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Olfactory stimuli and social behaviour in the guinea pig

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Olfactory Stimuli and Social Behaviour

in the Guinea Pig.

by

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SUMMARY

This report is concerned with the relationship between olfactory stimuli and social behaviour in the guinea pig.

The literature review outlines the history of the guinea pig and suggests why an animal so widely used in biomedical research was unpopular with the behavioural psychologists. Reasons for the resurgence of interest in this species are given. Investigations into varying aspects of social behaviour in the guinea pig are described.

The observations which led to the present investigation are outlined, followed by a discussion of experimental methods relevant to the present investigation.

The response of guinea pigs to specified olfactory stimuli under controlled conditions are detailed. It was found that male guinea pigs respond to the scent of male conspecifics with an aggression-related, species specific response, including scent marking, investigation, and increased locomotion. The animals were attracted to the odour. They preferred female odour to male odour, and responded with increased investigation and marking. The latter was significantly less than in response to male odour. They showed evidence of being able to distinguish between oestrous and non-oestrous urine. Data were obtained indicating that the female guinea pig increases her rate of marking at oestrus; the oestrous female may be attracted to the male.

The findings are discussed in relation to the work of other investigators with Cavia porcellus and Cavia aperea, and in relation to other mammalian species. The value of both natural and controlled investigations in the study of social behaviour is emphasized. It is concluded that olfactory stimuli are of major importance in the social life of the guinea pig, and are involved in territoriality, dominance relationships, sexual behaviour, and group cohesion. Suggestions for further research are made.

Acknowledgements

CONTENTS

INTRODUCTION

This investigation is concerned with the relationship between olfactory stimuli and social behaviour in the guinea pig.

Studies of group behaviour could be said to form the foundation of animal behaviour (Dimond, 1970). However, Dimond goes on to say that "they are often limited by a failure to penetrate beyond the descriptive level and a failure to advance the account of individual patterns within the social context". The controlled investigation therefore is important in the study of social behaviour in animals. There are problems, however, in that a controlled investigation may inhibit the expression of much of the animal's range of behaviour. Dimond (1970) writes "an experimental group may behave in a different fashion from a natural group, but this is not as serious an objection as it might seem, because cross-referencing can take place between natural and experimental groups, and knowledge about behaviour gained under controlled conditions can be substantiated by natural observation".

In the present investigation, therefore, the response of guinea pigs to specified olfactory stimuli are investigated under controlled conditions, and considered in relation to the findings obtained in laboratory, semi-naturalistic, and field studies. Thus although the behaviour of individual guinea pigs is investigated, the study as a whole is concerned not with the behaviour of the individual but with the role of olfactory stimuli in the social organization of the species.

The behaviour of the guinea pigs in this study are also compared with the behaviour of Cavia aperea, studied in the field by Rood (1972). C. aperea has been suggested as the ancestral species of C. porcellus (Weir, 1974).

The behaviour of the wild species may be of value in eval-
uating the findings obtained in the laboratory with C. porcellus:
there are no wild C. porcellus.   The comparison of the two species
will also indicate what effects domestication has had on the
social behaviour of the guinea pig.

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Before the experiments are described some information con-
cerning the historical and experimental background of the species
is given.   Investigations into aspects of social behaviour in the
guinea pig are described.   The reasons for beginning the present
study are outlined, and some consideration is given to experi-
mental design and the recording of data.

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Chapter 1

The Guinea Pig

Chapter 1

Part I

The guinea pig has been domesticated for several thousand years. The llama and the guinea pig may have been domesticated by 5500 B.C. (Kendall, 1973). However, it is not known which of the Indian civilisations began the process (Weir, 1972). Nor is it known from where the forerunners of the domestic guinea pig were obtained as there are no wild Cavia porcellus. However, a possible ancestor of the guinea pig, Cavia aperea, was present in South America since the Pleistocene (Rood, 1972).

Although the llama was used as food it was important in other ways and was not, therefore, eaten indiscriminately. The only regular meat supply available to the Indians was the guinea pig. They lived in Indian kitchens or houses and were fed on food scraps and green plants (Kendall, 1973). Guinea pigs were used by the Incas, as were llamas, for public sacrifice. Berryman (1974) reports that Mason (1940) writes that mummies of guinea pigs have been found dating from the Inca period.

By the time the Spanish arrived in Peru (1532) the guinea pigs varied in colour, whereas all forms of wild cavia have agouti dorsal pelage (Rood, 1972).

It is not known when the guinea pig was first brought to Europe, but it would seem likely that this happened soon after the invasion of South America by the Spanish. It is certain that the guinea pig was established in Europe by early in the seventeenth Century. Two guinea pigs feature in the painting the "Garden of Eden" by Jan Bruegel (1568-1625). These guinea pigs resemble those described by the Conquistadores in that they are multi-coloured. They are also clearly recognisable as the guinea pig of today. A photograph of these guinea pigs can be seen on page 3.

Thus it would seem that the guinea pig was brought to Europe in the latter half of the Sixteenth Century. Berryman (1974) reports that Mason (1940) writes that the first mention of the guinea pig in Europe was in 1551-1554.

The generic name of the guinea pig, "Cavia", would seem to derive from the name given to it by the Brazilians; in 1648 Marcgrave described an "aperea Brasiliensibus", and called it "Cavia cobaya" which is an adaptation of the name given to it by the Brazilian natives (Weir, 1972). Thus "Cavia" has become the generic name. The French name for the guinea pig is "le cobaye", retaining the Brazilian "cobaya". The Oxford English Dictionary (1969) still gives "Cavia cobaya" as the Latin name of the species. The animals described by Marcgrave were certainly of a domestic species as they were multi-coloured (Weir, 1972).

The name porcellus derives from the tenth Edition of Linneaus' Systema Naturae 1758 (Weir, 1972). Thus in accordance with the International Code of Zoological Nomenclature the species is termed Cavia porcellus. Where the term porcellus comes from it is not possible to say. However, it has been said that the Conquist-adores considered that the guinea pig resembled a small sucking-pig (Forrest, 1971). In view of the fact that porc with the suffix -ellus means "small pig" this is possibly the origin of the term. The species was known as the "guinea pig" in England as far back as 1664 (Oxford English Dictionary, 1969). The origin of the term "guinea" is obscure. Stuart-Paterson (1967) suggests it may come from Guiana, indicating, perhaps, a misunderstanding as to the country of origin of the original animals brought to Europe from Peru.

Guinea Pigs. Detail from The Garden of Eden.
by Jan Bruegel 1568-1625

The guinea pigs in South America are left to scavenge around the huts of the Indians. Weir (1972) writes that it can be assumed that this method of husbandry has always existed. There is no wild form of Cavia porcellus. Thus the only way to determine its origin is to compare porcellus with other species of Cavia on the assumption (Weir,1972) that the wild forms might not have changed greatly during the period of domestication. As Weir (1972) points out, the domestication process was not rigorous. It is possible therefore, that many of the characteristics of the ancestral species have been retained.

In view of the fact that the domestic guinea pig originated in South America it would be expected that the ancestral species is still living there. There are several species of Cavia and three have been suggested as possible ancestors of porcellus. These are Cavia cutleri (or Cavia tschudii) from Peru, Cavia rufescens from Brazil, and Cavia aperea from Argentina (Weir, 1972). Rood and Weir (1970) report that Huckinghaus (1962) concluded that C. porcellus, C. cutleri and C. rufescens are all conspecific with C. aperea. However, Rood and Weir (1970) point out that Huckinghaus' work was based on skull morphology and does not take into account work on the genetics of crosses between Cavia. When a C. aperea male is crossed with a C. porcellus female, the offspring of both sexes are fertile (Rood and Weir 1970), although numbers of infertile animals have been reported as occurring in the second to fifth generations (Guyenot and Duszynska-Wietrzykowska, 1935; in Rood and Weir, 1970). The reciprocal cross also produces fertile hybrids of both sexes (Weir 1972).

Weir (1972) writes that Castle and Wright (1916) report that
C. porcellus females crossed with C. cutleri males produce fertile
offspring. This is perhaps why Stuart-Paterson (1967) states
that Cavia cutleri is the ancestor of the domestic guinea pig.

Rood and Weir (1970) investigated the reproductive character-
istics of the four species. They found that "C. aperea has many
reproductive characteristics in common with C. porcellus; effect
of litter size on gestation length, a similar length of oestrus
cycle, and lack of a well-defined breeding season. C. aperea also
has the same chromosome number as C. porcellus and interspecific
crosses are fully fertile ... C. aperea would seem to be a more
probable ancestor of C. porcellus than, for example, C.rufescens, in
which the male offspring of crosses with C. porcellus are sterile."

Rood and Weir (1970) write that although the evidence suggests
that it is possible that C. aperea, C. rufescens and C. cutleri
may be conspecific, C. porcellus differs in that it has a longer
mean length of gestation than the three wild species of Cavia.
Weir (1972) concludes that C. porcellus may have been derived from
C. aperea and that it is probable that C. rufescens and C. cutleri
are conspecific with C. aperea.

This is supported by work on chromosomes (Weir 1974) which
indicates that C. aperea and C. porcellus are very closely delated.
Beauchamp, Criss and Wellington (1979) report that Carter (1972)
also found evidence that the two species are very closely related.

Thus it is concluded that C. porcellus and C. aperea are
closely related. It is possible that C. aperea is the ancestral
species.

As was indicated in the introduction, identification of the wild species from which C. porcellus is derived, or to which it is closely related, is of importance to the present investigation.

PART II

Whereas the guinea pig was used for food by the Incas, in Europe it has long been valued both as a pet and as a research animal.   It was in fact used as an experimental animal late in the 18th Century: Lavoiser used the guinea pig in 1780 for the measurement of heat production (Lane-Petter and Porter, 1963). It was not chosen in preference to the laboratory rat, but because "... the laboratory rat was not available at the dawn of biomedical research" (Rowlands 1972).   The guinea pig has been so widely used as to give rise to "... the proverbial association between an experiment and a guinea pig" (Rowlands 1972).   In recent times the guinea pig has been bred primarily for biological and medical research.   It is not within the scope of the present study to give details of the biological investigations involving guinea pigs, although these are extensive and include such fields as biochemistry, pharmacology, genetics, toxicology, endocrinology and immunology.

However, by the time psychologists began to use animals in behavioural research the laboratory rat was available, and was the animal most used by such investigators as Watson, Tolman, Hull and Skinner.   The rat has been used extensively since early in the Twentieth Century, and indeed it has become almost notorious in the role it has played in the development of psychological theories. Although the guinea pig had long been a laboratory animal, it seems to have held little interest for workers carrying out behavioural

investigations. Perhaps this was due to the fact that oaboratory workers assumed the guinea pig to be (as Becker, 1946, puts it) "....just plain stupid" or, as described by Minot (1891, cited in Berryman, 1974), an unintelligent animal.

However, in more recent years the guinea pig has been used in behavioural work at a steadily increasing rate.

Apart from the fact that the rat is easier to maintain in the laboratory, and multiplies at a faster rate than the guinea pig, why is it that those carrying out behavioural investigations showed so little interest in the guinea pig? Due to its wide-spread use in biological research laboratory strains were readily available.

Some suggestions will be made as to those characteristics of the guinea pig which resulted in it being so little used. Then some indication will be given of why workers again turned their attention to the guinea pig.

Pearson (1970) comments on the paucity of work carried out by experimental psychologists using the guinea pig as a subject, and suggests that this may be related to the "animal's propensity for becoming immobile at the least provocation and remaining so for an indefinite period of time". Hadley (1927) when carrying out some experiments on the transfer of training in guinea pigs found that some guinea pigs tended to become immobile when faced with a problem box. Hadley (1927) and Riess (1934) had to discard up to thirty per cent of the subjects because of a tendency to freeze. Even with the relatively successful subjects there were still problems due to lengthy hesitation and time involved when food was used as an incentive.

Glickman and Hartz (1964) and Tobach and Gold (1966) found that guinea pigs showed extensive freezing behaviour in the open field situation, and little exploratory activity. Dutch and Brown (1969) reported immobility, several deaths, and had to end two experiments because of the condition of the animals. In a 1969 study comparing exploratory behaviour in four species of rodent the writer recorded the same behaviour: the guinea pigs were largely immobile in both an open field and a Dashiell maze.

Pearson (1970) investigated guinea pigs' response to a strange environment. He found that both male and female subjects showed the immobility response for periods ranging from 15 seconds to 40 minutes. After an initial period of immobility most animals made a "frantic" dash to the side of the box, and occupied this position for the remainder of the test period.

Riess (1934) and Miles, Ratoosh and Meyer (1956) make the point that prolonged preliminary training is necessary with the guinea pig. This aids habituation of the immobility response in a strange environment and social isolation. Dutch and Brown (1969) recommend the provision of adequate opportunity to become used to the experimental situation. Jonson, Lyle, Edwards and Penny (1975) have also found it necessary to provide the guinea pigs with time for habituation to the laboratory, as well as extensive habituation to the experimental conditions.

Thus, although the immobility response can be countered by sufficient habituation periods, it is hardly surprising that many workers would prefer to use the rat. Providing habituation periods is time consuming. This is not the only difficulty encountered with the guinea pig.

Not only does the guinea pig tend to become immobile in a strange situation, it is also highly susceptible to auditory stimuli. Becker (1946) reports that Riess (1934) noted that extraneous noises were more likely to disrupt the behaviour of the guinea pig than that of the laboratory rat. King (1956) writes "... a strange sound provoked them to give a low-pitched rumble or purr and to freeze in position until all was quiet again". Ibsen (1967) describes the sensitivity of hearing of the guinea pig. "They are very sensitive to sound and hear the slightest rustle of green alfalfa." Miller and Murray (1966) point out that if the guinea pig has been thoroughly habituated to an environment and is engaged in ongoing activity, the introduction of a novel stimulus of sufficient strength will produce the immobility response. This response varies from a brief pause in ongoing activity to a full-blown response with a characteristic posture in which the back is arched, the head is up and the front legs are extended. Miller and Murray (1966) report that the immobility response of guinea pigs shows many features of tonic immobility and freezing. They conclude that "in comparison with other animals the guinea pig has an exaggerated tendency for these various forms of immobility".

Another reason for the lack of interest in the guinea pig as a research animal may be due to the fact that its learning ability has been questioned. If, as Becker (1946) suggests, the guinea pig was considered as stupid, then again it is hardly surprising that the rat was used in preference to the guinea pig.

Becker (1946) investigates learning ability in the guinea pig. He describes the work of Allen (1904) with newborn guinea pigs, and a discrimination problem. Allen (1904) demonstrated that memory is

functioning as early as the third day after birth. She concluded, however, that after the first week of life, learning in the guinea pig depends more on increased activity rather than increased ingenuity. Becker (1946) comments that this conclusion is hardly warranted. Allen did not test adult animals; also, the problems were so easy and so alike, that it is possible that little ingenuity was needed to solve them.

Jonson, Lyle, Edwards and Penny (1975) note that guinea pigs have been described as stupid animals; Scott (1958) claims that comparative psychologists have found it difficult to devise tests on which the guinea pig will show evidence of learning and intelligence. Jonson et al (1975) comment that Scott (1958) was "somewhat puzzled as to how its wild ancestors could have survived at all ! "

Riess (1934) and Fjeld (1934) compared the learning of several species of animal using the Jenkins problem box. The guinea pig did poorly compared with other species. Keehn and Webster (1967) had difficulty in maintaining bar-pressing avoidance behaviour in guinea pigs.

Gross (1952) carried out an investigation into the effects of cochlea lesions on the auditory response of guinea pigs.* The animals were trained to respond to a test tone by turning a rotatable drum-shaped cage. Some animals failed to reach the criterion of learning, while others required from 250 to 500 trials. Shock was used as reinforcement. However, Gross (1952) points out that the rotatable cage proved to be an unsuitable test instrument, suggesting that the design of the experimental

* The characteristics of the guinea pig are particularly
  suitable for this sort of investigation

situation was, at least in part, responsible for the poor per-
formance of the guinea pig.

Jonson et al (1975) point out that most of the studies where
guinea pigs have performed badly have used appetitive paradigms.
These include Allen (1904), Hadley (1927), Riess (1934) and
Dutch and Brown (1969). The majority of investigators have found
it difficult to motivate subjects with conventional reinforcers.
Becker (1946) found that even after starvation food did not prove
to be an adequate reinforcer, although guinea pigs have large
appetites and eat almost continuously. He also found water un-
suitable for technical reasons.

