	All-male	Mixed				Isolate	All-male	Mixed
Kagan and Beach (1953)	Sprague-Dawley	30-			30-160	18	10	7		
			30-		100-120	5	10		75	
Beach (1958)	?	14-	14- 76 +		90-105	5	10	62	75	
Zimbardo (1958)	Hooded	18-			75-140	4	10 *	<10		
Folman and Drori (1965)	Albino	30-	30-	30-	102-122	4	15 *	75	75	100
	Albino	30-	30-	30-	77-116	3	15 *	0	67	100
Gerall H.D. et al (1967)	Sprague-Dawley	14-	14-	14-	90-125	9	10	<20	100	100
Hard and Larsson (1968)	Albino	25-	25-	25-85 ++	95-120	25	30	72	94	100
Gruendel and Arnold (1969)	Albino	30-			200-228	4	20 *	35		

+ = Subsequently isolated.
* = Maximum as well as minimum duration.
++ = Females removed from groups.

Table 6.2
Summary of social experience effects on male rat ejaculation in mating tests.

Reference	Strain	Period of experimental housing (days of age).			Age at mating tests (days).	Maximum no. of tests.	Minimum duration of each test (mins).	Percentage of animals in each condition ejaculating by last test.		
		Isolate	All-male	Mixed				Isolate	All-male	Mixed
Duffy and Hendricks (1973)	Wistar	14-	14-100 +		105-135	7	15 *	25	100	
Spevak et al (1973)	Long Evans	26-	26-	26-	140-160	2	30 *	36	50	89
Wilhelmsson and Larsson (1973)	Wistar	10-		10-85 ++	95-121	26	15	85		90
Gruendel and Arnold (1974)	Albino	14-	14-100 +		120-141	4	15 *	10	35	
Thor and Flannelly (1977)	Sprague-Dawley	30-			90-106	8	20 *	100		
Chambers et al (1980)	Sprague-Dawley		23- 63 +		258-363	15	15		70	
			23-		258-363	6	15		100	

+ = Subsequently isolated.
* = Maximum as well as minimum duration.
++ = Females removed from groups.

Table 6.2 (continued)
Summary of social experience effects on male rat ejaculation in mating tests.

given mating tests as described in Table 6.2, in which none showed any copulatory behaviour at all. These results show that the absence of copulation in perinatally isolated male rats is not simply due to pre-weaning isolation. It seems more likely that the rats in Gruendel and Arnold's experiment were physically underdeveloped due to their artificial feeding and housing conditions, as they were significantly lighter in weight than their socially reared peers even at the age of 200 days.

Two studies have investigated the effects of brief periods of social experience during early isolation on subsequent copulatory ability. Kagan and Beach (1953) replicated their isolation experiment (see Table 6.2) using isolated rats which were exposed to either another male or to a receptive female for ten minutes per week from 30 to 100 days of age. In mating tests performed after 100 days, these animals copulated even less frequently than the complete isolates (i.e. less than seven percent copulated by the end of testing). They claimed that this was due to the prevalence of attempted play rather than copulatory behaviours during mating tests.

Zimbardo (1958) weaned and isolated male hooded rats at 18 days old. Half of these animals were subsequently given the experience of an anoestrous female for 24 hours, and then for fifteen minutes per day from 32-62 days of age. Mating tests were performed on these animals as shown in Table 6.2. Eighty percent of the rats with partial cohabitation experience had copulated by the end of the fourth mating test, as opposed to less than ten percent of the complete isolates.

The apparently conflicting results of Kagan and Beach (1953) and Zimbardo (1958) probably say more about rat play behaviour than about copulatory ability. A socially-housed rat will normally play for from ten to fifty minutes per day between the ages of twenty and forty-five days (Humphreys, 1982), so the rats in Zimbardo's (1958) experiment were allowed sufficient social contact time for them to be able to indulge in a large proportion of the normal amount of play. Kagan and Beach's (1953) rats, however, were only able to play for a very short period per week. This suggests that, if minimal play time is allowed, rats will continue to try to play with other individuals long after the normal age range for play. If no time for play is given at all (i.e. total isolation) during the prepubescent period, postpubescent male rats do not show this tendency to indulge in social play when confronted with a receptive female. Play deprivation leaves them no less capable of copulation in the long term (provided they are given a large number of mating tests, or are rehoused socially) than does late isolation of males which were housed in all-male groups during the play period (Beach, 1958; Chambers et al, 1982).

These results suggest that the retardation in production of copulatory behaviour in some isolated males could be due simply to their lack of familiarity with other rats rather than to a specific effect of isolation on copulatory ability. Also, housing in all-male groups apparently leads to only a slight reduction in copulatory ability as compared with housing in mixed groups, and this difference can be rapidly removed by a series of mating tests i.e. by sexual experience.

Although social experience has no lasting effect on copulatory ability, it may have a lasting effect on other aspects of copulatory behaviour. Beach (1958), Duffy and Hendricks (1973) and Wilhelmsson and Larsson (1973) observed that isolated males mounted and intromitted more before ejaculating than did males from all-male groups, even after up to twenty-six mating tests. Hard and Larsson (1968) found that males from all-male groups and isolated males which were slow to initiate copulation (i.e. took several mating tests to copulate) intromitted more before ejaculating than males from mixed groups. Isolated and all-male group animals which initiated copulation early in testing did not differ in this way from mixed-group males. Similarly, Gerall et al (1967) observed that isolates which were slow to initiate copulation oriented their mounts poorly, even after three weeks' housing with a female.

In contrast, Spevak et al (1973) found that on their second mating test, isolated rats actually took less time to ejaculate than did mixed-group males. However, it is possible that this result may have been due to sexual fatigue in the mixed-group rats.

Finally, Beach (1942a), Folman and Drori (1965), Gruendel and Arnold (1974) and Chambers et al (1982) claimed that their isolated rats showed no differences in frequency, latency or duration of copulatory behaviours from socially-housed males once they had commenced full copulation (i.e. copulation to ejaculation). Beach (1942b) actually found that more isolated males (isolated from 21 days) than all-male-reared or sexually experienced males intromitted on test, and also that the isolates intromitted earlier in a series of tests. In this experiment the all-male reared (and housed) males showed less copulatory behaviour or interest in the receptive females on test than did either the isolates or the sexually experienced males.

The only conclusion that can reasonably be drawn from these inconsistent results is that isolation and (to a lesser extent) all-male housing increases the variability in performance of certain mating behaviours in male rats. Whether this variability would be reduced by prolonged sexual experience is not clear. Nor is there any evidence as yet to indicate which factor or factors determine whether a particular rat's sexual performance will be impaired (even if only temporarily) by the experience of social isolation or all-male housing.

From the results of previous studies on the effects of isolation, all-male and mixed housing on the ability of male rats to achieve full copulation in mating tests, it seems that social isolation at any age does not have a long-term detrimental effect on this behaviour. Some isolated rats initiate copulation almost immediately, although others require a number of tests with oestrous females before copulating. Isolates which are slow to copulate are nevertheless usually very interested in the female even on their first mating test. In almost all cases, the initiation of mounting inevitably led to ejaculation, if copulation was allowed to follow its natural course.

Experience of all-male housing (i.e. social but not sexual experience) leads to only a slight reduction in the proportion of animals copulating in their first mating test, and this reduction is rapidly removed by further testing.

Thus it seems that male rat ability to copulate is affected more by maturation than by social or sexual experience, such that most mature animals are capable of copulation to ejaculation. Socially experienced animals initiate copulation more rapidly than isolates, which means that more of them initiate copulation within the period allowed on test. As in guinea pigs, the evidence from studies of early isolation in rats is more indicative of the existence of an optimal period (Moltz, 1973) than of a critical period for social experience to affect the development of copulatory ability.

Although isolation and all-male housing do not seem to have a long term effect on a male rat's ability to copulate, there is some evidence to show that certain copulatory behaviours are affected by social experience such that the variation in their performance is greater in isolated and all-male housed rats than in mixed housed males. No clear evidence is available as yet to indicate whether this is a long term effect. Also, it is not yet known what determines whether a rat's sexual performance will be impaired by its lack of social experience.

In chapter Eight, an experiment is described in which individual and group mating tests were performed on male rats during and after the experience of isolation, all-male and mixed housing. Temporal and frequency measures of copulatory behaviours were made in order to discover more about the effects of different social experiences on copulation.

Chapter Seven.

AN INVESTIGATION OT THE EFFECTS OF PRE- AND POST-PUBERTAL SOCIAL EXPERIENCE ON THE SOCIAL BEHAVIOUR AND SOCIAL STRUCTURE OF MALE GUINEA PIGS.

7a

General Introduction.

Previous research on rodents and other mammals has suggested that early social isolation has permanent effects on the non-social behaviour of some species, but only temporary effects i.e. effects that can be reversed by subsequent social housing, on others (see chapter Six). The animals which have so far been found to show permanent effects of early (but not late) isolation are all members of species which indulge in social play during the pre-pubertal period, while those for whom early isolation has only temporary effects are all from non-playing species (Einon et al, 1981; Chivers and Einon, 1982).

Most of the investigations of the effects of early isolation on social behaviours have focused on copulatory behaviour, though a few have looked at intermale aggression in brief neutral encounters (see chapter Six). None have studied the later intra-group social behaviour or social structure of early isolated male guinea pigs. The present study was designed to investigate the effects of early isolation on spontaneous male intra-group behaviour in guinea pigs. The data obtained were used not only to look at global effects on social behaviour frequency, but also to find out whether stable agonistic dominance hierarchies would be formed in the same way in early isolated animals as in semi-natural groups i.e. animals with continuous social experience from birth (Rood, 1972; Berryman, 1978; Colony Studies 2 and 3).

Another aspect of social experience which has received little attention in studies of rodents is that of all-male versus mixed housing. Previous studies of semi-natural colonies of guinea pigs have indicated that the agonistic dominance hierarchy formed in this species functions to allocate reproductive priority. Other studies have shown a relationship between intermale aggressiveness and reproductive activity when a female is present (see Chapters 1 to 5). However, no comparative evidence has yet shown whether males housed in all-male groups form the same type of agonistic dominance structure as do males housed in mixed groups with naturally-cycling females. The present study was designed, therefore, to investigate not only the effects of early isolation but also those of early and late all-male housing on male guinea pig social behaviour and structure.

Although the main focus of this study was on spontaneous intra-group behaviour, I also investigated courtship behaviour in individual and group tests, water competition and weight. In this way, global effects of early experience and all-male versus mixed housing on these behaviours could be looked at where appropriate, but more importantly the relationship between these behaviours, weight, and agonistic dominance could be studied. Berryman (1978) had previously found that agonistic dominance rank in a semi-natural group of guinea pigs did correlate with aspects of aggressiveness and courtship, but did not correlate with measures of water competition success or weight.

The studies of spontaneous intra-group behaviour (Observations of social behaviour), courtship behaviour in tests, and water competition are reported separately in Sections 7.1 to 7.3 (with weight test results included in Section 7.1). However, directional agonistic dominance hierarchies found in Section 7.1 are compared not only with spontaneous intra-group behaviour, but also with the results obtained from the courtship tests and water competition tests described in Sections 7.2 and 7.3.

7b

General Method.

Subjects.

Subjects were 24 male guinea pigs crossbred in this laboratory from outbred coloured males and Dunkin Hartley females. They were weaned and assigned to experimental conditions between 20 and 33 days of age. It was not possible to set up all the experimental groups at once because of the slow reproduction and small litter size of guinea pigs. However, the same four males and sixteen females were used to produce all the experimental subjects.

After weaning, isolated animals were kept in white plastic cages (Bowman; 39 x 29.5 x 17.5cm) and socially grouped animals in open-topped boxes made of white-painted half-inch chipboard (62.5 x 61 x 31.5cm).

Subjects were given access to food and water ad lib. except during courtship tests and in the 16 hour period of water deprivation preceding each water competition test. A light/dark cycle of 12L:12D was maintained. Animals in mixed groups were kept in a room with lights on between midnight and noon, and isolated and all-male group animals were kept in a room with lights on between 1000 and 2200 hours. No females were kept in the latter room.

Subjects were individually identified by their unique fur colour patterns.

Female guinea pigs used to form mixed groups were from the same breeding stock and of the same age range as the males they were grouped with.

Design and Procedure.

A summary of the design of this experiment is given in Figure 7.1.

At weaning, subjects were assigned to experimental groups such that littermates were, as far as possible, separated and distributed evenly among the different experimental conditions. Each group contained animals differing in age by less than seven days.

For the first part of the experiment, three housing conditions were set up. Each condition contained two groups of animals. A mixed group consisted of four males and two females, an all-male group of four males only, and an isolation 'group' was comprised of four isolated males.

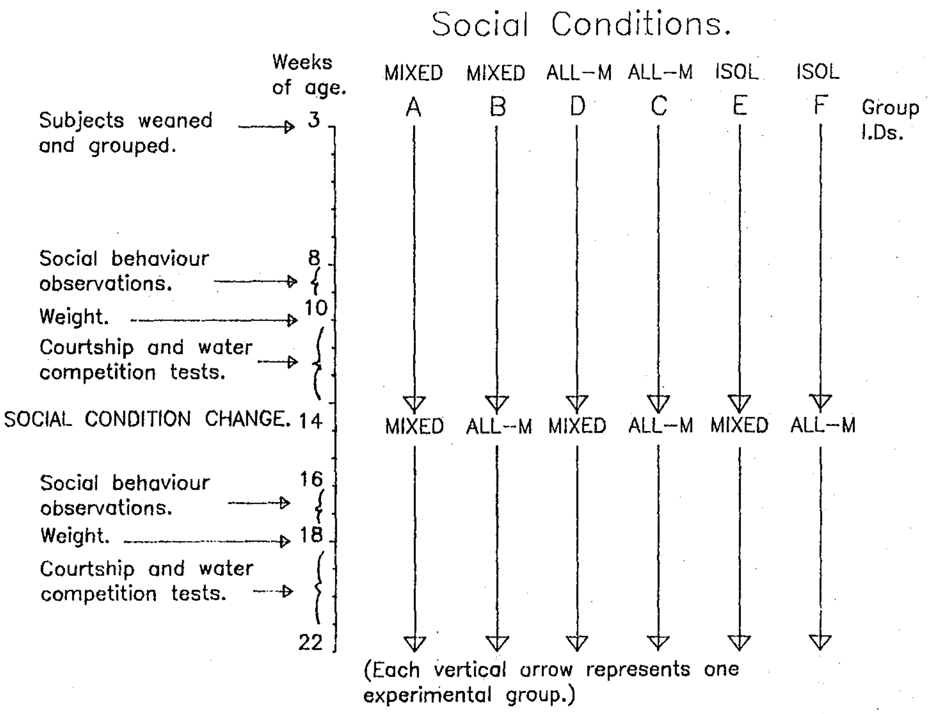

Figure 7.1.
Diagram of experimental design for guinea pigs.

For the duration of the first part of the experiment, these conditions were referred to as rearing/housing conditions (Rhconds), as they covered the period in each guinea pig's life from weaning to sexual maturity. During the second part of the experiment (after rehousing as described below), these initial conditions were referred to simply as rearing conditions (Rconds).

Between the fifth and seventh weeks postweaning, the socially-housed groups were observed for eight 30 minute sessions as described below. Each subject was weighed at the completion of all eight observation sessions (or seven weeks after weaning in the case of isolates). Over the next four weeks, individual and group courtship tests and water competition tests were carried out.

For the second part of the experiment, the housing conditions of the subjects were changed. The previously isolated males were grouped in fours and two females were added to one of the two groups thus formed. All females were removed from previously mixed groups, and a fresh pair of females was added to one of these groups. A pair of females was also added to one of the all-male Rhcond groups. (All the females added to experimental groups at this stage were nulliparous and had been housed with other females since weaning.) In this way, two new experimental conditions (all-male and mixed) were created, each containing the same number of groups from the three Rhconds (isolation, all-male and mixed). These two new experimental conditions were always referred to as housing conditions (Hconds), to distinguish them from the rearing conditions (Rconds) experienced by the animals during the first part of the experiment.

Between the second and fourth weeks after the change of experimental conditions, all groups were observed for eight 30 minute sessions. Each subject was then weighed again. Further individual and group courtship tests and a water competition test were carried out over the next four weeks.

7.1

Observations of Social Behaviour.

7.1.1

Introduction.

The aim was to study the individual spontaneous agonistic behaviours of the group housed male guinea pigs described in the previous section i.e. groups with different social experiential histories. The data were to be examined in two ways, so as to reveal any inter- and intra- group differences in social behaviour and structure.

Firstly, the overall frequencies of male behaviour under the different rearing and housing conditions were to be compared to see whether social experience affected the total frequency of interactions, and/or the proportionate frequencies of the separate behaviours. Studies by Hull et al (1973) and Fara and Catlett (1971) have suggested that early isolation might increase aggressiveness and the frequency of intermale ano-genital sniff/licking, though it was not certain whether these increases reflected proportionate increases in the production of these behaviours or were simply due to a general increase in social activity.

Observations of increased fighting between male guinea pigs when an oestrous female was present (Riss and Goy, 1957; Rood, 1972) have suggested that intermale aggression may be greater (either in absolute or proportional terms) in mixed than in all-male groups. In Colony Study 3 it was found that aggression by the dominant male to a subordinate was frequently induced by the subordinate courting a female.

No previous evidence has been reported as to the effect of all-male versus mixed housing on intermale courtship, so no predictions of this behaviour based on prior findings can be made.

The courtship of cohabiting females by isolation- or all-male reared male guinea pigs has not previously been studied, so again no precise predictions of these results can be made. Mating tests on animals with these types of early experience have shown that early isolates tend to ano-genital sniff/lick oestrous females less than do socially-reared males (Gerall, 1963). Whether this behavioural trend is permanent and would also be found with cohabiting females has not yet been shown.

The second way in which the data from the observational studies were to be investigated concerned intra-group comparisons of behaviour frequencies and dominance ranks. Studies of semi-natural groups have previously shown a close positive relationship between dominance rank and the initiation of aggressive behaviours (Rood, 1972; Berryman, 1978; Colony Studies 2 and 3). The relationship between dominance and received aggressive behaviours has been found to be more complex, however, probably beacause of the tendency of subordinate individuals to avoid conflict, expecially extended conflict, with their superiors, apparently by using some type of cue assessment (see Chapters 4 and 5). No previous studies have looked at the relationship between dominance rank and intermale courtship in guinea pigs.

A positive correlation between dominance rank and courtship of cohabiting females in semi-natural colonies has been found by Rood (1972), Berryman (1978), and in Colony Study 2. Less straightforward relationships between ranks and courtship have been found by Jacobs et al (1971), Jacobs (1976) and in Colony Study 3.

No previous studies have compared the social structures of guinea pigs after early isolation or under all-male housing conditions with those found in mixed groups, so it is not possible to predict the outcome of this investigation from earlier results. However, since it has been observed that the male guinea pig dominance hierarchy appears to function to allocate reproductive priority, it could be that such a hierarchy is only formed under conditions of reproductive competition i.e. in mixed groups. Alternatively, it is possible that functional pressures could have led to the evolution of the tendency for male guinea pigs to form a dominance hierarchy in anticipation of reproductive competition, rather than simply as a result of it. The results of this study should indicate which of these two hypotheses is closer to reality.

7.1.2

Method.

Eight 30 minute observation sessions were carried out on each socially-housed group of animals over a period of two weeks at the times indicated in Figure 7.1. These took place during the first two hours of darkness, at a time when considerable activity usually occurred. Each group was observed in its home box. The box was lit by a 40W red bulb in an Anglepoise lamp situated 40cm above one side of the box. The experimenter sat on a stool next to the lamp, positioned so that she could observe all the animals from above.

Social interactions were recorded on a check sheet in abbreviated form. Recordings were made in the form: agent (initiator); behaviour; recipient. Observations were written down in sequential order, and pauses of 10 seconds or more between acts were noted. The types of behaviour scored are listed and described in Table 4.1. Following and circling behaviours were not recorded in this experiment as they were too difficult to determine under the rather crowded housing conditions.

Treatment of results.

Social behaviour frequency: Inter-group comparisons.

A Mann-Whitney U test and a Kruskal-Wallis analysis of variance were performed respectively on the total intermale interaction data from Social Observation periods 1 and 2. Further Mann-Whitney U tests and Kruskal-Wallis analyses of variance were performed on the data for each social behaviour.

For the first Observation period, these analyses were made on the actual frequencies of behaviours, as no overall differences between conditions had been found in total interaction frequency. The total intermale interaction data for Observation period 2, however, showed nonsignificant, but nevertheless large, differences in the total frequency of interactions per condition. Thus it was decided to analyse the intermale social behaviour data after transforming them into percentages of each group's (i.e. each condition's) total interaction score. This meant that any significant effects found would indicate differences in proportionate behaviour production between experimental social conditions, rather than overall differences in social activity.

The Observation period 2 data were analysed further in order to find out whether there were any Rcond differences in the nature of male to female interactions between the three mixed Hcond groups. Kruskal-Wallis analyses of variance were performed on the total male to male/female interactions, the total male to female interactions and on each male to female social behaviour (except mounting, which was never observed) separately.

The medians of the interaction data analysed in these ways were tabulated.

Dominance and social behaviour frequency: Intra-group comparisons.

Socially grouped males were dominance ranked within each group, where possible, according to the direction of intermale interactions for each agonistic behaviour (see section 4.1.3). The results obtained for each behaviour were compared within each group. If there were missing or equal relationships on any behaviour, the rank trend of the data was compared with the ranks obtained for behaviours with no missing relationships. If one or more behaviours showed different directional rank orders in any group, that group was found not to have a dominance hierarchy.

Rank comparisons were carried out, using Friedman's two way analysis of variance (Siegel, 1956), on five sets of data for each group of animals: 1) initiated intermale agonistic behaviours; 2) received intermale agonistic behaviours; 3) initiated intermale courtship behaviours; 4) received intermale courtship behaviours; 5) courtship of cohabiting females by males (in mixed housed groups only). The agonistic behaviours compared were: displace, threat, chase, bite and runaway. The courtship behaviours compared were: rumba, ano-genital sniff/lick, and attempted mount. Rank 1 was assigned to the male which initiated most of each behaviour in the comparisons of initiated behaviours, and to the male which received the fewest of each behaviour in the comparisons of received behaviours (with the exception of runaway which was ranked in the opposite manner because it was the only defensive behaviour scored).

The rank ordering of the frequency of behaviours (discounting direction) was compared within groups both in groups with and without a dominance hierarchy. In the former case, if significant within group consistency of rank ordering across behaviours was found, an additional analysis was performed in which dominance rank was included with the ranked behaviour frequencies. If the results attained a higher level of significance than those of the preceding analysis (without dominance ranks), then a significant relationship between the behaviour frequencies and dominance status was found. In groups without dominance hierarchies, but with internally consistent initiated and received agonism, a further analysis of combined initiated and received agonism scores was made. The results of this analysis would show how close the relationship between initiating and receiving aggression was.

7.1.3

Results.

7.1.3.1

Observation period 1.

Social behaviour frequency: Inter-group comparisons.

Table 7.1 shows the medians and the results of Mann-whitney U tests for each intermale behavioural measure (and the total number of intermale interactions) for both socially-housed Rhconds in Observation period 1. There was a significant effect of Rhcond on the number of intermale rumbas, such that males in the all-male Rhcond rumba-ed to one another more frequently than did males in the mixed Rhcond. No other significant effects of Rhcond on intermale social behaviours were found.

In considering the significance of the Rhcond difference in rumba frequency, it is necessary to remember that nine tests were performed, so the chances of one test producing a significant result by chance were nearly one in two. These results should be replicated for verification.

Dominance and social behaviour frequency: Intra-group comparisons.

Tables 7.2 a-d show the results of attempts at directional ranking on each agonistic behaviour for each group of guinea pigs. The only group which reached the criterion for having a dominance hierarchy (i.e. no rank reversals between behaviours) was group A

Behavioural measure	Rhcond	Median score	U value (Rhcond)	P
Total no. of intermale interactions.	MF	42.0	27.5	NS
	M	70.5		
No. of intermale displacements.	MF	15.5	31.0	NS
	M	17.0		
No. of intermale threats.	MF	8.5	23.5	NS
	M	13.0		
No. of intermale runaways.	MF	6.0	14.5	NS
	M	9.5		
No. of intermale chases.	MF	2.0	31.0	NS
	M	1.5		
No. of intermale bites.	MF	0.0	24.0	NS
	M	0.5		
No. of intermale rumbas.	MF	0.0	10.5	<.05
	M	1.0		
No. of intermale ano-genital sniff/licks.	MF	2.5	18.5	NS
	M	1.0		
No. of intermale attempted mounts.	MF	0.0	22.5	NS
	M	0.0		

Rhcond = Rearing (and current housing) condition.
(MF = Mixed
M = All-male)
NS = Nonsignificant.

Table 7.1
Guinea pig Observation Period 1: Medians and results of Mann-Whitney U tests on frequencies of intermale behaviours.

	Rhcond			
	Mixed		All-male	
Group ID	A	B	C	D
	Displace	Threat	Threat	Threat Runaway

Table 7.2 a.
Intermale agonistic behaviours showing dominance rank order linearity with no missing or equal relationships.

	Rhcond			
	Mixed		All-male	
Group ID	A	B	C	D
	Bite (3) Runaway (1) Chase (2) Threat (1)	Runaway (2) Bite (3)	Displace (1) Chase (3) Bite (3)	

Table 7.2 b.
Intermale agonistic behaviours showing the same linear rank order as in Table 7.2 a, but with some missing or equal relationships (no. given in parentheses).

	Rhcond			
	Mixed		All-male	
Group ID	A	B	C	D
		Displace Chase (3)		Displace Bite (5) Chase (2)

Table 7.2 c.
Intermale agonistic behaviours showing different linear dominance rank orders to those in Table 7.2 a, (nos. of missing or equal relationships given in parentheses).

	Rhcond			
	Mixed		All-male	
Group ID	A	B	C	D
			Runaway	

Table 7.2 d.
Intermale agonistic behaviours showing non-linear dominance rank orders, with no missing or equal relationships.

Rhcond = Rearing/housing condition.

Tables 7.2 a-d
Guinea pig Observation period 1: Evidence for dominance hierarchies among males according to the direction of intermale agonistic interactions.

(one of the two mixed Rhcond groups). Even in this group, however, the data were unequivocal (i.e. with no missing or equal relationships) for only one behaviour: displacement. There were missing or equal relationships in all the other agonistic behaviours. Neither of the all-male Rhcond groups nor the other mixed Rhcond group (group B) showed evidence of a dominance hierarchy.

Table 7.3 summarises the results of the Friedman two way analyses of variance performed on the agonistic and courtship behaviours for each group. (This table is referred to throughout this chapter.) Group A (mixed Rhcond) showed consistent ranking on both the frequency of initiation and the frequency of reception of agonistic behaviours. Comparisons of these ranked frequencies with agonistic dominance rank gave increased Chi-r-squared values in both cases, indicating that initiated and received agonistic behaviour frequencies were both related to dominance status (positively and negatively, respectively). Initiated intermale courtship behaviours were not ranked consistently, so no comparison with agonistic dominance was made. Received intermale courtship did show internal rank consistency, but the inclusion of dominance rank in this calculation reduced the value of Chi-r-squared, indicating that received intermale courtship was not closely linearly related to dominance status. Courtship behaviour frequency to cohabiting females was found to be consistently ranked between the males of group A. Further analysis including dominance rank gave an increased Chi-r-squared value, indicating that this behaviour was positively related to dominance rank.

Group B (mixed Rhcond) showed consistent ranking on the frequencies of initiation of agonistic behaviours, and also on the

	Rearing/housing Condition.					
	Mixed		All-male		Isolation	
Group ID.	A	B	C	D	E	F
a) Initiated inter-male agonism.	9.36* 12.10**	9.06*	11.94*	6.90		
Received inter-male agonism.	9.24* 9.60*	9.24*	11.22*	4.14		
Initiated and received inter-male agonism.		14.85**	23.13**			
Initiated inter-male courtship.	5.80	X	3.8	X		
Received inter-male courtship.	11.40** 9.30*	X	4.5	X		
Courtship to cohabiting females.	8.50* 11.48**	X				
b) Individual Courtship Test 1.	3.88	6.97	9.38*	7.70	10.86* 8.85*	2.82
Initiated inter-male agonism and I.C. Test 1.			14.10**			
c) Group Courtship Test 1.	11.80** 12.82**	12.20**	7.50	10.40* 13.51**		
Initiated inter-male agonism and G.C. Test 1.		19.95**				
d) Water Competition Test 1.	5.80	8.20*	5.80	6.60		
Initiated inter-male agonism and W.C. Test 1.		14.96**				

* = p<.05, ** = p<.01
X = Insufficient data for analysis.
NB. Df= 3 for each analysis.
Scores for which agonistic dominance ranks were included in the analysis are underlined.

Table 7.3
Results of Friedman two way analyses of variance (Chi-r-squared) on rank ordered behaviour frequencies:
a) Guinea pig Observation Period 1; b) Individual Courtship Test 1; c) Group Courtship Test 1; d) Water Competition Test 1.

frequencies of reception of these behaviours. A further analysis of the combined scores for initiated and received agonism revealed consistent ranking across both. In particular, it was noted that the most aggressive male had the most consistent rank scores on both measures of behaviour frequency. Insufficient intermale courtship or courtship of cohabiting females was recorded for these behaviours to be analysed.

Group C (all-male Rhcond) showed consistent ranking on the frequencies of initiation and reception of intermale agonistic behaviours, but not on the frequencies of initiation and reception of intermale courtship. This group also showed consistent ranking across both initiated and received agonism, though in this case the most consistent ranking was seen in the least aggressive animal.