Jonson et al (1975) comment that the difficulties encountered
by investigators may have been contributed to by the failure to
use a satisfactory reinforcer. However, satisfactory reinforce-
ment for the guinea pig can be devised, and this is discussed on
page 15.

Thus the guinea pig has a propensity for becoming immobile,
and many workers have had difficulty in finding suitable rein-
forcement. It also has a record of poor performance, thus
supporting the view that its mental capacities are rather more
limited than those of the laboratory rat. These points will be
discussed shortly, but first some details of the advantages
the guinea pig has in comparison with other laboratory species
will be given. These account, in part at least, for renewed
interest in the guinea pig as a subject.

The guinea pig is a precocial species, and the advanced state
of its development at birth makes it useful in many studies. The
guinea pig's anatomically well-developed brain at birth permits

accurate assessment of pre-natally induced neurological interference. Also, the newborn guinea pig resembles to some extent the human neonate. Thus it can be used to investigate the effects of prenatal asphyxia on subsequent learning ability (Becker and Donnell (1952).

The advanced state of the guinea pig at birth also makes it useful in visual and behavioural studies very soon after birth (Jonson et al.1975). Thus Harper (1966) was able to study the effects of isolation from birth: the young guinea pigs were separated from their mothers at parturition.

Jonson et al.(1975) describe some of the areas in which the guinea pig is of particular value as a research animal. For example, it is possible to determine precisely the onset of oestrus and data of conception by inspection. This, together with the lengthy gestation period of 68 days, permits precise determination of critical neuro-embryological developmental periods in order to subject them to experimental treatment procedures.

Guinea pigs raise their young communally from birth, so it is possible to use cross-fostering techniques (for instance, in studies investigating the effects of pre-natal treatment on post-natal behaviour). The relatively long life of the guinea pig in comparison with other laboratory rodents might also be useful where projects extend over a relatively long period of time.

The structure of the ear is also particularly suitable for studies concerned with audition. Thus Gross (1952) used guinea pigs as subjects in investigating the effects of cochlea lesions.

Becker (1946) planned to carry out an investigation for which, due to certain aspects of reproductive anatomy and developmental

physiology, the guinea pig was particularly suitable. The
investigation required information on the learning ability of the
guinea pig. There was little information available. Becker (1946)
therefore carried out an investigation into the learning ability
of the guinea pig.

Becker (1946) points out that although the guinea pig did
poorly in the learning study using the Jenkins problem box, Fjeld
(1934) noted that it used a variety of techniques in its approach
to the problem which contrasted with the stereotyped approach of
the rat. Becker suggests that the problem box may not be suited
to the behaviour of the guinea pig. Muenzinger/(1928) provides evidence
of the plasticity of approach in the guinea pig compared with the
stereotypy of the rat. The animals were presented with problems
requiring latch lifting, burrowing under, use of teeth, and circum-
vention of barriers. The guinea pig was superior to the rat in
that its responses were plastic and variable, thus achieving
greater success than the rat which responded in a stereotyped
manner. Becker (1946) considered that if a suitable apparatus
were provided the guinea pig would be able to master it without
difficulty, and decided to use an alternating maze. Both positive
and negative reinforcement were used: electric shock in a blind
alley and dry alfalfa in the goal box. Becker (1946) describes
the combination as providing "adequate motivation".

Becker (1946) found that normal * animals did not take long
to master the maze. He also found that an adult guinea pig showed
perfect retention after eight weeks. Again, the animals showed

* other animals had been subjected to experimental manipulations,
  such as anoxia or concussion.

plasticity of approach to the learning situation, trying a new route
to the goal at each trial. Becker (1946) concludes that "... the
genus Caviae is not so dumb as you think".

Thus the particular advantage of the guinea pig for certain
types of investigation has led to a reappraisal of its mental
capacities, and an attempt to devise an experimental situation
suitable for the guinea pig. Becker's (1946) investigation
supports the view that inappropriate experimental conditions are
the reason for many a poor performance by a guinea pig and emphasize
the importance of providing adequate appropriate reinforcement.
Becker's (1946) findings also confirm the plasticity of behaviour
noted by Muenzinger (1928) and Fjeld (1934).

Jonson, Lyle, Edwards and Penny (1975) propound the same view
as Becker (1946). They write that the guinea pig is "not so lacking
in sagacity as many investigators have intimated". They report that
the guinea pig is able to learn in situations using appatitive
reinforcement. This has been revealed in more recent work (Jonson
1971; Jonson, Lyle, Edwards, Penny and Sosula 1974; Jonson, Lyle,
Edwards and Penny, 1976; Lyle, Jonson, Edwards and Penny (1973)
where in suitable experimental conditions* the guinea pig exhibits
serial discrimination learning which is comparable to that of other
mammalian species.

Jonson et al (1974) investigated spatial and non-spatial
reversal learning in guinea pigs. Reinforcement consisted of
cabbage juice with cabbage pulp and ascorbic acid added; its
reinforcing effect was enhanced by stopping the daily supply of
fresh vegetables to the animals. The guinea pigs responded with
increasing efficiency over the eleven reversals, and the results
correspond well with previous findings obtained with other mammalian

* my emphasis

species. However, Jonson et al (1974) report that their work demonstrates that behavioural research with the guinea pig requires extended periods of "intense experimental management".

There are several studies which indicate that the guinea pig may be successfully trained in operant studies using both appetitive and negative reinforcement. Norton, Daley and Wolff (1968) trained three guinea pigs to bar-press to avoid electric shocks to the feet. Pearl (1963) reported that the guinea pig has shown superior performance in shock avoidance to rats and hamsters. Burnstein and Wolff (1967) succeeded in conditioning a vocal response in male albino guinea pigs using intracranial stimulation as reinforcement. The guinea pig has shown higher overall rates of bar pressing for intracranial stimulation than the rat (Wolff, Burnstein, Flory and Mabry, 1966).

Valenstein (1959) used water as reinforcement. Miles, Ratoosh and Meyer (1956) used pelleted food as reinforcement. Berryman (1976c) devised an effective method of reinforcement for both adult and infant guinea pigs. Berryman writes that food and/or water deprived animals were unresponsive subjects. She found that a soupy solution consisting of one part Ostermilk, two parts Farex, & eight parts water, produced a reinforcer that was accepted by all her animals. A tiny drop was sufficient to keep her animals working on a lever-lifting task before becoming satiated. No deprivation was required.

Petersen, Prosen, Moody and Stebbins (1977) comment on the difficulties reported in training the guinea pig to perform simple operant tasks. Petersen et al found that it was possible to train the guinea pigs to be reliable observers in a demanding psychophysical task for determining absolute auditory thresholds. The animals were semi-deprived in that they were maintained on a restricted

diet, which was adjusted so as to keep each individual healthy and active. Food pellets proved effective reinforcement. Urbain, Poling and Thompson (1979) found that guinea pigs adapted readily to food deprivation. The animals were maintained on a fixed time (FT) schedule with either one or three food pellets per reinforcement. The guinea pigs produced reliable data across twenty-one consecutive months. In contrast to this report, Dutch and Brown (1974) found that although guinea pigs adjusted to a water deprivation schedule, they failed to adjust to a food deprivation schedule.

Many experimental procedures have been designed for use with the rat. The Skinner box is a notable example of this. Thus Valenstein (1959) experienced difficulty in training guinea pigs to press a bar with their forepaws. "This" write Jonson, Lyle, Edwards and Penny (1975) "is because the guinea pig, unlike the laboratory rat, does not normally lift its forepaws off the ground in the appetitive or consummatory phase of feeding." Kunkel and Kunkel (1964) report that in contrast to other rodents "the forepaws are scarcely used as 'hands' at all" by the guinea pig. Jonson et al (1975) note that Riess (1934) found it difficult to train guinea pigs to depress circular plates embedded in the floor of the apparatus, and suggest that the persistence of the non-adaptive behaviour shown by the guinea pigs in Riess' study was due to the unsuitablity of the task to the natural behaviour of the animal. Gross (1952) noted that the rotator[*] used in his study was an unsuitable test instrument for use with the guinea pig.

Jonson et al (1975) suggest that such difficulties could be overcome by modifying the apparatus to enable the guinea pig to use its snout. In their 1974 study the guinea pigs were required to nose open a pair of closed doors. Many learned to do this in one trial, and all in less than ten trials. Operant procedures

* See page 10.

could also be adapted to the natural behaviour of the guinea pig;
"... the bar in the Skinner box could be inverted so that it could
be raised by the normal appetitive response of nosing with the
snout, rather than depressing it with the paw".

The guinea pigs trained by Berryman (1976) were required to lift
a lever. Petersen, Prosen, Moody and Stebbins (1977) trained guinea
pigs to push a Gerbrands pigeon response key with the nose. Petersen
et al point out that this is utilising a naturally occurring response
of the animal: "... observation of the guinea pig in its home cage
revealed that the animal spends a good deal of time poking and
thrusting its nose into the various slots available in the enclo-
sure". The response keys were placed on the wall at "nose-level".

The value of being able to use operant techniques with the
guinea pig has been clearly demonstrated by Ruddy (1980) who used an
avoidance schedule to study the ability of male and female guinea
pigs to discriminate between odours of colony mates*

Thus it is possible to use the guinea pig in behaviour studies
providing that the experimental situation is designed with the
characteristics of the guinea pig in mind, and that care is taken,
when appropriate, in pr viding a suitable reinforcement. This would
seem to be self-evident. Whatever the species being studied, it is
necessary that the experimental situation be appropriate to its
natural range of behaviour. Nonetheless, investigations have been
carried out without sufficient knowledge of the species being used
as subjects.

Thus it is necessary that the investigator take into account
the characteristics of the species, and designs the investigation

* This work is discussed in Chapters 9 and 10

accordingly. Jonson et al (1975) list several factors which can be identified as important requirements for successful behavioural research with the guinea pig. These include the following: *

1. An initial habituation period of at least several weeks.

2. Adequate Vitamin C.

3. Adequate habituation to the experimental situation to minimize the influence of the characteristic immobility response.

4. The design of the experimental task to suit the natural habits of the guinea pig.

5. A soundproof laboratory.

Finally, Jonson et al (1975) point out that in comparison with the rat, behavioural research with the guinea pig requires more intensive management. These requirements are demanding, and suggest that the guinea pig should only be used when there are compelling reasons for doing so.

SUMMARY

The guinea pig has been domesticated for a very long time, but it is possible that its behaviour has not changed greatly. Cavia aperea has been identified as the possible ancestral species, or as very closely related to the guinea pig.

The guinea pig has been used in biological research for many years, but it has not been widely used in behavioural studies due to its propensity for becoming immobile. However, it has certain advantages and, under careful management, proves a satisfactory subject in behavioural investigation.

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* I have included those suggestions which are generally applicable to the guinea pig.

Chapter 2

Social Behaviour in the Guinea Pig

Chapter 2.

Sexual Behaviour

Much of the work on social behaviour in the guinea pig is concerned with its sexual behaviour. This is perhaps not surprising. Although, as has been indicated, the guinea pig is a difficult animal to work with, its sexual behaviour is relatively easy to investigate. Becker (1946) writes "The male guinea pig is always interested in sex. Here, the guinea pig is not so dumb ... the ardor of the buck is such that he will cross a high voltage barrier to reach a female in heat; food is likely to be insufficient incentive to persuade him to cross a considerably lower voltage".

It is possible to study sexual behaviour in the guinea pig without putting the animal into a novel environment. An oestrus female can be put into the male's cage and his behaviour recorded (Valenstein and Goy 1957). Furthermore, the study of sexual behaviour, of necessity, does not involve isolation of the animal. Pearson (1970) reports that immobility did not occur when more than one animal was present.

Avery (1925) and Louttit (1927, 1929) were the first to make detailed observations of the guinea pig. Avery describes the repertoire of sexual activity in both sexes. He writes that the diversity and variability of activities observed in male sexual behaviour is so great that a simple characterisation is not possible, and lists those types of response most frequently seen under laboratory conditions. These include pursuit, vocalisation,

circling, licking excretions and atypical mounting.*

Louttit (1927, 1929) investigated the sexual and reproductive behaviour of the guinea pig. He published details of the behaviour of the animals in response to one another, which include vocalisation, circling and swaying, rumping the female, kissing, and atypical mounting.*

A comprehensive list of the patterns of sexual behaviour in the guinea pig is given by Jacobs (1976). Jacobs subsumes the different items of behaviour under the general heading of courtship: licking and sniffing of the target animal's ano-genital region, pursuit, nosing or nibbling fur, swaying, circling, jumping over female, rumping, rump-attempt, kissing, nibbling ear, chin-rump follow, perineal drag, supracaudal rub, mounting, disoriented mounts, pelvic thrust, intromission, ejaculation.
However, Jacobs does not include vocalisation. This is included by Avery (1925), Louttit (1927), King (1956), Kunkel and Kunkel (1964), Pearson (1970), and Rood (1972) as part of the sexual behaviour of the guinea pig. It is generally described as a rumbling, purring sound which accompanies hip swaying and circling movements. While some investigators call it the "purr" (Pearson 1970; Berryman 1974), others term it the "rumble" (King 1956; Rood 1972). This sound is discussed further in the section on vocalization.

Beauchamp, Magnus, Shmunes and Durham (1977) include perineal sniff-chew and spritz (or epuresis or urine spraying) as part of the pattern of courtship. Pearson (1970) includes epuresis.

Despite differences in description and terminology inspection of the varying accounts (see Appendix 2) reveals that they refer to

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* A more detailed description of the behaviour patterns is given in Appendix 2.

the same basic patterns of behaviour. As Beauchamp et al (1977) write, the male guinea pig displays unusually complex pre-copulatory behaviour. The functional significance of this is not known.

Harper (1966) suggests that the mating behaviour of the guinea pig is stereotyped. He writes that the male and female patterns dovetail quite neatly. This would be predicted if one assumes that a strict sequence of mutually regulated responses on the part of each member of the pair is necessary to permit them to copulate. Harper (1966) supports the suggestion as to the stereotypy of mating behaviour in the guinea pig with his finding that improperly oriented mounts were preceded by different responses than were properly oriented attempts. Klein (1956) has reported that a strictly stereotyped pattern of behaviour is necessary for mating in rabbits.

Young and Grunt (1951) investigated the sexual behaviour of the male guinea pig. They describe some aspects of this in detail, but other items are lumped into a category "along with indifference" termed "other behaviour" on the grounds that they occurred to such a small extent. These behaviours include rumping, circling, pursuit, nudging and vocalization. This is unfortunate, as it means ignoring part of the characteristic mating pattern of the guinea pig (Avery,1925; Louttit, 1927;1929; Pearson, 1970; Jacobs, 1976) and may lead to misconceptions. In his review of sexual behaviour in the guinea pig Young (1969) points out that Young and Grunt (1951) saw all the responses listed by Avery (1925) and Louttit (1927) but deemed the responses described in their (1951) paper as sufficient. However, Young (1969) notes that abortive mounting was included by Valenstein, Riss and Young (1954), and subsequently all mating behaviour shown during a mating test was recorded.

Young and Grunt (1951) report that for much of a ten-minute test period the male guinea pig may sniff at parts of the female's body other than the ano-genital region, and he may nibble at the female's fur and ears. They suggest, therefore, that sniffing and nibbling should be regarded as sexual. This is supported by their observation that the decrease in sniffing and nibbling following ejaculation is as abrupt as the decrease in mounting, nuzzling and intromission. Jacobs (1976) includes these items in his list.

Young and Grunt (1951) observed that the receptivity of the female appeared to influence the pattern of behaviour shown by the male; also that the male-like mounting behaviour of the female during oestrus frequently stimulates the male to take the initiative. Young and Grunt (1951) also report that satiation in the guinea pig is almost invariably reached after a single ejaculation, which is usually achieved within a few seconds to ten minutes. This is in contrast to the rat which, say Young and Grunt (1951), requires from three to ten ejaculations and considerably more time. The median number of intro-missions required by the guinea pig for ejaculation was between three and four, although ejaculation commonly occurred during the first intromission. After ejaculation both animals indulge in anogenital grooming.

Young and Grunt (1951) point out the advantage of the guinea pig over the rat in a situation which requires ejaculation before the end of a test period. However, Avery (1925) reported great variability in sexual behaviour in males, and says it should never be assumed that one male will copulate at the first opportunity given by the female. Young (1969) points out that some animals require more than ten minutes

for ejaculation to occur, also that strain differences have been found in mating behaviour as shown by the amount of mounting, the number of intromissions and ejaculations, and latency to ejaculation (Valenstein, Riss and Young, 1954; Valenstein, Riss and Young, 1955). Mating in the male is also influenced by other males. Males living in unisexual groups for the first four months of life had uniformly higher mating scores than males living one to a cage (Riss and Goy, 1957).