No consistent ranking of the frequencies of intermale agonistic behaviours initiated or received was found in group D (all-male Rhcond). Insufficient intermale courtship behaviour was recorded in this group for analysis of these behaviours to be made.

7.1.3.2

Observation period 2.

Social behaviour frequency: Inter-group comparisons.

Intermale behaviours.

The medians of total intermale interaction frequency and percentage intermale interactions for each separate social behaviour are given in Tables 7.4 a-i.

Median scores.

	Rcond		
Hcond	MF	M	I
MF	27.5	51.0	38.5
M	52.5	70.5	92.5

Table 7.4 a.
Total no. of intermale interactions.

Median scores.

	Rcond		
	MF	M	I
MF	3.25	8.00	6.00
M	4.00	3.50	2.50

Table 7.4 b.
Percentage intermale displacements.

	Rcond		
Hcond	MF	M	I
MF	3.0	8.0	6.0
M	7.0	6.0	2.5

Table 7.4 c.
Percentage threats.

	Rcond		
	MF	M	I
MF	4.00	7.00	4.50
M	3.50	7.00	3.00

Table 7.4 d.
Percentage intermale runaways.

	Rcond		
Hcond	MF	M	I
MF	0.0	2.25	1.5
M	1.0	1.25	0.5

Table 7.4 e.
Percentage intermale chases.

	Rcond		
	MF	M	I
MF	0.50	1.25	3.50
M	0.00	1.50	0.50

Table 7.4 f.
Percentage intermale bites.

	Rcond		
Hcond	MF	M	I
MF	0.0	0.0	0.0
M	2.5	2.5	0.5

Table 7.4 g.
Percentage intermale rumbas.

	Rcond		
	MF	M	I
MF	0.75	0.00	0.00
M	1.00	1.00	1.50

Table 7.4 h.
Percentage intermale ano-genital sniff/licks.

	Rcond		
Hcond	MF	M	I
MF	0.0	0.0	0.0
M	0.0	0.0	0.0

Table 7.4 i.
Percentage intermale attempted mounts.

Rcond = Rearing condition.
Hcond = Housing condition.
(MF = Mixed, M = All-male, I = Isolation.)

Tables 7.4 a-i.
Guinea pig Observation Period 2: Median scores of intermale social behaviours (expressed as a percentage of the total no. of interactions for each group of animals).

Table 7.5 shows the results of Kruskal-Wallis analyses of variance performed on these data. Significant effects of Hcond were found for both intermale rumbas and ano-genital sniff/licks. In both cases the all-male Hcond males rumba-ed and sniff/licked each other proportionately more frequently than did the mixed Hcond males. No other significant effects of Rcond, Hcond or Group on intermale social behaviours were found, though it was noticed that group E (isolation Rcond x mixed Hcond) did show a (non-significantly) higher proportion of bites than did the other groups.

Once again, as nine tests were performed, these two significant results may have been due to chance. However, since the rumba result supports that found in Observation Period 1, and the ano-genital sniff/lick result was significant at $p<.005$, it seems probable that these results indicated genuine effects.

Courtship and agonistic behaviours to females.

Table 7.6 shows the medians and the results of Kruskal-Wallis analyses of variance of the male to female interaction data for the three mixed Hcond groups (of mixed, all-male and isolation Rconds respectively). No significant effect of Rcond was found for the total number of male to male/female or male to female interactions. Nor was there an effect of Rcond on the frequency data for male to female displacements, threats, runaways, chases, bites, rumbas, ano-genital sniff/licks or attempted mounts.

Behavioural measure	Variable	H value	Df	P
Total intermale interactions.	Rcond	0.25	2	.88
	Hcond	2.43	1	.12
	Group	3.01	5	.70
Percentage intermale displacements.	Rcond	0.21	2	.90
	Hcond	0.001	1	.98
	Group	0.43	5	.99
Percentage intermale threats.	Rcond	1.82	2	.40
	Hcond	0.10	1	.75
	Group	2.59	5	.76
Percentage intermale runaways.	Rcond	0.85	2	.65
	Hcond	0.001	1	.98
	Group	2.10	5	.83
Percentage intermale chases.	Rcond	0.85	2	.65
	Hcond	0.04	1	.84
	Group	1.02	5	.96
Percentage intermale bites.	Rcond	2.87	2	.24
	Hcond	2.17	1	.14
	Group	5.48	5	.36
Percentage intermale rumbas.	Rcond	0.20	2	.91
	Hcond	6.31	1	.01**
	Group	7.30	5	.20
Percentage intermale ano-genital sniff/licks.	Rcond	1.88	2	.39
	Hcond	8.17	1	.004**
	Group	11.07	5	.05
Percentage intermale attempted mounts.	Rcond	0.69	2	.71
	Hcond	0.16	1	.69
	Group	1.09	5	.96

Rcond = Rearing condition.
Hcond = Housing condition.
Group = Each group (i.e. rearing x housing condition) separately.
** = Significant at p<.01 level.

Table 7.5
Guinea pig Social Observation Period 2: Results of Kruskal-Wallis one-way analyses of variance on total intermale interactions (actual frequency) and on social behaviours (expressed as a percentage of the total no. of interactions for each group of animals).

Behavioural measure	Rcond	Median score	H value (Rcond)	Df	P
Total no. of male to male/ female interactions.	MF	83.0	0.12	2	.94
	M	79.0			
	I	137.0			
Total no. of male to female interactions.	MF	56.0	1.28	2	.53
	M	27.5			
	I	96.5			
No. of male to female displacements.	MF	4.0	0.41	2	.81
	M	5.0			
	I	15.0			
No. of male to female threats.	MF	2.0	1.05	2	.59
	M	1.0			
	I	2.0			
No. of male to female runaways.	MF	0.0	1.38	2	.50
	M	0.5			
	I	0.0			
No. of male to female chases.	MF	0.0	1.51	2	.47
	M	0.0			
	I	0.5			
No. of male to female bites.	MF	0.0	0.46	2	.79
	M	0.0			
	I	0.0			
No. of male to female rumbas.	MF	26.5	1.13	2	.57
	M	6.5			
	I	48.0			
No. of male to female ano-genital sniff/ licks.	MF	22.5	0.59	2	.75
	M	11.0			
	I	24.0			
No. of male to female attempted mounts.	MF	0.5	1.38	2	.50
	M	0.0			
	I	0.0			

Rcond = Rearing condition.
(MF = Mixed, M = All-male, I = Isolation.)

Table 7.6
Guinea pig Social Observation Period 2: Median scores and results of Kruskal-Wallis analyses of variance of male to female social interaction frequencies (mixed Hcond only).

Dominance and social behaviour frequency: Intra-group comparisons.

Tables 7.7 a-c show the results of directional ranking on each agonistic behaviour for each group of animals. It can be seen that all the mixed Hcond groups reached the criterion for having a dominance hierarchy, though in the case of group E (isolation Rcond x mixed Hcond), only one behaviour, displacement, showed this hierarchy unequivocally (i.e. with no missing or equal relationships). None of the all-male Hcond groups reached the criterion for dominance, as different behaviours indicated different dominance rank orders.

Table 7.8 summarises the results of the Friedman two way analyses of variance performed on the agonistic and courtship behaviours for each group. (This table will be referred to throughout this chapter.) Group A (mixed Rcond x mixed Hcond) showed consistent ranking on the frequencies of initiated intermale agonistic behaviours, but not on the frequencies of reception of these behaviours. Inclusion of agonistic dominance rank in the analysis of initiated behaviour led to an increase in the value of Chi-r-squared, thus indicating a close positive relationship between agonistic status and the frequency with which intermale agonistic behaviours were initiated. No significant rank trend was found for the frequencies of initiated or received intermale courtship behaviours, or in the frequency of courtship to cohabiting females.

The animals in group D (all-male Rcond x mixed Hcond) were consistently ranked across both initiated and received behaviour frequencies. The inclusion of dominance rank increased the values of

		Rcond	
Hcond	Mixed	All-male	Isolation
MF	Threat Runaway	Threat Runaway Displace Bite	Displace
M	Threat Displace	Runaway	Threat

Table 7.7 a.
Intermale agonistic behaviours showing dominance rank order linearity with no missing or equal relationships.

		Rcond	
Hcond	Mixed	All-male	Isolation
MF	Chase (3) Bite (3) Displace (1)	Chase (3)	Threat (2) Runaway (2) Chase (1) Bite (1)
M	Chase (2) Bite (5)	Bite (1) Chase (2)	Chase (3) Bite (1)

Table 7.7 b.
Intermale agonistic behaviours showing the same linear rank order as in Table 7.7 a, but with some missing or equal relationships (no. given in parentheses).

		Rcond	
Hcond	Mixed	All-male	Isolation
MF			
M	Runaway	Threat Displace	Displace Runaway

Table 7.7 c.
Intermale agonistic behaviours showing different linear dominance rank orders to those in Table 7.7 a, (nos. of missing or equal relationships given in parentheses).

Rcond = Rearing condition
Hcond = Housing condition
(MF = Mixed
M = All-male)

Tables 7.7 a-c
Guinea pig Observation period 2: Evidence for dominance hierarchies among males according to the direction of intermale agonistic interactions.

	Housing Condition	Rearing Condition. MF	M	I
a) Initiated intermale agonism.	MF	10.86* 13.65**	15.00** 18.00**	10.62* 13.30**
	M	9.84*	11.64*	3.15
Received intermale agonism.	MF	7.50	9.72* 12.20**	6.90
	M	12.76**	10.32*	0.78
Initiated and received agonism.	MF			
	M	19.35**	21.66**	
Initiated intermale courtship.	MF	1.30	X	X
	M	4.20	5.50	X
Received intermale courtship.	MF	1.70	X	X
	M	3.60	7.00	X
Courtship to cohabiting females.	MF	7.50	X	7.00
b) Weight Tests.	MF	8.10* 10.88*	5.30	1.00
	M	7.40	12.50*	0.90
Initiated agonism and Weight Tests.	MF			
	M		21.41**	
c) Individual Courtship Test 2.	MF	13.12** 15.49**	4.22	9.04* 10.95*
	M	5.21	7.34	1.00
d) Group Courtship Test 2.	MF	10.80* 13.85**	14.00** 16.60**	16.40** 17.64**
	M	12.60**	9.00*	2.70
Initiated agonism and G.C. Test 2.	MF			
	M	9.02*	20.08**	
e) Water Competition Test 2.	MF	8.20* 11.10*	8.20* 11.10*	7.30
	M	3.40	9.00*	4.20
Initiated agonism and W.C. Test 2.	MF			
	M		18.75**	

(MF = Mixed, M = All-male, I = Isolation)
* = p<.05, ** = p<.01
X = Insufficient data for analysis.
Scores including dominance ranks are underlined.

Table 7.8
Results of Friedman two way analyses of variance (Chi-r-squared) on rank ordered behaviour frequencies and weights: a) Guinea pig Observation Period 2; b) Weight Tests 1 and 2; c) Individual Courtship Test 2; d) Group Courtship Test 2; e) Water Competition Test 2.

Chi-r-squared for these measures, showing dominance status to be positively related to frequency of initiation of agonistic behaviours, and negatively related to frequency of reception of these behaviours. Insufficient data were available for similar analyses of intermale courtship or courtship to cohabiting females to be made.

Group E (isolation Rcond x mixed Hcond) showed the same pattern of results as group A (mixed Rcond x mixed Hcond) i.e. the rankings of initiated agonistic behaviours were internally consistent and were found to be closely related to dominance rank. Rankings of received agonistic behaviours showed no internal consistency. Insufficient intermale courtship was seen for these data to be analysed. No consistency between the rankings of courtship behaviours to females was found.

Groups B (mixed Rcond x all-male Hcond) and C (all-male Rcond x all-male Hcond) both showed consistent ranking of and between frequencies of initiation and reception of intermale agonistic behaviours. No consistent rank order was found in the frequencies of initiation or reception of intermale courtship behaviours in either group.

Group F (isolation Rcond x all-male Hcond) failed to show any consistency in ranking of frequencies of initiation or reception of intermale agonistic behaviours. Little intermale courtship was seen in this group, so that rank comparisons of this data could not be made.

7.1.3.3

Weight tests.

Weights and weight change: Inter-group comparisons.

Table 7.9 shows the medians and results of a Kruskal-Wallis analysis of variance of the guinea pig Test 1 weights. A significant effect of Rhcond was found such that the heaviest animals were those in the all-male condition and the lightest were those in the mixed condition. The isolated males were closer in weight, on average, to the mixed Rhcond than to the all-male Rhcond animals.

Tables 7.10 a-b and 7.11 give the medians and results of Kruskal-Wallis analyses of variance of the guinea pig Test 2 weights and of the change in weight between Tests 1 and 2. Significant effects of Rcond and Group (Rcond x Hcond) but not of Hcond were found for the Test 2 weights. The all-male Rcond males were still heavier than either the mixed or isolation Rcond animals. However, the difference in weight (on average) between the mixed and isolation Rconds had become negligible by the second weighing. The reduction in the difference in weight between the mixed and isolation Rcond males appeared to be due to the fact that the isolation Rcond x mixed Hcond males were very much lighter than the isolation Rcond x all-male Hcond males.

The analyses of variance of the weight change data revealed significant effects of Rcond, Hcond and Group (Rcond x Hcond), though that of Hcond was the weakest. The mixed Rcond males gained more weight between Tests 1 and 2 than did the all-male or isolation

Measure	Rhcond	Median	H value	Df	P
Test 1 weight.	MF	552.5	12.76	2	.002*
	M	695.0			
	I	597.0			

Table 7.9
Guinea pig weight Test 1: Median scores and results of Kruskal-Wallis analysis of variance on actual weights.

	Median scores.		
	Rcond		
Hcond	MF	M	I
MF	792.5	880.0	702.5
M	818.0	962.5	840.0

Table 7.10 a.
Test 2 weights (grams).

	Median scores.		
	Rcond		
	MF	M	I
MF	241.0	212.5	59.5
M	343.0	245.0	209.0

Table 7.10 b.
Weight change (grams).

Tables 7.10 a-b.
Guinea pig Weight test 2: Median scores and results of Kruskal-Wallis analyses of variance on actual weights and weight changes (Test 2 minus Test 1).

Measure	Variable	H value	Df	P
Test 2 weight.	Rcond	9.62	2	.008*
	Hcond	2.80	1	.094
	Group	13.43	5	.020*
Weight change (test 2-test 1 weights).	Rcond	11.65	2	.003*
	Hcond	4.32	1	.038*
	Group	16.07	5	.007*

Table 7.11
Guinea pig Weight test 2: Results of Kruskal-Wallis analyses of variance on actual weights and weight changes.

Rhcond = Rearing/housing condition.
Rcond = Rearing condition.
Hcond = Housing condition.
Group = Each group (i.e. rearing x housing condition) separately.
(MF = Mixed, M = All-male, I = Isolation.)
* = $p<.05$

Rconds. The all-male Rcond males gained more weight than did the isolation Rcond animals. The Hcond effect on weight change was such that the all-male Hcond males gained more weight than did the mixed Hcond males. The effect of Group (Rcond x Hcond) appeared to be due to the greater difference in weight change between the Hconds in the mixed and isolation Rconds than in the all-male Rcond. In particular, the isolation Rcond x mixed Hcond males gained very little weight (indeed, one animal actually lost weight between Tests 1 and 2), while the isolation Rcond x all-male Hcond males gained only slightly less weight than animals in other conditions. Also, the mixed Rcond x all-male Hcond males gained considerably more weight than did the animals in any of the other conditions.

Dominance, weights and weight change: Intra-group comparisons.

Table 7.8 presents the results of Friedman two way analyses of variance (Chi-r-squared) on the first and second weights and weight changes ranked within groups. (Ranks of 1 were assigned to the heaviest animals and the animal which gained the most weight between Tests 1 and 2 in each group.)

The only mixed Hcond group which had consistent ranks across the three weight measures was group A (mixed Rcond x mixed Hcond). When agonistic dominance ranks (the same for both Observation Periods in this group) were included in a further Friedman analysis, the value of Chi-r-squared increased, indicating a close relationship between first and second weights, weight change and dominance status i.e. the heavier animals had higher dominance ranks and gained more weight than did the lighter, lower-ranking males.

Although group E (isolation Rcond x mixed Hcond) showed no consistency of ranks across the three weight measures, perusal of the data revealed that the first and second weights actually showed a very close negative relationship with agonistic dominance (second Observation Period) order, while weight change was perfectly *positively* correlated with dominance rank. Thus it appeared that in this group dominance status was not determined by weight, but rather weight change was determined by dominance status (it should be remembered that this group was not socially housed until the second half of the experiment). It is possible to speculate that if this group had been studied for a longer period, the effects of dominance status on weight might have eventually caused the weights of the animals to become positively correlated with dominance order.

The only all-male Hcond group to show consistent ranking across weights and weight change was group C (all-male Rcond x all-male Hcond). Further analysis of this group's combined initiated agonism and weight results gave a very high Chi-r-squared value, indicating a very close relationship between first and second weights, weight gain and intra-group aggressiveness.

7.1.4

Discussion.

The absence of any significant differences in total intermale interaction frequency between groups or conditions shows that neither housing nor rearing condition affects total intermale behaviour frequency. If early isolation does increase social activity as suggested by Fara and Catlett (1971) and Hull et al (1973), then this increase must be only temporary, and removable by as little as two weeks' social housing.

Rearing condition was found to have no effect on the proportionate production of intermale agonistic and courtship behaviours, nor on such behaviours to females. This indicates that the increased intermale aggressiveness and ano-genital sniff/licking found by Fara and Catlett (1971) and Hull et al (1973) in brief neutral encounters between isolates are not permanent. Also, Gerall's (1963) observation of reduced ano-genital sniff/licking of females in mating tests by isolation-reared males was not supported by this study's findings with regard to cohabiting females.

Although rearing condition did not appear permanently to affect male social behaviour either quantitatively or qualitatively, housing condition did have a marked effect on intermale courtship frequency. All-male housed males rumba-ed to one another more frequently than did mixed housed males during both periods of the experiment, and all-male housed males also ano-genital sniff/licked each other more often during the second (post-pubertal) period. Two possible explanations can be given for this difference. Firstly, male guinea pigs may have some kind of sex drive which comes into operation with the increased secretion of testosterone around puberty, and which leads them to exhibit courtship behaviours to male conspecifics when no females are available. The results obtained here indicate that such a drive must operate independently of past experience of females. The second possible explanation is that intermale courtship may be important in establishing or maintaining the social organisation of all-male, but not of mixed groups.

The results of this study with respect to dominance hierarchies and consistent individual differences in agonistic behaviour frequencies suggest the existence of three levels of social organisation in male guinea pigs. Dominance hierarchies which show the normal close positive relationship with initiated agonistic behaviour, and less close negative relationship with received agonistic behaviour (such that the top ranking male receives least, but the bottom ranking male does not necessarily receive the most) are only found in pubescent or post-pubescent groups containing females. These groups usually show at least a weak relationship between dominance rank and courtship to females.

Dominance hierarchies based on the direction of agonistic behaviours are not found at the second level of social organisation, but consistent individual differences in frequency of initiation and reception of intermale agonistic behaviours are. The relationship between initiated and received agonism is closer than at the first level of organisation, and the animal which initiates the least aggression almost inevitably receives most. This suggests that a major difference between the first and second levels of organisation is in the performance of submissive acts, especially avoidance of highly aggressive individuals by less aggressive ones. It seems probable that the development of a dominance hierarchy and the organisation of submissive behaviour occur at the same time and are mutually dependent. Also, it seems that females must be present for a dominance hierarchy to be formed. The second level of organisation was found in one of the mixed and one of the all-male Rhcond groups during the first half of the experiment, and in two of the all-male Hcond groups (mixed Rcond x all-male Hcond, and all-male

Rcond x all-male Hcond) in the second half.

The third level of social organisation in male guinea pigs is actually one of apparent disorganisation, when no dominance hierarchy or consistent individual differences in initiated or received intermale behaviours are found. This disorganisation was found in one of the all-male Rhcond groups in the first half of the experiment, and in one of the all-male Hcond groups (isolation Rcond x all-male Hcond) in the second half. Thus it appeared that organisation to the second level required postpubescent housing of males together for several weeks at least. If females were present, however, social organisation progressed much more rapidly such that the isolation Rcond x mixed Hcond males developed a dominance hierarchy within a few weeks.

It was notable from the results of this experiment that intermale courtship showed little or no relationship either with dominance status or with consistent differences in initiated or received agonism (aggressiveness). Thus it appears that intermale courtship is not important in either the development or the maintenance of social organisation in male guinea pigs, even in all-male groups.

The results of this experiment suggest that the level of social organisation reached by a group of male guinea pigs depends mainly on their age and housing condition. Rearing condition appears to be unimportant. However, the effects of rearing condition and group (rearing x housing condition) on weight and weight change suggest that the housing of isolation-reared males with females is very stressful, possibly because the group is undergoing a very rapid period of social organisation. It was also observed that these animals showed more evidence of severe fighting outside Observation Periods in terms of body wounds (especially on the low-ranking males) than did any of the other groups.

Since the isolation reared x all-male housed males also did not gain as much weight as the socially-reared males in the second half of the experiment, it appears that the experience of cohabiting with other males was stressful to the isolation-reared animals, even though they had not yet become socially organised.

The results of intra-group comparisons of weights, weight change and social structure are particularly interesting. The observation that in two groups (A and C), the weight measures were positively correlated with social organisation (dominance status or aggressiveness) contradicts Berryman's finding that weight was not related to dominance rank. However, the fact that real weight was actually negatively related to present and future dominance rank in group E (isolation Rcond x mixed Hcond), while weight change was positively related to dominance status suggests that a male's weight does not determine his success in agonistic interactions, but rather that his success (or failure) does affect his future weight, probably by the physiological effects of stress. Thus the correlations found between weight, weight change and social status in groups A (mixed Rcond x mixed Hcond) and C (all-male Rcond x all-male Hcond) probably reflect the long-term effects of social position or of success in agonistic encounters on weight gain rather than a relationship between initial weight and future social status. The fact that groups A and C had both had constant group compositions since weaning might account for the closer relationship between weights, weight change and social status in these groups than in groups B (mixed Rcond x all-male Hcond) and D (all-male Rcond x mixed Hcond).

7.2

Courtship tests.

7.2.1

Introduction.

As with the first part of this experiment, the aim of investigating courtship behaviour was to make comparisons not only of the overall effects of early social isolation and all-male versus mixed housing on courtship, but also of individual performance in courtship tests with dominance rank and individual aggressiveness in the home group.

Most previous tests of male guinea pig sexual behaviour have involved actual mating tests, in which male guinea pigs were individually paired with an oestrous female. These tests have shown that early isolation (and to a lesser extent, all-male housing from weaning) reduces copulatory ability, and in particular reduces the amount of ano-genital sniff/licking of females (Gerall, 1963). All the evidence suggests, however, that these effects are only temporary and are removed by subsequent social housing or prolonged experience of mating tests (see chapter Six).

Only Riss and Goy (1957) have reported a group mating test in which a cohabiting group of sexually experienced males were simultaneously tested with one oestrous female. The results indicated that a similar pattern of behaviour occurred with this unfamiliar female as is usually seen during mating chases in semi-natural colonies of guinea pigs i.e. one male not only achieved the first copulation but also succeeded in keeping the other males away from the females most of the time.

In the present study, anoestrous females were used so that courtship rather than copulatory behaviour would be observed. It appears that male guinea pigs are attracted to anoestrous females in much the same way as to those in oestrus, and show courtship behaviours to both. Thus it was expected that early isolation or all-male rearing would have similar effects on male courtship behaviour to anoestrous females as on copulatory behaviour to females in oestrus. It has been suggested that male courtship of anoestrous females might in some way increase the probability of the male achieving first mating during oestrus (thus increasing his likelihood of reproductive success), though how this connection could be made is not yet clear (see chapter Five).

In this study, it was desired to compare frequency of courtship in group courtship tests with present and future aspects of male social structure, expecially dominance, according to social experience. A further important aspect of this study was to compare performance in individual courtship tests with group social structure. For the socially housed males, an individual test would mean that each animal was not under the influence of aggressive or other social pressure from other group members. Thus if differences in courtship performance seen in group tests or in spontaneous intra-group activity were due entirely to social factors rather than to individual differences in sexual activity, it would be expected that no relationship between individual courtship and intra-group dominance or aggressiveness would be found. If, on the other hand, an animal's sexual activity was affected not just by direct social pressure from the other members of its group, but also by its social position e.g. by means of 'confidence' level, then persistent differences in individual courtship (mirroring social position) might be found. The same results would also occur if social position and/or general aggressiveness were dependent on some innate factor which also determined sexual activity. It was thought that the results of the first individual courtship tests (i.e. before grouping) on the isolation- reared males might be particularly interesting in this respect, as these animals had not yet been influenced by group social structure. Their performance could, however, be compared with their future social position during subsequent grouping.

7.2.2

Method.

Test Females

Females used for the mating tests were from the same stock as the experimental males. They were nulliparous and aged from 3-8 months at the time of testing. Females were housed together in small groups in the same room as the mixed group experimental animals.

Whenever courtship tests were to be made, all the test females were checked for the presence or absence of a vaginal closure membrane (Stockard and Papanicolaou, 1919). Only those whose membrane was complete i.e. those which were anoestrous, were used for testing on that day. No female was used for more than one courtship test on any one day.

Apparatus.

Tests were carried out in the home room of the male/s to be tested. Each isolate male was tested in his home cage (Bowman white plastic; 39 x 29.5 x 17.5cm) which was placed with its top removed inside a circular open field for the duration of the test. This open field measured 70cm in diameter and 30.5cm in height and was painted matt black with white lines across the floor. The cage was lit by a 40W red bulb in an Anglepoise lamp situated 110cm above its base.

Group-housed males were tested in their open-topped home box (white-painted chipboard; 62.5 x 61 x 31.5cm). This box was lit by the Anglepoise lamp described above, positioned 110cm above the box's base.

Two Smiths stopclocks were used for timing the tests and for timing the total duration of purring by each male in the Individual Courtship tests.

A minute before testing, each male or group of males to be tested was temporarily transferred either to a clean white plastic cage (Bowman, described above) in the case of isolates, or to a circular open field (described above) in the case of grouped males.

Procedure

Testing was carried out during the dark period, between 1430 and 1630 hours.

Home group females (if any) were removed from the home box five hours before testing began in order to reduce possible effects of sexual fatigue. Food containers and water bottles were removed from the test cage or box immediately before testing. Only one test female was used per test, for both Individual and Group Courtship tests. The test female was placed in the test cage or box one minute before each test began so that she could become acclimatised to her surroundings.

For the Individual Courtship tests, a single male was placed in the test cage or box as one stopclock was started. The experimenter sat on a stool adjacent to the cage or box and recorded the male's behaviour on a check sheet. For 10 minutes the experimenter scored the latencies to first ano-genital sniff/lick, rumba and attempted mount and the frequencies of these behaviours. Frequencies were scored in 30 second blocks throughout the 10 minute period. Using the other stopclock, the experimenter also recorded the total amount of time the male spent purring (Berryman, 1978) during the test. At the end, the female was returned to her home cage, and the male was either left in his home cage (in the case of isolates) or removed to the open field (in the case of group-living males) until testing of the other males in his group was completed for the day. Home group females, food containers and water bottles were replaced when testing was over.

Group Courtship tests were carried out only after all the males in the group had been subjected to Individual Courtship tests, and never on the same day as any of these tests. The procedure for Group Courtship tests was the same as for Individual tests, with the following differences. All four males in a socially-housed group were replaced simultaneously in the test box and the stopclock started.

For the following 30 minutes the latencies to first ano-genital sniff/lick, rumba and attempted mount of the test female, and the frequencies of these behaviours, were scored for each male. Frequencies of behaviours were recorded in one-minute blocks. At the end of 30 minutes the test female was returned to her home cage, and food and water containers were replaced in the males' home box. Duration of purring was not recorded in the Group tests, because it was too difficult to determine which animals were purring at any one time.

Treatment of results.

Courtship behaviour frequency: Inter-group comparisons.

Medians for each experimental condition were tabulated for both the Individual and Group Courtship tests. In order to obtain these scores and to perform statistical analyses on the latency data, missing data (i.e. cases where an animal never showed one of the behaviours during a test) were replaced by maximum latency scores. Thus maximum scores of 600 and 1800 seconds were used for the Individual and Group Courtship tests respectively.

Kruskal-Wallis one-way analyses of variance were performed on the first and second Individual Courtship test frequency and latency data for ano-genital sniff/licks, rumbas and attempted mounts. The total time spent purring (duration of purring) was analysed similarly.

Mann-Whitney U tests and Kruskal-Wallis one-way analyses of variance were performed on the first and second Group Courtship test frequency and latency data for ano-genital sniff/licks, rumbas and attempted mounts.

Dominance and courtship behaviour frequency: Intra-group comparisons.

Seven behavioural measures taken in the Individual Courtship tests were each ranked within each group (Tests 1 and 2 treated separately) such that ranks of 1 were assigned to animals which performed any behaviour most often or at the shortest latency within each group. The behavioural measures used were frequency and latency to ano-genital sniff/lick, rumba and attempted mount, and total time spent purring.

Friedman two way analyses of variance were performed on these ranked scores in order to show whether they were internally consistent within each group. In cases in which significant consistency was found, and the group had also been shown to have an agonistic dominance hierarchy (from the Observation Period 2 data), a further analysis was carried out with dominance ranks included. If this analysis gave a greater Chi-r-squared value than the previous one, then a positive relationship between dominance status and Individual Courtship test behaviour was indicated. A similar analysis was performed in groups which did not have a dominance hierarchy, but which did have individually consistent scores on initiated aggression and Individual Courtship. In this case, the further analysis included both initiated agonism and Individual Courtship results so as to show how closely these measures were related to each other.