Grunt and Young (1952) carried out a study to determine whether or not there are circumstances in which a re-awakening of sexual activity can occur. It seemed that the most likely stimulus would be access to a second receptive female.

It was found that the sharp drop in activity which followed ejaculation was not significantly affected whether the female was left with the male, or whether she was removed and returned. However, evidence was obtained indicating that sexual activity in the male guinea pig can be restored when a second female replaces the first. The frequency of mounting increased, even when the second female was not on heat, and although the introduction of an oestrous female as opposed to a non-oestrous female would seem to have been the more stimulating, the comparison was not reliable. This is surprising in view of the fact that the behaviour of the oestrous and non-oestrous female varies considerably. Thus Young and Grunt (1951) observe that the behaviour of the female appeared to influence the response of the male; the oestrus female often shows male-like mounting behaviour (Avery, 1925; Louttit, 1929), and Young (1969) writes that in females

from genetically heterogeneous stock up to eighty per cent of the
females showed some masculine behaviour at oestrus.

Young (1969) comments that mating experience with females appears
to have a reinforcing effect on adult males. Young and Grunt (1951)
and Riss and Young (1953) found that mating performance in low score
males increased after they were housed with females for sixty days.
Sexual behaviour of males reared in isolation was not organised into
an effective pattern; subsequent contact with females permitted the
organisation of the sexual behaviour into an effective pattern
(Valenstein, Riss and Young, 1955; Valenstein and Goy, 1957).*

Testosterone is related to mating behaviour. Young (1969) notes
that mounting is most frequent in intact males, and in castrates given
testosterone.

Homosexual behaviour has been reported in guinea pigs. Louttit
(1927) found that six males of approximately the same age and size
showed it. At different times the same guinea pig might "play the
part" of a male or female. The male playing the part of a female did
not submit willingly, but usually ran or fought with his aggressor.
The male guinea pig will mount males and females indiscriminately
when these are first put into his home cage.

Rood (1972) reported that when a male was introduced into a social
group the C. porcellus male seemed unable to distinguish the sex of
the introduced males and responded to them sexually. He also found
that male guinea pigs will rumba ** to juveniles of both sexes. Kunkel
and Kunkel (1964) report that males court young animals until the

* This is discussed in greater detail on pages 47-49.
**rumba: part of the courtship pattern. The rumba would seem to include
  swaying, circling and treading. See Harper (1966), Rood (1972), and
  Jacobs (1976).

latter are sexually mature, but never try to copulate with them.

Male guinea pigs have also been reported as responding sexually to non-oestrous females. Thus Louttit (1927) reports that the male does not seem to differ in his response to oestrous and non-oestrous females. When a male was with two females, one of which was receptive, he was observed to approach either female indiscriminately. In his discussion of this behaviour Louttit (1927) reports that Loeb and Lathrop (1914) observed that if a male loses a receptive female among a group of animals he has no way of finding them except by trial. Avery (1925) writes that a male guinea pig shows "a minimum of discrimination between receptive and non-receptive females and a maximum of trial and error mounting". When a male loses a receptive female, in his search for her he tries almost any female until he discovers the right one.

Willis, Levinson and Buchanan (1977) found that alpha males courted non-receptive females, and conclude that courtship of non-receptive females is a normal aspect of guinea pig behaviour. Berryman (1978) also reported courtship by dominant males of non-receptive females, although she points out that few oestrous periods occurred during the observations. Jacobs (1976) found that all males courted non-receptive females. However, an increase in the rate of courtship towards the end of the gestation period was usually seen, with more courtship occurring during the four-day period approaching parturition (Beauchamp, Jacobs and Hess, 1971). Rood (1972) observed that the dominant male would start guarding the pregnant female during the period preceding parturition. He would chase away other males.

When living in social groups males usually confine mounting behaviour to oestrous females. Only three instances of mounting

of non-receptive females by males was observed during forty hours of observation (Beauchamp, Magnus, Shmunes and Durham 1977). King (1956) reported that adult males showed more selection of mates than did the juveniles, and tended to remain only with females in oestrus. Thus not all the evidence suggests that the male guinea pig is as likely to court an unreceptive female as a receptive one, or that males generally mount other males. Beauchamp et al (1977) suggest that novelty is an extremely important stimulus in eliciting mounting behaviour in guinea pigs.

There is some evidence that the sexual behaviour of the male is influenced by the behaviour of the female (Young and Grunt 1951). Louttit (1927) found some differences in the response of a male with a receptive female compared with a non-receptive female; using time analysis, Louttit found that when placed with a receptive female the male makes the first mount sooner and the subsequent mounts at shorter intervals. This difference is the most outstanding one in the behaviour with receptive and non-receptive females. Louttit (1927) suggests that it could be due to differential behaviour on the part of the female.

Thus the picture is somewhat confused with evidence that the male guinea pig is likely to mount male animals, and has difficulty in distinguishing oestrous from non-oestrous females. There is also evidence that in social groups he confines his courtship behaviour to oestrous females, and is able to distinguish a female shortly to give birth and, therefore, to come into postpartum oestrus. But again, there is evidence that while in a social group he may direct his attentions to a male animal, particularly if this is a juvenile or a stranger. This will be discussed further in the experimental section of this investigation.

There are differences to be found between <u>Cavia porcellus</u> and <u>Cavia aperea</u> with regard to sexual behaviour. Rood (1972) reports that overt sexual behaviour is less often expressed in <u>C. aperea</u>. The rumba is shorter, less frequent, and is not directed to young males. Mounts on non-oestrous females and homosexual mounting were not seen. Naso-anal licking was much less frequent than in the guinea pig.

Some <u>C. porcellus</u> males are slower to ejaculate than <u>C. aperea</u>. Rood (1972) suggests that this is possibly because, during domestication, no selective pressure exists for rapid ejaculation. One <u>C. porcellus</u> male never ejaculated as he kept on circling round the female until he was chased away by the dominant male.

<u>Female</u>

The sexual behaviour of the female guinea pig has received less attention than that of the male. Louttit (1927) lists behaviour shown by the receptive female. This includes mounting behaviour. He reports that it is possible to determine the receptive female by the posture she assumes (lordosis) when mounted by the male. Avery (1925) reports that posture lordosis is an unequivocal sign of receptivity in the female; he also reports that homosexual (mounting) behaviour occurred in no less than from ten to fifteen per cent of animals coming into oestrus. Young (1969) found that in females from genetically heterogeneous stock up to eighty per cent showed some masculine behaviour at oestrus. Pearson (1970) also describes the behaviour of the oestrous female which resembles that of the male. Beauchamp <u>et al</u> (1977) write that the following behaviour is associated with receptivity in the female: rumble sway, scent mark, mount.

Young (1969) describes the sexual behaviour of the females: in the dioestrum the female guinea pig may be relatively quiet and seemingly uninterested in her companions. As oestrus approaches there is a marked increase in her excitability. Vocalisation and movement increase, with a running pursuit after other animals, and frequent attempts to mount them. Such mounts often include pelvic thrusts. Young (1969) notes that the mounting behaviour has been seen for as long as fifty-three hours before oestrus, but is rarely displayed vigorously until two to three hours before. The amount of this behaviour shown is extremely variable.

With the onset of oestrus the female becomes quiet, and will show lordosis in response to appropriate stimulation. Young (1969) comments that during the early part of a strong oestrus, lordosis can be repeatedly elicited by the male or by stroking by the in-vestigator. The intensity of the response gradually diminishes.

Birke (1981) investigated changes in behaviour associated with the oestrous cycle. She found that several patterns of behaviour varied systematically with the oestrous cycle, and reports that oestrus is characterized by an increase in locomotion, anogenital dragging, and greater interest in conspecifics.*

Length of oestrus varies considerably. Young (1969) gives a mean length based on 1062 heat periods, of approximately 8 hours, with extremes of from 1 to 15 hours. However, despite this variation, Young notes that individual females tend to have heat periods of a relatively uniform length. Similarly, Young suggests that while the pro-oestrus activity varies widely from female to female, it is

* This work is discussed in Chapter 10

nearly constant for a given female from one cycle to another. The
extent of mounting behaviour and length of heat do not correlate.
Young (1969) comments on the possibility that copulation might
shorten oestrus, but says that there is no real evidence to suggest
that this is so.

Thus it would seem that within certain parameters there is
considerable variation in sexual behaviour in the guinea pig. Rood
(1972) reports that female mounting was occasionally observed in
guinea pigs, but was not seen in C. aperea.

Young (1969) points out that contact with other animals is
necessary for the organization of sexual behaviour in the female.
Contact with other animals later in life is not so effective as early
contact in the organization of sexual behaviour in the female. This
contrasts with the male (see page 49).

There is some evidence that the oestrous cycle of guinea pigs kept
in groups tends to become synchronised (Donovan and Kopriva, 1965).
The synchrony is not complete, however, and ablation of the olfactory
lobes did not affect the oestrous cycle, indicating that the sense of
smell is of little importance in mediating the oestrous cycle. Harned
and Casida (1972) observed female guinea pigs over two cycles, and
reported that synchronisation of oestrus occurred at a chance level
only, and Birke (1981) reports that she found no synchronisation of
oestrus, although she does point out that females housed singly
tended to have more irregular cycles than those housed in groups.

Jesel and Aron (1976) found that in female guinea pigs exposed
to the odour of female urine collected during the period of vaginal
opening, the period of vaginal closure was shortened, causing a

decrease in the duration of the oestrous cycle. The same effect was observed in females exposed to the odour of male urine. The shortening of vaginal closure did not occur in bulbectomized females exposed to male urine. Jesel and Aron (1976) conclude, therefore, that concentrated urine contains a pheromone capable of shortening the oestrous cycle.

Jesel and Aron (1976) also report that no difference in vaginal closure duration was found between bulbectomized and unoperated animals, and note that in this respect their results confirm those of Hamed and Casida (1972).

Harrison (1977) reports that synchronisation occurred to a partial extent in females housed in groups, and suggests that this occurs as a result of the shortening of some of the oestrous cycles; this appeared to take place during the first cycle after grouping. This shortening of the cycle would seem to correspond with the finding of Jesel and Aron (1976). Harrison suggests that both synchronisation and shortening of the cycle are due to olfactory stimuli.

Thus the data on synchronisation of the oestrous cycle are conflicting, although it would seem clear that given olfactory stimuli may shorten the oestrous cycle. Further research would clarify the position with regard to synchrony of oestrus and, if it occurs, whether it is mediated by olfactory stimuli.

Summary

The male guinea pig has a complex range of copulatory responses. There is a considerable amount of evidence which suggests that he

will direct his courtship behaviour to other males and to non-receptive females. However, reports vary concerning this. Sexual behaviour in male guinea pigs shows great variability.

The receptivity and behaviour of the female appears to affect the pattern of behaviour shown by the male. It has been suggested that sexual behaviour in the guinea pig is stereotyped.

The female tends to show considerable activity and male-like behaviour with the approach of oestrus. With the onset of oestrus she becomes quiet. There is considerable variation in the amount of activity shown, and in the length of oestrus. There is some evidence that synchronisation of oestrus may occur in females grouped together. However, the data are conflicting. If synchronisation does occur, it is possibly mediated by olfactory stimuli.

Contact with other animals would seem to be necessary for the organization of sexual behaviour in both male and female guinea pigs.

The domestic guinea pig and the wild species, Cavia aperea, vary with regard to certain aspects of sexual behaviour.

Agonistic behaviour

Much of the work concerned with agonistic behaviour resembles
that on sexual behaviour in that it is essentially descriptive.
Avery (1925) describes a fight between two strange male guinea pigs
that were put together. The account includes swaying of the hips
and tooth chattering or gnashing *. King (1956) also describes
fighting in the guinea pig. He reported that severe fights
developed among males which were previously strange to each other.
Some fights were particularly severe, frequently resulting in cut
lips, parts of the ears being torn off, and deep wounds on the rump.
King (1956) writes that these displays of aggression appeared
necessary for the establishment of territories, each being guarded
by a male. No territories developed, however.

Grant and Mackintosh (1963) describe the postures character-
istic of the guinea pig during fighting. They also report that
the bite of the guinea pig is less inhibited than that of the rat,
and can be quite damaging even at low level intensities of
aggression. Coulon (1975a) gives details of agonistic postures
observed during lengthy daily observations carried out for three
months. These postures include those of Grant and Mackintosh (1963).
Offensive and defensive postures are described.

Kunkel and Kunkel (1964) have also described the fighting
behaviour of the guinea pig. They observe that the guinea pig
shows several fighting and threatening gestures. Fighting is
described as unritualized and damaging. This is in contrast with
Coulon (1975a) who suggests a considerable degree of ritualization
in fighting. Pearson (1970) described in detail the pattern of
fighting between two males, and reports that it often results in

* Patterns of agonistic behaviour are given in greater detail
  in Appendix 2.

severe wounding .   At any time one of the males may "retire".

Thus it is clear that in certain situations the male guinea pig will fight fiercely.   This would seem likely to occur when the males are strangers to one another (Avery 1925; King 1956). Rood (1972) found that an introduced animal (that is, one that is unfamiliar) was attacked and chased by C. aperea.   Males attack males and females attack females.   Adult males placed in the C. aperea pen were usually attacked and killed; strange males were attacked by the C. porcellus males, but eventually became integrated into the group, at the bottom of the male hierarchy.

Coulon (1975b) studied the agonistic behaviour of dominant male guinea pigs confronted with a stranger male either on their own "territory" or on that of the stranger.   He suggests that an agonistic encounter starts with behaviour which establishes a dominance relationship between the antagonists.   Coulon (1975b) reports that the dominant male displays ten times as many offensive postures as defensive ones, whereas in the subordinate animal this ratio is balanced.   He also reports that offensive postures in one male tend to evoke defensive postures in its opponent, and defensive postures of the subordinate male evoke offensive ones in the dominant animal.   Coulon (1975b) suggests that agonistic displays are an expression of an aggression-escape conflict. Further, that agonistic displays provide a means of solving the conflict and establishing dominance relations by selecting postures adapted to the situation and consequently to the antecedent reactions of the opponent.   Coulon (1975b) reports that the characteristics of the opponent appear to be more important than

the territory where the encounter takes place.

Geissler and Melvin (1977) investigated aggression between home-cage resident guinea pigs and an intruder. Resident animals were housed in male-male or male-female combinations. The male intruders were introduced singly into the home-cage of the resident male-male or male-female pairs. The resident males won significantly more of the encounters than did the intruders. In the male-male resident pairs one male became dominant and fought the intruder while the other resident remained passive. The sexual composition of the resident pairs did not affect the aggressive behaviour.

Geissler and Melvin (1977) point out the resemblance of the "home-cage effect" to the natural phenomenon in which an intruder into a territory is often defeated, even when the resident is smaller.

The findings of Geissler and Melvin (1977) suggest that the area where an agonistic encounter between guinea pigs occurs is an important factor in determining its outcome, whereas Coulon (1975b) reports that the characteristics of the opponent are more important. Geissler and Melvin (1977) report that intruders which were housed in isolation elicited more aggression than intruders housed with another male, and suggest that this was due to a greater level of activity shown by the isolated intruders, although they were not more aggressive than the socially housed intruders. Thus the behaviour of the intruder may be a relevant factor in an encounter.

Rood (1972) reports that in Cavia aperea many agonistic postures provide visual stimuli which elicit appropriate behaviour

in conspecifics. The curved body posture characteristic of
threat stimulates nearby animals of similar dominance status to
assume the same posture.

Thus it would seem that in certain circumstances the male
guinea pig is an aggressive animal. He will fight a stranger
(Avery, 1925; King, 1956; Rood, 1972), and fighting occurs in the
establishment of dominance. However, Rood (1972) reports that
aggression was rare in feeding groups of C. aperea. King (1956)
reports that several animals would feed together on a single
carrot. As Rood (1972) points out, this lack of aggression during
feeding permits efficient detection of predators and communication
of the alarm response.

Boxing with the snout is seen in many situations where agg-
ression is relatively low; it is seen in both sexes when the
animals are jostling for food. It may also be shown by females
avoiding the attempts of infants to suckle (Berryman, 1976a).