The behavioural measures obtained from the Group Courtship tests were treated in the same way as those from the Individual Courtship tests. The Group Courtship measures used in the analysis of courtship consistency within groups were the frequencies and latencies to ano-genital sniff/lick, rumba and attempted mount.

7.2.3

Results.

7.2.3.1

Individual courtship test 1.

Courtship behaviour frequency: Inter-group comparisons.

Table 7.12 gives the medians and the results of the Kruskal-Wallis analyses of variance for each behavioural measure obtained for each Rhcond in Individual Courtship test 1.

Significant effects of Rhcond were found on the frequencies of rumbas and attempted mounts, and on the latencies to first attempted mount. Males in the all-male Rhcond rumba-ed most frequently while those in the mixed Rhcond rumba-ed least frequently. Males in the isolation Rhcond showed a rumba frequency midway between those of the other social conditions. The effect of Rhcond on frequency and latency of attempted mounting appeared to be due to the complete lack of production of this behaviour by the isolated males.

The Kruskal-Wallis results for the frequency of ano-genital sniff/licks and the latency to first ano-genital sniff/lick revealed effects of Rhcond which approached significance. Mixed Rhcond males sniff/licked most often, and the isolated males showed very little

Behavioural measure	Rhcond	Median score	H value (Rhcond)	Df	P
No. of ano-genital sniff/licks.	MF	14.0	5.21	2	.07
	M	9.5			
	I	1.5			
No. of rumbas.	MF	7.5	6.26	2	.04*
	M	17.5			
	I	11.0			
No. of attempted mounts.	MF	2.5	7.36	2	.03*
	M	2.5			
	I	0.0			
Duration of purring.	MF	169.5	0.23	2	.89
	M	86.0			
	I	112.0			
Latency to first ano-genital sniff/lick.	MF	29.5	5.50	2	.06
	M	101.0			
	I	278.5			
Latency to first rumba.	MF	96.0	0.11	2	.95
	M	94.0			
	I	57.5			
Latency to first attempted mount.	MF	153.5	7.27	2	.03*
	M	188.5			
	I	600.0			

* = $p<.05$

Rhcond = Rearing/housing condition.

(MF = Mixed, M = All-male, I = Isolation

Chi-r-squared scores for which agonistic dominance ranks were included are underlined.

Table 7.12

Guinea pig Individual Courtship test 1: Median scores and results of Kruskal-Wallis one-way analyses of variance.

sniff/licking of the test females. The median score of the all-male Rhcond fell between those of the other two conditions. This frequency effect may have been due to the fact that mixed Rhcond males initiated sniff/licking very early during their tests, while the all-male Rhcond and isolated males took considerably longer. The isolated males were slower to sniff/lick than were the all-male Rhcond animals.

Dominance and courtship behaviour frequency: Intra-group comparisons.

Table 7.3 gives the results of the Friedman two way analyses of variance performed on the ranked courtship behaviours from Individual Courtship Test 1. Only two groups, group C (all-male Rcond x all-male Hcond) and group E (isolation Rcond x mixed Hcond) showed significantly consistent ranking across the measures of courtship behaviour. When second Observation Period agonistic dominance ranks were included in a further analysis of group E′s data, the value of Chi-r-squared was reduced (though still reached significance), indicating that the animals′ courtship behaviour was not very closely related to their future dominance ranks. Further analysis of group C′s combined initiated agonism and Individual Courtship Test 1 results gave a higher Chi-r-squared value than had been found for either set of data independently. This indicated a close relationship between intra-group aggressiveness and Individual Courtship.

7.2.3.2

Individual courtship test 2.

Courtship behaviour frequency: Inter-group comparisons.

Tables 7.13 a-g and 7.14 give the median scores and the results of Kruskal-Wallis analyses of variance respectively of the data obtained in the second Individual Courtship tests.

None of the behavioural measures showed significant effects of Rcond, Hcond or Group (Rcond x Hcond). However, there was a trend approaching significance for males from the mixed Rcond to ano-genital sniff/lick less frequently than the all-male and isolation Rcond males. This trend appeared to be due to a considerable increase in ano-genital sniff/licking by the all-male and isolation Rcond males in the second test as compared with their low scores in the first Individual Courtship test (see Table 7.12). The scores for the mixed Rcond males showed little change between tests 1 and 2.

Dominance and courtship behaviour frequency: Intra-group comparisons.

Table 7.8 gives the results of the Friedman two way analyses of variance on the ranked Individual Courtship Test 2 behaviours. Two of the three mixed Hcond groups, group A (mixed Rcond x mixed Hcond) and group E (isolation Rcond x mixed Hcond) showed consistent within group ranking on the measures taken. Further analyses of these results in which agonistic dominance ranks were included gave increased Chi-r-squared values for both group A and group E, indicating close relationships between dominance status and Individual Courtship test 2

Median scores.

	Rcond		
Hcond	MF	M	I
MF	15.5	22.0	18.5
M	8.5	20.0	20.0

Table 7.13 a.
No. of ano-genital sniff/licks.

Median scores.

	Rcond		
	MF	M	I
MF	14.0	6.5	17.5
M	15.5	11.5	11.0

Table 7.13 b.
No. of rumbas.

	Rcond		
Hcond	MF	M	I
MF	0.5	0.5	17.5
M	4.0	0.5	1.0

Table 7.13 c.
No. of attempted mounts.

	Rcond		
	MF	M	I
MF	99.0	61.0	118.0
M	174.0	70.0	82.5

Table 7.13 d.
Duration of purring (secs).

	Rcond		
Hcond	MF	M	I
MF	54.5	12.5	46.0
M	11.5	21.0	89.0

Table 7.13 e.
Latency to first ano-genital sniff/lick (secs).

	Rcond		
	MF	M	I
MF	59.0	18.0	49.0
M	65.0	11.5	62.5

Table 7.13 f.
Latency to first rumba (secs).

	Rcond		
Hcond	MF	M	I
MF	278.5	512.0	127.5
M	320.0	395.0	212.5

Table 7.13 g.
Latency to first attempted mount (secs.).

Rcond = Rearing condition.
Hcond = Housing condition.
(MF = Mixed, M = All-male, I = Isolation)

Tables 7.13 a-g.
Guinea pig Individual Courtship test 2: Median scores.

Behavioural measure	Variable	H value	Df	P
No. of ano-genital sniff/licks.	Rcond	5.92	2	.05
	Hcond	0.56	1	.45
	Group	6.74	5	.24
No. of rumbas.	Rcond	4.93	2	.09
	Hcond	0.19	1	.67
	Group	7.57	5	.13
No. of attempted mounts.	Rcond	4.19	2	.12
	Hcond	0.24	1	.62
	Group	7.78	5	.17
Duration of purring (secs).	Rcond	4.97	2	.08
	Hcond	0.40	1	.53
	Group	6.41	5	.27
Latency to first ano-genital sniff/lick (secs).	Rcond	4.28	2	.12
	Hcond	0.14	1	.71
	Group	9.12	5	.10
Latency to first rumba (secs).	Rcond	4.09	2	.13
	Hcond	0.30	1	.58
	Group	4.43	5	.49
Latency to first attempted mount (secs).	Rcond	2.63	2	.27
	Hcond	0.19	1	.67
	Group	3.42	5	.64

Rcond = Rearing condition.
Hcond = Housing condition.
Group = Each group (i.e. rearing x housing condition) separately.

Table 7.14
Guinea pig Individual Courtship test 2: Results of Kruskal-Wallis one-way analyses of variance.

behaviours.

Group D (all-male Rcond x mixed Hcond) showed no consistent ranking across the courtship behaviour measures.

None of the all-male Hcond groups (B, C and F) showed internally consistent ranking on these measures.

7.2.3.3

Group courtship test 1.

Courtship behaviour frequency: Inter-group comparisons.

Table 7.15 shows the medians and results of Mann-Whitney U tests of the data for both the mixed and all-male Rhconds in the first Group Courtship test (n.b. the isolation Rhcond was not tested at this stage). No effect of Rhcond was found on the frequencies of, or latencies to, ano-genital sniff/lick, rumba or attempted mount.

Dominance and courtship behaviour frequency: Intra-group comparisons.

Table 7.3 presents the results of Friedman two way analyses of variance on the ranked Group Courtship test 1 behavioural measures.

Groups A (mixed Rhcond), B (mixed Rhcond) and D(all-male Rhcond) showed consistent ranking across behavioural measures. Further analyses of group A's and group D's data in which second Observation Period agonistic dominance ranks were included (these ranks were the same for group A in both Observation Periods) produced increased

Behavioural measure	Rhcond	Median score	U value (Rhcond)	P
No. of ano-genital sniff/licks.	MF	7.5	29.5	>.05
	M	9.5		
No. of rumbas.	MF	2.0	27.5	>.05
	M	6.0		
No. of attempted mounts.	MF	0.0	27.0	>.05
	M	0.0		
Latency to first ano-genital sniff/lick (secs.).	MF	88.5	26.0	>.05
	M	83.5		
Latency to first rumba (secs).	MF	446.0	29.0	>.05
	M	651.0		
Latency to first attempted mount (secs).	MF	1800	28.0	>.05
	M	1800		

Rhcond = Rearing/housing condition.
(MF = Mixed, M = All-male)

Table 7.15
Guinea pig Group Courtship test 1: Medians and results of Mann-Whitney U tests.

Chi-r-squared values in both groups. These results indicated that in group A, Group Courtship behaviour was closely related to present and future dominance status, while in group D this behaviour was closely related to future dominance status. A further Friedman analysis of group B's combined ranked Group Courtship test 1 and initiated agonism scores gave an increased value of Chi-r-squared (see Table 7.3). This indicated that there was a close relationship between aggressiveness and Group Courtship behaviour in this group.

Group C (all-male Rhcond) showed no within group consistency of ranking across the courtship behaviours.

7.2.3.4

Group courtship test 2.

Courtship behaviour frequency: Inter-group comparisons.

The medians of behaviour scores for each social condition in the second Group Courtship tests are given in Tables 7.16 a-f. Table 7.17 shows the results of Kruskal-Wallis analyses of variance on these data. No effects of Rcond, Hcond or Group (Rcond x Hcond) were found on any of the behavioural measures taken.

Dominance and courtship behaviour frequency: Intra-group comparisons.

Table 7.8 gives the results of Friedman two way analyses of variance on the ranked Group Courtship test 2 behavioural measures.

All three mixed Hcond groups (A, D and E) showed consistent

Median scores.

		Rcond	
Hcond	MF	M	I
MF	9.5	12.5	7.5
M	15.5	12.5	14.0

Table 7.16 a.
No. of ano-genital sniff/licks.

Median scores.

		Rcond	
	MF	M	I
MF	4.5	3.5	2.0
M	9.5	3.0	2.5

Table 7.16 b.
No. of rumbas.

		Rcond	
Hcond	MF	M	I
MF	3.5	0.5	3.0
M	0.5	0.0	0.0

Table 7.16 c.
No. of attempted mounts.

		Rcond	
	MF	M	I
MF	40.0	155.5	504.5
M	41.5	64.5	176.0

Table 7.16 d.
Latency to first ano-genital sniff/lick (secs).

		Rcond	
Hcond	MF	M	I
MF	665.0	551.0	1093.5
M	85.0	522.0	547.5

Table 7.16 e.
Latency to first rumba (secs).

		Rcond	
	MF	M	I
MF	261.5	1175.0	1175.0
M	1519.0	1800*	1800*

Table 7.16 f.
Latency to first attempted mount (secs).

* 1800 = substituted maximum score for animals which never attempted to mount on test.
Rcond = Rearing condition.
Hcond = Housing condition.
(MF = Mixed, M = All-male, I = Isolation).

Tables 7.16 a-f.
Guinea pig Group Courtship test 2: Median scores.

Behavioural measure	Variable	H value	Df	P
No. of ano-genital sniff/licks.	Rcond	0.42	2	.81
	Hcond	0.07	1	.80
	Group	1.33	5	.93
No. of rumbas.	Rcond	0.76	2	.68
	Hcond	0.10	1	.75
	Group	2.14	5	.83
No. of attempted mounts.	Rcond	1.20	2	.55
	Hcond	3.10	1	.08
	Group	4.54	5	.47
Latency to first ano-genital sniff/lick (secs).	Rcond	1.37	2	.51
	Hcond	1.02	1	.31
	Group	3.31	5	.57
Latency to first rumba (secs).	Rcond	0.21	2	.90
	Hcond	0.24	1	.62
	Group	1.12	5	.95
Latency to first attempted mount (secs).	Rcond	1.42	2	.49
	Hcond	2.71	1	.10
	Group	4.33	5	.50

Rcond = Rearing condition.
Hcond = Housing condition.
Group = Each group (i.e. rearing x housing condition) separately.

Table 7.17
Guinea pig Group Courtship test 2: Results of Kruskal-Wallis one-way analyses of variance.

ranking across the courtship measures and also increased values of Chi-r-squared when agonistic dominance ranks were included in the analyses. Thus Group Courtship behaviour appeared to be closely related to dominance status in all the mixed Hcond groups.

Two of the all-male Hcond groups, group B (mixed Rcond x all-male Hcond) and group C (all-male Rcond x all-male Hcond) showed significant within group consistency of ranking across the measures of courtship behaviour. Group F (isolation Rcond x all-male Hcond), however, showed no within group consistency of courtship ranking. Further analysis of group B's combined initiated agonistic and Group Courtship test 2 results gave a lower (though still significant) Chi-r-squared value than had been found for either independent analysis. This suggested that the relationship between individual intra-group aggressiveness and Group Courtship was not very close in Group B. A similar analysis performed on group C's data, however, gave a very high Chi-r-squared value, indicating a very close relationship between individual intra-group aggressiveness and Group Courtship in group C.

7.2.4

Discussion.

The inter-group comparisons of courtship behaviour in Individual Courtship test 1 revealed a similar effect of early isolation to that found by Gerall (1963) i.e. a reduction in ano-genital sniff/licking to test females. The all-male reared males also showed a reduction in this behaviour, but to a lesser extent. Corresponding differences between the rearing conditions in latency to first sniff/lick suggest, however, that this effect of early experience on courtship behaviour did not necessarily represent a specific behaviour change, but rather was due to the unfamiliarity of the stimulus females to these males. It seems likely that the isolation and all-male Rhcond males were somewhat retiscent at first to approach a strange-smelling (i.e. female) animal sufficiently closely to sniff it.

The greater number of rumbas shown by the all-male Rhcond males (and to a lesser extent by the isolation Rhcond males) than by the mixed Rhcond males to females in Individual Courtship test 1 had not previously been reported. It is possible to speculate that the unfamiliar stimulus of a female both frightened and excited these males at first, so that they resorted to performing a courtship behaviour which did not require such close proximity as sniffing.

The observation that the isolation Rhcond males did not rumba as much as the all-male Rhcond males may have been due to the non-specific reduction in sexual activity found in isolated males by Riss and Goy (1957). Also, each isolated male was in a much more confined space (i.e. his small home cage) with the test female than were the socially-housed males. This enforced proximity may have inhibited courtship behaviour by the isolates even more.

The mixed Rhcond males seemed to ano-genital sniff/lick and attempt to mount the females more often than they rumba-ed to them. The absence of attempted mounts by isolation Rhcond males was probably due to their inexperience of conspecifics, which had made them cautious of physical contact. Also, their lack of social experience may have prevented them from reaching a mature state of sexual behaviour organisation.

None of these effects of early experience on courtship behaviour was permanent, as all had disappeared by Individual Courtship test 2, i.e. after a period of social housing for the isolates. The differences between all-male and mixed Rhcond male courtship found in Individual Courtship test 1 were not evident in Group Courtship test 1, possibly because the all-male Rhcond animals had lost their retiscence to approach females by then.

The results of the Group Courtship tests on mixed housed males showed that group courtship behaviour was very closely related to group social structure as previously reported in semi-natural colonies by Rood (1972), Berryman (1978) and in Colony Study 2. In all groups in which a dominance hierarchy had been found, this hierarchy was very closely related to group courtship behaviour. Correspondingly, in the only mixed housed group without a dominance hierarchy (group B in test 1), group courtship was closely related to individual intra-group aggressiveness.

These results could be due either to the influence of other group members on each individual's behaviour or to individual differences in sexual activity (either innate or due to 'confidence'), or to a combination of these factors. The observation that neither of the mixed Rhcond groups (A and B) showed a relationship between Individual Courtship test 1 results and social structure suggests that any innate differences in sexual activity which might have existed cannot have been of overriding importance. Equally, 'confidence' cannot have been of paramount importance, at least not at that stage in the experiment.

However, the observation that two out of three mixed Hcond groups (A and E) showed a close relationship between Individual Courtship test 2 results and dominance status indicates that individual 'confidence' level may affect sexual activity, expecially in adult males with a stable dominance hierarchy. Additionally, the fact that group E's (isolation Rhcond) Individual Courtship test 1 results showed consistent individual differences in courtship which were slightly related to future dominance status suggests that if innate individual differences between members of a group are sufficiently great, these differences may influence the development of a social structure within that group.

The absence of a relationship between social structure and courtship behaviour in group D's (all-male Rcond x mixed Hcond) Individual Courtship test 2 results shows that 'confidence' cannot have been the only factor affecting sexual activity at that time.

The results of courtship tests on all-male housed males were somewhat more variable than those on mixed housed males. In Group Courtship test 1, only one all-male Rhcond group (D) showed consistent individual differences in courtship behaviour. This group did not show consistent differences in initiated agonism in Observation Period 1, so no comparison between group courtship behaviour and aggressiveness could be made. However, a comparison of group D's group courtship results with future dominance status did reveal a close relationship between these factors. This suggests either that group D's social structure became more organised, e.g. to the second level of organisation, between Observation Period 1 and Group Courtship Test 1, or that individual differences in sexual activity did not necessarily correspond to similar differences in aggressiveness. The observation that group D did not quite show consistent individual differences in Individual Courtship Test 1 (which was given shortly before Group Courtship Test 1) suggests that the former hypothesis is more probable.

In Group Courtship Test 2, two of the all-male Hcond groups, B (mixed Rcond x all-male Hcond) and C (all-male Rcond x all-male Hcond) showed consistent differences in individual courtship behaviour. Both of these groups showed consistent individual differences in initiated agonism in Observation Period 2, but only in group C was this found to be closely related to group courtship behaviour, as also observed by Riss and Goy (1957). Neither group B nor group C showed consistent differences in behaviour in Individual Courtship test 2, thus replicating the findings of Riss and Goy (1957). Group F (isolation Rcond x all-male Hcond) showed no consistent individual differences in any of the courtship tests.

These results for all-male housed groups are difficult to interpret precisely in terms of social structure. However, they may indicate different stages in social organisation between disorganisation (group F) and the level of consistent individual differences in courtship to females and in initiated and received agonism (group C).

In conclusion, it seems that both innate individual differences and 'confidence' from previous agonistic experience can influence the courtship behaviour of male guinea pigs in individual tests, though innate differences are not often great enough to have much effect. In group tests, courtship behaviour appears to reflect the level of social organisation of the group such that it is closely correlated with either dominance status or with individual aggressiveness in groups which have reached sufficiently high levels of social organisation.

Three factors could contribute to this close correlation between group courtship and agonism: direct intermale aggression, which is probably increased by competition for the female (Riss and Goy, 1957; Rood, 1972; Colony study 3); 'confidence' level from previous agonistic experience, which appears to affect courtship as well as agonistic behaviour; innate differences in sexual activity, which might correspond to innate differences in aggressiveness.

The extent to which individual aggressiveness and dominance status are caused by innate differences between animals is not clear from this experiment. However, the limited evidence available suggests that innate differences (possibly hormonal) may, when they are large enough, have some initial effect on group social structure, particularly on the speed with which a group attains a high level of social organisation. Agonistic experience may then act on these innate differences by a process of change in 'confidence' level so that the individual differences become larger and more consistent.

7.3

Water competition tests.

7.3.1

Introduction.

Water Competition tests were carried out in this experiment so that comparisons of agonistic dominance or aggressiveness and priority of access to water could be made.

The principle role of dominance in guinea pigs has been shown to be the allocation of reproductive success (Rood, 1972; Martan and Shepherd, 1976; Berryman, 1978). The long gestation period and small litter size of guinea pigs means that competition for reproductive success will always be strong, but the presumed natural habitat of guinea pigs does not normally have shortages of food or water (Rood, 1972). Thus it might be speculated that competition for food and water would be rare, and that females, especially pregnant females, may well have priority over males should this situation arise (Bates et al, 1973). However, if males are forced to compete with each other for food or water, it would be expected that agonistic dominance relationships might at least influence the outcome of the competition. After all, the 'confidence' of an individual and his perception of other males' cues will be no different in this situation than in any other, so if a high-ranking male approached a small water source, a subordinate already at that source would be expected to flee.

Berryman (1978) is the only person who has previously reported a comparison between colony water competition and dominance and aggressiveness in male guinea pigs. She found a weak relationship between these measures, (especially the number of drinking bouts), and intra-group dominance. In the present study, similar measures of success in a water competition were used as in Berryman's study. However, in this case, the measures of water gain were compared with one another to establish whether or not individual differences in success on these measures were consistent. If consistent individual differences were found, then these were subsequently compared with intra-group dominance or aggressiveness.

7.3.2

Method.

Apparatus.

A 500ml glass drinking bottle with a 9mm diameter spout was used for these tests. This was the type of water bottle which was normally used in the guinea pig boxes. Since a guinea pig places its mouth over the end of the spout in order to drink, only one animal could drink from the bottle at a time.

Tests were timed using a Smiths stopclock.

Procedure.

These tests were carried out in the home box during the first three hours of darkness, at least one day after the Group Courtship test. The box was lit by red light and the experimenter positioned as described above for the courtship tests. The water bottle was removed

16 hours prior to testing and was replaced at the beginning of the test. The test lasted 10 minutes, during which the experimenter scored the identity of the drinking animal every 5 seconds on a check sheet.

Treatment of results.

The results were analysed to give three measures of priority of access to water: total time spent drinking, mean drinking bout length, and order of first access to the water spout within each group. All three measures were ranked within each group of animals such that ranks of 1 were assigned to the males which spent most time drinking, had the longest mean drinking bout length and reached the water spout first. Friedman two way analyses of variance were performed on these ranks in order to find out whether the animals in each group were consistently ranked on these measures. In groups for which an agonistic dominance hierarchy had been found (see sections 7.1.3.1-2 above) and the Friedman analysis indicated consistent ranking over the three measures of water access priority, the dominance ranks were included in an additional analysis. This would indicate whether ranking on priority of access to water was related to agonistic dominance order.

7.3.3

Results.

7.3.3.1

Water competition test 1.

Table 7.3 gives the results of the Friedman two way analyses of variance performed on the first water competition data. No significant consistency of ranking was found in the three measures of water access priority for group A (mixed Rhcond).

Group B (mixed Rhcond) showed a significant consistency of rank order on the three measures of priority of access to water. Further analysis of combined initiated aggression and water competition results gave a high Chi-r-squared value, indicating a close relationship between these two measures.

Neither group C (all-male Rhcond) nor group D (all-male Rhcond) showed consistent ranking across time spent drinking, mean drinking bout length and order of access to the water spout. However, it was noted that the animals in group D were ranked identically for both time spent drinking and mean bout length.

7.3.3.2

Water competition test 2.

Table 7.8 presents the results of the Friedman two way analyses of variance performed on the second water competition data.

Groups A (mixed Rcond x mixed Hcond) and D (all-male Rcond x mixed Hcond) both showed significantly similar ranking on the three measures of water access priority. Increased values of Chi-r-squared were found when the agonistic dominance ranks of these groups were included in the analyses, indicating that agonistic dominance was closely related to water access priority in both groups A and D.

Group E (isolation Rcond x mixed Hcond), however, did not show consistent ranking on the three measures of water access priority.

Neither group B (mixed Rcond x all-male Hcond) nor group F (isolation Rcond x all-male Hcond) showed consistent ranking between the three measures of water access priority. However, the animals in group C (all-male Rcond x all-male Hcond) were identically ranked across all these measures. Further analysis of group C's combined water competition and initiated aggression results gave a very high Chi-r-squared value, indicating a very close relationship between these measures.

7.3.4

Discussion.

In all the cases where consistent ranking across the three measures of water priority was found, this order was also closely related to the group's social structure i.e. to dominance status or to aggressiveness. Also, in all these cases, group courtship behaviour had been found to be closely related to social structure. These results show a closer correlation between water priority and dominance or aggressiveness than was found by Berryman (1978).

None of the groups which did not show a high level of social organisation (i.e. an agonistic dominance hierarchy , or closely related individual differences in initiated and received aggression) was found to have consistent ranking across the three measures of success in water competition.

These findings suggest that priority of access to water is closely related to social structure, so long as the group concerned has reached a sufficiently high level of social organisation. This supports the theory that the dominance hierarchy (or social organisation approaching the level of the dominance hierarchy) should influence success in water competition. In groups with dominance hierarchies this would occur because of the tendency of low-ranking males to avoid high-ranking males through a process of both cue assessment and 'confidence'.

In organised groups which have not yet developed a dominance hierarchy, it is presumed that different levels of 'confidence' would cause males to be more or less hesitant to approach others and more or less ready to flee from them. 'Confidence' level may also be related to hesitancy to approach the water spout, thus the more 'confident' males would tend to reach the spout first and not be challenged by less 'confident' males while they were there.

7c

General Discussion.

This experiment has shown that the experience of isolation or all-male housing on male guinea pigs between weaning and puberty has no permanent effects on either the courtship of females or the initiation of agonistic behaviours to cohabiting males. However, males in all-male groups court each other significantly more often than do males in mixed groups, no matter what their previous social or sexual experience. This intermale courtship bears no relation to intra-group social structure in terms of initiated or received agonism and appears to be due to some kind of sex drive which is probably associated with increased testosterone secretion after puberty.

The small number of groups studied in this experiment makes it difficult to draw full conclusions about the effects of social experience on male guinea pig social structure. However, the results do give strong indications of different levels of social organisation which seem dependent on current housing condition, innate individual differences and the length of time for which tha animals have been housed together. Rearing condition (from weaning to puberty) has no apparent effect on social organisation, though the grouping of males after early isolation stresses them considerably (as shown by unusually small weight gain and an increased number of wounds).

It appears that male guinea pig social organisation progresses from a state of disorganisation through a state of agonistic consistency without dominance to the final state of the dominance hierarchy. Disorganisation is shown by the absence not only of consistent directional dominance, but also of consistency in frequency of initiation and reception of agonistic behaviours. The animals in disorganised groups also tend not to show consistent courtship behaviour frequency differences in either Group or Individual courtship tests, nor are they consistently ranked on measures of priority of access to water. This stage was found only in all-male groups which had either just reached puberty or had only been housed together for a couple of weeks.

The second stage of social organisation, agonistic consistency without dominance, is shown by consistent differences between individuals in the frequency of initiation and reception of agonistic behaviours. Also, initiation and reception frequency are very closely related such that the least aggressive male is likely to receive most aggression. Despite this, consistent directional dominance across the various agonistic behaviours is not found. At this stage, group courtship behaviour is closely related to aggressiveness, but individual courtship usually is not. Water competition success shows a relationship with aggressiveness only in some of these groups. In the present experiment, agonistic consistency without dominance was found in one pubescent all-male group, and in both the mature all-male groups which had been housed together since weaning. It was also found in one pubescent mixed-housed group.

The final stage of social organisation, the dominance hierarchy, is shown by consistent directional dominance across all the agonistic behaviours. Initiated agonism and group courtship behaviour are closely related to dominance rank, and individual courtship behaviour is also often correlated with dominance status. However, received agonism is often not closely related to dominance as the lower-ranking males do not usually receive the most aggression. At this stage, water competition success is usually related to dominance. Dominance hierarchies were found in one pubescent mixed-housed group and in all three mature mixed groups (even after as little as two weeks' cohabitation).

From the evidence of this experiment, it appears that when several male guinea pigs are first housed together, small innate differences in aggressiveness (equivalent, perhaps, to innate 'confidence') between animals will influence the outcome of initial agonistic interactions between them. These innate differences in aggressiveness seem to be related to similar differences in sexual (courtship) activity. As more agonistic interactions are experienced, individual differences in 'confidence' become magnified until they reach the stage of agonistic consistency without dominance. At this point, 'confidence' consistently affects the initiation and reception of agonism, and courtship performance when other group members are present, but is rarely strong enough to influence courtship in individual courtship tests.

The final stage of social organisation, the dominance hierarchy, requires not just consistent individual differences in 'confidence', but also assessment of the resource holding power (Barnard and Burk, 1979; Parker, 1974; Popp and DeVore, 1979) of other group members. Thus the less successful (in agonistic terms) animals actively avoid their superiors, and all animals tend to initiate interactions mainly with closely ranked individuals. It seems that this stage is only reached when females are present in the group. It is possible that active competition for females in a group leads to more intense intermale agonism, thus accelerating the process of social organisation. In groups with dominance hierarchies, win/loss experience, or 'confidence', affects animals to the extent that their social status influences not only their courtship performance when grouped, but often also their courtship behaviour in individual courtship tests. it is possible that this correlation between Individual courtship behaviour and dominance status in mixed groups may be at least partly caused by aversive learning. Thus, if the subordinate males are frequently chased and/or bitten by their superiors (especially by the alpha male) when they court the group females (cf. Colony Study 3), this may condition them against courting females.

The three states of social organisation described above are not intended as all or none stages in the development of social structure, but rather are thought of as positions on a continuum. Thus the time it takes to progress from disorganisation to agonistic consistency without dominance is thought to depend on both the degree of innate difference between group members and the frequency and intensity of intermale interactions. In this experiment, males in mixed groups with dominance hierarchies were not found to interact more frequently than others, suggesting that frequency of interaction might not be the chief factor concerned in progress to this stage of organisation i.e. to cue assessment. However, since no data were obtained on interaction frequency immediately after group formation, it is possible that males in mixed groups did interact more (and possibly more intensely) at that time, so enabling social organisation and the development of cue assessment to take place very fast. Alternatively, males may not be able to assess each other's resource holding power cues unless females are present, no matter how frequently they interact, thus making directional dominance in all-male groups improbable. However, the mechanism by which males might assess cues when females are present is as yet unknown.