Kunkel and Kunkel (1964) report that guinea pigs spray con-
specifics with urine, and describe this as an expression of weak
or blocked aggression, in which an escape tendency is lacking.
Rood (1972) describes the "tail-up", where the perineal region is
raised, as a form of defensive aggression which typically repulsed
the approaching male. It was sometimes accompanied by urine-
spraying. It was observed to occur more frequently in C. aperea
than in C. porcellus. Pearson (1970) describes the behaviour of
a non-oestrous female when placed with a male. As she seeks to
avoid his attentions she may kick out at the male, or eject a
stream of urine backwards into his face. Pearson (1970) comments
that urine-squirting is often shown by a male in a male-male en-

counter. This may be shown by both animals as they simultaneously try both to mount and to avoid the other.

Female C. aperea are considerably more aggressive than C. porcellus females. Rood (1972) found that there is a well-defined dominance hierarchy of a straight-line type in female C. aperea. They are aggressive to one another, and particularly to subordinate females. C. porcellus females were observed foraging with another female considerably more often than were C. aperea. C. aperea are also more aggressive in their relations with young animals. They are likely to be aggressive to the young of another female. Adolescent females may be chased by adult females, but Rood (1972) reports that C. porcellus females never chased juveniles: C. porcellus are generally amiable to the young of other animals. King (1956) reports mild antagonism among females. He reports that they varied both individually on different occasions and from one animal to another. Some females were able to dominate others when conflict did occur, and displayed a weak and flexible social hierarchy. Young (1969) reports that a female may be quite vicious and aggressive towards a strange female, snapping and biting.

Perusal of the findings obtained by King (1956) and Rood (1972) reveal that Cavia aperea is considerably more aggressive than Cavia porcellus. King(1956) suggests that domestication is likely to result in greater social tolerance. This is perhaps why the domestic guinea pig (Cavia porcellus) is generally less aggressive than C. aperea.(This point will be discussed further in connection with the studies of King (1956) and Rood (1972).

Summary

The aggressive behaviour of the guinea pig is complex and

includes postures which have been described by several workers. It is possible to divide them into offensive and defensive postures.

Aggression is shown to animals of the same sex. A male guinea pig will fight a strange male. Fighting also occurs during the establishment of dominance hierarchies.

The place where an agonistic encounter occurs is important in determining its outcome, with an intruder likely to be chased and defeated by the resident animals. The behaviour of the intruder would also seem to be relevant in an agonistic encounter.

While female _C. aperea_ are aggressive to young and adolescent females, this is less true of _C. porcellus_. However, domestic females do show mild aggression, and the occurrence of considerable aggression has been recorded.

The data suggest that some of the postures observed during fighting are ritualized, and communicate information to others of the species.

Dominance

Naturalistic studies, or semi-naturalistic studies, where animals are maintained as a group rather than one or two to a cage, and where the behaviour of the animals to one another is observed, have revealed that guinea pigs form dominance hierarchies.

Avery (1925) observed that when male guinea pigs were reared together, one or two usually became dominant in the group, and all the others gave way to them. Kunkel and Kunkel (1964) observed guinea pigs in groups of varying sizes and recorded that dominance hierarchies were formed. These were mainly of the straight-line type, but triangular relationships were also recorded. Young males were observed to become involved in rank order conflict when they first engaged in sexual activity.

Rood (1972) found that both Cavia aperea and Cavia porcellus formed stable dominance hierarchies of the straight-line type, but observed no triangular dominance relationships. Occasionally, dominance ralationships were not clearly defined at the lower levels, generally because no aggressive interactions were recorded. Rood also recorded that female C. aperea were aggressive and showed a well-defined dominance hierarchy. This was stable with only two reversals of dominance and one triangular relationship observed during the study. The C. porcellus females were less aggressive, and did not form dominance relationships. King (1956) wrote that the female guinea pigs are less antagonistic than the males, and display a weak and flexible social hierarchy. Kunkel and Kunkel (1964) reported a rank order among the females, although less clearly than among the males. Bates, Langenes and Clark (1973) found reliable linear dominance hierarchies in both male and female juvenile guinea pigs. In competition for water females were likely to be dominant over males.

Coulon (1975) observed groups of C. percellus for several hours a day for three months. He found a straightline hierarchy existing in the male animals. This was generally stable but could change during periods of sexual activity stimulated by an oestrous female. Greatest aggression occurred between the alpha and beta males. The beta male was also the most frequently attacked male. The lower ranked males were less aggressive.

Coulon (1975a) suggests that each male is aware of the position of all other males in the hierarchy. He also reports that the behaviour sequences are ritualized to a considerable extent, but that these vary characteristically between different pairs of opponents. Coulon (1975a) describes his results as not fundamentally different from those of Rood (1972).

Jacobs (1976) however, reports a considerable difference between his data and those of Rood (1972). Jacobs studied guinea pigs in groups of varying size and composition, and most of these groups were observed daily for a period of several months. Unlike Rood (1972) who reported that mating was promiscuous and that permanent bonds were not formed between male and female animals, Jacobs (1976) recorded long term associations between a male and a female. A significant interaction was recorded between these male/female associations and the dominance hierarchy. The associating male became more aggressive as parturition and the post-partum oestrus of his female approached. If the associating male was not the normal alpha male he often assumed the alpha position on the day of parturition or, if this did not occur, he moved up the hierarchy. The newly acquired rank usually fell soon after the day of parturition.

The dominance hierarchy was subject therefore to considerable
fluctuation.   Rood (1972) reported that in undisturbed groups of
male guinea pigs no dominance reversals were recorded.   Thus the
data obtained by Jacobs (1976) differ from those of Rood (1972) on
two counts: one, in that in Jacobs' study long term pair assoc-
iations were formed, whereas Rood described mating as promiscuous
with no permanent associations; and two, in that Jacobs observed a
dominance hierarchy characterised by frequent changes (dominance
reversals), whereas Rood recorded a stable dominance hierarchy
with no reversals observed during the course of the study.

It is hard to account for the fact that Jacobs' (1976) findings
should differ so markedly from those of Rood (1972), although
Jacobs (1976) suggests that the discrepancy is due to the fact that
he kept daily records over periods of several months, whereas Rood
observed the animals for relatively short periods of time at widely
spaced intervals.   Coulon's (1975a) data are interesting in this
context.   He observed the animals daily for three months, and his
data seem to be intermediate between those of Rood (1972) and
Jacobs (1976).   Coulon (1975a) reports changes in dominance due to
periods of sexual activity stimulated by an oestrous female.   He
makes no mention of enduring associations between male and female
guinea pigs.

It is perhaps possible that in a more natural environment the
alpha male would be more successful in driving away a number of
subordinate males, and in keeping away the remaining subordinate
males from the females during oestrus.   Where a group of animals
is maintained in a pen the alpha male cannot drive away the other
males.   As females come into oestrus the aggression in the

subordinate males increases, resulting in fighting and temporary shifts in dominance.

Berryman (1978) suggests that the context in which the animals are observed may be of importance in producing social dominance. She points out that it might be difficult (less feasible) for a single animal to defend a territory in group situations where animals are maintained at a relatively high density, due to the number of animals likely to intrude during random movements. In support of this there is some evidence to suggest that where the number of males in a group is low, stable dominace is established. In an investigation into post-partum breeding which lasted several months, Rowlands (1962) found that in groups of ten or fifteen females and two boars, one male became dominant and prevented any attempt by the other to mate. Geissler and Melvin (1977) report that when males were caged together in pairs, one male became dominant.

Berryman (1978) studied dominance in guinea pigs in a variety of situations. They were observed during daily interactions in the pen where they were housed at a fairly high density, also in groups and pair-wise testing situations, including interactions at a single water source. Berryman found that the male guinea pigs formed a fairly stable linear hierarchy, as indicated by a variety of behaviours. This was particularly consistent in aggressive and sexual contexts. The position in the hierarchy and the degree of courtship were linked: domimant males generally showed more courtship, and courted a greater number of females. The dominant male was responsible for forty per cent of the courtship recorded, most of it to unreceptive females, as few oestrus periods occurred during the observations. The male at the bottom of the hierarchy was not observed to court an adult female. As

Berryman points out, such total inhibition was not observed by Jacobs (1976).

Purring was found to be a fairly reliable indicator of the domimance status of an individual in a sexual or aggressive context.* Competition for water also revealed a linear hierarchy, with a positive correlation between the time spent drinking, and boxing and biting. No significant correlation was found between drinking and fighting and purring, and Berryman (1978) suggests that dominance in this context may be governed by causal factors different from those giving rise to dominance in the sexual or aggressive situations.

In contrast to those investigators who report the formation of dominance hierarchies (Kunkel and Kunkel,1964; Rood, 1972; Bates, Langenes and Clark, 1973; Coulon, 1975; Jacobs, 1976, and Berryman, 1978), Fuchs (1981) reports that in a group of six male and eight female guinea pigs, no dominance hierarchy developed. One male became dominant: the remaining males were of equal rank. Fuchs' (1981) animals were maintained in an outside pen measuring 12 x 12 metres square, and he suggests that the rank order found by other investigators is due to the animals being kept in a smaller space, leaving them no option but to fight. In such conditions rank order, suggests Fuchs, would reflect fighting ability rather than resource-related competition.

It would seem that dominance hierarchies in the guinea pig are influenced by several factors. The size of the area in which the animals are maintained would seem to be important, also the density of

* Purring in relation to dominance is discussed more fully in the section on vocalisation.

the population. It is likely that dominance is affected by the
ability of the male to defend an area. In a high density popu-
lation random intrusions by animals would render this less feasible,
as Berryman (1978) suggests. The occurrence of oestrus in female
guinea pigs would also seem to be significant. The ratio of males
to females is possibly of importance, with dominance more likely to
remain stable where the proportion of males is low. The context in
which dominance is observed is important, whether in an aggressive
or sexual situation, or an appetitive one, as in competition for
water. Although some workers have reported triangular dominance
in the guinea pig (Kunkel and Kunkel, 1964), the bulk of the evidence
suggests that male guinea pigs typically form a linear hierarchy.

No link has been found between body weight and dominance
(Geissler and Melvin, 1977; Berryman, 1978).

Summary

The work of the majority of investigators suggests that male
guinea pigs living in social groups form dominance hierarchies,
generally of a straight-line type. These have also been observed
in both male and female _Cavia aperea_ and in female guinea pigs.
However, some workers have reported that the female guinea pigs
did not form dominance hierarchies.

The evidence concerning the stability of these hierarchies is
conflicting. There are some data which indicate that dominance
fluctuates with the occurrence of oestrus in the females. Reports
on this vary, however, and it is probable that dominance is in-
fluenced by several factors.

Early Environment and adult behaviour

The guinea pig is a precocial animal, and it is perhaps this fact in conjunction with the guineapig's tendency to follow conspecifics (King, 1956; Rood, 1972) that suggests the possibility that imprinting may occur in this species. As Harper (1966) points out, the young of several nidifugous birds tend to develop a following response to their conspecifics during what is termed a "critical period" after hatching. The characteristics of the object become "imprinted" on the young bird. As a consequence, these characteristics may become the stimuli to which the bird will eventually direct its social responses, including sexual behaviour. Birds which fail to imprint may show a permanent disturbance of behaviour.

Shipley (1963) reported a process resembling classical imprinting in the guinea pig. Infant guinea pigs isolated from their mothers and siblings were observed to show attachment and social behaviour to a rotating block. This was still in evidence at six weeks of age. Shipley (1963) points out that his data suggest that this is a gradually learned phenomenon rather than a "one-shot" process, and suggests that it is a matter of personal preference whether the term imprinting is used to describe processes of attachment occurring after the first few days of life.

Louttit (1929) provides data on the ages at which the different components of sexual behaviour in the guinea pig first appear. Rumping, for example, appears earlier than atypical mounting. The earliest sexual responses to appear include nosing, pursuit, and licking of the ano-genital region. Next to appear are kissing, biting, circling, swaying, and jumping, followed by

the copulatory responses.   This sort of data provides a means of determining whether critical periods exist in the guinea pig for the development of sexual behaviour.   Experimental manipulations can be carried out at the time a given item of behaviour typically first appears.

This section looks at studies investigating the effects of early experience on the behaviour of the adult.   The work to be discussed will also clarify the situation with regard to imprinting and critical periods in the guinea pig.

Louttit (1929) investigated the effect of isolation on sexual behaviour in the male guinea pig.   Several pairs of isolated animals were put together at 30 days of age.   They had been isolated since they were removed from their mothers at ten days of age.   In all cases they showed on the first day of being with a female all the responses one would expect at that age.   Louttit (1929) concluded that "physical maturation is of more importance in the development of the reproductive behaviour pattern in the guinea pig than experience gained from association with animals of the opposite sex".   However, Kunkel and Kunkel (1964) report that males reared in isolation show abnormal responses to other guinea pigs.   Gerall (1963) found that the percentage of isolated guinea pigs showing inadequate sexual behaviour increased as the duration of isolation before the first mating test was extended from 30 to 80 days of age.   Subjects isolated for seventeen days showed essentially normal sexual behaviour.   Gerall (1963) suggests that there is a period between approximately 17 to 80 days of age during which various processes occur which are important for the display, and perhaps development, of normal sexual behaviour.

Gerall (1965) compared hand reared guinea pigs isolated at 2 days with hand-reared guinea pigs kept together. It was found that fewer isolated animals made posterior mounts and ejaculated. Gerall (1963) found that twenty out of twenty-nine males tested at 17 days mated normally. Only four out of twelve isolated at 2 days mated normally (Gerall, 1965). As Harper (1968) points out the effects of isolation appear to be increasingly disruptive for males, according to how early isolation is begun, and for how long it is maintained. Gerall (1965) also reports that physical restriction of young guinea pigs affects sexual behaviour in the adult.

Valenstein, Riss and Young (1955) carried out four experiments to determine whether sexual behaviour is "innately organised in the male guinea pig or whether contact with other animals plays a role in its organization into an effective pattern". Male guinea pigs were reared in isolation or in the company of males and females. They were separated from other members of the litter at birth until weaning and were subjected to complete isolation for given periods thereafter. The results indicated that the isolated males had difficulty in mating. Contact with males as well as with females generally provided adequate experience for the organization of copulatory behaviour. Valenstein et al (1955) point out that the isolated animals gave evidence of being as much aroused by the presence of the female as those from the social groups. Nor was there any evidence of emotional disturbance which might have interfered with the display of sexual behaviour. Valenstein et al (1955) conclude that the sexual

behaviour of the isolated animals had not been organized into an effective pattern.   In clarification of this they point out that the socially reared male orients himself to the posterior end of the female.   When mounting he approaches from the rear.   Although isolated male guinea pigs show many of the components of sexual behaviour they are not organized in such a way as to permit copulation. They pursue the female, but they frequently circle around her and attempt to mount her head or side.

However, pursuit and circling form part of the pattern of sexual behaviour in the guinea pig (Avery 1925; Louttit, 1927, 1929; Pearson 1970).   Atypical mounting is also reported by these workers as part of the normal pattern.   Thus the behaviour described by Valenstein et al.(1955) may not have been so aberrant as it seemed, and a longer test period may have resulted in the emergence of the full pattern.

There are difficulties attendant upon studies using isolation as a means of assessing the importance of contact with others for the development of a given behaviour pattern.   Isolation may have a generalised effect.   Thus Valenstein and Goy (1957) note the possibility that the inability of the isolated males to copulate might be due to an effect of the prolonged isolation, rather than to a limited opportunity to organize their sexual behaviour.   Or the performance of the animals in the tests might be due to insufficient opportunity to engage in a form of pre-copulatory activity, such as nuzzling and sniffing.   If more tests were allowed, thus providing the opportunity for such activity, the full copulatory pattern might have emerged.   Valenstein and Goy (1957) investigated these possibilities.

Repeated testing of isolated males did not give rise to the full pattern of sexual behaviour. However, when these animals were caged with others for twenty days or more, they generally achieved copulation in subsequent tests. It was also found that older males isolated in infancy can display the full copulatory pattern if they are caged with other animals for a time.

Males reared with spayed females did significantly less well than males reared with either male or female cage mates. Valenstein and Goy (1957) suggest that this provides evidence of the stimulatory role of female mounting behaviour during the development of sexual behaviour.

The results indicate that prolonged isolation per se does not prevent a male from displaying the full copulatory pattern, providing that the necessary skills had been acquired previously. Thus a male reared with females and subsequently isolated shows the full mating pattern. The pattern can also be acquired by older animals, isolated in infancy. This shows that the development of copulatory behaviour is not restricted to a critical development period. This, therefore, casts doubt on the concept of imprinting in relation to the guinea pig. However, the data obtained by Valenstein and Goy (1957) suggest that prior experience with animals is involved in the organization of copulatory behaviour in male guinea pigs.

Harper (1966) investigated the effects of isolation from birth on approach and sexual behaviour. His study differed from those already mentioned in that the infant guinea pigs were removed from their mothers at birth, and reared alone until they were eighty days old. The subjects comprised six male and seven

female animals.   Tests were carried out in a 5 feet diameter
circular arena and habituation periods of twenty minutes were
provided daily between the ages of seventy and seventy-nine days.
To measure approach behaviour between the ages of eighty and eighty-
nine days all the animals were placed in the arena with an animal
of the same sex tethered in the centre.   To investigate mating
behaviour, when the male guinea pigs were one hundred days old
they were given three periods of ten minutes in the arena with a
free-moving, receptive female.   Similarly, the female subjects
were given three periods of ten minutes with a male of proved
potency.   The behaviour of the isolated animals was compared with
that of eight male and nine female socially reared control animals.

Harper (1966) found that the approach behaviour of the isolated
animals to a conspecific was not significantly different from that
of the control animals.   When the isolated animals were paired
with an animal of the opposite sex their performance did not differ
significantly from the modal control mating pattern.   However, three
of Harper's experimental and four of his control animals failed to
copulate in the first block of three pairings.   Even after being
housed with a female which they inseminated during her first oestrus,
it took further tests before they would copulate in the test
situation.   One isolate and two controls never copulated in the
test situation.   This suggests that the test situation is failing
to elicit the behaviour in some of the animals, both experimental
and control.   Harper (1966) concluded that the only real difference
between the control and experimental males' reaction to a receptive
female lay in the greater playfulness and curiosity of the experi-

mental animals compared with the tendency of the control animals
to freeze. The test arena was in the same building as the iso-
lates, whereas the controls were housed in another building. Thus
the test situation was more unfamiliar to the controls who, despite
habituation trials, were more likely to freeze. Harper (1966)
suggests that this factor may have influenced his results.

Coulon's (1972) findings resemble those of Harper (1966). Like
Harper, Coulon isolated a group of animals from birth, providing
them with artificial milk. When tested as adults their sexual
behaviour was intact, in that the necessary patterns of behaviour
were present. However, the behaviour showed a lack of sequential
organisation and much play behaviour. Cohabitation with a female
resulted in full recovery of normal sexual behaviour. The
increase in play and exploratory behaviour in the isolates reported
by Coulon (1972) parallels the increase in playfulness and curiosity
reported by Harper (1966).

The female guinea pigs isolated from birth by Harper (1966)
tended to lordose longer in response to a male than did the
socially reared females. However, Harper (1966) found that the
reverse occurred in response to stroking by the experimenter: the
socially reared controls maintained lordosis for longer than the
experimental females. The behaviour of the isolated females did
not differ from that of the socially reared females except in that
they showed significantly less post-copulatory grooming and sig-
nificantly more play responses. Little mounting was observed in
the isolated females, and too little in the controls "to warrant
discussion".

Young (1957) looked at the effects of early social deprivation
on female guinea pigs. Female guinea pigs were spayed within five
days of birth and raised by their mothers, without siblings, until

they were 25 days old. They were then placed in individual cages until they were 150 days of age. When they were compared with spayed females reared in a social environment, it was found that the isolated females took longer to come into oestrus after injections, maintained lordosis for shorter periods of time, and showed less mounting behaviour.

The difference between Young's (1957) findings and those of Harper (1966) is possibly due to differences in experimental procedure. The females in the former study lordosed in response to the experimenter, whereas in the latter study a male guinea pig was used to elicit the response. Harper's (1966) results were reversed when lordosis was elicited by stroking by the experimenter, and Harper suggests that Young's (1957) findings may have been due to the isolates having experience with humans rather than to their having been prevented from interacting with conspecifics.

Harper (1966) concludes that the opportunity to interact with other guinea pigs is not a necessary condition for the development of approach or copulatory behaviour in either the male or the female guinea pig. With regard to the male this is supported by Coulon's (1972) data.

Harper's (1966) findings are in contrast with those of Valenstein et al (1955), Young (1957) and, to some extent, Gerall (1963) and Gerall (1965). The resulting picture, therefore, is not clear. It is possible that some factor of the experimental design might have contributed to the earlier findings. Valenstein et al (1955) limited their test periods to ten minutes on the assumption that the guinea pig will ejaculate within a few seconds to ten minutes (Young and Grunt, 1951). However, other workers have reported considerable variation in the sexual performance of the male guinea pig. Thus Avery (1925) writes that assumptions that a male will

copulate at the first opportunity should not be made, unless the "male in question has been thoroughly and recently tested with receptive females". Pearson (1970) reports that although the full pattern of behaviour plus ejaculation usually occurred in ten minutes it was sometimes more than this. Rood (1972) found some variation in guinea pigs' sexual behaviour. One male never ejaculated because he circled the female excitedly instead of mounting, and was chased away by the alpha male. It is also possible that the behaviour of the test females varied. The behaviour of the female is likely to affect that of the male (Young and Grunt,1951; Valenstein and Goy,1957). Rood (1972) reports that if a female does not promptly give lordosis the male may climb over her, may rump her, or crawl under her.

Thus, as has been suggested earlier in this section, a longer test period may have resulted in the isolated males copulating successfully. Louttit (1929) allowed considerably longer than ten minutes.

It is not known whether experience of the scent and sound of conspecifics is necessary for the organization of sexual behaviour. Harper's (1966) and Coulon's (1972) animals were not isolated from the auditory and olfactory stimuli of other guinea pigs. Harper (1966) points out that certain exogenous stimuli available to the infant guinea pig at a particular stage of development may constitute a necessary condition for the development or consolidation of social responses, and suggests that olfactory and auditory stimuli may serve to maintain social contact in some species either in addition to or in the absence of more direct contact. King (1956) concluded that the guinea pig's "chirping" call acted as a means of maintaining contact with conspecifics in a semi-natural environment.

It is clear that experience with conspecifics during infancy is not a necessary condition for guinea pigs to interact and to

mate successfully. It also seems likely that an animal which has had no previous contact with a conspecific can mate successfully. It is not known whether experience of the scent and sound of conspecifics is necessary for the organization of copulatory behaviour. It is clear also that critical periods for the development of sexual behaviour do not exist in the guinea pig.

It is not possible to explain why some isolated male guinea pigs fail to mate normally, although some suggestions have been made to account for these findings. Further, as Harper (1968) points out, there are "grounds for considering that conditions for the development of coital behaviour to be independent of those facilitating its expression". It is clearly essential that the testing situation is maximal for eliciting mating behaviour. Factors which may affect this are the test area itself and the behaviour of the female.

Although the majority of investigations into the effects of early experience on behaviour in the adult guinea pig would seem to be concerned with sexual behaviour, this is not always the case.

Berryman (1974) reports an interesting experiment which she carried out into the effects of isolation during infancy on the maternal behaviour of the adult female guinea pig. She hand-reared two female fuinea pigs in isolation for six months, when they were returned to the colony. They reared the young subsequently born to them with the same facility as did females which had been reared in the colony. Berryman (1974) points out that although her sample was small, she was convinced that differences between isolated and socially reared animals in maternal care are minimal.

Carter and Marr (1970) investigated the effect of rearing guinea pigs with litter mates characterized by an artificial odour on subsequent preference behaviour. The duration of exposure and age at which the animals were exposed to the odour was systematically varied. It was found that the longer the length of exposure to the odour, the more effective it was in producing a preference for the artificial odour. Also, the first days of life were found to be more sensitive to "olfactory imprinting" than later exposure periods. However, all groups of subjects tended to prefer the natural odour when tested at sixty days of age.

Beauchamp and Hess (1971) reared neonates with a chick, an adult female guinea pig, or the natural mother and siblings. They were then required to discriminate weekly between an unfamiliar chick and a guinea pig. For the first 3 weeks the subjects preferred the species with which they were reared. At 5-7 weeks the preference had disappeared even though the experimental animals continued to live with the chick, and by 10-17 weeks all subjects preferred the guinea pig.

If the initial preference shown during testing for the artificial odour and for the chicken occurred as a result of imprinting, it would be expected that the preference would be a permanent one. At least, this would be expected if one accepts Lorenz' (1937) characterization of imprinting: Beauchamp and Hess (1971) point out that this includes the hypothesis that the object to which the bird is imprinted may become the most potent releaser of some adult behaviour, such as sexual behaviour. This is clearly not so in the guinea pig. Thus Pettijohn (1979) suggests that

research shows that the early attachments of the guinea pig are not strong and do not last. Nagy and Misanin (1970) conclude that guinea pigs do not imprint on objects or other guinea pigs as do precocial birds. Instead they appear to develop preferences or attachments to objects to which they have been continually exposed. This has been reported in other mammals (Cairns, 1966), and fits with Shipley's (1963) description of the process of imprinting as a gradual one.

The findings that the attachments or preferences of the guinea pig do not persist, together with the evidence that critical periods do not exist in the guinea pig, suggest that imprinting does not occur in this species. However, this is not intended as a firm conclusion and Sluckin and Fullerton (1969) suggest that the term imprinting is retained with regard to the guinea pig. They point out that this does not involve an explanation of such attachment, but illustrates the similarity between such attachments in precocial mammals and precocial birds. Berryman (1974) suggests that the term imprinting is not a useful one as far as the guinea pig is concerned. Such terms as "attachment" or "preference behaviour" would seem to be more appropriate.

Finally, the work of Vince (1979) should perhaps be mentioned here. She investigated the effects of prenatal auditory stimulation on the response of young guinea pigs to a natural sound alien to guinea pigs. The prenatal stimulation was found to reduce the response of the young animals to the sounds in comparison with the responses of control animals. This is described more fully in the section on vocalization in the guinea pig.

Summary

It would seem that early isolation of the guinea pig may affect his behaviour as an adult. Although the data are conflicting, it is clear that critical periods do not exist for the development of, for example, sexual behaviour in the male guinea pig. There are less data concerning the female, but early isolation does not appear to have a marked effect.

Although the young guinea pig shows preference behaviour, the fact that this does not persist, in conjunction with the apparent lack of critical periods, suggests that imprinting does not occur in this species. Whether or not the term imprinting is used to describe the preference behaviour of the guinea pig would seem to depend on whether Lorenz' (1937) characterization is accepted as definitive.

Mother and young

During parturition other females sometimes sit with the female giving birth, and help to clean the membrane from the young. They are not aggressive at this time. Rood (1972) reports this of both C. porcellus and C. aperea.

The infant guinea pig is homeothermic soon after birth, and does not need to be kept warm (Berryman 1974). However, the mother is needed to stimulate eliminative behaviour in the infant guinea pigs which she does by licking the anal region of the young (King 1956).

The infant guinea pig is also dependent on milk for nourishment during the first four days of life (King 1956), although the young animals may nibble at food within a few hours of birth. Therefore the role of the mother in the first four days is to provide nourishment, and the necessary stimulation for elimination to occur.

King (1956) reports that ties between mother and young are strong. The mothers often stayed by their young when they were being weighed. At these times the mothers seemed solicitous of the young, running about "nervously" while the other animals ran away. However, this response was not immediate or well directed. In contrast Rood (1972) reports that C. porcellus mothers "typically ignored" their young when they were placed in a trap in the home pen, where they emitted a series of bubbling squeaks grading to whistles. This presumably is the same as the attention-seeking call (et-epilemetic) described by King (1956) who writes that the request for attention is well-developed in guinea pigs. The call appears first in the young when alone. The young may not whistle when the mother leaves them but will do so when hungry, or

when the mother comes near them. As the young grow and wander about they often give this call when in a strange place.

Kunkel and Kunkel (1964) report that care of the young is not pronounced. Females may reject the young of another, or treat it as their own. In large groups the young were mothered indiscriminately by all lactating females. Rood (1972) observed that although C. porcellus would suckle the young of another female, C. aperea females typically chased away the young of other females.

Female guinea pigs are especially likely to allow young other than their own to suckle in the first few days after parturition (Fullerton, Berryman and Porter, 1974). This occurs even though it has been shown that mother guinea pigs show a preference for their own young (Fullerton et al, 1974). Berryman (1974) suggests that the ability to suckle from another would enhance the chance of survival. Clearly this is dependent on a female permitting it.

Investigations have been carried out into the nature of the bond between mother and infant guinea pigs. Berryman (1974) found that lactating females were responsive to the calls of young other than their own. However, the mothers are able to recognise their own young. Thus Porter, Fullerton and Berryman (1973) studied maternal-young recognition in guinea pigs, and the role of olfactory cues in such recognition. Infant guinea pigs showed no preference, but the mother guinea pigs preferred their own litter to another of the same age. This suggested that while the mother is able to distinguish her own young, the young are not able to recognize their own mother. Porter et al (1973) report also that the females preferred an odour which had previously been applied to their own young rather than a

novel odour. They suggest, therefore, that it is the mother who is responsible for maternal-young interactions and that olfactory stimuli are important in maternal recognition of the young. Berryman (1974) has shown that female guinea pigs are able to recognize their young by distal cues but it is not known whether olfaction or vision is involved. She reports that evidence was not found suggesting that mother guinea pigs could distinguish their own young on the basis of voice.

Fullerton, Berryman and Porter (1974) demonstrated that preference for the female's own young continued to be shown even when the animals were permanently housed with another female and her litter. Female C. aperea distinguish between their own and the young of another female, and may respond aggressively to the latter (Rood, 1972).

Further to their earlier paper (Porter, Fullerton and Berryman, 1973), Fullerton, Berryman and Porter (1974) present data which indicate that the young guinea pigs are able to recognise their mother when they are close to her. Thus Fullerton et al (1974) found that while infant guinea pigs housed with their mother and another lactating female showed no preference for their mother in their initial approach behaviour after a period of separation, time analysis revealed that the young spent more time with their own mother than with the other lactating female. This preference was independent of the response of the mother to her young. Fullerton et al suggest, therefore, that the infant guinea pig may be able to recognize the mother by proximal cues only. Olfaction would seem to be a likely cue. Berryman (1974) reports that her data indicate that the infant guinea pig does not respond to the sight of the female; even

at a distance of 12 inches an infant may pass by the female.

Berryman (1974) points out that the vocalizations are extremely important in maintaining contact between mother and young. Kunkel and Kunkel (1964) report that the guinea pig mother is in constant vocal contact with her young. Berryman (1974) writes that the vocal behaviour of the female reflects a readiness to respond to the infants' calls. Seward and Seward (1940) investigated the strength of "maternal drive" as measured by the willingness of the mother to cross a barrier to reach her young. They found wide individual differences, but report that there was a general decline in readiness to cross the barrier over the three weeks post-partum. Berryman (1974) also reports data which indicate that the female's readiness to respond to her young declines. She found that locomotion and vocalization associated with the care of the young declined over the four weeks post-partum. However, the behaviour of the infants showed no evidence of a decline of interest in the mother. It seems likely that as the interest of the mother wanes, the young start to seek her out. Pettijohn (1979) found that time spent close to the mother declined over the two months post-partum suggesting that attachment weakens as the infant matures. This does not conflict with Berryman (1974) as she investigated the behaviour of the young over the first four weeks of life. Rood (1972) found that whistling in juvenile guinea pigs declined as they matured, and King (1956) reports that as the infant guinea pig matures it will follow adult guinea pigs other than its mother. Both these findings support the finding of Pettijohn (1979) that as young guinea pigs mature they become less attached to their mother.

Berryman and Fullerton (1976) investigated interactions between adult and young guinea pigs. It was found that young could distinguish adults by distal cues, and after a period of separation the infants preferred the mother to the other adult guinea pigs. Berryman and Fullerton suggest that the infants may recognize classes of animals at a distance, but that proximal cues are needed to distinguish individual animals; also that the infant guinea pig may play a more important role in mother-young interactions than had been thought.

Little has been said of the role of the male in relation to young guinea pigs. Although he is tolerant of the young (Blythe, 1962; Sole, 1969), there are no data which suggest that he is involved in caring for the young. Pettijohn (1977) reports that the males do not respond at all to the distress calls of the young. However, Sole (1969) reports that the male will permit the young to make physical contact, and it is clear from the work of Berryman and Fullerton (1976) that the male will permit the young to remain near him. There are also data which suggest that although the male is not involved in caring for the young his presence is nevertheless of importance with regard to the development of social behaviour. Thus Levinson, Buchanan and Willis (1979) observed guinea pigs from birth to 60 days in a colony containing no adult males. Levinson et al (1979) report that in contrast with their earlier study (Willis, Levinson and Buchanan, 1977) where the young were raised with other guinea pigs of all ages including adult males, the appearance of aggressive behaviour was delayed from weaning to about the onset of puberty. Sexual behaviour also showed some delay. Levinson et al (1979) conclude therefore that the presnce of adult males is

associated with the earlier appearance of social behaviours, and
suggest that enhanced behavioural development stems from the adult
males stimulating activity in others by their constant high levels
of interaction. Levinson et al also report some evidence of inhib-
ition of mounting when young are reared in the presence of males,
and suggest that this inhibition is due to the competitive nature
of mounting. Thus it would seem that the development of social
behaviour (sexual and aggressive) is affected by the presence of
adult males as well as by physiological factors.