In conclusion, this experiment has answered the questions posed in Chapter 5 to the extent that; a) the presence of females does appear to be necessary for the formation of a dominance hierarchy among male guinea pigs, probably because it enables them to assess each other's resource holding power cues; b) males in all-male groups become socially organised to the level of agonistic conistency without dominance, apparently by a process of changes in 'confidence' level as a result of agonistic experience; c) the addition of females to an established all-male group allows them to develop a dominance hierarchy, but whether the removal of females from a mixed group changes its social structure is not clear. In addition, it has been shown that early experience of isolation or all-male housing does not have a permanent affect on agonistic courtship behaviour or on the ability to develop normal social organisation after puberty.

The question still remains as to why the males in all-male groups show any agonistic behaviour to one another at all. Their behaviour does not appear to relate to competition for an immediate resource. However, the fact that their aggressiveness is related to the amount of courtship they show to females in a group courtship test suggests that the development of social organisation to the level of agonistic consistency without dominance in all-male groups functions to accelerate allocation of priority of access to a female when one becomes available. Thus it appears that some social organisation develops in all-male groups in anticipation of competition for females, but that females must actually be present before full organisation to the level of the dominance hierarchy takes place.

Chapter Eight.

AN INVESTIGATION OF THE EFFECTS OF PRE- AND POST-PUBERTAL SOCIAL EXPERIENCE ON THE SOCIAL BEHAVIOUR AND SOCIAL STRUCTURE OF MALE RATS.

8a

General Introduction.

The design of this experiment is essentially the same as that of the experiment on guinea pigs described in chapter Seven.

Rats have previously been found to show permanent effects of early isolation on aspects of non-social behaviour (see chapter Six) and on overall intragroup intermale agonistic behaviour during subsequent social housing (Wahlstrand et al, 1983). These effects have been related to the lack of experience of social play during the postweaning period (Einon et al, 1981; Wahlstrand et al, 1983). The present study was intended to extend these findings with regard to the effects of early isolation on intermale behaviour by looking not only at the overall agonistic behaviour of groups of previously isolated animals, but also at the aggressiveness of the individuals in each group, and at the nature of their interactions. By comparing these results with those obtained from socially reared animals, it could be shown whether early isolates exhibit proportionate as well as absolute differences in their production of agonistic behaviours, and also whether they develop the same type of social structure (in terms of agonistic interactions) as socially-reared males.

In addition to investigating the effects of social isolation, this experiment was designed to look at the influence of the presence of females (both pre- and post-pubertally) on intra-group intermale behaviour. Previous studies have generally indicated an increase in the intensity (and possibly the frequency) of male aggression to intruders and to cohabitants when females are present (see section 1.1.1.4). The present study investigated possible differences in the proportionate production of intermale agonistic behaviours and in male social structure between mixed and all-male groups of rats.

Investigations of early and late social experiences in rats have frequently looked at their effects on mating behaviour. The results of these studies have indicated a general temporary reduction in copulatory ability in isolation and all-male reared rats (see section 6.2.2). Other studies have investigated the relationship between aggression, social structure and reproductive priority (see section 1.2.5.2.2). In the present experiment, mating tests were carried out in an attempt to provide further information not only on the overall effects of social experience on copulatory behaviour, but also to relate reproductive behaviour and priority to the social structures developed in rats with different social experiential histories. Weights and priority of access to water were also measured so that these, too, could be examined in relation to male rat social structure. In this way, it was hoped to build up an overall picture of the nature and function of male rat social behaviour and relationships, and to determine the effects of early isolation or all-male rearing on these factors.

The studies of spontaneous intra-group behaviour (Observations of social behaviour), mating behaviour in tests, and water competitions are reported separately in sections 8.1 to 8.3 (with weight test results included in section 8.1). Information regarding social structure (i.e. aggressiveness and dominance) gained from the social behaviour observations (section 8.1) was compared with the results obtained from the mating and water competition tests (sections 8.2 and 8.3).

8b

General Method.

Subjects

Subjects were 96 male Lister hooded rats bred in this laboratory from stock obtained from Olac, Bicester. They were weaned and assigned to experimental conditions between 21 and 31 days of age. Owing to the large number of animals required it was not possible to set up all the experimental groups at once. However, the same breeding animals (five males and ten females) were used to produce all the experimental subjects.

For three weeks after weaning, isolated animals were kept in NKP M3 white plastic cages (48 x 15 x 13cm.) and socially grouped animals in NKP RB1 white plastic cages (45 x 28 x 22cm.). Thereafter, isolated animals were transferred to NKP RB1s and socially grouped animals to galvanised steel colony cages (Bowman: 80 x 41 x 23.5cm.).

Subjects were given access to food and water ad lib. except during mating tests and in the 16 hour period of water deprivation preceding each water competition test. A light/dark cycle of 12L:12D was maintained. Animals in mixed groups were kept in a room with lights on between midnight and noon, and isolated and all-male group animals were kept in a room with lights on between 1000 and 2200 hours. No females were kept in the latter room.

Subjects were individually identified by the unique patterns of black fur on their backs. Female rats used to form mixed groups were from the same breeding stock and of the same age range as the males they were grouped with.

Design and Procedure.

A summary of the design of this experiment is given in Figure 8.1.

At weaning, subjects were assigned to experimental groups such that littermates were, as far as possible, separated and distributed evenly among the different experimental conditions. Each group contained animals differing in age by less than five days.

For the first part of the experiment, three rearing/housing conditions were set up: mixed; all-male; isolation. Each condition contained eight groups of animals. A mixed group consisted of four males and two females, an all-male group consisted of four males only, and an isolation 'group' was comprised of four isolated males.

For the duration of the first part of the experiment, these conditions were referred to as rearing/housing conditions (Rhconds), as they covered the period in each rat's life from weaning to sexual maturity. During the second part of the experiment (after rehousing

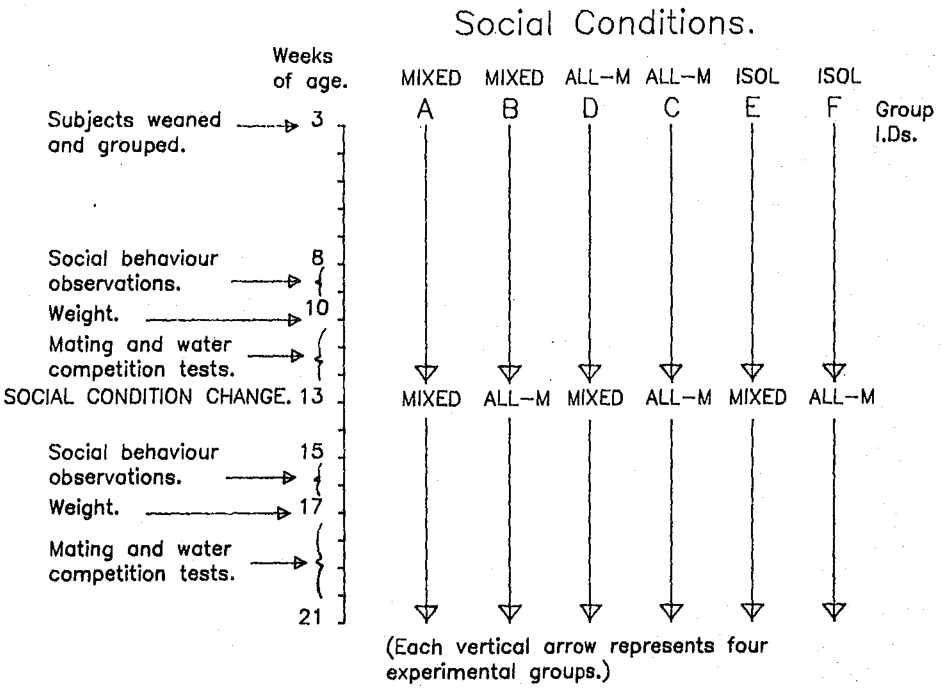

Figure 8.1.
Diagram of experimental design for rats.

as described below), these initial conditions were referred to simply as rearing conditions (Rconds).

Between the fifth and seventh weeks postweaning, the socially housed groups were observed for eight 30 minute sessions as described below. Each subject was weighed at the completion of all eight observation sessions. Over the next three weeks, individual and group mating tests and water competition tests were carried out.

For the second part of the experiment, the housing conditions of the subjects were changed. The previously isolated males were grouped in fours and two females per group were added to half of the groups thus formed. All females were removed from previously mixed groups, and fresh pairs of females were added to half of these groups. Pairs of females were also added to half the all-male Rhcond groups. (All the females added to experimental groups at this stage were nulliparous and had been housed with other females since weaning.) In this way, two new experimental conditions (all-male and mixed) were created, each containing the same number of groups from the three Rhconds (isolation, all-male and mixed). These two new experimental conditions were always referred to as housing conditions (Hconds), to distinguish them from the rearing conditions (Rconds) experienced by the animals during the first part of the experiment.

Between the second and fourth weeks after the change of experimental conditions, all groups were observed for eight 30 minute sessions. Each subject was then weighed again. Further individual and group mating tests and water competition tests were carried out over the next month.

8.1

Observations of social behaviour.

8.1.1

Introduction.

The spontaneous intra-group social behaviour of the group housed male rats described in the previous section was studied in order to investigate the effects of different social experiential histories on social behaviour. The intention was to look at both absolute and proportionate inter-group differences in social, especially agonistic, behaviours, and also to examine the nature of intra-group social structure.

Earlier studies have shown that male rats in established groups rarely attack one another fiercely, but do frequently indulge in low-key aggressive acts such as boxing, on-top-of, and aggressive grooming (Seward, 1945a; Alberts and Galef, 1973; Luciano and Lore, 1975). Correlations between the frequency of initiation of these behaviours have been found by Drews and Dickey (1977), Drews and Wulczyn (1975), Flannelly and Lore (1975) and Militzer and Reinhard (1979). These observations have caused people to speculate that these behaviours may be important in developing and maintaining the social structure (possibly a dominance hierarchy) in each group. Indeed, Meaney and Stewart (1981) have claimed that a linear dominance hierarchy, shown by on-top-of postures, develops in rats during the play period, and is maintained in adulthood by the same behaviours.

Other evidence regarding male rat social structure is less clear, however. All-male housed groups of four or fewer males have frequently been found to have linear agonistic dominance hierarchies, but larger groups have not (Grant and Chance, 1958). Some studies of semi-natural and wild colonies have suggested that these animals are not organised into linear hierarchies, but rather have a system of ranked subgroups (Barnett, 1958b; Flannelly and Lore, 1977). Telle (1966) found no evidence of a social hierarchy in wild rats at all.

In this study, agonistic dominance was looked for in strictly directional terms such that a linear dominance hierarchy would only be found where no intransitive relationships existed (see section 1.2.4). Groups of four male rats (with and without females) were used, so it was anticipated that linear dominance hierarchies would develop in the all-male, and possibly also the mixed groups, which had been socially reared. Mixed group males were predicted to be more aggressive to one another than all-male group males (see section 1.1.1.4). The early-isolated males were expected to show increased intermale agonism when subsequently housed in all-male groups (Wahlstrand et al, 1983), though whether they would develop a dominance hierarchy was unknown. The effect of mixed housing on the agonistic behaviour and social structure of early-isolated males could not be predicted, as no similar studies had previously been made. However, it was thought that the combined effects of isolation rearing and the presence of females might lead to an increase in intermale agonism.

Although male rats have not been found to court females in the manner of guinea pigs, the observation that male rat agonistic dominance may be linked with reproductive priority (see section 1.2.5.2.2) suggested that there may be intra-group correlations between intermale agonistic behaviour and spontaneous sexual behaviour to cohabiting females. In order to investigate this possibility, male-female sexual interactions in mixed groups were compared with the results obtained regarding male agonism and social structure.

In addition, it was thought that isolation or all-male rearing might affect the way in which male rats subsequently interact with cohabiting females. Thus overall frequencies of male-female and female-male interactions in groups with different histories of early experience were compared.

8.1.2

Method.

Eight 30 minute observation sessions were carried out on each socially-housed group of animals over a period of two weeks. These took place during the first two hours of darkness, at a time when considerable activity usually occurred. Each group was observed in its home cage. The cage was lit by a 40W red bulb in an Anglepoise lamp situated 40 cm away from the front of the cage. The experimenter sat on a stool next to the lamp, positioned so that she could observe the animals at eye-level.

Social interactions were recorded on a check sheet in abbreviated form whenever they occurred. Recordings were made in the form: agent (initiator)-behaviour-recipient. Observations were written down in sequential order, and pauses of 10 seconds or more between acts were noted. The types of behaviour scored are listed and described in Table 8.1.

BEHAVIOUR CATEGORY	EQUIVALENT TERMS USED BY: Experimenter	Grant and Mackintosh (1963)	DESCRIPTION
Aggressive	Aggressive groom	Aggressive groom	Agent grooms recipient vigorously, usually about the head, neck or ventral regions. Agent appears to tug at recipient's skin with his teeth.
	On-top-of	Agent: Aggressive posture. Recipient: Submissive posture.	The agent stands with his fore paws on top of the recipient. The recipient is lying on his back or side.
	Box	Agent: Offensive upright posture. Recipient: Defensive upright posture.	Both animals stand on hind legs, facing one another and boxing with their fore paws. The agent is the animal which appears to initiate this behaviour.
	Chase	Chase	Self-explanatory.
	Bite	Bite	Agent lunges open-mouthed at recipient. Recipient usually shrieks, though there is normally no apparent injury.

Table 8.1
Description of the rat behaviours recorded in Chapter 8.

BEHAVIOUR CATEGORY	EQUIVALENT TERMS USED BY: Experimenter	Grant and Mackintosh (1963)	DESCRIPTION
Sexual	Ano-genital sniff	Sniff	Agent establishes naso-anal contact with recipient.
	Attempted mount		Male mounts with or without hip thrusting, but lordosis is not shown by the recipient.
	Mount		Only includes male-female interactions where female exhibits lordosis in response to the male's mount. Hip thrusts always occur.
Other Social	Social groom	Social groom	Most commonly occurs when one animal is lying on another. The agent grooms the recipient's dorsal or neck fur with gentle movements of his mouth.

Table 8.1 (continued)
Description of the rat behaviours recorded in Chapter 8.

Treatment of Results.

Intermale behaviour frequency: Inter-group comparisons.

The behaviour interaction data were typed onto an Apple II microcomputer in their raw form, and the computer was used to produce all subsequent information about interaction and behaviour frequencies in each experimental group.

Total intermale interaction frequency in the different conditions was compared using t tests (Observation Period 1) and analyses of variance (Observation Period 2) to show whether this was affected by social rearing and/or housing condition.

For both observation sessions, only four of the recorded behaviours occurred sufficiently often between males to be statistically analysable. These behaviours were: aggressive groom; on-top-of; box; ano-genital sniff. The scores for aggressive groom, on-top-of and box approximated to a normal distribution, but those for ano-genital sniff did not. Thus parametric tests were used to analyse aggressive groom, on-top-of and box scores, while non-parametric tests were used for all ano-genital sniff scores (including those directed to male rats by females).

In order to investigate possible differences in the nature of intermale interactions between the different experimental conditions, individual frequency scores were recoded as percentages of the total male-male interactions for each experimental group of four males.

Dominance and intermale behaviour frequency: Intra-group comparisons.

An attempt was made to assign dominance ranks within each group to socially grouped males, according to the direction of intermale interactions for each commonly-occurring agonistic behaviour. The results obtained for each behaviour were compared within each group. If there were missing or equal relationships on any behaviour, the rank trend of the data was compared with the ranks obtained for behaviours with no missing relationships.

Previous research on dominance hierarchies in male rats has focused on the on-top-of behaviour as being most indicative of the hierarchical relationship between two males (Grant and Chance, 1958; Meaney and Stewart, 1981). It was decided, therefore, to look at the evidence for directional dominance not only in the total intermale agonistic interactions, but also in the direction of on-top-of 'wins'. In every unbroken sequence of interactions between two males (i.e. every sequence of behaviours occurring within ten seconds of each other) , the last male to be on-top-of the other was scored as winning the sequence, while the receiving male was scored as losing it. The microcomputer was used to draw up a table of wins for each group of four males. These tables were then examined to see if a perfect linear hierarchy existed in any of the groups.

If one or more of the agonistic behaviours and the measure of on-top-of 'wins' showed different directional rank orders in any group, then that group was found not to have a dominance hierarchy.

Groups which were not found to have a dominance hierarchy were also checked for evidence of despotism. If one male in any group showed directional dominance over all three other males in aggressive groom, box and on-top-of interactions, then that male was said to be a despot.

Rank comparisons of behaviour frequency rather than direction were carried out using Friedman's two way analysis of variance (Siegel, 1956) on the initiated and received agonistic behaviours, to show whether there were consistent individual differences in aggressiveness within groups. The agonistic behaviours compared were: aggressive groom, on-top-of and box. Rank 1 was assigned to the male which initiated most of each behaviour in the comparisons of initiated behaviours, and to the male which received fewest of each behaviour in the comparisons of received behaviours.

In any group which showed a directional dominance hierarchy and also showed significantly consistent individual differences in initiated or received aggression frequency, the dominance ranks were included in a further Friedman analysis of the ranked behaviour frequencies. If the result attained a higher level of significance than that of the preceding analysis (without directional dominance ranks), then a significant relationship between the behaviour frequencies and dominance status was found. In groups without dominance hierarchies, but with internally consistent initiated and received agonism, an analysis of combined initiated and received agonism scores was made. The results of this analysis would show how close the relationship between initiating and receiving agonism was.

Frequency of interaction with cohabiting females: Inter-group comparisons.

These comparisons were only made on the Observation Period 2, mixed Hcond data.

Inspection of the male to female interaction data for the mixed Hconds revealed that while ano-genital sniffing and attempted mounting took place in many of the observation sessions, actual mounting occurred in only a few of the half hour periods. It was assumed that such mounting only took place when at least one of the females in the group was in oestrus. It seemed probable that an oestrous female might receive an unusually large number of male behaviours, so the following data correction was made to enable comparisons between the scores of all groups to be made. For each group, all male-female interaction data in any half hour observation session when mounting occurred were replaced by mean scores obtained from the no-mounting sessions.

Analyses of variance were performed on the corrected data to compare the total number of male-male and corrected male-female interactions in each Rcond. Chi-squared tests were used to compare the numbers of males in each Rcond which showed any ano-genital sniffing or attempted mounting to their anoestrous group females.

Corrected male-female ano-genital sniff and attempted mount scores were recoded as percentages of each group's total number of interactions. Since these scores did not appear to be normally distributed, they were analysed using the Kruskal-Wallis one-way analysis of variance by ranks.

Behaviours received by males from females were treated in a similar way to those received by females from males. Total female-male interaction and ano-genital sniff scores were corrected to remove possible effects of oestrus. An analysis of variance was performed on the total numbers of female-male interactions.

Female-male ano-genital sniff scores were recoded as percentages of each group's total number of female-male interactions. These data were then subjected to a Kruskal-Wallis analysis of variance by ranks, so as to show whether the females behaved differently to males from different Rconds.

Dominance and the frequency of interactions with cohabiting females: Intra-group comparisons.

The uncorrected scores for male-female ano-genital sniff, attempted mount and mount were ranked (when scores existed for all three behaviours) according to frequency within each group of four mixed Rhcond or mixed Hcond males. Rank 1 was assigned to the male which exhibited most of each behaviour. Friedman's two way analyses of variance by ranks were performed on these ranked scores to show whether the males in each group were consistently ranked across the three behaviours i.e. showed consistent individual differences in sexual activity. If consistent differences were found, a further analysis was performed in which either the group's dominance ranks (if the group had a dominance hierarchy) or ranked initiated agonism scores (if these were consistent) were included. If this further test gave a higher value of Chi-r-squared than the previous test, then sexual activity was found to be closely related either to dominance status or to initiated agonism (i.e. aggressiveness).

8.1.3

Results.

8.1.3.1

Observation period 1.

Intermale behaviour frequency: Inter-group comparisons.

The following social behaviour results were obtained from the mixed and all-male Rhconds only, as the isolated males had no opportunity for social interactions and so were not subject to observation.

Preliminary examination of the total frequencies of male-male and male-male/female interactions showed considerable differences in the variances as well as in the means between the mixed and all-male Rhconds (Table 8.2). F tests performed on the data revealed the variance in total interaction scores in the all-male Rhcond to be significantly greater than that in the mixed Rhcond for both male-male ($F=4.915$, $df=31/31$, $p<.01$) and male-male/female ($F=2.324$, $df=31/31$, $p<.05$) interaction frequencies.

Owing to these unequal variances, a normal Student's t test could not be performed on these results. Instead, the Cochran and Cox t test (Ferguson, 1976) was used. A highly significant difference between the means of the two Rhconds was found for both male-male and

Behavioural Measure	Rhcond	Mean score.	Standard error.
Total male-male interactions.	MF	29.56	3.69
	M	110.22	8.17
Total male-male/female interactions.	MF	61.94	5.36
% Aggressive groom.	MF	6.34	0.67
	M	6.84	0.43
% On-top-of.	MF	5.97	0.65
	M	6.56	0.39
% Box.	MF	9.41	1.15
	M	7.16	0.46

Rhcond = Rearing/housing condition.
(MF = Mixed, M = All-male.)

Table 8.2
Rat Observation Period 1: Means and standard errors of total male-male and male-male/female interactions, and of intermale agonistic behaviours (expressed as percentages of each group's total intermale interactions).

Behavioural Measure.	Rhcond	Median score.	Range
% Ano-genital sniff.	MF	1.00	0- 6
	M	3.00	1-12

Rhcond = Rearing/housing condition.
(MF = Mixed, M = All-male.)

Table 8.3
Rat Observation Period 1: Medians and ranges of intermale ano-genital sniffs (expressed as percentages of each group's total intermale interactions).

male-male/female interaction frequencies (Table 8.4). Males in the all-male Rhcond interacted with one another more frequently than did males in the mixed Rhcond. Indeed, mixed Rhcond males initiated interactions with both males and females less often than all-male Rhcond males did with each other. This finding could be due to an inverse relationship between group size or population density and frequency of social interaction. Alternatively, it could reflect continuing play behaviour or as yet unresolved social structures in the all-male groups, compared to greater social stability in the mixed groups. A third possible explanation for the reduced frequency of social interactions in the mixed groups is that females may have an inhibitory effect on intermale aggression, possibly by being aggressive themselves.

F tests were performed on the percentage intermale aggressive groom, on-top-of, and box scores (Table 8.2) to ascertain if their variances were equal for both the mixed and all-male Rhconds. Significant differences between variances were found for aggressive groom (F=2.88, df=31/31, p<.005), on-top-of (F=2.81, df=31/31, p<.005) and box (F=5.83, df=31/31, p<.0001). For all three behaviours the variance in percentage scores was greater in the mixed than in the all-male Rhcond.

Cochran and Cox t tests showed no significant differences between the mean percentage scores of the mixed and all-male Rhconds for aggressive groom, on-top-of and box (Table 8.4). Thus it appeared that males in both the all-male and mixed Rhconds showed similar mean proportions of these behaviours in their total social interactons. However, there was greater variation in scores in the mixed Rhcond

Behavioural Measure	Rhcond Score	Df	P
Total male-male interactions.	t= 8.99	31/31	<.001
Total male-male/female interactions.	t= 4.94	31/31	<.001
% Aggressive groom.	t= 0.59	31/31	>.2
% On-top-of.	t= 0.79	31/31	>.2
% Box.	t= 1.54	31/31	>.1
% Ano-genital sniff.	U=323.00	31/31	<.05

Rhcond = Rearing/housing condition.

Table 8.4
Rat Observation Period 1: Results of t and U tests on total male-male and male-male/female interactions (corrected for oestrus) and on intermale social behaviours (expressed as percentages of the total no. of intermale interactions in each group).

groups than in the all-male Rhcond groups.

A Mann-Whitney U test performed on the percentage scores for male-male ano-genital sniffs (Table 8.3) showed that the proportion of ano-genital sniffing shown by male Rhcond animals was significantly greater than that shown by mixed Rhcond animals (Table 8.4). It was thought that the lower proportions of male-male ano-genital sniffing in the mixed groups might be due to preferential male-female sniffing. Total male-female interaction and male-female ano-genital sniff scores were corrected to remove any possible effects of oestrus (as described above) and male-female ano-genital sniff scores were expressed as a percentage of each mixed group's total number of male-male/female interactions. A Mann-Whitney U test for large samples (Robson, 1973) was used to compare the proportionate male-male/female (mixed Rhcond only: median, 5.5%) and male-male (all-male Rhcond only: median, 2.5%) ano-genital sniff scores. This showed that males in the mixed Rhcond showed a higher proportion of ano-genital sniffing than did males in the all-male Rhcond ($U=278$, $z=3.142$, $p<.05$).

This latter result is not surprising, as ano-genital sniffing is considered to be primarily a sexual behaviour. It is interesting, however, that males in the all-male condition ano-genitally sniffed each other more often than did males in the mixed condition.

Dominance and intermale behaviour frequency: Intra-group comparisons.

Tables 8.5 a-f show the results of attempts at directional ranking on each agonistic behaviour, and on on-top-of 'wins' for each group of rats. None of the groups reached the criterion for having a

Rhcond	Mixed				All-male			
Group ID.	A1	A2	A3	A4	C1	C2	C3	C4
		Box		Agro	Oto	Agro	Oto	Oto Win
Group ID.	B1	B2	B3	B4	D1	D2	D3	D4
			Box		Box	Agro Box		Box

Table 8.5 a.
Intermale agonistic behaviours showing dominance rank order linearity with no missing or equal relationships.

Hcond	Mixed				All-male			
Group ID.	A1	A2	A3	A4	C1	C2	C3	C4
			Agro(3) Oto(2)	Oto(3)	Win(1)		Box(1)	Agro(1)
Group ID.	B1	B2	B3	B4	D1	D2	D3	D4

Table 8.5 b.
Intermale agonistic behaviours showing the same linear rank order as in Table 8.5 a, but with some missing or equal relationships (no. given in parentheses).

Hcond	Mixed				All-male			
Group ID.	A1	A2	A3	A4	C1	C2	C3	C4
		Win			Agro	Win		
Group ID.	B1	B2	B3	B4	D1	D2	D3	D4

Table 8.5 c.
Intermale agonistic behaviours showing different linear dominance rank orders to those in Table 8.5 a and to each other, with no missing or equal relationships.

Rhcond = Rearing/housing condition.
Oto = On-top-of.
Agro = Aggressive Groom.
Box = Box.
Win = On-top-of 'win' (see text).

Tables 8.5 a-f.
Rat Observation period 1: Evidence for dominance hierarchies among males according to the direction of intermale agonistic interactions.

		Mixed		Hcond		All-male		
Group ID.	A1	A2	A3	A4	C1	C2	C3	C4
	Agro(2) Oto(1) Box(3)			Win(1)			Agro(1) Win(1)	
Group ID.	B1	B2	B3	B4	D1	D2	D3	D4
	Box(1)	Agro(3) Oto(2) Box(4) Win(2)	Agro(2) Oto(2) Win(2)				Agro(1)	

Table 8.5 d.
Intermale agonistic behaviours showing different linear dominance rank orders to those in Tables 8.5 a and 8.5 c and to each other, with some missing or equal relationships (no. given in parentheses).

		Mixed		Hcond		All-male		
Group ID.	A1	A2	A3	A4	C1	C2	C3	C4
		Agro	Win	Box	Box	Oto Box		Box
Group ID.	B1	B2	B3	B4	D1	D2	D3	D4
	Oto			Win	Agro Oto Win	Oto Win	Oto Win	Agro

Table 8.5 e.
Intermale agonistic behaviours showing non-linear dominance rank orders, with no missing or equal relationships.

		Mixed		Hcond		All-male		
Group ID.	A1	A2	A3	A4	C1	C2	C3	C4
	Win(2)	Oto(2)	Box(1)					
Group ID.	B1	B2	B3	B4	D1	D2	D3	D4
	Agro(1) Win(1)			Agro(2) Oto(1) Box(2)			Box(1)	Oto(1) Win(1)

Table 8.5 f.
Intermale agonistic behaviours showing non-linear dominance rank orders, with some missing or equal relationships (no. given in parentheses).

Rhcond = Rearing/housing condition.
Oto = On-top-of.
Agro = Aggressive Groom.
Box = Box.
Win = On-top-of 'win' (see text).

Tables 8.5 a-f. (continued)
Rat Observation period 1: Evidence for dominance hierarchies among males according to the direction of intermale agonistic interactions.

dominance hierarchy (i.e. no rank reversals between behaviours). Indeed, only 15 occurrences of linearity in behaviour ranking were found out of a possible 64 (no. of groups (16) x no. of behaviours (4) assessed) i.e. 23%, which is less than the 37.5% level expected by chance (Appleby, 1983).

No evidence of despotism was found in any group.

Table 8.6 presents the results of Friedman's two way analyses of variance on ranked agonistic behaviour frequencies. Only two mixed Rhcond (A2 and A3) and three all-male Rhcond (D1,D2 and D3) groups showed consistent individual differences across the initiated intermale agonistic behaviours (on-top-of, aggressive groom and box). One mixed Rhcond (B1) and three all-male Rhcond (C1, D1 and D4) groups showed consistent individual differences across the received intermale agonistic behaviours. A further analysis to compare the combined initiated and received agonism results of group D1 revealed no relationship between the two sets of data.

Dominance and the frequency of interaction with cohabiting females: Intra-group comparisons.