In their (1976) investigation Berryman and Fullerton found that
although most interactions occurred between the young and their
mother, the young also interacted with other adult guinea pigs (a
male or non-lactating female). However, these interactions tended
to differ from those between the young and their mother. Suckling
and responses involving physical contact were directed mainly at
the mother, while "near responses" (near an adult but not in
physical contact) occurred more often in relation to the other
adult. The infants preferred the male guinea pig to the non-
lactating female. Berryman and Fullerton (1976) suggest that this
is perhaps due to the fact that the virgin females showed marked
avoidance of the young

Pettijohn (1978) studied social interactions in young guinea pigs
living with their parents, from birth to eight weeks. During the
first four weeks while still nursing the young the mother occasionally
attacked the father when he came close to the litter. Also during the
first four weeks the young directed most approach and following be-
haviour to the mother or littermates. In the second four weeks this

was also directed at the father, although at a lower rate than to the mother or littermates. Pettijohn (1979) tested infant guinea pigs to see how much time they would spend close to two familiar social objects, the mother and father, during the first two weeks of life. Significantly more time was spent with the mother; the reaction to the male seemed to be random.

Although the male is tolerant of the young the only behaviour he would seem to direct at the young is courtship. Kunkel and Kunkel (1964) report that the male is initially reserved towards the young; as they begin to mature they court them until they are sexually mature, but never try to copulate with them. Rood (1972) observed that adult male C. aperea rumba to young females at about two weeks of age, while adult male guinea pigs would rumba to both sexes when less than a week old. Pettijohn (1978) also reports that the father attempted some courtship with the young of both sexes during the eighth week, but states that this was minimal.

Summary

The bond between mother and young is loose, and weakens from early in life. The evidence suggests that the mother will begin to lose interest in the young before the young lose interest in her. However, as the young guinea pigs mature their interest in the mother wanes, and responses are directed towards other adult guinea pigs as well as to the mother.

The female is able to distinguish her own young, and the infant guinea pigs seem able to recognize their mother when they are close to her. Vocalization is important in maintaining contact between mother and young.

Female guinea pigs are generally amiable to the young of another female, and will often allow them to suckle. However, female <u>Cavia aperea</u> are aggressive to young other than their own.

The male guinea pig would not seem to have any specific role in the care of the young. However, his tolerant attitude towards the young, permitting young close to him, or to follow him, would seem to contribute to the cohesion of the group. Adult males court young of both sexes, but do not copulate with them. There is evidence which suggests that the presence of adult males is important in that it contributes to the development of sexual and aggressive behaviours. These would seem to be delayed in the absence of an adult male.

Vocalization in the guinea pig

The guinea pig is capable of producing a range of sounds.
These occur in a variety of situations. Allen (1904) is reported
by King (1956) as referring to the whistle given by young guinea
pigs as a hunger call. Loeb and Lathrop (1914) refer to the
"sociable clucking" of guinea pigs, also to a "complaining squeal".
Both Avery (1925) and Louttit (1927) report the occurrence of
vocalization in the guinea pig during courtship behaviour: Avery
describes a low guttural sound, Louttit a characteristic purring
note made by the male during conditions of sexual excitement.
While these two descriptions vary, they would seem to be referring
to the same vocalization as it occurs in the same context, and this
purring sound has been widely documented by investigators studying
sexual behaviour in the guinea pig. Kunkel and Kunkel (1964)
report the purring sound made during courtship behaviour. As
Berryman (1974) points out this vocalization has become associated
with sexual behaviour; in fact it occurs in situations other than
the sexual one.

Without a more exact means of defining a given vocalization,
the investigator will do so by describing the call verbally and
stating the context in which it is consistently found to occur.
This has made it difficult to obtain a coherent picture of
vocalization in the guinea pig. Guinea pigs emit a wide range
of sounds (King 1956; Kunkel and Kunkel 1964; Pearson 1970; Coulon, 1973;
Rood 1972; Berryman 1974). The names given to these calls vary
also, which further confuses the picture.

King (1956) reports that when guinea pigs are in a group they
occasionally utter a series of chirp-like sounds, and suggests

that this vocalization serves the function of keeping the colony together.   He also describes a whistle given by young guinea pigs, and refers to this as the et-epilemetic whistle, and says that it may be given at any time as a demand for attention, whether the animals are hungry or not.   Kunkel and Kunkel (1964) report that the guinea pig mother is in constant vocal contact with her young.   They suggest that the voice is the main means of contact between guinea pigs.

Pearson (1970) carried out an investigation into the vocalization of guinea pigs.   He recorded vocalizations on tape-recorders, and analysed them by means of sound spectrograms produced on a sonagraph.   Pearson grouped the guinea pig calls into two main types, although he points out that the grouping was somewhat arbitrary as there were intermediate sounds.   The calls were named as follows:

> clucks, chirrups, purrs, whimpers, warbles, whistles and squeals.

Pearson comments that during chirruping and purring the animal's body vibrates in synchrony with the staccato noise produced. It is likely that this was what Avery (1925) was referring to in his description of a fight when he reported that both animals "trembled greatly".

Pearson (1970) also attempted to study the causation of a given vocalisation in guinea pigs, and their response to vocalizations.   To do this he played tape-recordings to the animals but the initial response to chirrups, purrs and tooth-chattering (the latter not strictly vocal behaviour) was similar to that in response to any novel stimulus.   Pearson (1970) suggests

that there was a lack of fidelity in relaying the sounds.

Clucks, warbles and whistles resulted in locomotion and interest in the vicinity of the loudspeaker. The responses resembled those made during encounters between two amimals with visual stimuli obscured. Pearson (1970) concluded that vocalization is an attention-producing stimulus. Calls seem to be recognized in that they indicate the presence of another animal, and give rise to attempts to locate that animal.

Pearson (1970) investigated whistling, the sound described by King (1956) as attention-seeking. Pearson's animals readily learned to whistle in response to a sound which had originally caused them to chirrup (described as an alarm call), but which now signalled the arrival of food to two 24-hour deprived adults, milk to two infants, and a cage-mate to an animal isolated over-night. Thus Pearson (1970) concluded that whistling seemed to be related to anticipation rather than to any specific facet of the reward. Pearson's (1970) investigation represents the first attempt to do more than describe the calls and the situations in which they occur.

Coulon (1973) studied the vocal behaviour of the guinea pig. Coulon recorded the vocalizations and analyzed them by means of a sonagraph. He distinguished thirteen different sounds based on their physical structure and the behavioural situation in which they typically occur. Coulon presents sonagramsof the calls and gives their frequency (H_z) and durations; he also describes each sound, the posture of the animal emitting the sound, and the type of situation in which each vocalization is given. The thirteen sounds distinguished by Coulon, together with details of the

situation in which they occur, are given in Table 1.

Table 1

Vocalization	Situation in which the sound is given.
1. Signal de menace: entrechoquement des dents*	Occurs in agonistic situations. Prelude to combat. Implies conflict in vocaliser.
2. Cri de cohésion sociale	Given by all animals during exploration. Given by mothers in response to cries of new-born young.
3. Cri de quête (a) and sifflement d'appel	Both (a) and (b) emitted when animal separated from group. (a) often precedes (b).
4. Sifflement de détresse	Given by animals of both sexes when attacked by conspecific.
5. Trille d'inconfort	Given by alarmed animals, particularly males. (Was also recorded in animals with intestinal trouble, therefore in pain?)
6. Cri de cobaye saisi brusquement	Given when animals (mainly young ones) are picked up (gently) by a human.
7. Cri aigu de contact social	Given by guinea pig in response to actual physical contact. Can develop into 8.
8. Cri rhythmique de contact social	Suggests that an animal is slightly disturbed. Frequently given by females nosed by a male.
9. Cri de "dérangement"	Tends to follow 8. Given when animal is really annoyed. For example: non-receptive female importuned by a male; animal bitten and sheltering in a corner; given by animal trying to escape aversive stimulation.
10. Cri de jeune léché par la femelle	Given by young being licked by mother in ano-genital region.

* Coulon points out that tooth chattering is not a vocal sound.

Table 1 (continued)

11. Cri rythmique sexuel: purren,   Given by adult males during
                          purring   courting behaviour

12. Cri rythmique de tétée   Given by young suckling.
                                  Accompanied by lordosis and
                                  evagination of ano-genital
                                  region.

13. Cri rythmique d'immobil-   Given in response to a sudden
                isation   loud noise. Followed by pro-
                                  longed immobility.

Coulon also studied the response of animals to vocalizations. These findings are presented in Table 2. These data indicate that the calls evoke specific responses in the recepient.

Table 2

Signal emitted	Meaning of signal	Response of the recipient
Sifflement d'appel	Appel	Phonoréponse Orientation Exploration Attraction
Cri rythmique sexuel	Sexualité	Phonoréponse sous forme de signal de menace des mâles dominants
Signal de menace	Agressivité	Phonoréponse des immobilite des femelles
Cri de cohésion sociale	Cohésion sociale	Phonoréponse Orientation Attraction Emission du cri d'appel

Coulon (1973) suggests that there are continuing series of vocalizations which correspond with gradual modification of the initial stimulation (for example, Cri aigu de contact social, cri rythmique de contact social, and cri de "dérangement").

Coulon writes that the calls provide a good picture of the motivational status of the vocalizer. Some calls, suggests Coulon, seem to convey specific information; they convey the sexual and hierarchic relationships between guinea pigs, and can contribute to the structure and maintenance of the social group.

Berryman (1974)*conducted a detailed investigation into vocalization in guinea pigs. Berryman recorded samples of vocalizations, analysed them by means of a sonagraph, and classified them according to their physical structure. She points out that the advantage of this is that it avoids the problem of defining a call in terms of its function. Each call occurs in a wide variety of situations, but as has been indicated, calls have tended to become associated with a given behavioural situation.

Berryman (1974) observed the behaviour of the guinea pig in a wide variety of situations, and the vocalizations emitted were recorded. Eleven basic calls were identified. She describes them in detail providing the necessary information for other workers to identify the calls, including the frequency (H_z) and duration of the calls. The postures associated with the calls are also described, together with details of the situations in which they are likely to occur. Berryman (1974) does not include tooth-chattering in her list of eleven vocalizations. She also makes essentially the same point as Pearson (1970) that the calls are not entirely discrete, but form part of a continuum. At points along the continuum calls tend to occur more often. It is these

* see also Berryman, 1976b.

clumps which have been defined. The eleven calls defined by
Berryman are:

> chut, chutter, whine, low whistle, whistle, squeal,
> scream, purr, drrr, chirrup and tweet.

Berryman (1974) points out that the whistle is not really a
whistle but that she has retained the terminology because of its
wide usage. She found no evidence of ultrasounds in the guinea
pig.

The definition of the calls is followed by a detailed exam-
ination of their occurrence. The sort of situations where
vocalization occurs include separation, greeting, contact seeking,
sexual encounters, aggressive encounters, mother-young inter-
actions, disturbance and pain.

Berryman (1974) is particularly concerned with the vocalizations
of mother and infant guinea pigs. Infants appeared to respond to
various kinds of call of adult guinea pigs in a way different
from their response to unfamiliar tones. It was found that vocal-
ization in lactating females was increased by the presence of
infants' calls. Exploratory behaviour was directed to the source
of the sound. Berryman (1974) suggests that audition may be the
significant modality for keeping animals in contact with one
another.

Vocalizations in mothers and infants were found to change over
the four weeks post partum. The females' vocalizations generally
decreased, while infant calls remained stable or increased. Calls
were associated with particular forms of behaviour in this context.
After separation females greeted the young with the chut, and
infants purred as they suckled from the mother. Berryman (1974)

suggests that the calls may be functionally classified as follows:

a. Increasing physical proximity;   purr
    contentment   tweet (only occurs
                                          in the young)

b. Greeting; proximity maintaining   chut

c. Proximity regaining   low whistle
                                       whistle

d. Distress calls   chutter
                                       whine

                                       squeal ⎫
                                       scream ⎭ injury

e. Alarm calls   drrr
                                       (possibly the chirrup)

Berryman (1974) concludes that "infant sounds are useful in keeping mother and infant animals together, and sounds appear to be of importance in enabling females to locate young". Although no evidence was found suggesting that female guinea pigs could distinguish their own young by voice, it seemed that vocalization is important in initiating searching for infants.

The calls of the young show a marked similarity to those of adults. Berryman (1974) comments that this is surprising: in altricial species which have been studied the calls of the infants are specific and unlike those of their parents. However, this specificity is possibly not so necessary in the guinea pig which requires considerably less maternal care.

Rood (1972) reported that the guinea pigs in his study were not heard to emit chirps, a series of which are emitted by C.aperea in response to a possible predator. It would seem possible that the grunt mentioned by Rood (1972) is the same as the "low pitched rumble or purr" described by King (1956) in response to a strange

noise; also   the "chirrup" of Pearson (1970) which he describes as commonly given in response to any sudden or unusual sound; or again, Berryman's (1974) drrr. The Table on page 75 shows those calls given different names by different workers, which are in fact equivalent.

If Cavia aperea is the ancestral species or closely related to C. porcellus then it would seem as though domestication has resulted in a greater degree of vocalization. This might imply that, to some extent, vocalization is of less relevance to the social life of this species than the range and complex nature of the calls suggest.

There is evidence that the unborn guinea pig can hear the calls of the adults. Rawdon-Smith, Carmichael and Wellman (1938) secured a cochlea electrical response in a fifty-two day old foetus.

Vince (1979) investigated the effect of prenatal auditory stimulation. The heart rate was used in addition to observed responses. Pregnant guinea pigs were stimulated with a recording of a natural sound alien to the guinea pigs, namely the feeding call of the bantam hen, together with the feeding calls of the chicks. This sound pattern has been shown to result in startle, flight and /or freezing and a slowing of the heart rate in adult guinea pigs. Young guinea pigs which had been stimulated before birth with these sounds and unstimulated controls were tested with a series of the sounds. Changes in the heart rate indicated that the prenatally stimulated animals responded less to the alien sounds then did the controls. Re-testing of the controls with the stimulus resulted in their responses diminishing over the five test days. Vince (1979) reports that the behaviour of the guinea

Table 3

Berryman 1974	Pearson 1970	Rood 1972	King 1956
chut	cluck	grunt?	
chutter		bubbly squeaks	chirplike sounds
whine	warble		
low whistle	whimper		
whistle	whistle	whistle	whistle
tweet			high-pitched series of squeaks
squeal	squeal	squeal	
scream			
drrr	chirrup	grunt?	low-pitched rumble
purr	purr	rumble	
chirrup		chirp?	
teeth chatter	teeth chatter	tooth chatter	tooth chatter

Based on Berryman, 1974.

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pigs indicates that bantam calls suppress vocalising in the guinea pig, whereas guinea pig calls tend to increase it.

Vince (1979) concludes that if the response of the prenatally stimulated animals had waned before birth, then it seems that the external sound environment of the foetus may affect the behaviour of the neonate. Thus if the young adapt to naturally occurring background sounds they will be relatively unaffected by them and will be more likely to respond to cues involved in establishing bonds between mother and young.

Vocalization is clearly of importance in maintaining the

relationship between mother and young. It is further mentioned in the section concerned with the relationship between mother and infant guinea pigs.

Summary

The guinea pig produces a wide range of sounds, which can be divided into eleven basic sounds (Berryman, 1974) or into thirteen sounds, including tooth-chattering (Coulon, 1973).

The calls are possibly of importance in social relationships between the animals, particularly between mother and young, and one call would seem to function as an alarm call. The function of some calls is not clear, although the situations in which they occur are well-documented, and the calls indicate the motivational status of the vocalizer. It is possible that specific information is communicated by some calls, and vocalization may be of importance in maintaining group cohesion.

The guinea pig is considerably more vocal than Cavia aperea, and it is possible that the greater vocalization in the guinea pig is a result of domestication.

Naturalistic Studies

Two investigations will be described. They provide a great deal of information about the guinea pig which will be drawn on in this investigation.