Table 8.6 gives the results of Friedman's two way analyses of variance on ranked frequencies of sexual behaviours (ano-genital sniff, attempted mount and mount) to cohabiting females (mixed Rhcond only). (This table will be referred to throughout this chapter.) Group A3 was the only group to show consistent individual differences across these behaviours. A further analysis to compare group A3's initiated agonism and sexual behaviour scores gave a very high value

	Rhcond															
	Mixed								All-male							
Group ID.	A1	A2	A3	A4	B1	B2	B3	B4	C1	C2	C3	C4	D1	D2	D3	D4
a) Initiated inter-male agonism.	6.3	8.2*	8.2*	5.8	6.7	7.4	3.3	5.8	6.6	0.8	5.0	7.4	8.2*	9.0*	8.5*	7.4
Received inter-male agonism.	3.7	2.5	6.1	7.0	8.2*	1.9	1.0	5.7	8.5*	2.7	1.2	6.9	8.5*	7.3	7.3	9.1*
Initiated and received inter-male agonism.													5.0			
Sexual behaviour to cohabiting females.	X	X	8.1*	1.8	X	X	3.1	7.0								
Initiated inter-male agonism and sexual behaviour to cohabiting females.			16.3**													
b) Individual Mating Test 1.	3.5	1.6	12.1**	13.5**	1.7	13.6**	13.6**	4.4	9.2*	5.4	12.6**	2.0	12.6**	8.3*	7.1	4.9

Rhcond = Rearing/housing condition.
* = p<.05
** = p<.01
Df = 3 for each comparison.

Table 8.6
Results of Friedman two way analyses of variance (Chi-r-squared) on ranked behaviour frequencies: a) Rat Observation period 1; b) Individual Mating Test 1; c) Group Mating Test 1; d) Water Competition Test 1.

	Rhcond															
	Mixed								All-male							
Group ID.	A1	A2	A3	A4	B1	B2	B3	B4	C1	C2	C3	C4	D1	D2	D3	D4
Initiated intermale agonism and I.M. Test 1.			16.7**										12.8**	11.3*		
c) Initiated intermale agonism and Group Mating Test 1.		3.1	8.0*										10.9*	13.9**	4.4	
d) Water Competition Test 1.	2.2	2.2	5.8	8.2*	8.2*	9.0*	1.8	5.8	7.4	8.2*	8.2*	3.8	3.9	1.9	3.4	5.0

	Rhcond							
	Isolation							
Group ID.	E1	E2	E3	E4	F1	F2	F3	F4
b) Individual Mating Test 1 (continued).	1.0	2.2	X	5.8	X	4.4	X	7.3

Rhcond = Rearing/housing condition.
* = p<.05
** = p<.01
Df = 3 for each comparison.

Table 8.6 (continued)
Results of Friedman two way analyses of variance (Chi-r-squared) on ranked behaviour frequencies: a) Rat Observation period 1; b) Individual Mating Test 1; c) Group Mating Test 1; d) Water Competition Test 1.

of Chi-r-squared, indicating a close relationship between aggressiveness and sexual behaviour to cohabiting females.

8.1.3.2

Observation Period 2.

Intermale behaviour frequency: Inter-group comparisons.

For the second Observation Period, scores of social behaviour were obtained for all three Rconds (mixed, all-male and isolation) as the previously isolated animals had now been grouped. Data presented in this section have been analysed in terms of both the animals' rearing conditions (Rconds) and their current housing conditions (mixed or all-male Hconds).

Initial analysis of variance of the total number of male-male interactions (Table 8.7c) during the second Observation Period showed highly significant effects of Rcond and Hcond. Further analysis of this data using the Newman-Keuls test (Ferguson, 1976) revealed that the mixed Hconds were not significantly different from one another. However, in the all-male Hconds the isolation Rcond males interacted significantly more frequently with one another than did the socially-reared males (isolation Rcond v mixed Rcond; $Q=4.98$, $df=90$, $p<.01$: Isolation Rcond v all-male Rcond; $Q=2.86$, $df=90$, $p<.05$). These results show that males housed in all-male groups still interacted much more frequently than did males housed in mixed groups, even if they had had previous experience of living in a mixed group. Previously isolated males interacted very often when rehoused in all-male groups.

	Rcond		
	MF	M	I
Hcond			
MF	31.06 (5.41)	20.94 (6.58)	20.31 (2.95)

Table 8.7a
Total no. of male-female interactions (corrected for oestrus).

	Rcond		
	MF	M	I
MF	63.38 (8.10)	59.88 (11.53)	78.06 (8.36)

Table 8.7b
Total no. of male-male/female interactions (corrected for oestrus).

	Rcond		
	MF	M	I
Hcond			
MF	32.31 (4.51)	38.94 (5.87)	57.75 (8.56)
M	69.13 (8.66)	85.50 (9.04)	107.56 (8.51)

Table 8.7c
Total no. of male-male interactions.

	Rcond		
	MF	M	I
MF	6.69 (1.02)	8.69 (0.89)	8.81 (1.18)
M	7.56 (1.14)	9.50 (0.93)	8.31 (0.76)

Table 8.7d
Percentage intermale aggressive grooms (means).

	Rcond		
	MF	M	I
Hcond			
MF	4.56 (0.76)	5.69 (0.85)	7.56 (1.12)
M	5.81 (0.85)	6.31 (0.67)	8.81 (0.97)

Table 8.7e
Percentage intermale on-top-ofs (means).

	Rcond		
	MF	M	I
MF	10.56 (1.58)	7.88 (1.20)	7.19 (0.93)
M	7.63 (1.00)	5.19 (0.71)	6.38 (0.57)

Table 8.7f
Percentage intermale boxing (means).

	Rcond		
	MF	M	I
Hcond			
MF	2.00	1.50	1.00
M	2.50	2.00	1.00

Table 8.7g
Percentage intermale ano-genital sniffs (medians).

Rcond = Rearing condition.
Hcond = Housing condition.
(MF = Mixed, M = All-male, I = Isolation).
Standard errors are given in parentheses.

Tables 8.7a-g
Rat Observation Period 2: Mean scores of total male-male, male-male/female and male-female interactions. Also mean intermale aggressive grooms, on-top-ofs and boxing, and median scores of intermale ano-genital sniff (expressed as percentages of each group's total intermale interactions).

Analysis of variance of the total number of male-male/female interactions showed a similar pattern (Tables 8.7b and c), though the differences between the two Hconds were considerably reduced. Significant effects of Rcond and Hcond (Table 8.8) were found. The total number of interactions initiated by males was greater in all-male Hcond groups than in mixed Hcond groups, even though the number of animals in the former groups was smaller (four instead of six).

Analyses of variance were performed on the percentage scores for intermale aggressive groom, on-top-of, and box (see Tables 8.7d-f). No significant effects of Rcond or Hcond were found for aggressive groom (Table 8.8).

On-top-of showed a significant effect of Rcond but no effect of Hcond (Table 8.8). Further analysis of the on-top-of scores using the Newman- Keuls test showed that a significantly greater proportion of isolation Rcond than of social Rcond intermale interactions involved on-top-of behaviour (isolation Rcond v mixed Rcond; Q=4.83, df=93, p<.01: isolation Rcond v all-male Rcond; Q=3.52, df=93, p<.05). No difference existed between the all-male and mixed Rconds (Q=1.31, df=93, p>.05).

Box showed significant effects of both Rcond and Hcond (Table 8.8). The trend here was for males in the mixed Rcond to show a greater proportion of boxing than did all-male or isolation Rcond animals. Also, mixed Hcond males showed a greater proportion of boxing behaviour than all-male Hcond males.

Behavioural Measure	Condition	Score	Df	P
Total male-male interactions.	Rcond	F= 8.79	2/90	<.001
	Hcond	F=49.66	1/90	<.0001
	Rc x Hc	F= 0.38	2/90	>.6
Total male-male/-female interactions.	Rcond	F= 3.25	2/90	<.05
	Hcond	F= 4.17	1/90	<.05
	Rc x Hc	F= 1.03	2/90	>.3
% Aggressive groom.	Rcond	F= 2.09	2/90	>.1
	Hcond	F= 0.24	1/90	>.6
	Rc x Hc	F= 0.30	2/90	>.7
% On-top-of.	Rcond	F= 6.18	2/90	<.005
	Hcond	F= 2.09	1/90	>.1
	Rc x Hc	F= 0.08	2/90	>.9
% Box.	Rcond	F= 3.62	2/90	<.05
	Hcond	F= 6.27	1/90	<.05
	Rc x Hc	F= 0.61	2/90	>.5
% Ano-genital sniff.	Cond	H= 6.88	5	>.2

Rcond(Rc) = Rearing condition.
Hcond(Hc) = Housing condition.
Cond = Experimental (Rc x Hc) condition.

Table 8.8
Rat Observation Period 2: Results of analyses of variance on total male-male and male-male/female interactions, and on intermale social behaviours (expressed as percentages of each group's total intermale interactions).

A Kruskal-Wallis one-way analysis of variance by ranks was performed on the proportionate intermale ano-genital sniff scores (Table 8.7g). No significant difference between the six experimental (rearing x housing) conditions was found (Table 8.8).

The increased proportion of on-top-of behaviours found in isolation reared males might again reflect instability in these animals' social structures, as the on-top-of action is usually taken as indicative of one animal's domination of another. Alternatively, it could indicate heightened aggression between these males either within an established dominance order or independently of such organisation.

Dominance and intermale behaviour frequency: Intra-group comparisons.

Tables 8.9 a-f show the results of attempts at directional ranking on each agonistic behaviour, and on on-top-of 'wins' for each group. Only one group (E1) reached the criterion for having a dominance hierarchy (i.e. no rank reversals between behaviours). Overall, the number of occurrences of linearity in behaviour ranking was found to be 36 out of a possible 96 i.e. 37.5%. This is exactly the proportion expected by chance (Appleby, 1983).

Groups A1 (mixed Rcond x mixed Hcond), D3 (all-male Rcond x mixed Hcond) and E4 (isolation Rcond x mixed Hcond) fulfilled the criteria for having a despot.

Table 8.10 presents the results of Friedman analyses of variance performed on the ranked frequencies of initiated and received

		Rcond											
Hcond		Mixed				All-male				Isolation			
Mixed	Group ID.	A1 Oto Agro Win	A2 Oto	A3 Box	A4 Box	D1 Oto Win	D2	D3 Agro	D4 Agro	E1 Oto Box Win	E2	E3	E4 Box
All-male	Group ID.	B1 Oto Win	B2 Agro	B3	B4	C1	C2	C3 Agro	C4 Oto Win	F1	F2 Win	F3 Oto Win	F4 Oto Agro Win

Table 8.9 a.
Intermale agonistic behaviours showing dominance rank order linearity with no missing or equal relationships.

		Rcond											
Hcond		Mixed				All-male				Isolation			
Mixed	Group ID.	A1	A2 Win(1)	A3	A4	D1	D2	D3 Oto(2) Win(2)	D4	E1 Agro(1)	E2 Oto(1) Win(1)	E3 Box(1)	E4
All-male	Group ID.	B1	B2	B3 Agro(1) Box(1)	B4	C1	C2	C3	C4	F1	F2 Oto(1)	F3	F4

Table 8.9 b.
Intermale agonistic behaviours showing the same linear rank order as in Table 8.9 a, but with some missing or equal relationships (no. given in parentheses).

Rcond = Rearing condition.   Hcond = Housing condition.
Oto = On-top-of.   Agro = Aggressive groom.
Box = Box.   Win = On-top-of 'win' (see text).

Tables 8.9 a-f.
Rat Observation period 2: Evidence for dominance hierarchies among males according to the direction of intermale agonistic interactions.

Hcond						Rcond							
		Mixed				All-male				Isolation			
Mixed	Group ID.	A1 Box	A2	A3	A4 Agro	D1	D2	D3	D4	E1	E2	E3	E4
All-male	Group ID.	B1 Agro	B2	B3	B4	C1	C2	C3	C4 Agro Box	F1	F2	F3 Agro	F4

Table 8.9 c.
Intermale agonistic behaviours showing different linear dominance rank orders to those in Table 8.9 a and to each other, with no missing or equal relationships.

Hcond						Rcond							
		Mixed				All-male				Isolation			
Mixed	Group ID.	A1	A2 Box(1) Agro(2)	A3 Oto(2) Agro(2) Win(2)	A4	D1 Agro(1) Box(1)	D2 Oto(2) Box(3) Win(2)	D3 Box(2)	D4 Oto(1) Win(1)	E1	E2	E3 Agro(2)	E4 Oto(1) Win(1)
All-male	Group ID.	B1	B2 Win(1)	B3 Oto(1) Win(2)	B4 Win(2)	C1	C2 Win(1)	C3	C4	F1 Agro(1) Box(1)	F2 Agro(1) Box(1)	F3 Box(1)	F4

Table 8.9 d.
Intermale agonistic behaviours showing different linear dominance rank orders to those in Table 8.9 a and 8.9 c and to each other, with some missing or equal relationships (no. given in parentheses).

Rcond = Rearing condition. Hcond = Housing condition.
Oto = On-top-of. Agro = Aggressive groom.
Box = Box. Win = On-top-of 'win' (see text).

Tables 8.9 a-f. (continued)
Rat Observation period 2: Evidence for dominance hierarchies among males according to the direction of intermale agonistic interactions.

							Rcond						
		Mixed					All-male				Isolation		
Hcond **Mixed**	Group ID.	A1	A2	A3	A4	D1	D2 Agro	D3	D4 Box	E1	E2 Agro Box	E3 Oto Win	E4 Agro
All-male	Group ID.	B1 Box	B2 Box	B3	B4 Oto	C1 Box	C2 Agro Box	C3 Oto Win	C4	F1 Oto	F2	F3	F4

Table 8.9 e.
Intermale agonistic behaviours showing non-linear dominance rank orders, with no missing or equal relationships.

							Rcond						
		Mixed					All-male				Isolation		
Hcond **Mixed**	Group ID.	A1	A2	A3	A4 Oto(2) Win(2)	D1	D2	D3	D4	E1	E2	E3	E4
All-male	Group ID.	B1	B2 Oto(1)	B3	B4 Agro(2) Box(1)	C1 Agro(2) Oto(1) Win(1)	C2 Oto(1)	C3 Box(1)	C4	F1 Win(1)	F2	F3	F4 Box(2)

Table 8.9 f.
Intermale agonistic behaviours showing non-linear dominance rank orders, with some missing or equal relationships (no. given in parentheses).

Rcond = Rearing condition.
Oto = On-top-of.
Box = Box.

Hcond = Housing condition.
Agro = Aggressive groom.
Win = On-top-of 'win' (see text).

Tables 8.9 a-f. (continued)
Rat Observation period 2: Evidence for dominance hierarchies among males according to the direction of intermale agonistic interactions.

		Rcond											
	Hcond	Mixed				All-male				Isolation			
a) Initiated intermale agonism.	Mixed	A1 7.0	A2 5.4	A3 6.3	A4 3.4	D1 7.4	D2 1.6	D3 7.5	D4 8.2*	E1 7.7	E2 9.0*	E3 7.5	E4 7.0
	All-male	B1 4.2	B2 8.1*	B3 8.5*	B4 1.0	C1 7.5	C2 3.1	C3 4.5	C4 8.2*	F1 6.6	F2 3.3	F3 7.5	F4 7.4
Received intermale agonism.	Mixed	A1 8.2*	A2 2.1	A3 5.4	A4 5.8	D1 4.5	D2 7.3	D3 0.6	D4 7.9*	E1 7.3	E2 9.0*	E3 5.3	E4 2.5
	All-male	B1 1.2	B2 7.7	B3 4.9	B4 7.3	C1 5.8	C2 8.5*	C3 7.4	C4 6.3	F1 2.3	F2 4.7	F3 6.6	F4 4.0
Initiated and received intermale agonism.	Mixed	A1	A2	A3	A4	D1	D2	D3	D4 11.2*	E1	E2 1.8	E3	E4
	All-male	B1	B2	B3	B4	C1	C2	C3	C4	F1	F2	F3	F4
Sexual behaviour to cohabiting females.	Mixed	A1 X	A2 X	A3 X	A4 X	D1 X	D2 X	D3 X	D4 4.1	E1 X	E2 X	E3 X	E4 X

Rcond = Rearing condition.
Hcond = Housing condition.
A1-F4 = Group IDs.
* = p<.05
** = p<.01
X = Insufficient data for analysis.
Df = 3 for each comparison.

Table 8.10
Results of Friedman two way analyses of variance (Chi-r-squared) on ranked behaviour frequencies and weights: a) Rat Observation period 2; b) Weight Tests 1 and 2; c) Individual Mating Test 2; d) Group Mating Test 2; e) Water Competition Test 2.

		Rcond											
	Hcond	Mixed				All-male				Isolation			
b) Weight Tests.	Mixed	A1 7.3	A2 6.6	A3 1.3	A4 5.8	D1 5.8	D2 0.6	D3 5.0	D4 4.2	E1 6.6	E2 5.8	E3 5.7	E4 9.0*
	All-male	B1 8.2*	B2 6.6	B3 3.4	B4 8.5*	C1 7.4	C2 7.3	C3 2.2	C4 5.8	F1 4.9	F2 6.7	F3 7.0	F4 7.9*
c) Individual Mating Test 2.	Mixed	A1 8.1*	A2 1.1	A3 4.7	A4 7.0	D1 2.3	D2 9.2*	D3 2.5	D4 9.7*	E1 6.8	E2 5.8	E3 2.2	E4 7.8
	All-male	B1 4.1	B2 0.7	B3 6.4	B4 3.3	C1 7.3	C2 4.9	C3 4.0	C4 3.2	F1 7.8	F2 3.2	F3 4.9	F4 4.5
Initiated inter-male agonism and I.M. Test 2.	Mixed	A1	A2	A3	A4	D1	D2	D3	D4 11.6**	E1	E2	E3	E4
	All-male	B1	B2	B3	B4	C1	C2	C3	C4	F1	F2	F3	F4
d) Initiated inter-male agonism and G.M. Test 2.	Mixed	A1	A2	A3	A4	D1	D2	D3	D4 7.4	E1	E2 5.1	E3	E4
	All-male	B1	B2 8.2*	B3 6.8	B4	C1	C2	C3	C4 4.9	F1	F2	F3	F4

Rcond = Rearing condition. Hcond = Housing condition.
A1-F4 = Group IDs. * = p<.05 ** = p<.01
X = Insufficient data for analysis.
Df = 3 for each comparison.

Table 8.10 (continued)
Results of Friedman two way analyses of variance (Chi-r-squared) on ranked behaviour frequencies and weights: a) Rat Observation period 2; b) Weight Tests 1 and 2; c) Individual Mating Test 2; d) Group Mating Test 2; e) Water Competition Test 2.

		Rcond											
	Hcond	Mixed				All-male				Isolation			
Dominance ranks and G.M. Test 2.	Mixed	A1	A2	A3	A4	D1	D2	D3	D4	E1 3.3	E2	E3	E4
	All-male	B1	B2	B3	B4	C1	C2	C3	C4	F1	F2	F3	F4
e) Water Competition Test 2.	Mixed	A1 7.0	A2 5.0	A3 7.0	A4 3.4	D1 7.2	D2 5.0	D3 2.2	D4 8.2*	E1 1.8	E2 3.4	E3 5.1	E4 4.2
	All-male	B1 4.2	B2 4.2	B3 2.2	B4 5.0	C1 3.6	C2 6.6	C3 0.6	C4 1.0	F1 1.8	F2 4.5	F3 5.4	F4 3.8
Initiated intermale agonism and W.C. Test 2.	Mixed	A1	A2	A3	A4	D1	D2	D3	D4 14.0**	E1	E2	E3	E4
	All-male	B1	B2	B3	B4	C1	C2	C3	C4	F1	F2	F3	F4

Rcond = Rearing condition. Hcond = Housing condition.
A1-F4 = Group IDs. * = p<.05 ** = p<.01
X = Insufficient data for analysis.
Df = 3 for each comparison.

Table 8.10 (continued)
Results of Friedman two way analyses of variance (Chi-r-squared) on ranked behaviour frequencies and weights: a) Rat Observation period 2; b) Weight Tests 1 and 2; c) Individual Mating Test 2; d) Group Mating Test 2; e) Water Competition Test 2.

intermale agonistic behaviours (on-top-of, aggressive groom and box). (Table 8.10 is referred to throughout this chapter.) Groups B2 and B3 (mixed Rcond x all-male Hcond), C4 (all-male Rcond x all-male Hcond), D4 (all-male Rcond x mixed Hcond), C2 (all-male Rcond x all-male Hcond) and E2 (isolation Rcond x mixed Hcond) all showed consistent individual differences across initiated agonistic behaviours.

Only groups A1 (mixed Rcond x mixed Hcond), D4 (all-male Rcond x mixed Hcond) and E2 (isolation Rcond x mixed Hcond) showed consistent differences across received agonistic behaviours.

Further analysis of the combined ranks of initiated and received agonistic behaviours of group D4 gave a high value of Chi-r-squared, indicating a close relationship between initiated and received aggression in this group. Similar analysis of group E2's combined ranks on initiated and received agonism showed no such relationship (Table 8.7).

Frequency of interaction with cohabiting females: Inter-group comparisons.

The following data were obtained only from animals from all three Rconds which were housed in the mixed Hcond for the second part of this experimant.

The analysis of variance performed on the corrected mixed Hcond scores for intermale and male-female interactions (Tables 8.7c and a) gave the following results. A significant effect of interactee gender was found (F=21.29, df=1/45, p<.005) as well as a significant interaction between Rcond and gender (F=6.54, df=2/45, p<.005), but no significant effect of Rcond alone (F=1.05, df=2/45 p>.3). This shows that in the mixed Hcond, animals from all three Rconds showed similar total interaction scores, but the proportions of these interactions directed at males and at females differed significantly between Rconds. Isolation Rcond males interacted more with each other than with the females in their groups, whereas mixed Rcond males interacted slightly more with their cohabiting females than with each other. All-male Rcond males interacted more with each other than with females, but the difference here was much less marked than in the isolation Rcond.

It is possible that isolation Rcond males were still trying to establish normal social structures within their groups and so concentrated their social attentions on one another rather than on the females in their groups. Alternatively, the females might have identified these males as being in some way 'abnormal', and so might have behaved aggressively towards them when the groups were first formed, thus inhibiting the males from interacting further with them. The latter explanation gives no reason for increased intermale interactions amongst the isolation Rcond males, however, and so seems rather unlikely.

No difference between Rconds was found for the number of males which ano-genital sniffed (Chi-squared=.14, df=2, p>.9), or attempted to mount (Chi-squared=4.57, df=2, p>.1) cohabiting females. The actual numbers of males (out of sixteen) in each Rcond which showed ano-genital sniffing were: mixed,15; all-male,13; isolation,14. The numbers which showed attempted mounting were: mixed,11;

all-male,7; isolation,3.

Kruskal-Wallis analyses of variance by ranks performed on the proportionate scores for male-female ano-genital sniff and attempted mount gave no significant difference between Rconds for ano-genital sniffing (median scores: mixed, 14.5%; all-male, 12.5%; isolation, 10%. H=2.02, df=2, p>.3) and a significant difference for attempted mounting (median scores: mixed, 3.5%; all-male, 0%; isolation, 0%. H=9.59, df=2, p<.01). All the females in all the mixed groups conceived either before or during Observation Period 2, so the reduced proportion of attempted mounting shown by isolation Rcond males to cohabiting anoestrous females cannot have been due to total sexual inactivity.

The analysis of variance performed on the total male-male/female and female/male interaction scores showed no significant difference between Rconds (F=2.10, df=2,45, p>.1), though there was a trend for the number of female-male interactions to decrease from the mixed Rcond (mean:7.75) to the all-male Rcond (mean:6.19) to the isolation Rcond (mean:4.81). It is notable that these female-male interaction frequencies are very small - even in the mixed Rcond groups - , averaging less than one female-male interaction per female per half hour observation session.

The Kruskal-Wallis analysis of variance by ranks performed on the proportionate female-male ano-genital sniff scores showed no significant difference between Rconds (median scores: mixed, 7%; all-male, 2%; isolation, 4.5%. H=.52, df=2, p>.7).

Dominance and the frequency of interaction with cohabiting females: Intra-group comparisons.

Only group D4 (all-male Rcond x mixed Hcond) showed all three sexual behaviours (ano-genital sniff, attempted mount and mount) to its cohabitee females. Since it is necessary to have ranked scores on at least three behaviours in order to obtain significance with the Friedman two way analysis of variance by ranks, (with groups of four animals) only group D4's data could be analysed in this way. Table 8.10 presents the results of this analysis which showed no consistent differences in sexual activity between individual males.

8.1.3.3

Weight tests.

Weights and weight change: Inter-group comparisons.

Analyses of variance were performed on the Test 1 and Test 2 individual weights and weight changes (Test 2 minus Test 1) (Tables 8.11 and 8.12). There was no effect of Rhcond on the Test 1 weights, nor of either Rcond or Hcond on the Test 2 weights (Table 8.13). There was no effect of Rcond or Hcond on weight change (Table 8.13).

Weights and weight change: Intra-group comparisons.

Friedman two way analyses of variance were performed on the ranked Test 1 and 2 weights and weight changes for each group. (Ranks of 1 were assigned to the greatest weights and weight change in each group.) The results are presented in Table 8.10. Only groups B1 and B4 (mixed Rcond x all-male Hcond), E4 (isolation Rcond x mixed Hcond),

	Rhcond	Mean	Standard error.
Weight 1 (grams)	MF	317.3	4.7
	M	315.9	5.5
	I	329.8	5.2

Table 8.11
Weight test 1: Means and standard errors.

Weight measure.	Hcond	Rcond		
		MF	M	I
Weight 2 (grams).	MF	393.9 (11.4)	389.6 (8.8)	415.1 (12.4)
	M	404.0 (9.7)	387.3 (8.6)	399.1 (11.9)
		MF	M	I
Weight change (grams). (Wt2-Wt1)	MF	74.9 (11.1)	70.9 (5.1)	83.4 (9.0)
	M	88.4 (7.9)	74.3 (6.2)	70.6 (6.7)

Table 8.12
Weight test 2 and weight change: Means and standard errors.

Weight measure.	Condition	F value	Df	p
Weight 1.	Rhcond	2.31	2/90	>.1
Weight 2.	Rcond	1.57	2/90	>.2
	Hcond	0.10	1/90	>.7
	Rc X Hc	0.76	2/90	>.5
Weight change (Wt2 - Wt1)	Rcond	0.68	2/90	>.5
	Hcond	0.05	1/90	>.8
	Rc x Hc	1.46	2/90	>.2

Table 8.13
Weight tests 1 and 2 and weight change: Results of analyses of variance.

Rhcond = Rearing/housing condition.
Rcond(Rc) = Rearing condition.
Hcond(Hc) = Housing condition.
(MF = Mixed, M = All-male, I = Isolation.)
Standard errors in Table 8.12 are given in parentheses.

and F4 (isolation Rcond x all-male Hcond) showed significantly consistent individual differences in weights and weight change. Since none of these groups had been found to show consistent individual differences in initiated aggression during Observation Period 2, nor to have dominance hierarchies, no further Friedman comparisons of combined weight and initiated agonism/dominance scores were made.

8.1.4

Discussion.

The finding that isolation-reared male rats interacted more frequently, using a greater proportion of on-top-of postures, than their similarly housed socially-reared peers replicates that of Wahlstrand et al (1983). The observation that mixed housed males interacted less often, and with a higher proportion of boxing behaviour than all-male housed animals was contrary to that predicted from earlier studies (see section 1.1.1.4). However, the previous studies of the aggressiveness of mixed housed males had all involved intruder or neutral arena tests, whereas the present investigation looked at intra-group intermale aggression. Thus it appears that the presence or recent experience of females may increase aggression to unfamiliar males, but not to cohabiting males.

The reduction in intermale interaction frequency in mixed housed groups is contradictory to Barnett's (1958b) finding, and difficult to explain. To some extent, it seems that the males' interest in the females distracted them from their fellow males. However, it is also possible that the females themselves inhibited overall group activity in such confined colony housing (with no nest boxes). Inevitably, the females were almost always pregnant and so were liable to show fierce aggression to animals which approached them, especially when they were resting or feeding (Barnett, 1958b; Calhoun, 1963). This may have effectively reduced total movement about the cage.

The proportionate differences in production of agonistic behaviours between isolation-reared and socially-reared (especially mixed-reared x mixed housed) males suggests that there was a qualitative difference in the form of agonistic interactions within isolation- and socially-reared groups. Previous observations of a mixed group revealed extended boxing and threat posturing before the on-top-of posture was adopted in a series of agonistic interactions (Thor and Flannelly, 1977). The present results suggest a similar pattern in socially-reared males, while isolation-reared animals seem to have reached the on-top-of posture more frequently, showing fewer other agonistic behaviours. Since the on-top-of posture is thought to be most representative of dominance relations in rats (Grant and Chance, 1958; Baenninger, 1966; Flannelly and Lore, 1977b; Meaney and Stewart, 1981) it would appear that the interactions of early isolated males were more concerned with dominance than were those of the socially-reared males, possibly because they had been housed together for a much shorter period.

The effect of rearing condition on frequency of interaction (both absolute and relative) with cohabiting females found in this experiment also suggests that the early isolated males may have been more interested in establishing some kind of social relationships with one another than they were in showing sexual or other behaviours to females. All-male-reared males showed a slight tendency towards the same pattern. This behaviour cannot have been due to sexual inadequacy or lack of sexual interest, as all the cohabiting females in all groups were impregnated shortly after grouping.