That of King (1956) investigates the behaviour of the guinea pig under semi-natural conditions. Rood (1972) studied the ecology and behaviour of three genera of Caviinae in Argentina for two and a half years. One of these is Cavia aperea * which Rood and Weir (1970) suggest might be the ancestral species of Cavia porcellus, the guinea pig. By comparing the behaviour of the wild and domestic species, C. aperea and C. porcellus respectively, Rood (1972) intended to ascertain the possible effects of domestication. The study was enlarged to include the two other genera. Rood compared the behaviour and social organization of all three genera in order to ascertain the evolution of social behaviour in the Caviinae. Rood also studied C. aperea x C. porcellus hybrids.

The purpose of King's (1956) study was to reveal the behaviour of the genus Cavia under natural conditions. King points out that the social behaviour of a species may be modified by domestication. Patterns of social behaviour undergo changes due to artificial selection and disuse. Thus 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. With regard to Cavia porcellus, King suggests that the conditions imposed by domestication probably enhance the survival of social tolerance while having little effect on other social traits. The fact that there is no close selection

* The other genera were Microcavia australis and Galea musteloides.

for social behaviour in the guinea pig during its domestication should ensure that many of the social characteristics of its progenitors are preserved. King (1956) claims that in a semi-natural environment these basic patterns of social behaviour should be shown by the domestic guinea pig, and may be comparable to a closely related species. This point is important to the present investigation which is concerned with interpreting experimental data in the light of the natural environment, and the behaviour of the free living ancestral species. The behaviour of the domestic guinea pig in a semi-natural environment is also likely to be helpful in assessing the data obtained in the laboratory.

It is of interest to compare Rood's (1972) work on C. aperea with both the C. porcellus in his study, and the C. porcellus in King's (1956) study. If King's point that domestication is most likely to enhance social tolerance while having little effect on other social traits is correct, then one would anticipate that this would reveal itself in lower levels of agonistic behaviour in the guinea pig, while the remaining patterns of behaviour are much the same. If C. aperea is the ancestral species one would expect to find considerable similarities in behaviour between the two species.

The semi-natural environment used by King (1956) consisted of a 2,500 foot square area of open field with four huts in each corner. Supplementary food was available for the animals.

The animals studied consisted of a male and two pregnant females of each of three strains placed in three of the huts. All the descendants of these nine animals were included in the data. These were collected for a year, although most of the data presented

by King were obtained during the first four months.   Observations
were initially made at intervals throughout the day.   Later they
were made at 9 a.m. and at 4 p.m.

In Rood's Argentine study Cavia aperea were observed in field
study areas and in outdoor pens.   In addition colonies of guinea
pigs and of C. aperea C. porcellus hybrids were maintained in the
pens.   Observations of individually marked animals in field study
areas were made with binoculars from a car at a distance of
approximately 20 metres.   Field notes were taken by hand.   The
animals in the pens were given commercial rabbit pellets and oats
and water constantly.   A selection of fresh food was provided
daily.   Shelters were provided in each pen.

Rood obtained two types of data: "colony watches", where the
entire colony was observed, and "individual watches" where the
interactions of one individual were recorded.   The colony watches
were to determine dominance hierarchies and relationships, to note
seasonal changes in social behaviour, and organisation, and to
obtain quantitative data on specific behaviour patterns.

The individual watches provided more accurate data on behaviour
patterns and social interactions in order to compare species.
Individual animals were observed and all their social interactions
were tape-recorded and transcribed.   The animals were observed
continuously, thus an accurate record of all the encounters and
interactions of the individual being watched was obtained.

This brief outline of the scope of Rood's study shows what
a very detailed and thorough investigation it was.   It has provided
a considerable amount of information concerning both the three

wild species studied and the domestic guinea pig. The findings

obtained by King (1956) and by Rood (1972) will not be discussed

here as their work will be referred to on several occasions during

the forthcoming chapters.

However, a brief indication of their conclusions will be

given, also some information concerning the general activity of

C. aperea and C. porcellus. This is relevant to the design of

experiments carried out in the laboratory.

The daily activity of the wild and domestic species was very

similar. Thus King found that daily activity in the guinea pigs

seemed to be governed partly by temperature and intensity of

sunlight. During Summer they were inactive during the heat of

midday. During cloudy days they were active at intervals throughout

the day, and during Winter activity increased at midday and at

twilight. They were not active at night. King described them

as predominantly crepuscular.

Similarly, the sun appeared to inhibit activity in Cavia aperea.

They were seen more on cloudy than on sunny days. They were never

seen to be active between 10.00 and 16.00 hours in March to January

(Summer). In August occasional activity was seen throughout the

day, probably due to the colder temperatures. Thus both the wild

and domestic species seem to avoid sunshine. Both species tend

to be crepuscular.

Nicholls (1922) reports that the guinea pig is active for as

much as 90 per cent of the day, and has no diurnal or nocturnal

rhythm. The guinea pigs divide time into continuous and inter-

mittent activity. No tendency was found for inactivity at the

same time of day, and Nicholls writes that extensive enquiry among

laboratory workers revealed that none had ever seen a guinea pig
sleep.   Pellet and Béraud (1967) report that the guinea pig was
active for 72 per cent of the day and that no diurnal or nocturnal
rhythm was present.   They write that polyphasism is the dominant
characteristic of the activity-rest rhythm of the guinea pig.
It is possible that these reports are due in part to the artificial
conditions in which laboratory animals are maintained.   The
variation of temperature of the natural environment is excluded
from the laboratory environment.   It would seem to be certain that
significant changes in temperature would affect the behaviour of
the animals.   Nicholls (1922) found a decided decrease in activity
associated with an increase in temperature.   In a natural or semi-
natural environment therefore the guinea pig tends to be crepuscular,
and avoids high temperatures.   The artificial day-night cycle of
the laboratory does not provide the conditions for this rhythm to
develop.   However, the fact that the guinea pig is basically a
crepuscular animal should be taken into account when carrying
out experimental investigations, both with regard to the time of
day, and to the level of lighting.

Both C. aperea and C. porcellus make runways through grass.
Animals of both species appear to feed at the same time.   Also,
both species often feed together in groups.   King reports groups
of from four to seven, and Rood, groups of five to nine animals.
Aggression was rare in feeding groups.

Both species show similar behaviour in response to danger.
C. aperea frequently interrupts feeding to dash to the nearest
cover.   They typically dashed to cover in response to bird alarm
calls, and an alarmed C. aperea will freeze at the edge of cover.

A potential predator is sometimes allowed within a few metres before the animal finally disappears. The guinea pigs behave in a similar way. King writes that they show both escape and freezing behaviour when startled.

King found little contactual behaviour in C. porcellus, although Rood observed female guinea pigs sitting side by side nibbling one anothers pelage. This was rare in C. aperea.

Rood writes that populations of cavies are characterized by a high rate of turnover, thus relationships between individuals tend to be transitory. Permanent social binds are not formed: cooperation is minimal and social groups are "typically non-cohesive, often consisting of nothing more than aggregations" about a food source. However, Rood goes on to say that social attraction may contribute to such aggregations since cavies, particularly C. aperea, tend to feed in groups even when food resources appear to be evenly distributed.

There is additional data to suggest that the groupings are more than a mere aggregation. Thus guinea pigs tend to give the et-epilemetic call (King 1956) when separated from conspecifics. Burnstein and Wolff (1967) found it necessary to use a second guinea pig in conjunction with reinforcement in an operant conditioning situation to help induce vocalization in the guinea pig, and Pearson (1970) reports that guinea pigs are less likely to freeze when they are in the presence of conspecifics.

As has been indicated in those pages discussing agonistic behaviour in the guinea pig, C.aperea is considerably more aggressive than C. porcellus. This supports King's (1956) suggestion that domestication is likely to result in greater social tolerance.

Aggression directed towards older juveniles and adolescents in the natural environment is adaptive in that it aids dispersal.

Rood (1972) concludes that if C. aperea is, or closely resembles the ancestral species of the guinea pig, it appears that domestication has resulted in a trend towards larger animals, longer gestation, greater tolerance of conspecifics, more frequently expressed overt sexual behaviour, and a lower threshold for vocalizations. Rood points out that many of these changes would be expected if those who originally domesticated the guinea pig for food selected the largest animals for breeding and eliminated aggressive troublemakers. The changes in vocalizations and sexual behaviour may be due to the lack of those pressures which operate in nature. Both vocalizations and sexual behaviour directed to animals other than receptive females may render the cavy conspicuous and be selected against in the wild state.

A table which summarises the difference in the behaviour of C. aperea and of C. porcellus can be seen on page 84.

Table 2

	Cavia aperea	C. porcellus
Agonistic behaviour		
Male agression to strangers	To males & occasionally females	To males only
Female aggression to strangers	To females & occasionally males	Not observed
Female dominance hierarchy	Stable	Undefined
Female high intensity aggression to young	Common	Not observed
Female defensive aggression to males	Common	Occasional
Sexual behaviour		
Rumba to females	Less common; Shorter duration	Common
Rumba to juvenile males	Not observed	Common
Males mount non-oestrus females	Not observed	Occasional
Homosexual mounting	Not observed	Occasional
Naso-anal licking	Rare	Common
Contactual-neutral behaviour		
Interaction between females	Rare	Common
Social grooming	Rare	Occasional
Nursing	Typically nurse own young only	Indiscriminate

Summary of behaviour differences between Cavia aperea and Cavia porcellus (based on Rood, 1972)

Conclusion

Although the guinea pig has been domesticated for a very long time it is possible that its social behaviour has not changed greatly during domestication. Cavia aperea, a wild species found in Argentina, is either the ancestral species of, or very closely related to, the guinea pig.

The review reveals that the guinea pig is now used in several areas of research; it is of particular value in certain fields of investigation. It does, however, present problems to the investigator.

With regard to the guinea pig itself interest in its behaviour has grown. While early investigations into its social behaviour seemed to concentrate mainly on its sexual activities, in more recent years several areas of social behaviour in the guinea pig have been investigated. The possibility that imprinting occurs in this species has been studied, also the effects of early environment on adult behaviour. Mother-young relationships have been examined.

Naturalistic and laboratory studies have yielded much data concerning the behaviour of guinea pigs in paired encounters or in groups. There is a considerable degree of agreement concerning some aspects of guinea pig behaviour, while there is some disagreement over others, but there is no doubt that the male guinea pig is aggressive and that dominance hierarchies are formed. It is also clear that the social behaviour of the guinea pig is complex.

Methods of investigating behaviour vary. It is possible that in certain cases the methodology has affected the results,

and is responsible for conflicting reports.

Research into the vocal behaviour of the guinea pig reveals a complex range of sounds, of which some appear to be of considerable importance to the guinea pig, especially in mother-young interactions. The function of some of the calls is not clear.

It would seem likely that, as in other rodents, olfaction is of communicatory importance to the guinea pig.   Since 1971-1972 when the work for this investigation was carried out, the amount of information concerning olfactory stimuli and their relation to social behaviour in the guinea pig has grown considerably.   This is in large part due to the work of G. K. Beauchamp and his associates.   This work will be described in relation to the present investigation.   Olfaction, therefore, has not been included in the Review of the Literature.   To have done so would have involved a great deal of repetition.

Chapter 3.

The Research Topic

Introduction

This chapter explains why this particular research topic came to be chosen.   A period spent observing adult male guinea pigs is outlined.   The line of enquiry suggested by the observations and a preliminary attempt to investigate this is described.   It is concluded that this attempt be repeated using a more rigorous experimental design and more suitable apparatus.

The chapter concludes with a glossary of the behaviour noted during the period of observation.

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Chapter 3

The present study evolved out of a period of observation of ten male guinea pigs. Initially it had been intended to carry out a rather different investigation from the present one. There were inevitable delays before this work could begin, and this waiting time was used to study the literature and to observe the day to day behaviour of the animals. As Hutt and Hutt (1970) write: "The behavioural scientist beginning his study of any species, requires a preparatory period of acquaintance with the animal of study. This should be true equally of the observer of cockroaches and children ... only by intimate and sustained contact with his subjects can the lone investigator hope to evolve a consistent and reliable activity vocabulary".

A brief description will be given of the sort of observations that were made.

The animals were kept in plastic cages with metal tops. Each animal was given a clean cage twice weekly. It was observed that when the animals were placed into the clean cage the guinea pigs would drag the ano-genital area over the fresh bedding. This might happen two or three times on being placed into the clean cage. The animals were occasionally seen to do this during their normal daily activity, in the absence of the stimulus of a clean cage.

In order to give an animal a clean cage, both the clean and the soiled cages were placed side by side on the floor. The animal was lifted from the one into the other, and the metal top was replaced onto the clean base. With the top removed the

cage was only seven inches deep and the guinea pigs had no diffi-
culty in jumping out of the base of the cage, and onto the floor.
The initial hesitancy of their movements soon disappeared, and
the guinea pigs would explore the floor, sniffing and biting at
any objects they came across.

They also spent a considerable amount of time sniffing and
licking at the floor, and frequently showed anogenital dragging
and defaecation. The animals were generally vocal, and the hair
at the back of the neck was raised.

The behaviour was noted carefully and shorthand forms devised
to facilitate recording. These were kept as simple as possible,
and most of them were obvious abbreviations, such as D for defae-
cation. Some were not so obvious: for example, it was noted that
when the guinea pigs dragged the anogenital area along the ground
they occasionally deposited a few drops of urine. The shorthand
sign which was devised for this is $\cup$ whereas U denotes elimin-
ative urination. Descriptions of the behaviour and the shorthand
forms are given at the end of this chapter.

The incidence of defaecation varied. The fact that defaecation
occurred was considered to be of interest, as novelty tends to
inhibit defaecation in the guinea pig (Tobach and Gold, 1965;
Pearson, 1970; personal observation). It seemed that an increase
in the occurrence of defaecation correlated with anogenital dragging
and the perseverative sniffing and licking (or s-nosing *). This in
turn seemed to increase according to the state of the floor: the
floor was washed twice a week, so by noting when it was washed it
was possible to compare the behaviour of the animals on a
washed floor with their behaviour on an unwashed floor.

Although no clear pattern emerged it seemed

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*The rationale for this terminology is discussed in Chapter 5, pp.
146-147

that the animals were reacting to the smell of the other guinea
pigs which they could detect on the floor.   This supposition
was supported by the fact that on one occasion a guinea pig jumped
into an empty cage recently vacated by another guinea pig in
which fresh carrot had been placed.   The animal ignored the
carrot and showed a high rate of both ano-genital dragging and
s-nosing behaviour in the conspecific's cage.   It seemed as though
the animals were scent-marking, thus conveying information to con-
specifics by chemical means, in response to the odour of another
male.   The s-nosing was stereotyped and suggested intense interest
in conspecific odour.   It was decided, therefore, to investigate
the hypothesis that ano-genital dragging and s-nosing will occur
in response to the smell of a male conspecific;   also that the
rate of defaecation will increase in response to the odour in
comparison with no odour.

This study will be mentioned briefly.*   It is not included
in the experimental section as the experimental data are not
available.   It is included at all because in conjunction with a
subsequent experiment (I, Chapter 5), it demonstrates the difficulty
of adequately controlling odour, and was influential in the design
of the apparatus used in the present investigation.

Ten male guinea pigs were used, of the tortoiseshell and white
variety.   They were kept in the animal room where the temperature
was maintained at 68°F.   The animals were kept on a twelve hour
day/night cycle and food and water was provided ad libitum.
Carrots were given twice daily.

* The findings of this study formed part of a paper given to the
  Association for the Study of Animal Behaviour in November, 1972.

The apparatus consisted of a round open field constructed of plywood and hardboard; the hardboard wall was fixed to the plywood base by means of wooden struts. The field was painted two shades of flat grey, the base being darker than the wall. The field was 31 inches in diameter, with 9 inch high walls. The paint was water-resistant so that it could be washed between subjects. It was placed in the animal room, against the wall opposite the guinea pig cages.

The counterbalanced design was used with both animals taking both conditions. Thus the animals were divided into two groups, a and b.

	Trial 1	Trial 2
Group a	Experimental condition	Control condition
Group b	Control condition	Experimental condition.

Experimental condition: Odour of conspecific present

Control condition: Open field washed to remove odour

The odour was provided by the predecessor animal undergoing the Control condition. Each trial lasted two minutes and was timed with a stopwatch.

Each animal was placed into the open field by the experimenter, and at the end of the trial was returned to its cage. Faecal pellets were removed, and the second animal was placed into the field. At the conclusion of the two trials the field was thoroughly cleaned to remove the odour in preparation for the next odour-free trial. It was first cleaned with absorbent paper, thoroughly washed with detergent, rinsed, and allowed to dry in the open air for several hours.