Despite the observation that recently formed groups of isolation-reared males showed more on-top-of behaviour than other groups, suggesting that they may have been in the process of developing dominance hierarchies (Meaney and Stewart, 1981), only one such linear hierarchy was found (in terms of consistent directional ranking of four agonistic measures) in a total of forty groups investigated. The dominance ranks of this group were not related to individual aggressiveness or sexual behaviour to cohabiting females. This scarcity of finding dominance hierarchies might have been due to the use of the wrong criterion in determining agonistic dominance in male rats. However, since none of the agonistic measures independently showed consistent linear ranking in any of the experimental conditions, it seems more likely that dominance hierarchies were not found because they did not exist. Linear hierarchies had previously been found using only the on-top-of measure in all Grant and Chance's (1958) groups of four male rats, and in half of Baenninger's (1966) similar groups. Using the same criterion, 19% of the groups in Observation Period 1 and 33% of the groups in Observation Period 2 of this study showed linear dominance. These results do not exceed the chance occurrence of linearity (37.5%) expected from the measurement of linearity in a single behaviour (Appleby, 1983).

These results do not support Meaney and Stewart's (1981) claim that rats develop dominance hierarchies (determined by on-top-of behaviour) during the play period. Meaney and Stewart also suggested that these hierarchies are maintained by the same behaviour in adulthood. The present study shows no evidence of such hierarchies in groups of rats housed together continuously from weaning, nor in males isolated from weaning until after puberty, despite the fact that the latter animals showed a high frequency (both proportionate and absolute) of on-top-of behaviour.

The very low occurrence of despotism found in this experiment could have been entirely due to chance. However, since it was only found during the second part of the experiment and only in mixed groups, it is possible that it indicated a very slow process of social organisation (faster in mixed than in all-male groups) to either a despotic, or even ultimately a hierarchical, system.

Investigation of the intra-group consistency of initiation of agonistic behaviours revealed such consistency in only 20-30% of groups, with no more groups showing consistency in one experimental condition than in any other. The same was true of consistency of received agonism. Only one group showed a consistent relationship between aggressiveness and sexual behaviour to cohabiting females. This overall level of consistency in aggressiveness suggests either a tendency towards an effect of win/loss experience on future agonistic behaviour (i.e. changes in 'confidence' at a very low level), or differential rates of maturation of aggression between individuals. It seems, therefore, that the experience of winning and losing encounters within an established group cannot have as great an effect on future aggressiveness in male rats as does similar experience with a succession of unfamiliar males (see section 1.1.2).

The results of weight tests on the male rats in this experiment showed no overall differences in weights or weight change between conditions. Nor were there consistent intra-group differences in these measures. This implies that the different housing/rearing conditions did not produce very great differences in stress. A previous study had found that intruders into mixed colonies lost more weight, apparently through the adverse physiological effects of stress, than did intruders into all-male colonies (Thor and Flannelly, 1976). These results again suggest that territorial aggression may be increased in mixed groups of rats, while intra-group aggression is not.

8.2

Mating tests

8.2.1

Introduction.

Previous research has shown that early (postweaning) isolation reduces a male rat's copulatory ability such that many animals fail to copulate on test. All-male housing over a similar period also reduces copulatory ability, but to a smaller extent. These effects of early experience on copulation have been shown to be only temporary, however, as extended experience of mating tests, or subsequent group housing (preferably mixed) leads to full copulation in almost all animals (see section 6.2.2).

Some controversy still exists on the question of whether early isolation or all-male housing affects copulatory behaviours permanently or only temporarily. The aspects of pre-ejaculatory behaviour which have been investigated most are the frequency and latency of intromissions (see section 6.2.2). In the present study, the behaviour of male rats with different postweaning and postpubertal social experiences (including early isolation) was investigated in individual and group tests. By these means, each rat's pre-ejaculatory behaviours as well as its ability to copulate could be measured to see whether early experiences had any permanent effects.

Another reason for carrying out these tests was to look at the relationship between intra-group social structure i.e. dominance status or individual differences in aggressiveness, and copulation.

Most previous studies involving competition for one oestrous female by more than two males have suggested that relative reproductive success (i.e. reproductive priority) is determined by reproductive strategy rather than by overt aggression (see section 1.2.5.2.2). In this experiment, elements of group mating behaviour thought to be most indicative of reproductive priority were compared with each male's social status and aggressiveness. It was hoped to show, in this way, whether there was a relationship between male rat social organisation and reproductive priority, and whether this relationship was affected by early experience or all-male housing. Social status was also compared, where possible, with each rat's copulatory behaviour in the individual mating tests, to show whether it was related in absolute terms to reproductive ability as well as to competitive reproductive priority.

8.2.2

Method.

Test Females.

Females used for the mating tests were from the same stock as the experimental males. They were nulliparous and aged from 2-6 months at the time of testing. Females were housed together in small groups in the same room as the mixed group experimental animals.

The oestrus cycle of each female was determined by vaginal smears taken every morning. Mating tests were carried out between 1700 and 2100 hours on the day of proestrus. As a double check of receptivity, all females to be used were first tested with a stud male. If any female showed aggression towards the male or failed to exhibit lordosis when mounted, she was discarded for that day.

Females which did not become pregnant as a result of a mating test were used again. Those which did become pregnant were kept until their litters were born and were subsequently killed.

Apparatus

Tests were carried out in a room separated from the main animal wing. Experimental animals and test females were transported to and from this room in their home cages. Testing took place in a circular open field (diam. 70 cm: ht. 30.5 cm) painted matt black with white lines across the floor. The open field was lit by a 40W red bulb in an Anglepoise lamp situated 120 cm above its base. A Smiths stopclock was used to time the tests.

After individual testing, each male from a socially-housed group was put into a white plastic carrying cage (Bowman: 39 x 29.5 x 17.5 cm) until testing of his group was finished for the day.

Procedure

Testing was carried out during the dark period, between 1630 and 2030 hours.

The open field was thoroughly cleaned with diluted Tego Amphocide before and after each test. Home group females (if any) were removed from the home cage six hours before testing began. This procedure was intended to reduce possible effects of sexual fatigue.

Only one test female was used per test, for both Individual and Group Mating tests. The test female was placed in the open field one minute before each test began in order to acclimatise her to her surroundings.

For the Individual Mating tests, one male was placed in the centre of the field as the stopclock was started. The experimenter sat on a stool adjacent to the open field and recorded the male's behaviour on a check sheet. For 10 minutes the experimenter scored the latencies to first ano-genital sniff and full mount (with penis-licking), and the frequencies of these behaviours. Frequencies were scored in 30 second blocks throughout the 10-min. period. If a male had started mounting but had not yet ejaculated after 10 mins., the test was continued until ejaculation occurred. Only the frequency of mounting and the time of ejaculation were scored after the initial 10 minutes. Any animal which had started a second series of mounts before the 10 minutes were up was allowed to continue until a second ejaculation took place.

Group Mating tests were carried out only when all the males in a group had been subjected to Individual Mating tests, and never on the same day as any of these tests. In a Group Mating test, all four males in a socially-housed group were placed simultaneously in the centre of the open field and the stopclock started. For the following 30 minutes the latency to mount the test female and frequencies of mounting and ejaculation were scored for each male in one-minute blocks. The occurrence, but not the frequency, of male-male mounting was noted. At the end of 30 minutes the males were returned to their home cage.

Treatment of results.

Mating behaviour: Inter-group comparisons.

The percentages of males in each condition which exhibited ano-genital sniff (Individual Mating tests only), mount, and ejaculation were calculated. Chi-squared tests were peformed on the results to show whether there were significant effects of Rhcond, or of Rcond and Hcond on these measures.

T tests and analyses of variance were performed on the latencies and frequencies of behaviours scored during the Individual and Group Mating tests respectively. These were intended to show whether rearing/housing conditions affected copulatory performance.

Dominance and mating behaviour: Intra-group comparisons.

For the Individual Mating tests, each group's scores on the latencies to first ano-genital sniff, mount and ejaculation, and their numbers of ano-genital sniffs to first mount, and of mounts to first ejaculation were ranked. Ranks of 1 were assigned to the shortest latencies and the smallest frequencies of these behaviours. Friedman two way analyses of variance were performed on these five ranked scores in order to show whether there were consistent individual differences in speed of copulation (considered to be a measure of sexual activity and therefore possibly related to reproductive success, see section 1.2.5.2.2) within each group.

If a dominance hierarchy or consistent individual differences in initiated agonism had been found for any of the groups which showed significant differences in speed of copulation, then a further Friedman analysis of variance was performed on the combined Individual Mating and initiated agonism (or dominance) scores. If this resulted in an increased Chi-r-squared value, then a close relationship between speed of copulation and aggressiveness (or dominance) was found.

In the Group Mating tests, two measures thought to be most representative of reproductive success (see Section 1.2.5.2.2) were ranked within each group. These measures were: number of ejaculations; number of ejaculations followed by at least four minutes in which the female received no intromissions. If a dominance hierarchy or consistent individual differences in initiated agonism had been found for any of the groups, then a Friedman analysis of variance of the combined ranked Group Mating and initiated agonism (or dominance) scores was performed. If this resulted in an increased Chi-r-squared value (over that obtained for initiated agonism alone), or a significant Chi-r-squared value (for comparisons with dominance status), then a close relationship between reproductive success and aggressiveness (or dominance) was found.

8.2.3

Results.

8.2.3.1

Individual mating test 1.

Mating behaviour: Inter-group comparisons.

Chi-squared tests performed on the percentage of males in each Rhcond which showed ano-genital sniff, mount and ejaculation (see Table 8.14) gave the following results. Significant differences between Rhconds were found on all three measures: ano-genital sniff (Chi-squared=28.39, df=2, p<.001); mount (Chi-squared=14.86, df=2, p<.001); ejaculation (Chi-squared=46.42, df=2, p<.001). In all cases, a high percentage of males from the mixed Rhcond showed the behaviour, and a low percentage of isolation Rhcond males showed mating behaviour during the test. Males from the all-male Rhcond gave an intermediate score.

Analyses of variance were performed on the following measures: number of ano-genital sniffs in 10 minutes; number of ano-genital sniffs to first mount; latency to first ano-genital sniff; latency to first mount; latency to first ejaculation; number of mounts to ejaculation; time from first mount to ejaculation; mount rate to ejaculation (Table 8.15). Significant effects of Rhcond were found for all these measures except for number of mounts to ejaculation (Table 8.16).

The pattern of results was the same for the three latencies and

		Rhcond	
Behaviour	Mixed	All-male	Isolation
Ano-genital sniff	96.88	90.63	37.5
Mount	84.38	53.13	15.63
Ejaculation	81.25	50.0	12.5

Table 8.14
Individual Mating Test 1: Percentages of males showing copulatory behaviours.

Behavioural Measure	Rhcond	Mean score.	Standard error.
No. of ano-genital sniffs in 10 mins.	MF	9.44	0.96
	M	17.63	2.37
	I	3.53	1.11
No. of ano-genital sniffs to first mount.	MF	6.85	0.63
	M	9.53	1.12
	I	0.00	0.00
Latency to ano-genital sniff (secs).	MF	56.32	9.51
	M	99.55	16.70
	I	247.83	56.56
Latency to mount (secs).	MF	115.0	19.96
	M	214.1	18.07
	I	317.0	54.21
Latency to ejaculation (secs).	MF	453.6	32.6
	M	699.3	50.9
	I	922.5	72.9
No. of mounts to ejaculation.	MF	14.88	1.58
	M	14.69	1.02
	I	18.0	3.67
Time from first mount to ejaculation (secs).	MF	370.5	30.5
	M	500.7	43.1
	I	667.5	80.7
Mount rate to ejaculation (mounts per minute).	MF	2.40	0.14
	M	1.94	0.16
	I	1.64	0.29

Rhcond = Rearing/housing condition.
(MF = Mixed, M = All-male, I = Isolation.)

Table 8.15
Individual Mating test 1: Means and standard errors of copulatory behaviours.

Behavioural Measure	Rhcond F value	Df	P
No. of ano-genital sniffs in 10 mins.	19.22	2/93	<.0001
No. of ano-genital sniffs to first mount.	13.14	2/46	<.0001
Latency to ano-genital sniff.	15.03	2/69	<.0001
Latency to mount.	12.28	2/46	<.0005
Latency to ejaculation.	17.40	2/43	<.0001
No. of mounts to ejaculation.	0.40	2/43	>.5
Time from mount to ejaculation.	7.49	2/43	<.005
Mount rate to ejaculation.	3.80	2/43	<.05

Rhcond = Rearing/housing condition.

Table 8.16
Individual Mating Test 1: Results of analyses of variance.

between Rhconds to be significant at at least the .05 level for the number of sniffs in 10 minutes. For the number of ano-genital sniffs to first mount, the Newman Keuls comparisons revealed no significant difference between the mixed and all-male Rhconds (Q=2.41, df=46, p>.05) and highly significant differences between these Rhconds and the isolation Rhcond (isolation Rhcond v all-male Rhcond; Q=7.62, df=46, p<.01 : isolation Rhcond v mixed Rhcond; Q=5.16, df=46, p<.01). None of the five isolated males which mounted during this test showed any ano-genital sniffing before their first mount.

Dominance and mating behaviour: Intra-group comparisons.

Groups A3, A4, B2, B3 (mixed Rhcond), C1, C3, D1, and D2 (all-male Rhcond) showed consistent individual differences in speed of copulation (Table 8.6). Further analysis of the combined initiated agonism and I.M. test 1 scores of groups A3, D1 and D2 yielded increased values of Chi-r-squared in all three cases (Table 8.6). These results indicated a close relationship between aggressiveness and speed of copulation in these groups.

8.2.3.2

Individual mating test 2.

Mating behaviour: Inter-group comparisons.

Chi-squared tests of Rcond x Hcond performed on the percentage of males in each condition which showed ano-genital sniff, mount and ejaculation (see Table 8.17) gave the following results. The null hypothesis that no association between Rcond and Hcond existed was for the time from first mount to ejaculation. Males from the mixed Rhcond were fastest and isolate males were slowest to ano-genital sniff, mount and ejaculate, and to reach ejaculation after starting a series of mounts. Similarly, mixed Rhcond males mounted most rapidly while isolate males had the slowest mounting rate. Further analysis of the latencies to first ano-genital sniff using the Newman Keuls method of multiple comparisons (with Bancroft's (1968) use of the harmonic mean to correct for unequal sample sizes; Ferguson, 1976) showed no significant difference between the mixed and all-male Rhconds ($Q=1.88$, $df=69, p>.05$), and highly significant differences between these groups and the isolates (isolation Rhcond v all-male Rhcond; $Q=7.29$, $df=69$, $p<.01$): isolation Rhcond v mixed Rhcond; $Q=9.17$, $df=69$, $p<.01$).

Similar analysis of the latencies to first mount and to ejaculation yielded significant differences at at least the $p<.05$ level between all Rhconds. Newman Keuls comparison of the times from mount to ejaculation gave a significant difference between the scores for mixed Rhcond and isolation Rhcond males ($Q=5.37$, $df=43$, $p<.01$), but not for either of the other two comparisons (mixed Rhcond v all-male Rhcond; $Q=2.36$, $df=43$, $p>.05$: all-male Rhcond v isolation Rhcond; $Q=3.02$, $df=43$, $p>.05$). The Newman Keuls test showed no difference between the three Rhconds on mount rate.

A different pattern of results emerged for the ano-genital sniff frequency scores (number of ano-genital sniffs in 10 minutes and number of ano-genital sniffs to first mount). Males from the all-male Rhcond gave the highest scores and isolates the lowest scores on both measures. Newman Keuls analyses showed all possible comparisons

Behaviour	Hcond	Rcond Mixed	 All-male	 Isolation
Ano-genital sniff	Mixed	100	87.5	87.5
	All-male	93.75	87.5	87.5
Mount	Mixed	100	100	93.75
	All-male	93.75	75.0	81.25
Ejaculation	Mixed	100	100	93.75
	All-male	93.75	68.75	75.0

Rcond = Rearing condition.
Hcond = Housing condition.

Table 8.17
Individual Mating Test 2: Percentages of males showing copulatory behaviours.

accepted for all three measures (ano-genital sniff; Chi-squared=.13, df=2, p>.9: mount; Chi-squared=1.15, df=2, p>.5: ejaculation; Chi-squared=2.14, df=2, p>.3).

It is apparent that in the two experimental conditions which had not been housed with females at any stage during the experiment (all-male Rcond x all-male Hcond, and isolation Rcond x all-male Hcond), fewer males achieved full mating behaviour than in the other conditions. Nevertheless, the experience of social housing in the isolation Rcond x all-male Hcond males has increased the percentage of males achieving ejaculation on test from 12.5% to 75%. This suggests that familiarity with other rats is the most important factor affecting a male rat's ability to mate in a 10 minute test, while familiarity with female rats in particular is less important.

Analyses of variance were performed on the same measures as in the first Individual Mating test (Tables 8.18a-h). There was no significant effect of either Rcond or Hcond on the number of ano-genital sniffs in ten minutes (Table 8.19). This implies that social housing and as little as 10 minutes' experience of a female had been sufficient to produce normal overall levels of ano-genital sniffing in the isolation Rcond x all-male Hcond males.

Rcond had a significant effect on the following scores: number of ano-genital sniffs to first mount; latency to mount; latency to ejaculation, time from first mount to ejaculation; mount rate to ejaculation. Measures showing a significant effect of Hcond were: latency to ano-genital sniff; number of mounts to ejaculation; mount rate to ejaculation (Table 8.19).

	Rcond		
Hcond	MF	M	I
MF	9.56	9.38	12.31
	(1.96)	(1.67)	(2.78)
M	7.19	20.50	12.75
	(1.55)	(7.20)	(2.60)

Table 8.18a
No. of ano-genital sniffs in 10 mins.

	Rcond		
	MF	M	I
MF	3.31	4.13	9.60
	(0.68)	(0.84)	(2.31)
M	3.73	5.25	7.00
	(0.97)	(2.40)	(2.24)

Table 8.18b
No. of ano-genital sniffs to first mount.

	Rcond		
	MF	M	I
Hcond			
MF	23.00	30.79	19.29
	(8.90)	(17.93)	(4.00)
M	62.73	71.00	51.36
	(32.07)	(34.65)	(15.28)

Table 8.18c
Latency to first ano-genital sniff (secs).

	Rcond		
	MF	M	I
MF	56.5	38.4	134.8
	(25.4)	(4.1)	(25.6)
M	55.8	90.4	194.8
	(11.8)	(28.9)	(37.1)

Table 8.18d
Latency to first mount (secs).

	Rcond		
	MF	M	I
Hcond			
MF	382.5	560.7	597.9
	(50.0)	(67.7)	(37.6)
M	464.1	515.4	737.4
	(61.9)	(79.1)	(89.1)

Table 8.18e
Latency to ejaculation (secs).

	Rcond		
	MF	M	I
MF	16.06	16.94	14.73
	(2.44)	(1.11)	(2.18)
M	20.47	18.09	21.00
	(2.18)	(2.72)	(2.88)

Table 8.18f
No. of mounts to ejaculation.

	Rcond		
	MF	M	I
Hcond			
MF	343.2	538.2	459.9
	(48.0)	(67.0)	(42.3)
M	420.0	433.5	579.9
	(54.9)	(73.2)	(73.0)

Table 8.18g
Time from first mount to ejaculation (secs).

	Rcond		
	MF	M	I
MF	2.90	2.20	1.90
	(0.19)	(0.21)	(0.13)
M	3.14	2.70	2.26
	(0.23)	(0.19)	(0.20)

Table 8.18h
Mount rate to ejaculation (mounts per minute).

Rcond = Rearing condition, Hcond = Housing condition.
(MF = Mixed, M = All-male, I = Isolation.)
Standard errors are given in parentheses.

Tables 8.18a-h
Individual Mating test 2: Means and standard errors of copulatory behaviours.

Behavioural Measure	Condition	F value	Df	P
No. of ano-genital sniffs in 10 mins.	Rcond	1.75	2/90	>.1
	Hcond	1.12	1/90	>.2
	Rc x Hc	2.02	2/90	>.1
No. of ano-genital sniffs to first mount.	Rcond	4.88	2/81	<.05
	Hcond	0.07	1/81	>.7
	Rc x Hc	0.70	2/81	>.5
Latency to ano-genital sniff.	Rcond	0.25	2/81	>.7
	Hcond	4.27	1/81	<.05
	Rc x Hc	0.02	2/81	>.9
Latency to mount.	Rcond	13.10	2/81	<.0001
	Hcond	3.54	1/81	>.06
	Rc x Hc	0.99	2/81	>.3
Latency to ejaculation.	Rcond	7.14	2/79	<.005
	Hcond	1.04	1/79	>.3
	Rc x Hc	0.58	2/79	>.5
No. of mounts to ejaculation.	Rcond	0.08	2/79	>.9
	Hcond	4.75	1/79	<.05
	Rc x Hc	0.58	2/79	>.1
Time from mount to ejaculation.	Rcond	3.09	2/79	<.05
	Hcond	0.32	1/79	>.5
	Rc x Hc	1.98	2/79	>.1
Mount rate to ejaculation.	Rcond	12.67	2/79	<.0001
	Hcond	5.89	1/79	<.05
	Rc x Hc	0.25	2/79	>.9

Rcond(Rc) = Rearing condition.
Hcond(Hc) = Housing condition.

Table 8.19
Individual Mating Test 2: Results of analyses of variance.

The latencies to mount and ejaculation, and time from first mount to ejaculation showed the same pattern in this test as in Individual Mating test 1 (I.M.test 1). The isolation Rcond males were slowest and the mixed Rcond males fastest, with the all-male Rcond males giving intermediate scores. Newman Keuls comparisons between Rconds showed the isolation-reared males to be significantly slower to mount than the socially-reared males (isolation Rcond v all-male Rcond; $Q=6.08$, $df=84$, $p<.01$: isolation Rcond v mixed Hcond; $Q=6.35$, $df=84$, $p<.01$), with no significant difference between mixed and all-male Rcond males ($Q=.27$, $df=84$, $p>.05$). Newman Keuls analysis of latency to ejaculation and time from first mount to ejaculation gave no further significant differences between Rconds.

It seems that there may be some residual effect of isolation rearing on the time it takes for a male to initiate mating behaviour when confronted by an oestrous female, even when he has been socially housed for the previous five weeks. When comparing the isolation Rcond x all-male Hcond males with other groups, however, it must be remembered that these animals had had less experience of females than any of the other males, as they had neither been housed with females nor had they been subjected to a 30 minute Group Mating test during the first part of the experiment (see Figure 8.1).

The effect of Rcond on the number of ano-genital sniffs to first mount was markedly different in I.M. test 2 than in the I.M. test 1, as the isolation-reared males ano-genital sniffed more often than the socially-reared males during the second test. This difference between isolation- and social-rearing was shown to be significant by Newman Keuls comparison (isolation Rcond v all-male Rcond; $Q=3.30$, $df=84$, p<.05: isolation Rcond v mixed Rcond; Q=4.25, df=84, p<.01), while no difference was found between the two socially-reared conditions (Q=.95, df=84, p>.05).

The experience of social housing had obviously been sufficient for isolation-reared males to learn to investigate another rat by ano-genitally sniffing it. However, the observation that the isolation Rcond males ano-genital sniffed the test females more before mounting than did the other males suggests that they may have required more olfactory stimulation than socially-reared males before they were sure of the sexual status of the female.

The pattern of results for latency to ano-genital sniff was different in I.M.test 2 from that found in I.M. test 1, showing an effect of Hcond but not of Rcond (Table 8.19). All-male Hcond males were slower to sniff the test females than were mixed Hcond males. Possibly, lack of recent experience of females might have caused the all-male Hcond males to hesitate longer before approaching them and investigating then by ano-genital sniffing.

The number of mounts to ejaculation also showed a different pattern in I.M. test 2. All-male Hcond males mounted more times before ejaculating than did mixed Hcond males (Table 8.18f). This would appear to be an effect of recent practice. The mixed Hcond males were probably better at achieving accurate intromission than the all-male Hcond males, and so required fewer mounts before ejaculating.

The only measure to show effects of both Rcond and Hcond was mount rate to ejaculation (Table 8.19). All-male Hcond males mounted more rapidly than mixed Hcond males. Mixed Rcond males mounted more rapidly than all-male Rcond males, and the latter animals mounted more rapidly than isolation Rcond males (Table 8.18h). This finding can be looked on as the combined effects of Rcond on time from first mount to ejaculation and of Hcond on the number of mounts to ejaculation.

Dominance and mating behaviour: Intra-group comparisons.

Groups A1 (mixed Rcond x mixed Hcond), D2 and D4 (all-male Rcond x mixed Hcond) showed consistent individual differences in speed of copulation (Table 8.10). Further analysis of group D4's combined mating and initiated agonism scores gave an increased Chi-r-squared value, indicating a close relationship between aggressiveness and speed of copulation in this group (Table 8.10).

8.2.3.3

Group mating test 1.

Mating behaviour: Inter-group comparisons.

Chi-squared comparisons between Rhconds performed on the percentages of animals exhibiting mount and ejaculation during this test (see Table 8.20) gave the following results. No significant difference between Rhconds was found for either measure (mount; Chi-squared=.86, df=1, p>.3: ejaculation; Chi-squared=2.00, df=1, p>.1), although slightly fewer males in the all-male Rhcond groups showed these behaviours than in the mixed Rhcond groups. This finding differs from that of I.M. test 1 in which significantly fewer of the all-male than mixed Rhcond males showed mating behaviour. The improved performance of these animals in the Group Mating test could

Behaviour	Rhcond	
	Mixed	All-male
Mount	96.88	84.38
Ejaculation	96.88	78.13

Rhcond = Rearing/housing condition.

Table 8.20
Group Mating Test 1: Percentages of males showing copulatory behaviours.

be due to their previous experience of females in the I.M. test, the longer duration of the Group Mating test (giving more time in which to habituate to the unfamiliar female), or to the presence of the other group males, or to a combination of these factors.

Six measures of mating behaviour were obtained for the mixed and all-male Rhcond males during this test. These were: latency to mount; latency to first ejaculation; number of mounts to first ejaculation; time from first mount to ejaculation; number of ejaculations in thirty minutes (Table 8.21). A large difference in variance of the latencies to mount was found between conditions, so a Cochran and Cox t test was performed on this data. Student's t tests were carried out on the data for the other measures. Significant differences in scores between the mixed and all-male Rhconds were found for all measures (see Table 8.22). The mixed Rhcond males were quicker to mount and ejaculate than the all-male Rhcond males, and took less time from first mount to ejaculation. They also mounted fewer times and more rapidly before ejaculating than did the all-male Rhcond males, and ejaculated more often in the thirty minute test.

In general, these results indicate that males in all-male Rhcond groups were quite capable of mating, but that they were slower to initiate mating behaviour. This slowness could have been due to lack of practice, as the animals had only had the previous sexual experience of one Individual Mating test.

Only one of these results differs from those obtained for the all-male and mixed Rhconds in I.M. test 1. In the Individual Mating test, no difference between conditions was found in the number of

Behavioural Measure	Rhcond	Mean	Standard error.
Latency to mount (secs).	MF	148.8	38.4
	M	309.2	76.2
Latency to ejaculation (secs).	MF	582.6	52.6
	M	1032.0	86.7
No. of mounts to ejaculation.	MF	13.77	1.00
	M	19.32	1.66
Time from first mount to ejaculation (secs).	MF	474.2	38.3
	M	859.2	62.6
Mount rate to ejaculation (mounts per minute).	MF	1.85	0.10
	M	1.37	0.08
No. of ejaculations in 30 mins.	MF	2.91	0.19
	M	1.50	0.20

Rhcond = Rearing/housing condition.
(MF = Mixed, M = All-male, I = Isolation.)

Table 8.21
Group Mating test 1: Means and standard errors of copulatory behaviours.

Behavioural Measure	t value	Df	P
Latency to mount.	10.01	56	<.001
Latency to ejaculation.	4.62	54	<.0001
Number of mounts to ejaculation.	2.96	54	<.005
Time from first mount to ejaculation.	5.46	54	<.0001
Mount rate to first ejaculation.	3.53	54	<.001
Number of ejaculations.	5.19	62	<.0001

Table 8.22
Group Mating Test 1: Results of t tests.

mounts to first ejaculation, whereas in the Group Mating test the all-male Rhcond males mounted more times before ejaculating than did the mixed Rhcond males.

Although no precise quantitative data on male-male mounting are available for this test, the observer wrote down her overall impression of its frequency at the end of each Group Mating test. The impression gained was that male-male mounting was very common in the all-male Rhcond groups and infrequent in the mixed Rhcond groups. In both cases, frequency of male-male mounting decreased towards the end of the test.

It is possible that this common occurrence of male-male mounting in the all-male Rhcond groups may have led to their larger number of male-female mounts before ejaculation. The experience of mounting a male, with obvious lack of intromission, may reduce a male rat's state of arousal. The male-male mounting in the all-male Rhcond groups gave every impression of being accidental. In a state of excitement while chasing the female, a male would inadvertently mount another male which was in front of him. After mounting a male, the mounter would frequently appear confused and spend some time ano-genitally sniffing the other males and the female before attempting to mount the female again. Possibly, lack of cohabitation experience of females at this stage led to poor discrimination between males and females, except by ano-genital sniffing.

Dominance and mating behaviour: Intra-group comparisons.

Friedman two way analyses of variance were performed on the combined initiated agonism and Group Mating test 1 behaviour measures for groups A2, A3 (mixed Rcond x mixed Hcond), D1, D2 and D3 (all-male Rhcond). Increased Chi-r-squared values were found for groups D1 and D2, indicating a close relationship between initiated agonism and reproductive success in these groups (Table 8.6).

8.2.3.4

Group mating test 2

Mating behaviour: Inter-group comparisons.

Chi-squared comparisons of the number of males in each experimental condition which showed mounting and ejaculation during this test (see Table 8.23) gave the following results. No significant association between Rcond and Hcond was found for either measure (mount;Chi-squared=.56, df=2, p>.7: ejaculation; Chi-squared=1.21, df=2, p>.5). The percentages of animals showing full mating behaviour in each condition were almost identical to those for I.M. test 2. The males Which had never been housed with females were least likely to mate.

Analyses of variance were performed on the same measures as for G.M. test 1 (see Tables 8.24a-f). Effects of Rcond were found for latency to ejaculation, time from first mount to first ejaculation, mount rate to ejaculation and number of ejaculations in thirty minutes (Table 8.25).

Behaviour	Hcond	Rcond Mixed	 All-male	 Isolation
Mount	Mixed	100	100	93.75
	All-male	100	87.5	93.75
Ejaculation	Mixed	100	87.5	93.75
	All-male	100	75.0	75.0

Hcond = Housing condition.
Rcond = Rearing condition.

Table 8.23
Group Mating Test 2: Percentages of males showing copulatory behaviours.

	Rcond		
Hcond	MF	M	I
MF	48.4	83.7	72.9
	(8.0)	(43.7)	(11.3)
M	105.4	230.3	266.1
	(27.2)	(111.3)	(75.0)

Table 8.24a
Latency to mount (secs).

	Rcond		
	MF	M	I
MF	348.8	510.0	572.0
	(29.6)	(48.2)	(70.5)
M	532.5	535.0	930.0
	(45.8)	(70.0)	(107.5)

Table 8.24b
Latency to ejaculation (secs).

	Rcond		
Hcond	MF	M	I
MF	10.75	19.57	14.40
	(0.87)	(2.82)	(2.10)
M	16.63	14.75	16.83
	(1.20)	(1.64)	(1.72)

Table 8.24c
No. of mounts to first ejaculation.

	Rcond		
	MF	M	I
MF	337.5	497.2	532.0
	(27.9)	(47.3)	(69.6)
M	453.7	490.0	775.0
	(28.4)	(66.9)	(96.3)

Table 8.24d
Time from first mount to ejaculation (secs).

	Rcond		
Hcond	MF	M	I
MF	2.00	2.33	1.65
	(0.15)	(0.20)	(0.13)
M	2.22	1.90	1.47
	(0.17)	(0.17)	(0.23)

Table 8.24e
Mount rate to ejaculation (mounts per minute).

	Rcond		
	MF	M	I
MF	3.50	2.31	2.81
	(0.16)	(0.28)	(0.25)
M	2.94	2.06	1.56
	(0.21)	(0.36)	(0.29)

Table 8.24f
No. of ejaculations in 30 mins.

Rcond = Rearing condition.
Hcond = Housing condition.
(MF = Mixed, M = All-male, I = Isolation.)
Standard errors are given in parentheses.

Tables 8.24a-f
Group Mating test 2: Means and standard errors of copulatory behaviours.

Behavioural Measure	Condition	F value	Df	P
Latency to mount.	Rcond	1.59	2/86	>.2
	Hcond	8.08	1/86	<.01
	Rc x Hc	0.84	2/86	>.4
Latency to ejaculation.	Rcond	11.67	2/79	<.0005
	Hcond	12.36	1/79	<.001
	Rc x Hc	4.08	2/79	<.05
Number of mounts to first ejaculation.	Rcond	2.09	2/79	>.1
	Hcond	0.92	1/79	>.3
	Rc x Hc	4.59	2/79	<.05
Time from first mount to ejaculation.	Rcond	9.60	2/79	<.0005
	Hcond	5.51	1/79	<.05
	Rc x Hc	2.74	2/79	>.06
Mount rate to ejaculation.	Rcond	6.32	2/79	<.005
	Hcond	0.34	1/79	>.5
	Rc x Hc	1.88	2/79	>.1
Number of ejaculations in 30 mins.	Rcond	10.04	2/90	<.0005
	Hcond	10.04	1/90	<.005
	Rc x Hc	1.85	2/90	>.1

Rcond(Rc) = Rearing condition.
Hcond(Hc) = Housing condition.

Table 8.25
Group Mating Test 2: Results of analyses of variance.

Effects of Hcond were found for latency to mount, latency to ejaculation, time from first mount to ejaculation and number of ejaculations in thirty minutes (Table 8.25). There was a significant interaction between Rcond and Hcond for latency to ejaculation and number of mounts to first ejaculation (Table 8.25).

The scores for latency to ejaculation and time from first mount to ejaculation showed an almost identical pattern (Tables 8.24b and d). Newman Keuls multiple comparisons performed on both sets of data showed the isolation Rcond x all-male Hcond males to be significantly slower than males in all the other conditions (latency to ejaculation; Q>4.2, df=79, p<.01: time from mount to ejaculation; Q>5.7, df=79, p<.01). No significant difference existed between any of the other conditions. This effect, therefore, appears to have been due to the reduced sexual experience of those males which had neither been housed with females nor had the experience of Group Mating test 1.

The all-male Hcond males were slower to mount than were the mixed Hcond males on this test, and also ejaculated fewer times (Tables 8.24a and f). The effect of Rcond on ejaculation frequency was such that mixed Rcond males ejaculated more often than all-male and isolation Rcond males, but no difference existed between the latter two Rconds (Table 8.25). These results indicate that recent experience of cohabiting with females is important in determining how long it takes for a male rat to initiate mating behaviour, and possibly also how frequently he can ejaculate. This effect of recent experience appears to be more important than the experience of being reared with females, as far as latency to mount is concerned. Frequency of ejaculation seems to depend on total amount of sexual experience (i.e. duration of cohabitation with females and number of mating tests taken).

The pattern of results for number of mounts to ejaculation was unique (Table 8.24c). For both the mixed and isolation Rconds, the all-male Hcond males mounted more often before ejaculating than did the mixed Hcond males. For the all-male Rcond, however, this trend was reversed. There is no obvious explanation for this phenomenon.

Newman Keuls comparison between Rconds on the mount rate scores revealed no difference between the mixed and all-male Rcond males ($Q=.18$, $df=82$, $p>.05$) and significant differences between both of these conditions and the isolation Rcond males (isolation x mixed; $Q=4.29$, $df=82$, $p<.01$: isolation x all-male; $Q=4.46$, $df=82$, $p<.01$).

In general, these results are very similar to those obtained in Individual Mating test 2. The mating performance of isolation Rcond males seemed to depend more on their recent housing conditions i.e. whether they had been housed with males only or in mixed groups, than on their lack of social experience during the period from 3-10 weeks of age. Male rat mating behaviour appears to be affected partly by experience of females at any previous time, but mostly by recent sexual experience.

Dominance and mating behaviour: Intra-group comparisons.

Friedman two way analyses of variance were performed on the combined initiated agonism and Group Mating test 2 behaviour measures (number of ejaculations, and number of ejaculations followed by four minutes in which the female was not intromitted) for groups B2, B3 (mixed Rcond x all-male Hcond), C4 (all-male Rcond x all-male Hcond), D4 (all-male Rcond x mixed Hcond) and E3 (isolation Rcond x mixed Hcond). A marginally increased Chi-r-squared value was found for group B2, indicating quite a close relationship between initiated agonism and reproductive success in this group (see Table 8.10).

Friedman two way analysis of variance of group E1's (isolation Rcond x mixed Hcond) dominance ranks combined with the two ranked measures of Group Mating test 2 reproductive success showed no significant relationship between dominance and reproductive success (Table 8.10).

8.2.4

Discussion.

The first Individual Mating test (I.M. test 1) showed, as predicted, that very few of the early isolated and only about half of the all-male reared males initiated copulation within the time allotted. In the first Group Mating test (G.M. test 1), the proportions of males from the mixed and all-male Rhconds which copulated were not significantly different, though they still showed the same trend.

Rearing/housing condition affected not only the proportion of males copulating in the first mating tests, but also their pre-ejaculatory behaviour. The isolates which copulated were very slow to initiate mounting and mounted at a slower rate before ejaculating than did the all-male or mixed Rhcond males. The all-male Rhcond animals were slower to start mounting and mounted at a slower rate than the mixed Rhcond males. In G.M. test 1, the all-male Rhcond males ejaculated fewer times than the mixed Rhcond males, and also mounted more times before achieving ejaculation.

These results partially support those of Beach (1958), Duffy and Hendricks (1973) and Wilhelmsson and Larsson (1973) with regard to the number of mounts to ejaculation. They do not, however, agree with Hard and Larsson's (1968) finding that isolated and all-male housed males which copulated early in testing (i.e. on their first test) did not exhibit differences in copulatory behaviours from mixed reared males. In the present study, early-copulator isolates and all-male Rhcond males did show diffences in copulatory behaviour when compared with mixed Rhcond males.

The finding that the isolation Rhcond males which copulated in I.M. test 1 did not ano-genital sniff their females before mounting, and indeed ano-genital sniffed very little at all, is new. This, combined with the observation that all-male Rhcond males sniffed the females more than the mixed Rhcond males suggests that ano-genital sniffing may be a learnt behaviour facilitating recognition of an animal's sexual identity and condition rather than an integral and necessary part of pre-ejaculatory behaviour.

In general, these results indicate that sexual performance in the first mating tests was best in males with previous sexual experience, and better in those with social experience of other males than in isolation-reared males. That the mixed Rhcond males had had previous sexual experience was confirmed by the fact that all their cohabiting females had conceived prior to testing.

The results of the second Individual and Group Mating tests showed that the experience of social housing for four weeks plus at least one mating test were sufficient to cause most early isolated males to copulate in subsequent testing. They also showed, however, that postpubertal housing condition (all-male or mixed) had an important effect on copulatory behaviour, at least in individual tests, no matter what previous social experience the animals had had. All-male Hcond males were slower to ano-genital sniff, and mounted at a slower rate before ejaculating than mixed Hcond males. They also ejaculated fewer times in G.M. test 2. This suggests that recent sexual experience may be important in determining a male rat′s copulatory behaviour.

Most of the apparent effects of rearing condition on the second mating test results seem to have been actually due to amount of sexual experience, as the greatest differences were found in the mixed Rcond x mixed Hcond and isolation Rcond x all-male Hcond males. The former animals had had continuous sexual experience since puberty, while the latter males had only experienced oestrous females during I.M.tests 1 (and 2). One effect of Rcond did not seem easily explicable in terms of sexual experience, however. This was the finding that isolation-reared males ano-genital sniffed more before mounting during I.M. test 2 than did the socially-reared males. It seems possible, therefore, that males which learn to identify other animals' sexual status by ano-genital sniffing after puberty do not use the information gained as efficiently as do males which learnt this means of identification early in life. Thus they require frequent ano-genital sniff 'checks' before embarking on copulatory behaviour.

Investigation of intra-group differences in speed of copulation in individual tests revealed that in eight of the twenty-four groups tested in I.M. test 1 (i.e. 33%), consistent individual differences existed. In all three groups which also showed consistent individual differences in initiated agonism, these two factors (aggressiveness and speed of copulation) were closely related. Also, four groups (out of five for which comparison was possible) showed a close relationship between initiated agonism and reproductive priority in G.M. test 1.

Similar investigations of intra-group differences in the second mating tests yielded different results, however. Only three out of twenty-four groups (i.e. 12.5%) showed consistent individual differences in speed of copulation in I.M. test 2, and in only one was the speed of copulation related to initiated agonism. Only one significant relationship (out of a possible five) between initiated agonism and reproductive priority was found. No such relationship was found between dominance status and reproductive priority (one group only). It was notable that the only intermale aggression seen during the group mating tests occurred after incidents of male-male mounting. Such occurrences were almost always in the all-male housed groups in which the males apparently had greater difficulty in distinguishing the female from the other males than did males from mixed groups. Thus any differences in reproductive priority in these groups were not due to direct aggression.

These results suggest that male rats' aggressiveness and sexual behaviour may develop simultaneously during the pubertal period, causing individual differences to be greatest at this time. At maturity, the animals seem to attain a more similar level of aggressiveness and sexual competence such that individual differences are reduced and less consistent.. Early experience of isolation or all-male housing does not appear to affect the rate of maturation of aggressive and sexual behaviour.

A drawback in the design of the mating tests in this experiment must, however, be borne in mind when considering these results. This was that neither the individual nor (more importantly) the group tests were continued until satiation had been reached. Group mating tests to satiation would have produced more precise data relating to individual differences in reproductive success or priority,. It is possible that these differences may only be shown during the later stages of an ejaculatory series in mature males rats (Thor and Carr, 1979; McClintock et al, 1982a and b). Also, if several group tests had been performed consecutively on each group, reproductive priority could have been shown either to be consistent over time, or purely due to chance differences on each test.

8.3

Water competition tests.

8.3.1

Introduction.

Success in water competition (usually measured by length of time spent drinking) in cohabiting male rats has previously been compared with a ratio measure of aggressiveness (Baenninger, 1970), an unspecified measure of agonistic dominance rank (Lore and Flannelly, 1977), agonistic dominance in colony intruder tests (Blanchard et al, 1984), and copulation rank as measured by frequency of intromission (Gärtner et al, 1981) in attempts to establish whether social dominance in rats is consistent across priorities of access to different resources. No correlations were found between these measures and priority of access to water.

In the present study, three ways of measuring priority of access to water were used and compared with one another in order to find out whether they produced consistent results. If no consistent results were found, then it was assumed that access to water was randomly determined. If non-random (i.e. consistent) priority of access to water was found, then this was compared with results obtained concerning agonistic dominance and aggressiveness.

The task used for obtaining water in these tests involved drinking from the same spout as was habitually used by the rats, so it was thought that animals' success in drinking would not be due to differential abilities to perform the required task (Syme, 1974).

8.3.2

Method.

Apparatus

A cylindrical aluminium restrictor (length;2.5 cm: diam. 2.5 cm) was placed over the end of the water bottle spout for the duration of each test. The restrictor was also put on the spout for at least 24 hours during the week preceding the water competition test so that the animals could get used to it. This restrictor did not alter the manner in which rats drank from the spout, but merely prevented more than one rat from drinking simultaneously.

The tests were timed using a Smiths stopclock.

Procedure

The Water Competition tests were carried out in the home cage during the first two hours of darkness, at least one day after the Group Mating tests. The cage was lit by red light and the experimenter positioned as described in section 8.1.2 above. The water bottle was removed 16 hours prior to testing and was replaced, with the restrictor attached, at the beginning of the test. The test lasted 10 minutes, during which the experimenter scored the identity of the drinking animal every five seconds on a check sheet.

Treatment of results.

The results were analysed to give three measures of priority of access to water; total time spent drinking, mean drinking bout length, and order of first access to the water spout within each group. All three measures were ranked within each group of animals such that ranks of 1 were assigned to the males which spent most time drinking, had the longest mean drinking bout length and reached the water spout first.

Friedman two way analyses of variance were performed on these ranked scores in order to find out whether the animals in each group were consistently ranked on these measures of water access priority. A further Friedman analysis was performed for any group for which either an agonistic dominance hierarchy or consistent individual differences in initiated agonism had been found, and for which the Friedman analysis of drinking priority indicated consistent ranking. This analysis combined dominance ranks or ranked initiated agonism scores (as relevant) with drinking priority scores so as to indicate whether ranking on priority of access to water was related to these measures. If the value of Chi-r-squared in this analysis exceded that obtained from the Water Competition data alone, then a close relationship between priority of access to water and dominance status and/or aggressiveness was found.

8.3.3

Results.

8.3.3.1

Water competition test 1.

Groups A4, B1, B2 (mixed Rhcond), C2, and C3 (all-male Rhcond) showed consistent ranking across the three measures of water access priority (see Table 8.6). Since none of these groups had been found to have dominance hierarchies or consistent individual differences in initiated agonism, no further analyses were performed.

8.3.3.2

Water competition test 2.

Only group D4 (all-male Rcond x mixed Hcond) showed consistent ranking across the three measures of priority of access to water (see Table 8.10). Inclusion of D4's initiated agonism scores in a further analysis yielded a higher value of Chi-r-squared, indicating a close relationship between water access priority and aggressiveness in this group (Table 8.10).

8.3.4

Discussion.

The results of the first Water Competition tests (performed on the socially-housed Rhconds only) showed consistent individual differences in priority of access to water in five groups out of sixteen (i.e. 31.25%), with no difference in the number of groups showing consistency between Rhconds. None of these groups had been found to have agonistic dominance hierarchies or consistent individual differences in initiated agonism (aggressiveness), so no comparisons between these measures could be made.

The second Water Competition results only revealed one group out of twenty-four (4.17%) to have consistent individual differences in priority of access to water. The results of this one group showed a close relationship with individual aggressiveness.

These results confirm that water access priority is not generally found in rats (Blanchard et al, 1984), and that even when it does occur, it is not often associated with other aspects of social behaviour or organisation. Indeed, bearing in mind the large number of groups tested, it seems probable that the few consistent results found may have been due to chance. Replication of these tests would have provided further information as to whether or not this was the case.

8c

General Discussion.

Previous studies of the social organisation of the male rat have taken two different approaches. One of these has been to investigate intra-group aggression and directional dominance (e.g. Grant and Chance, 1958; Baenninger, 1966), and the other to look at aggression to colony intruders (Blanchard et al, 1975, 1977, 1984; Blanchard and Blanchard, 1980). Barnett (1958b) and Flannelly and Lore (1977) looked at both of these aspects of organisation. Both of these approaches have been concerned with relating their findings to priorities of access to resources, especially to reproductive priority, as a way of explaining the evolution of male rat agonistic behaviour in functional terms.

The present study gave little indication of the existence of either agonistic dominance hierarchies or consistent individual differences in aggressiveness within groups of four males with or without females. These results contradict those of Grant and Chance (1958) who found dominance hierarchies in all their groups. However, the difference between the present results and those of Baenninger (1966) was not so great, as only half of her groups showed directional dominance. Baenninger's study spanned both the observation periods used in this experiment (8-10 and 15-17 weeks of age), whereas Grant and Chance's only looked at social behaviour up to the age of twelve weeks. Thus it is possible that apparent dominance most often occurs during the late play/early pubescent period, a time when it was frequently found by Meaney and Stewart (1981).

The results of my study indicate that individual differences in aggressiveness are greater and more consistent during this period (8-10 weeks) than later on (15-17 weeks). This suggests that such differences are due to different rates of maturation of adult aggressive behaviour, rather than to the effects of agonistic experience and developing social organisation within groups. Although no linear dominance hierarchies at all were found at the earlier age range in this experiment, dominance hierarchies would be more likely to occur by chance at this stage then later on if individual differences in aggressiveness were large. This would be especially true if dominance were measured by one behaviour alone (Landau, 1951a; Appleby, 1983), thus explaining Grant and Chance's (1958), Baenninger's (1966) and Meaney and Stewart's (1981) findings.

Flannelly and Lore's (1977b) results from a group of mature rats housed under semi-natural conditions indicated that rats do not always show the same functional social structure. For the first period of their study, one male dominated all the others in agonistic encounters, and was also more aggressive to an intruder. This dominant male copulated most with colony females. After this animal's death, the other males changed their relationships with one another such that another dominant male emerged. This time, however, all males copulated equally. Thus no dominance hierarchy existed in Flannelly and Lore's group, but degrees of despotism did exist both in terms of frequency and severity of intra-group aggression and of territorial aggression to intruders. Howver, the most aggressive rat did not always have reproductive priority over the colony females.

The sparse occurrence of despotism in mixed groups of mature animals was slightly reminiscent of Flannelly and Lore's (1977b) results and of Barnett's (1958b) finding of fewer 'alpha' males (i.e. greater despotism) in mixed than in all-male groups.

Studies of male rat aggression in the colony-intruder situation have consistently shown that most aggression is directed to the intruder by one male (Barnett, 1958b; Blanchard et al, 1975, 1977, 1984; Blanchard and Blanchard, 1980). It has also been found that both the length of time a colony has been together and previous experience of intruders intensify this phenomenon (Blanchard et al, 1977). The latter result should not be surprising, as other studies have shown that male rat aggressiveness towards intruder males is altered by their experience of attacking intruders and of being attacked as intruders (see section 1.1.2). No relationship between aggressiveness to intruders and priority of access to food or water has been found, but the most aggressive male usually copulates most in a group mating test, though he does not monopolise the female (Blanchard et al, 1984).

These findings suggest that male rat social organisation is more important in protecting the colony from intruders than in determining intra-group relationships. It seems that this function is pronounced when the colony contains females, as intruders into mixed colonies lose more weight than intruders into all-male groups (Thor and Flannelly, 1976). This observation complements that of frequently found reproductive priority for the most intruder-aggressive males (Flannelly and Lore, 1977b; Blanchard et al, 1984).

The results of the present experiment have indicated that the effects of agonistic experience within a group on agonistic and sexual behaviour, even when females are present, are very small, especially in comparison with those of agonistic experience with an intruder. This observation of different effects of intra- and extra-group agonistic experience could be related to differences in the intensity of aggression in these two situations.

That some relationship between intra-group and intruder aggression exists has been shown by Barnett (1958b), Flannelly and Lore (1977b) and Blanchard et al (1977). In particular, the latter's observation that prolonged colony housing of mature males increases the tendency for only one male to attack an intruder (even when they have not previously experienced one) suggests that notable differences in individual aggressiveness may emerge over a long period of intra-group interaction. The length of time necessary for significant differences to develop may depend on innate differences between rats, thus producing the considerable inter-group (or colony) variation in the degree of intra-group organisation (measured by agonism and reproductive priority) observed. (For instance, only one group of mature males (group D4) showed consistent (related) differences in agonistic and sexual behaviour.) The presence of females may also reduce the time taken for significant individual differences to develop, as Barnett (1958b) observed fewer 'alpha' males (usually only one) in mixed than in all-male colonies. It is also possible that experience of intruders may increase intra-group differences in aggression and thus intra-group structure, though this has yet to be shown conclusively. The latter two possibilities suggest that severity of aggressiveness experienced may also play an important part in the development of social organisation (by increasing individual differences in aggressiveness) in male rats.

The present experiment has shown that there are no differences in intra-group structure between isolation- and socially-reared male rats with no experience of intruders, though there is evidence of qualitative differences in the production of intermale social behaviours. The early-isolated males showed more on-top-of behaviours than the others. Since the isolation-reared males had not been housed together for as long as the other males, this result could simply have been due to group instability. However, the fact that Wahlstrand et al (1983) had observed the same effect in their groups of early-isolated rats, in which length of total cohabitation (rather than of cohabitation since puberty, as in this experiment) was controlled, suggests that the effect is genuine and permanent.

Previous studies investigating the effect of early experience on colony intruder aggression have shown abnormally low aggression to all intruders in isolation-reared colonies, and abnormally high aggression to isolation-reared intruders in colonies of socially-reared rats (Luciano and Lore, 1975). Observation of socially-reared colonies has shown that on-top-of behaviour is rare in attacks on intruders (Blanchard et al, 1984). This suggests that isolation-reared males respond inappropriately both to, and as, intruders, possibly using an excess of on-top-of instead of more severe attacking behaviour to intruders, and not producing adequate submissive behaviours when attacked. It is also possible that isolation-reared males are not able to distinguish properly between other group members and intruders, perhaps through a deficit or reduction in olfactory discriminative ability. Such a deficit was suggested by the results of the second Individual Mating tests in the present experiment. Early-isolated rats may also not develop social organisation in response to intruder experience in the normal way.

Although early isolation does appear to have a permanent effect on intermale social behaviour, the results of the present experiment confirm that it does not have such an effect on copulatory behaviour. The temporary effects of isolation on ability to mount and ejaculate are removed by subsequent social or sexual experience. In addition, qualitative and quantitative differences in copulatory behaviour between rearing/housing conditions are apparently due to different amounts and recency of experience of oestrous females, and not to isolation- or all-male rearing.

In conclusion, no evidence for male rat organisation into functional dominance hierarchies (in terms of intermale agonistic behaviour and its relationship with priorities of access to resources) was found in any of the rearing/housing conditions investigated in this experiment. The results did give some support to Barnett's (1958b) findings of greater despotism in mixed than in all-male groups, however.

Early isolated male rats showed qualitative differences from socially reared animals in intermale behaviour and in ano-genital sniffing of oestrous females. This finding supports the hypothesis that there is a permanent effect of play deprivation on agonistic behaviour. However, copulatory ability and behaviour is determined both by total sexual experience and by recency of sexual experience, and is not permanently affected by early isolation.

Comparison of these results concerning male rat social organisation with those of other studies leads to the conclusion that agonism is more important, intense and organised in the exclusion of intruders from a group than in establishing intra-group relationships. Agonism is also probably slightly more organised in mixed than in all-male groups, as more evidence of despotism is found under mixed conditions. The processes involved in such greater organisation are as yet unknown.

Chapter Nine.

DISCUSSION AND CONCLUSIONS.

The aims of this thesis were a) to investigate more closely the relationship between aggressive behaviour, courtship behaviour and social organisation in male guinea pigs under semi-natural conditions, and b) to make similar investigations of both male guinea pigs and rats under laboratory conditions in which early and late social experiences were controlled. By examining the results obtained, further information regarding the causes and functions of social behaviour and the natural organisation of these two species was gained. In addition, speculations as to the importance of early social experience (as compared to isolation) were made for both the rat (a playing species) and the guinea pig (a non-playing species).

The results pertaining to the causes and functions of social behaviour in male guinea pigs and rats are summarised and discussed, particularly with respect to theories of social ecology, below.

9.1

The social behaviour and organisation of male guinea pigs.

9.1.1

Causative factors.

9.1.1.1

The presence of females.

The presence of females was found to affect male guinea pig social organisation and courtship behaviour. Males cohabiting with females developed a directional dominance hierarchy such that each individual responded differentially to each other male in his group (chapters Four and Seven). When females were not present, such directional organisation and apparent cue recognition was not found (chapter Seven).

The experience of cohabiting with females early in life (from weaning to puberty) was not important for the normal development of copulatory or agonistic behaviour. Males reared in all-male groups and subsequently housed in mixed groups were not noticeably different in behaviour and social organisation from those which had been housed in mixed groups from weaning. Current housing conditions were more important than rearing conditions in determining social behaviour and organisation.

Despite the causative relationship between the presence of females and social organisation, courtship to familiar cohabiting females did not show the close relationship with dominance status nor the evidence of male-female associations reported in previous studies (chapters Four and Seven). However, courtship to unfamiliar females _did_ show such a relationship, both when the whole group of males was present and when each male was alone with a strange female (chapters Three, Four and Seven).

Males from all-male groups in which consistent individual differences in aggressiveness were found showed a relationship between courtship to unfamiliar females and individual aggressiveness when the whole group was tested together, but not when males were tested individually (chapter Seven).

The presence of females cohabiting with males affected intermale courtship. Male-male courtship occurred much more frequently in all-male than in mixed groups, but was not related to social organisation.

9.1.1.2

Weight.

Individual differences in weight before groups were formed did not predict aggressive behaviour or subsequent social organisation (chapter Seven). However, the social status of a male did affect his weight gain. Thus, in established groups, weight was often closely related to dominance status or aggressiveness.

9.1.1.3

Water competition.

Aggression during water competition tests was not measured in the study reported in chapter Seven. However, success in water competition was found to be related to dominance status in some mixed groups, and also to aggressiveness in some all-male groups. This means that although water competition has not been shown initially to cause aggression or the development of social organisation in male guinea pigs, it is influenced by previously established social structures.

9.1.1.4

Experience of winning or losing.

Although the ultimate cause of aggression obviously cannot be aggression, it is possible for agonistic experience to cause changes in the nature of subsequent aggressive/submissive behaviour i.e. aggressiveness. The experience of living in a group led to changes in male guinea pig aggressiveness such that individual differences became more consistent over time (chapter Seven). This was interpreted as signifying effects of winning or losing on subsequent agonistic behaviour, a process compatible with the theory of individual 'confidence' levels (Barnard and Burk, 1979).

The mechanism underlying these changes in aggressiveness is uncertain. It could involve learning (see Barnett, 1958b, for a discussion of the learning of social behaviour), hormonal changes interacting with the central nervous system (see Leshner, 1975, 1980 and Brain, 1980) or a combination of both learning and changes in relative hormonal levels.

The observation that dominance was often closely related to courtship in individual tests with strange females (chapter Seven) suggests that agonistic 'confidence' levels resulting from sufficiently intense win/loss experience also affect aspects of a male's sexual behaviour. Once again, this could be due either to aversive conditioning (since subordinate courtship is often followed by attack by the alpha male; see chapter Four), or to hormonal changes, or both.

9.1.2

Functional aspects.

9.1.2.1

Priority of access to females.

Although courtship of cohabiting females does not appear to be closely related to dominance status, it seems that dominance does function to allocate mating priority in male guinea pigs (Rood, 1972; Martan and Shepherd, 1976; Berryman, 1978). This may come about through direct agonistic competition when a female is in oestrus, and also through female preference for proximity with dominant males. Preferential proximity was not shown by resting associations in huts (chapter Three), but was indicated by the observation that females followed the alpha colony male more than they followed other males (chapter Four). The absence of such an observation from the hut association study could have been due to the fact that only two heated huts were available to about ten adults and their young. This restricted the possibility for detecting resting associations because of the overcrowded resting conditions.

The behavioural data from Colony study 3 (chapter Four) did not reveal any action performed by the alpha male which incited females to follow him. Rather it was suggested that the females may have been responding to the same physical and/or behavioural cues produced by this male which induced the other males to behave submissively towards him. Proximity of a female to a dominant male would benefit the male by enhancing his chances of copulating first with her at oestrus (and hence probably siring all or most of her litter), and would benefit the female by ensuring that she received a copulation from a healthy male early in oestrus and before any mating chase began.

Males housed in all-male groups were observed to develop consistent differences in aggressiveness as a result of agonistic experiences (chapter Seven), though the cause of this fighting was uncertain. Dominance hierarchies were not found in these groups. However, the relationship between aggressiveness and courtship of a strange female in group tests suggested that the low level of social organisation developed in established all-male groups functioned to allocate priority of access to a female when one became available.

9.1.2.2

Weight change.

The observation that male guinea pigs of low social status gained less weight than their superiors suggested that they were suffering the physiological effects of stress (chapter Seven). They may also have been less successful than the higher-ranking males in obtaining food and water. Under more natural circumstances, this type of stress would probably have the function of dispersing animals to a greater extent than was possible under the cramped laboratory housing conditions. Thus it would be expected that differences in weight change would be less extreme in the wild, and that subordinate males would live peripherally to the dominants.

9.1.2.3

Priority of access to water.

The social organisation developed in groups of male guinea pigs did show some relationship to priority of access to water, though this was not as close as the relationship between social organisation and courtship of strange females (chapter Seven). Nevertheless, the results obtained showed a closer relationship between dominance, aggressiveness and water competition success than was found by Berryman (1978).

This finding supported the idea that male guinea pigs respond agonistically to one another in dominance hierarchies according to their perception of each other's resource holding power (RHP) cues. While dominance hierarchies and RHP assessment may develop chiefly as a result of reproductive competition (or aggression induced by the presence of females), it would be expected that they would respond in a similar way to one another under other circumstances as well. Thus if all the guinea pigs in a group are motivated by thirst to approach a water spout, it would be anticipated that the subordinate individuals would still flee from a higher-ranking male if he got there first, or if he approached them while they were drinking. Thus male dominance would function to allocate water (and probably also food and resting site) access priority.

The observation that aggressiveness (in males from all-male groups) was similarly related to success in water competition can be explained in a similar manner, though in this case 'confidence' is more important than cue assessment in determining one individual's reaction to another. Thus although individual differences in agonistic 'confidence' are not sufficient for the development of a dominance hierarchy, they are sufficient to be of functional use in determining priorities of access to scarce resources.

9.1.2.4

Experience of winning or losing.

Initially, it might appear that to become less aggressive, more submissive and less active in terms of courtship as a result of losing fights with other males would not be advantageous, as the submissive male would be unlikely to achieve reproductive success and so increase his inclusive fitness. However, if the male is unable to escape from his superiors because of environmental restrictions (or would suffer a greater risk of predation were he to do so), then he would be better off avoiding escalated fights which would be likely to cause him severe damage. Similarly, since courtship incites attack from alpha-ranking males, the subordinate would suffer fewer damaging attacks if he courted females less. Although such submissive behaviour would undoubtedly reduce his reproductive success relative to the more dominant males, he would nevertheless have a greater opportunity of achieving some successful copulations during mating chases or even of later improving his dominance status if he avoided damage and stayed as near as possible to the females than if he risked death from predation or from severe wounding.

Thus it can be seen that the modification of aggressive behaviour as a result of agonistic experience functions to enhance the inclusive fitness of the subordinate males in a group.

9.1.3

Early isolation.

Early isolation of guinea pigs did not permanently affect male courtship behaviour or the development of male social organisation, but it did increase the severity of aggression and social stress experienced in subsequent mixed groups of males as compared to males in other social conditions. This was shown by a non-significant increase in observed intermale biting, low weight gain and more conspicuous bodily wounding. It seems that early isolation (from weaning to puberty) reduces social tolerance of other males. This becomes most evident when females are present, as the presence of females increases the intensity of aggression even among males which have grown up together (chapter Seven).

Since guinea pigs do not play socially when young (Einon et al, 1981), this reduction in intermale social tolerance cannot be due to lack of play experience. It seems likely to be an exaggeration of the normal aggressive response of adult males to unfamiliar conspecifics. This response occurs even when (as in the present study; chapter Seven) the males concerned first meet on neutral ground (Fara and Catlett, 1971; Hull et al, 1973), although it is considerably less intense than when one of the animals is on home territory i.e. when territoriality is an additional aggression-inducing factor (Rood, 1972). Quite why early isolation should apparently have a greater effect than late isolation on aggression between unfamiliar males on neutral ground (Hull et al, 1973) has yet to be ascertained. The present study expands Hull et al's findings by showing that the increased aggression of early isolated males to one another does not only occur immediately after meeting, but continues over a period of several weeks' cohabitation.

9.1.4

The social ecology of the guinea pig.

Any investigation of the causes and functions of social behaviour and social organisation under laboratory or semi-natural conditions is only useful if it can be related to the natural ecology of the species concerned. The guinea pig (C.porcellus) is a domesticated animal believed to be a conspecific of C.aperea (Huckinghaus, 1961; cited in Rood, 1972). For thousands of years, guinea pigs have been kept as pets and for food, medicinal and ceremonial purposes by South American Indians. These animals are usually unpenned, living in and around Indian houses (Gilmore, 1952). Since the beginning of the twentieth century, guinea pigs have also been bred in laboratories for scientific purposes. In addition, many have been caged as pets by Europeans. Thus in considering the implications for the social ecology of the species, it is necessary to take account of the possible consequences of prolonged domestic breeding. As King (1956) pointed out

> "a domestic species retains those social characteristics which are selected for under the conditions imposed by domestication, and those which are least affected by the new environment."

It should be added that a domestic species may also gain those social characteristics which are not selected against (through predation) under domestic conditions.

King (1956) suggested that, for the guinea pig, the process of domestication would have led to an enhancement of social tolerance and little change in other social traits. Rood (1972) found this to be the case in as much as dominance hierarchies were less well defined among female C.porcellus than among female C.aperea, and that male C.porcellus were less likely to severely wound or kill one another in fights than were male C.aperea. However, since the social organisation of males of both subspecies was the same under semi-natural colony conditions (i.e. a dominance hierarchy) it seems probable that the increase in social tolerance in C.porcellus may be greater in females than in males.

Although it seems probable that the innate aggressive behaviour of guinea pigs has not been altered greatly by domestication, it is possible that perceptual factors or cues pertaining to agonistic reactions might have changed through reduced selective pressure. Rood (1972) found some evidence of reduced olfactory discriminatory powers of male guinea pigs as compared to their wild counterparts in that they showed less behavioural distinction in their courtship response to male and female juveniles. Despite this, Beauchamp (1973) has shown that domestic males can distinguish between the urine of male and female juveniles over the age of 18 days, and can also distinguish their own urine from that of other males. In addition, they showed a preference for female urine over male urine, and for the urine of low-androgen males over that of intact males. Thus it seems that olfactory ability in close encounters between males should be adequate to function in the normal way in determining agonistic responses. Also, it seems that the domesticated animals still produce distinct olfactory cues in their urine depending on their age, gender and sexual status.

It is possible that, if hormones (especially androgens) are important in determining agonistic responses (e.g. Brain, 1980; Leshner, 1980), then the observed increase in social tolerance (most noticeable in females) and reduction in adult male ability to distinguish between male and female young could be due to generally lowered androgen levels in domesticated guinea pigs. This reduction in androgen level may be proportionately greater in females and in young than it is in adult males, thus producing greater differences in female behaviour and juvenile olfactory cues than in those of adult males.

Further evidence of differences between C.porcellus and C.aperea from colony studies (Rood, 1972) suggests that domesticated males rumba more to females than do wild males, and also are generally more vocal than their wild conspecifics. Both of these differences could have come about through reduced predatory selection against animals which give away their presence by excessive noiseness.

In general, the differences found by Rood (1972) between C.porcellus and C.aperea were sufficiently small that he felt it permissible to use data obtained from both subspecies in an attempt to describe the social ecology of the species. Studies of a wild population of C.aperea revealed home ranges (larger in males than in females) as opposed to territories. Nevertheless, males in captivity did exhibit apparent territorial fighting. Little interactive behaviour was seen in the wild owing to the fact that the natural habitat consists mainly of long grass and reed beds (protective to a small non-burrowing rodent), so Rood's deductions about social behaviour and organisation were based on his observations of densely populated, captive colonies. He concluded that co-operation is minimal (with promiscuous mating and no pair bonds), populations of cavies often

> "consisting of nothing more than aggregations about a natural resource."

Conversely, he also stated that

> "social attraction...tends to lead to grouped feeding, even when food is evenly dispersed.."

He claimed that males are attracted to females and young and tend to maintain proximity with near-oestrous females. Rood also stated that the 'principal organising factor' in cavy society is the dominance-subordination relationship which determines reproductive fitness. The chief factors determining social relationships were said to be gender, age and previous experience.

From his study of a semi-natural colony of guinea pigs, King (1956) concluded that

> "the social organisation of wild *Cavia* may be a polygynous group consisting of one adult male with several adult females and their young."

Each such group is thought to inhabit a territory (despite the fact that King found no evidence of territoriality within his colony) which is patrolled by the resident male. This male drives away strange males (though occasionally a stranger may defeat him and take over the territory) and accepts strange females at all reproductive stages onto his territory. King claimed that young males are prevented from copulating by the resident adult male, and most leave the territory at maturity and roam about attempting to acquire a territory of their own. A few may, however, remain sexually inactive (i.e. subordinate) on their birth territory.

Rood's conflicting conclusions of social disorganisation and of social attraction and dominance in wild cavies do not give a satisfactory account of their social ecology. King's suggestions are more cohesive, but his idea that guinea pigs defend definite territories does not tie up either with Rood's field observation of home ranges, or with Coulon's (1975b) finding that individual male aggressive attributes were more important than territory ownership in determining the outcome of fights between pairs of (dominant) males.

My own observations of domesticated animals, combined with those of other researchers on both domesticated and wild cavies, lead me to suggest the following social ecology for the wild form of guinea pigs. Although no territories are held, each male has a home range which encompasses or overlaps the ranges of several females. The most desirable areas (i.e. those with the best natural resources of food, water and shelter) are occupied by the dominant males in the population i.e. those males which have been most successful in fights with other males. These areas attract females and are occupied by the most successful females in interfemale competition. They may also support a higher density of females than poorer regions. It is probable that it is the presence of a high density of fertile females in a desirable area which attracts males to that area.

Competition caused by the presence of females leads to the establishment of a dominance order amongst the males, causing them to disperse accordingly. The most successful male remains in the preferred area, while the second-ranking male moves to the next most desirable site which is far enough away from the alpha to avoid persistent conflict. Thus it is thought that, although male guinea pigs do not occupy territories in the true sense of the word, the severity of conflict between high-ranking males will ensure that their home ranges overlap very little. The weakest and least successful males may either occupy ranges on the edge of the habitat, or remain in the more desirable areas by acting submissively and evasively towards their superiors and showing less courtship to females.

Dominant males court the females living within their home range to some extent, but focus more attention on any strange female who comes within reach. Females are attracted to the most dominant male on their home range and tend to follow him around. Subordinate males rarely obtain first matings with oestrous females, but achieve some reproductive success in subsequent matings. Each locally dominant male sires most of the offspring born within his home range.

Females born within a dominant male's home range are courted by him, but may sometimes have to disperse to another area as a result of competition with their female elders for food or shelter. Young males, on the other hand, are forced in the same way as non-related weaker males either to disperse to the edge of the habitat until they can acquire a home range in a desirable area, or to remain submissively in the area of their birth.

This proposed social ecology of the guinea pig is in many ways similar to that of King (1956). However, the organisation is seen as less rigid, requiring fewer simpler mechanisms for its establishment and maintenance. The chief factors responsible for guinea pig social organisation are a) attraction of females to and competition between females for areas of rich natural resources of food and shelter; b) attraction of males to females, their proximity being increased by courtship; c) attraction of females to dominant males by some assessment process involving cues related to aggressiveness and courtship; d) the capacity of males to alter their agonistic (and to a lesser extent sexual) behaviour (i.e. their 'confidence') according to intermale agonistic experience; e) the ability of males to respond appropriately to one another's RHP cues, leading to dominance-subordination relationships when females are present. The competition between females for proximity to rich resources of food and shelter is thought to be weaker than that between males for proximity to females. The flexibility of organisation found in guinea pigs (e.g. the formation of dominance hierarchies rather than severe despotism under crowded laboratory or semi-natural conditions which would rarely be found in nature) can be accounted for by factors d) and e) above, which may operate largely through hormonal change and perceived differences in olfactory, behavioural and other cues.

9.2

The social behaviour and organisation of male rats.

9.2.1

Causative factors.

9.2.1.1

The presence of females.

Male rats cohabiting with females had reduced total intermale interaction frequencies and showed an increased proportion of boxing in their interactions. They also ano-genitally sniffed one another less frequently while pubescent than did males housed in all-male groups. The effect of the presence of females on total intermale interaction frequency could well have been due to the aggressive interference of the (usually) pregnant females who, having no nest boxes to retreat to and defend, tended to attack all animals which passed close to them.

Little effect of the presence of females on intermale social organisation was observed, though there was very slight evidence suggesting greater agonistic despotism in mixed than in all-male groups (similar to that found by Barnett, 1958b). Neither mixed nor all-male groups showed significant evidence of male agonistic dominance hierachies.

Early experience of cohabitation with females was not important in the development of sexual or agonistic behaviour. Amount and recency of sexual experience at any age influenced sexual activity much more than did early experience of females.

9.2.1.2

Weight.

Consistent individual differences in male weight or in weight change were rare in either mixed or all-male groups of rats (chapter Eight). Also, few similar differences in individual aggressiveness or other signs of social organisation were found. Thus no causative relationship between weight, weight gain and social status or aggressiveness was established.

9.2.1.3

Water competition.

Aggression during water competition tests was not scored in the study reported in chapter Eight. Since no reliable evidence of social organisation was found in laboratory groups of rats, no relationship between organisation and water competition could be established. The observation that very few groups showed consistent individual differences in water competition success indicated that water deprivation did not normally lead to the development of such differences.

9.2.1.4

The experience of winning or losing.

Only a small proportion of rat groups showed consistent individual differences in aggression, and a very few exhibited agonistic despotism. Thus there was little evidence of win/loss experience leading to changes in subsequent aggressiveness under the conditions of this study (chapter Eight). However, other studies involving colony intruder tests have indicated that win/loss experience with intruders does lead to modification of agonistic behaviour (e.g. Blanchard et al, 1975, 1977, 1984).

9.2.2

Functional aspects.

9.2.2.1

Priority of access to females.

The rare occurrence of social organisation into dominance hierarchies in the present study meant that no general functional relationship between agonistic dominance and priority of access to females could be found. No such relationship was found in the only group which did have a dominance hierarchy. In some of the groups which showed consistent individual differences in initiated aggression, this measure of aggressiveness was found to be closely related to speed of copulation in individual tests and (more occasionally) to a measure of reproductive priority in group tests. Such findings, however, were more common during the early phase of the experiment (i.e. around puberty) than later on. Thus it seemed more likely that the consistent individual differences in agonistic and sexual behaviour (and their relatedness to one another) were due to different rates of maturation of these behaviours rather than to functional differences in adult behaviour.

It must be remembered, however, that in the present study the mating tests were given quite short time limits, so rats were not allowed to complete copulatory series. Recent evidence (Gartner et al, 1981) suggests that differences in mating behaviour leading to differences in reproductive success (mating priority) may be revealed late in a copulatory series, so it is possible that existing differences in reproductive priority may have passed unnoticed because of inadequate testing procedures.

9.2.2.2

Weight change.

No difference in weight or weight change was found between mixed and all-male groups. Nor was there a relationship between social status and weight or weight change (though since little evidence of social organisation was found, it cannot be said that such a relationship would never exist under different conditions e.g. after colony-intruder experience). It appears, therefore, that there were not sufficient differences in stress between mixed and all-male housing, or between individuals within groups to produce physiological symptoms. Thus the cramped housing conditions of this laboratory study (chapter Eight) did not apparently restrict natural dispersal in the manner suggested for guinea pigs (section 9.1.2).

9.2.2.3

Priority of access to water.

Very few groups of rats showed consistent individual differences in water competition success, and in only one group was this related to aggressiveness. The only group to have an agonistic dominance hierarchy showed no correlation between dominance status and priority of access to water. Thus there was very little evidence of social organisation functioning to allocate priority of access to water in rats under the conditions of the present study (chapter Eight).

9.2.2.4

Experience of winning or losing.

There was very little evidence of changes in aggressiveness as a result of win/loss experience in the present study (chapter Eight). Thus, on this evidence alone, it could not be said that functional changes in aggressiveness caused by agonistic experience occurred in rats as in guinea pigs (see section 9.1.2). The evidence from colony intruder tests (e.g. Blanchard et al, 1975, 1977, 1984; Flannelly and Lore, 1977b), however, suggests that changes in aggressiveness caused by fights with intruders may function to develop a semi-despotic system of territorial defence and even, occasionally, of intra-group dominance.

9.2.3

Early isolation.

Early isolation (from weaning to puberty) did not permanently affect the copulatory ability or behaviour of male rats. It did seem to affect pre-copulatory ano-genital sniffing, however. It was suggested that this might have reflected reduced efficency in the use of ano-genital sniffing in the identification of an animal's sexual status. Thus there may be a critical period for the learning of fully functional ano-genital sniffing during early life. The present studies (chapter Eight) could not show whether this critical period occurred during the play period (17 to 60 days max.) or around puberty (approximately 40 to 70 days). However, ano-genital sniffing is rarely seen in young rats until about 55 days of age, and does not normally occur in play (Humphreys, 1982), so it seems unlikely that it is the playful experience of ano-genital sniffing which is important for its normal development.

Evidence of intermale social organisation was very rare in all conditions of the present study (chapter Eight), and no differences in social organisation attributable to early isolation were found. However, early isolated rats showed a significantly greater proportion of intermale on-top-of behaviour than socially-reared rats when subsequently rehoused in all-male or mixed groups (chapter Eight; Wahlstrand et al, 1983). Once again, the precise period of social isolation responsible for this behavioural change could not be ascertained from this study. However, Wahlstrand et al's finding that isolation during the period from 17 to 41 days (i.e. at the time when most social play occurs) caused this change in behaviour, while isolation from 41 to 68 days did not, suggests that it is the lack of social play which causes abnormal social behaviour in adults. The present study (chapter Eight) adds to Wahlstrand et al's (1983) findings by showing that intermale on-top-of behaviour is increased not only in all-male, but also in mixed groups of early-isolated male rats.

An additional effect of early isolation on male rat social behaviour was found in the mixed groups where males interacted much more often with one another and less often with their cohabiting females than did socially-reared males (chapter Eight). The latter difference was not due to lack of sexual interest or ability. It is possible that the high frequency of intermale interactions may have represented a reduction in habituation to novel social stimuli, similar to that found for inanimate objects (Einon and Morgan, 1977; Einon et al, 1978, 1981). This explanation, however, cannot account for the reduced frequency of interaction with cohabiting females, and so does not seem very plausible.

9.2.4

The social ecology of the rat.

As stated in section 9.1.4, it is felt that laboratory investigations of the causes and functions of social behaviour and organisation are only useful if they can be related to the natural ecology of the species. The rats used in the present study (chapter Eight) were laboratory bred from a strain which has probably been bred in captivity since the turn of the century (UFAW, 1967). Unlike guinea pigs, which have mostly been bred for food or pets, rats have been domesticated chiefly for use in laboratory studies of learning and physiology. Thus most of the artificial selection which has undoubtedly occurred over the years must have been for ease of handling and, to a lesser extent, for reduced intraspecific aggression (since it is usually more economical to house rats in group cages rather than separately). Laboratory breeding of rats usually only involves keeping one male with two or three females for a week (i.e. until all the females have had at least one oestrus) and then returning the male to an all-male colony cage. Thus laboratory rats have probably had less opportunity to escape selection for intermale docility than have laboratory guinea pigs, in which the long anoestrous and gestation periods and the difficulty of predicting parturition have led to the common use of permanent one-male breeding groups (UFAW, 1967). It should be noted, however, that house mice (Mus musculus) have been laboratory bred and artificially selected in the same way as rats, but no noticeable reduction in intermale hostility has occurred. A resident male laboratory mouse will still frequently kill or severely injure a strange male intruder, or even a previously familiar male from which it has been separated for a couple of days (UFAW, 1967). Thus it seems that there must be an innate difference in intermale tolerance between rats and mice which is largely resistent to artificial selection.

Several studies using a variety of laboratory strains have attempted to quantify and qualify the social behavioural differences between wild and laboratory rats. It has been suggested that domesticated rats (especially males) show reduced intraspecific aggression and increased intraspecific gregariousness and tolerance

(Harkins et al, 1974; Boreman and Price, 1972; Barnett and Stoddart, 1969; Barnett, 1960, 1969, 1975; Calhoun, 1961). Contrary to these findings, Blanchard et al (1975, 1977, 1984) claimed apparently 'normal' attack of intruders by the dominant males of established colonies of albino rats. In general, the results of these studies show that, when put into a sufficiently 'natural' environment, domesticated rats will behave in a very similar manner to wild rats (Flannelly and Lore, 1977b; Blanchard et al, 1975, 1977, 1984), though they are less likely to kill or severely injure male intruders and seem to require more win/loss experience to achieve the same alteration in their agonistic behaviour. It has been suggested that these changes may be due either to higher thresholds for the production of some social behaviours (Boice, 1972) or to reduced sensory abilities (Harkins et al, 1974). It is certainly true that the vision of albino rats is very poor, but in hooded and other pigmented laboratory rats it is probably nearly normal (Barnett, 1975). Differences in olfactory or auditory abilities have rarely been measured. However, it has been shown that albino rats are able to discriminate between rats using olfaction (Hepper, 1983), so it seems unlikely that olfaction is severely impaired in domesticated rats.

Using evidence from studies of domesticated and wild rats, a variety of theories have been proposed with regard to the natural social ecology of rats. The results of studies claiming linear male dominance hierarchies within groups of rats (Grant and Chance, 1958; Baenninger, 1966; Meaney and Stewart, 1981) have all been shown to be explicable in terms of chance, poor measurement methods and differential individual rates of development of agonistic and sexual behaviour rather than to a genuine tendency to develop such functional structures (see sections 8.1 and 8c). Instead, rats seem to have a semi-despotic structure in which most aggression to male intruders is initiated by one male (Barnett, 1958b, 1975; Flannelly and Lore, 1977b).

In wild rats, territorial aggression has been observed by Calhoun (1948, 1950), Barnett (1958b) and Telle (1966), though Telle claimed that a rat territory consisted of a series of paths instead of an area of land. Rats holding territories closest to food sources are generally larger and have better reproductive success than their smaller peers, probably because they obtain more food and receive less aggression (Calhoun, 1950). Robitaille and Bovet (1976), on the other hand, thought that territoriality in their wild rats (living on a rubbish tip at a density of 2-3 per square metre) would have been overcostly and impracticable. However, they had no definite observations to support their claim, and indeed their reports of frequent agonistic encounters between animals could provide evidence to the contrary.

Barnett (1975) and Calhoun (1948, 1950, 1963) claimed that, under favourable conditions, rats may live in very dense populations, but that population density never reaches the maximum possible according to food supplies, showing that social factors including territoriality must play a part in density regulation and dispersal. All the people who have found territoriality in the rat have claimed that these territories are inhabited by mixed groups rather than by harems, pairs or individuals (Barnett, 1958b, 1975; Calhoun, 1948, 1950, 1963; Lore and Flannelly, 1977). Lore and Flannelly suggested that wild rats live in small (territorial) groups of less than twenty animals within large societies.

Barnett's observations of reduced aggression between littermates and between animals housed together from before maturity led him conclude that family groups of rats develop within colonies, and that separate territories are held by each group. He suggested that the members of each family group distinguished one another from strangers by means of a 'colony odour'. Lore and Flannelly (1977) generally agreed with Barnett's conclusions, but thought that individuals can recognise one another individually rather than by a common odour. Thus they proposed that group size was largely limited by the rats' capacity for recognising individuals.

Hepper (1983) has shown that individual recognition is possible in the rat, though he did not show whether there was any limit on the number of individuals a rat could discriminate between at any one time. The present study (chapter Eight) has indicated that rats do not normally use this ability to develop an agonistic intragroup hierarchy, suggesting that there is little adaptive pressure on them to do so. Hepper also showed that rats learn to recognise their kin (and other animals with which they have lived from an early age) and discriminate between these and other animals in terms of huddling, play and mating preferences. Thus it seems likely that rats in territorial groups within large colonies are able to recognise one another individually, but that they are also able to use genetic identifiers learnt in early life to discriminate kin from non-kin as well as familiar from non-familiar rats. In this way, the cohesion of family groups would generally be maintained, though some immigration and emigration of young animals would be permitted as these are not attacked by adult males. Emigration between neighbouring groups would ensure that group members did not become too closely related, and that most breeding took place between individuals related at about the level of first cousins (as suggested by Hepper, 1983). This level of relatedness, combined with the high reproductive rate of rats, would considerably reduce the evolutionary pressure for reproductive competition between group members.

In conclusion, I would suggest that the most important mechanisms involved in establishing and maintaining rat social organisation are a) male and female attraction to and tolerance of closely related rats and rats familiar from early life; b) adult male aggression to strange adult males; c) adult male tolerance of juvenile males; d) general attraction of rats to a wide variety of rich habitats. It is notable that females appear to show more defense of their nest burrows than of their group's whole territory (Barnett, 1958b, 1975), though they may occasionally fight adult female intruders away from the nest (Blanchard et al, 1984). The modification of male aggressiveness through win/loss experience does occur, probably in a similar way to the guinea pig (see section 9.1.4), but is much less important in rats than in guinea pigs, especially in determining intra-group relationships. It seems to occur mainly as a result of experience of territorial attack, and may lead to one male becoming noticeably more aggressive than the other males on that territory. This male sometimes dominates other group males in competition for food or females, though such findings are far from universal. He may also gain greater reproductive success incidentally through being sexually more vigorous than the others i.e. having more ejaculations over a longer period than them (Blanchard et al, 1984).

No information is available as yet to indicate the normal size of a territorial group of rats, nor of the ratio of males to females in such a group.

9.3

Conclusions and suggestions for further research.

A general conclusion of this thesis is that in all investigations of social behaviour and social organisation it is necessary to identify individuals so that the nature and direction of individual interactions can be scored. Also, it has been shown that the measurement of agonistic dominance hierarchies must be strictly controlled for the effects of chance (especially in small groups), and so should involve the investigation of more than one agonistic behaviour. The finding of dominance hierarchies in captive populations does not necessarily mean that the animals studied would naturally exhibit similar hierarchies in cohabiting groups in the wild. Further field studies of both wild rats and the closest wild relations of the guinea pig, (C.aperea), are needed to determine whether their natural social ecologies are as predicted in sections 9.1.4 and 9.2.4. These field studies must allow for the accurate identification of individual animals.

Differences between male guinea pig (C.porcellus) and rat (R.norvegicus) social behaviour have been found which suggest, when combined with the results of previous studies, that the male rat is more socially tolerant of its male conspecifics than is the male guinea pig. In the natural state, male rats are only socially tolerant of familiar (usually related) individuals. This study has shown that male rats deprived of social contact during the post-weaning to pubescent period interact abnormally (in terms of the proportionate behaviours produced), but not more fiercely, with like-reared peers than do socially-reared males. The effect of early isolation on male guinea pigs was different. They became even more socially intolerant than usual, fighting each other in a more damaging way.

Hepper (1983) suggested that play in rats occurs mostly between familiar, related animals (usually siblings) and functions to increase recognition of such animals. He speculated that this increased recognition might improve group cohesion in adult life. However, if play functioned to improve group cohesion through recognition, it might be expected that rats deprived of the chance to learn to recognise one another during the play period would later act more aggressively than usual to other males (as did the guinea pigs) and would not be able to form a cohesive group with them. The present studies did not show early-isolated males to be more aggressive to one another than socially-reared males. Also, they did not reveal any differences in group organisation between early-isolated and other rats, but then no social organisation was found at all, probably because no intruder experience was given. Luciano and Lore's (1975) colony intruder studies showed that early-isolated (grouped) rats did not exhibit the normal aggressive response to intruders. Thus it appears that early isolation (including play deprivation) actually causes <u>less</u> rather than <u>more</u> intense intermale aggression in rats.

Further experiments are needed to investigate these findings. Controlled studies of both individual intra-group social behaviour and aggression towards male intruders in mixed groups of rats should be made using males with and without social experience during the play period. Some of these rats should be housed in constant groups from weaning, and others rehoused with unfamiliar like-reared peers at puberty. This would show how specific the effects of playing with other males are to future behaviour and group organisation. The groups used for this proposed experiment should be housed in larger cages than were used in the present study, and these cages should have nest boxes attached so that abnormal aggressive interference by pregnant females would be reduced.

The main contributions of the work described here are to show that many of the methods previously used in the study of animal social behaviour and organisation are inadequate, and to suggest more robust techniques for present and future use. The advantages of scoring behaviour sequentially have been shown with respect to the determination of the causes and functions of social behaviour, particularly under semi-natural or natural conditions.

Using these techniques, it has been shown that male agonistic dominance hierarchies do not occur in confined groups of rats, and are only found in similar groups of guinea pigs when females are present. In general, the presence of females appears to be more important in the establishment of male guinea pig than rat social organisation, particularly if the rat groups have no experience of intruders.

The evidence from the present studies of early isolation does not lead to any clear conclusions about the functions of social play in rats, but points to the previously-suggested possibility that early social experience including social play may be important in the development of social group cohesion (Hepper, 1983) such that intruders can be identified as such and attacked. Also, since no evidence of male agonistic dominance hierarchies was found in groups of rats housed together from weaning, it seems unlikely that social play can function to develop dominance relationships as suggested by Meaney and Stewart (1981).

A problem posed by this study of adult agonistic behavour in rats is that several of the 'agonistic' behaviours observed (e.g. boxing, on-top-of, and aggressive groom) do not appear to cause dispersal or to be related to dominance, despite previous claims that 'on-top-of' does indicate dominance (see chapter Eight). Further studies of the detailed sequential behaviour of wild rats are needed, preferably under natural or semi-natural conditions, to provide information as to the causes and functions of these behaviours.

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