All subjects showed the same range of behaviour.   Ano-genital
dragging, vocalisation, s-nosing, sniffing, defaecation, pilo-
erection and locomotion.   There was no real difference between the
control and experimental conditions.   In both the experimental
and control situations perseverative sniffing and licking (s-nosing)
was directed at the base of the field.

These findings appeared to indicate either that the hypothesis
was false, of that the experiment was inadequately controlled.   A
possible variable affecting these results was the fact that the
investigation had been carried out in the animal room, within
scent and sound of the conspecifics.

However, the perseverative sniffing and licking at the base
of the field suggested there was an odour there which the animals
could detect.   It seemed at this stage incumbent upon the
experimenter either to abandon this line of investigation, or
to assume that the experimental variable had not been adequately
controlled, and to try again, using apparatus which it was
possible to clean adequately, leaving no trace of the odour of
male guinea pigs.   It had seemed at the time that the cleansing
of the open field had been adequate;   certainly considerable care
had been given to this.   However, if the lack of a difference
between the control and experimental situations was due to the
persistence of odour left by previous subjects then the cleaning
had failed in its object.   It seemed possible that the water-
resistant paint over plywood was an unsuitable substance for
this type of experiment in that it absorbed odour.   Thus it
would be necessary to use material which would not retain odour,

and to design the apparatus in such a way as to permit its thorough cleansing.

It would also be necessary to carry out the experiment in a separate room, where no evidence of conspecifics would be present.

A look at the relevant literature suggests that the majority of investigators have not encountered this problem of residual odour affecting the behaviour of a subsequent animal, nor that they have had difficulty in removing such an odour. The cleaning of apparatus seems generally to be cursory or inadequate. Thus Topping and Cole (1969) use a damp sponge to clean their apparatus. Glickman and Hartz (1964) cleared the floor of the apparatus of debris between subjects. Halliday (1967) used a damp cloth smelling of disinfectant to clean his maze.

Some investigators take more care. Satinder (1969) writes that the floor of the open field was cleaned and washed twice with clean water and dried with a sponge. Whittier and McReynolds (1965) discuss the problem of residual odour. They carried out two experiments designed to investigate the effects of odour trails left in apparatus by one mouse might have on the behaviour of a subsequent mouse. They found that a significant proportion of mice spent more time on that half of the enclosure which had held a predecessor mouse. This was not linked to the sex of predecessor or subject. A second experiment was carried out to determine the effectiveness of washing the apparatus with clear water to remove odour cues. This was not found to be effective.

In their review of the olfactory control of behaviour Schultz and Tapp (1973) emphasize the importance of olfactory stimuli on the behaviour of rodents. They write that to "say that odor exists as simply another cue to be controlled grossly understates

the situation.   Odor removal techniques will have to be vastly
improved from the current state of the art".

There is variation in the methods used to clean apparatus.
Thus while many experimenters use water or a damp sponge or cloth,
Thiessen, Blum and Lindzey (1969) use a 70% Ethanol solution.

While deciding on the form of apparatus which would permit
adequate cleansing, the use of alcohol as a cleaning substance was
considered.   It was concluded that to clean the apparatus by
wiping it with cotton wool soaked in Ethanol might result in
partially dissolving the substance that the experimenter was
trying to remove, and to spread it over the area, rather than
actually to remove it.

There was yet another factor to be taken into account in
designing the experiments.   Guinea pigs maintained in natural-
istic conditions are crepuscular (King, 1956: Rood, 1972).
Although Nicholls (1922) and Pellet and Béraud (1967) report that
there is no nocturnal or diurnal rhythm in the guinea pig, it
would seem advisable to assume that the species is crepuscular
when determining the most suitable time of day in which to carry
out the experiments.   Pearson (1970) found that it was possible
to reduce the immobility response by reducing the level of illu-
mination.   The animals studied by King (1956) and Rood (1972)
avoided bright sunlight.

Glossary of items of Guinea Pig behaviour relevant
to the open field experiments of the present
investigation*
  The Shorthand symbol is given in brackets.

LOCOMOTION This includes any movement which moves the animal by
            at least half a body length from its original position.
            When the animal is walking the ventral surface may be
            touching the ground.   This behaviour does not have a
            shorthand symbol.

SNIFFING   This includes movements of the snout over, but not
            touching, any surface; also movements of the snout
            in the air, accompanied by movements of the external
            naries. (S)

S-NOSING   Perseverative sniffing and licking of an area.   It
            is clearly distinguishable from sniffing.   Beauchamp
            (1973) describes it as "very stereotyped head bobbing
            behaviour".   Pearson (1970) terms it "nodding
            movements", and Berryman (1974) as "nodding", "rhythmic
            and stereotyped movements of the snout over a surface.
            Often seen where an animal is exploring the urine or
            faeces of another animal." (N)

DEFAECATION   Deposition of faecal pellets (D)

ANO-GENITAL   Dragging the ano-genital area along the ground for
DRAGGING approximately 2 to 18 inches.   The back legs are
            flexed and the perineal pouch everted thus spreading
            secretion from the perineal glands.   Possibly includes
            secretion from the supracaudal gland which is situated
            above the anus.   This behaviour has also been described
            as "rump dragging" (Berryman, 1970).   (T)

URINATION Dragging the ano-genital area along the ground as described
ASSOCIATED above, but including a line of drops of urine.   (ᴜ-)
WITH
DRAGGING

URINATION The animal urinates, motionless, with the ano-genital
            region thrust out to the rear. (U)

PILO-ERECTION   The hair in the region around the neck is raised.
            It is similar in appearance to the raised hackles of
            a dog. (H)

* These descriptions are based on the period of observation described
   in Chapter 3, and the descriptions of Pearson (1970) and Berryman
                                                              (1974)

FREEZING*   The animal is motionless.   The eyes are wide open, and respiration is reduced so that respiratory movements are barely observable, except for small movements of the nostrils.   This may last from a few seconds to many minutes. (F)

PAUSING*   The animal remains still, but is not motionless.   Small movements of the head or feet may occur, and there may be some sniffing of the air.   It may last for many minutes. (P)

GROOMING   Stereotyped movements of the paws over the snout, head and ears, sides and back of the animal.   They are returned to the mouth where they are licked.   This category also includes licking and nibbling of the fur. (G)

TOOTH   A horizontal movement of the lower jaw against the upper
CHATTERING   jaw so that the teeth scrape over one another. (Ch)

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*   Despite the definition of freezing and pausing, the one behaviour seems at times to grade into the other, and it is not possible to determine whether the animal is freezing or not.   These two behaviours will, therefore, be combined as immobility.

Chapter 4

Experimental Design

Introduction

Chapter 4 gives details of the apparatus used in the majority
of experiments which form the subject matter of this account.
The method of recording data is then discussed and consideration
is given to sample size and experimental design.

General information is given concerning the experimental
procedure and the subjects of the experiments.   Those details
relevant only to some of the experiments are given in the
appropriate chapters.

Chapter 4

Apparatus

This consists of a square open field and was used throughout
the entire series of experiments, with minor modifications which
will be described in the relevant chapters.

The most important factor governing the design of the field
was the necessity of being able to remove all olfactory stimuli
used in the experiments.   This has been discussed in Chapter 3.
This determined both the materials used in the building of the
field, and   the design of the field.   Also governing the
design of the field was the need to allow the animals sufficient
space in which to move around freely, and yet not so large as to
facilitate the immobility response.

As the experiments are concerned with the effects of odour on
behaviour, it is clearly necessary to be able to remove all trace
of odour from the apparatus.   As has been indicated in Chapter 3
this is not easy.   The first requirement is a material which does
not absorb odours, and for this reason perspex was chosen.
Secondly, it is necessary that the apparatus can be thoroughly
cleaned and to this end a field was designed that could be readily
taken apart.   A drawing of the open field can be seen on page 100.

The open field was constructed of opaque grey perspex.   As this
is shiny the walls were buffed so as to eliminate reflection.   The
field was 3 feet 3 inches square, with 12 inch high walls.   The
four walls were not fixed but held together by two hooks and eyes
in each corner.   The hooks and eyes were mounted on wood nailed
to the perspex.   The wood was on the outside walls and did not reach
the base, and was not therefore in a position where it would be

DIAGRAM 1
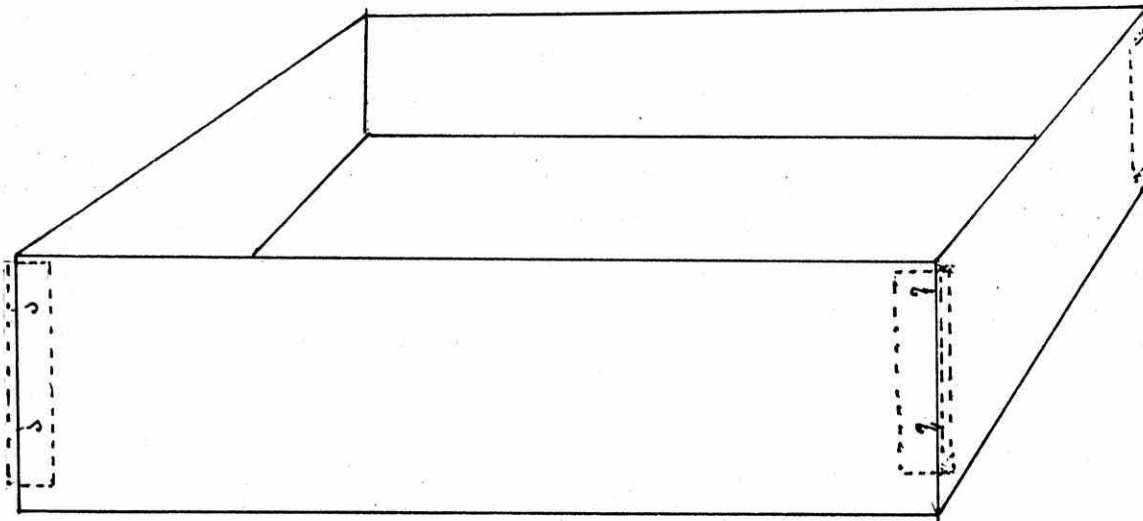
The open field

contaminated by the olfactory stimuli used in the experiments.

Once assembled, the four walls of the field were self-supporting. They stood on a formica base. As with perspex this is non-absorbent and readily cleaned. As the formica was slippery it was covered with a sheet of white cartridge paper.

The apparatus was situated in a square tent-like structure, 3 feet 6 inches square and 4 feet high. (See diagram on page 102). This tent consisted of a square wooden frame attached to the wall, covered with parachute nylon* . It was possible for the side curtain to be in an open or closed position, and the covering could be removed easily. The tent served three purposes:

    i.   It provided a uniform extra-field environment.
    ii.   It helped to diffuse the light over the field.
   iii. It concealed the experimenter from the animals.

After each experimental session the paper was discarded and the apparatus was washed. Each portion of the open field, including the formica base, were treated as follows:

1. Scrubbed with hot water amd a deodorant soap.
2. Rinsed in clear water.
3. Washed in the detergent customarily used for cleaning the home cages.
4. Rinsed.
5. Dried.

After use the cloths used for washing and drying were washed in the detergent and then rinsed. They were replaced regularly. During the cleaning procedure rubber gloves were worn to avoid contaminating the apparatus, also a clean overall kept especially for this purpose.

The above process may sound arduous, but was adopted as a

* parachute nylon was ideal for this purpose as it is sufficiently opaque to both conceal the experimenter and diffuse the light, while at the same time permitting sufficient light to permeate through to the open field.

DIAGRAM 2

wooden struts attached
to wall

wooden frame

double
layer of
nylon

parachute nylon
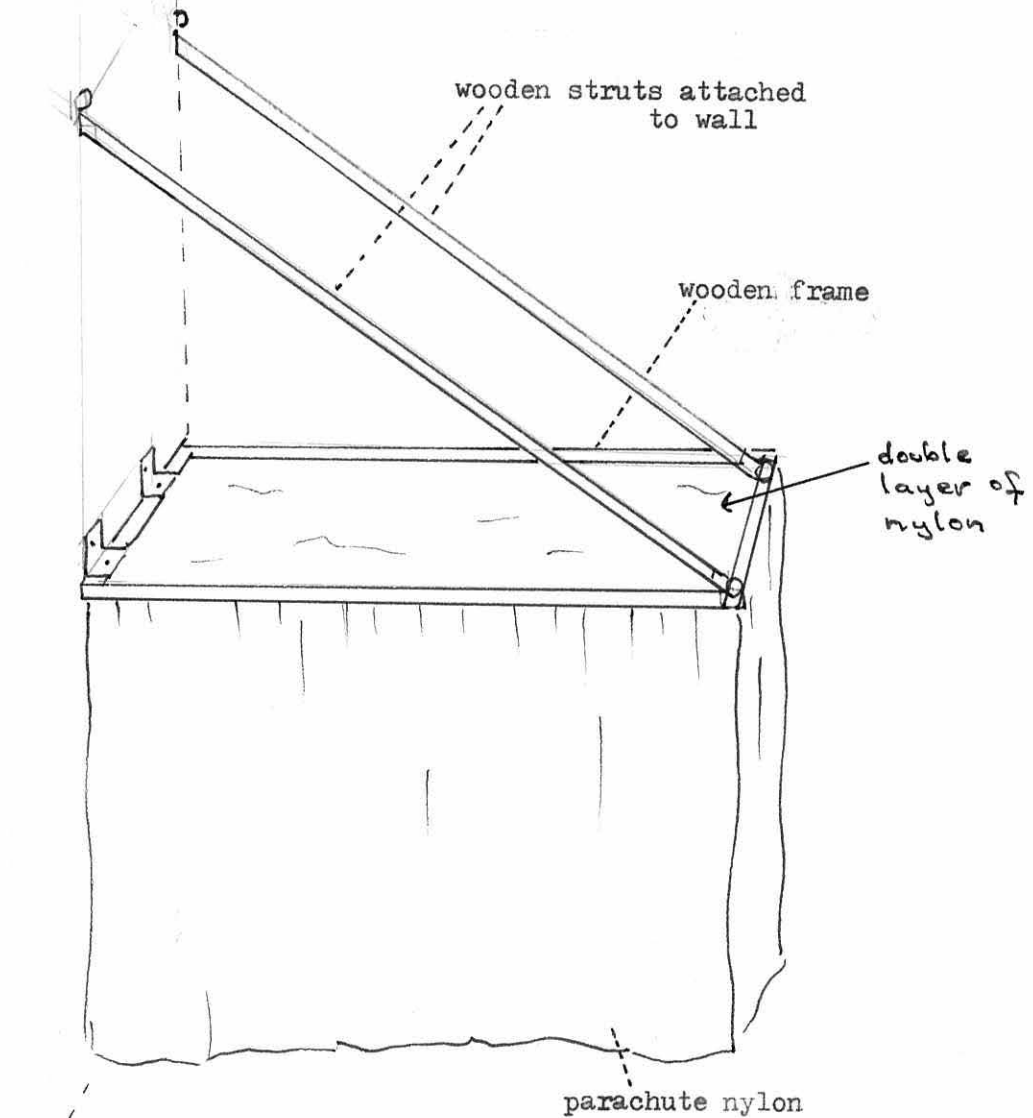
The tent surrounding the open
field

result of the findings described in chapter 3. The rationale of using both soap and detergent was that the scrubbing with soap followed by rinsing would remove all substance adhering to the apparatus. The washing with detergent provided an additional safeguard and, moreover, as it was also used to clean the animals' home cages any residual odour left by the cleaning materials themselves would be familiar to the animals and therefore unlikely to excite interest.

It is important to remember that in studying the effect of odour on behaviour the important variable is the presence or absence of the odour being investigated. The amount of odour is relatively unimportant, but it is essential that in the control condition there is no odour whatsoever.

Lighting

This was provided by two lamps standing on opposite sides of the open field, outside the tent. The level of illumination was measured with a Universal Exposure Meter Western Master V. Dimmer switches on each lamp were used to adjust illumination over the field to a uniform level. Readings were taken systematically in different areas of the field and at different heights (see Diagram on page 104). The level of lighting was lower than the general level pertaining in the animal room where readings ranged from 3 to 4." It was higher than in the animals' cages where the reading was 0.5. The level of illumination permitted the experimenter to see the animals clearly yet was dim enough not to alarm them. As has been indicated in Chapter 2 the guinea pig

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* Unfortunately it has not been possible to convert these readings into foot candles. However, by using the same light meter the level of lighting of this study can be replicated.

DIAGRAM 3

Illumination of open field *

+ lamp

```
*           *           *




*           *           *




*           *           *
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+ lamp
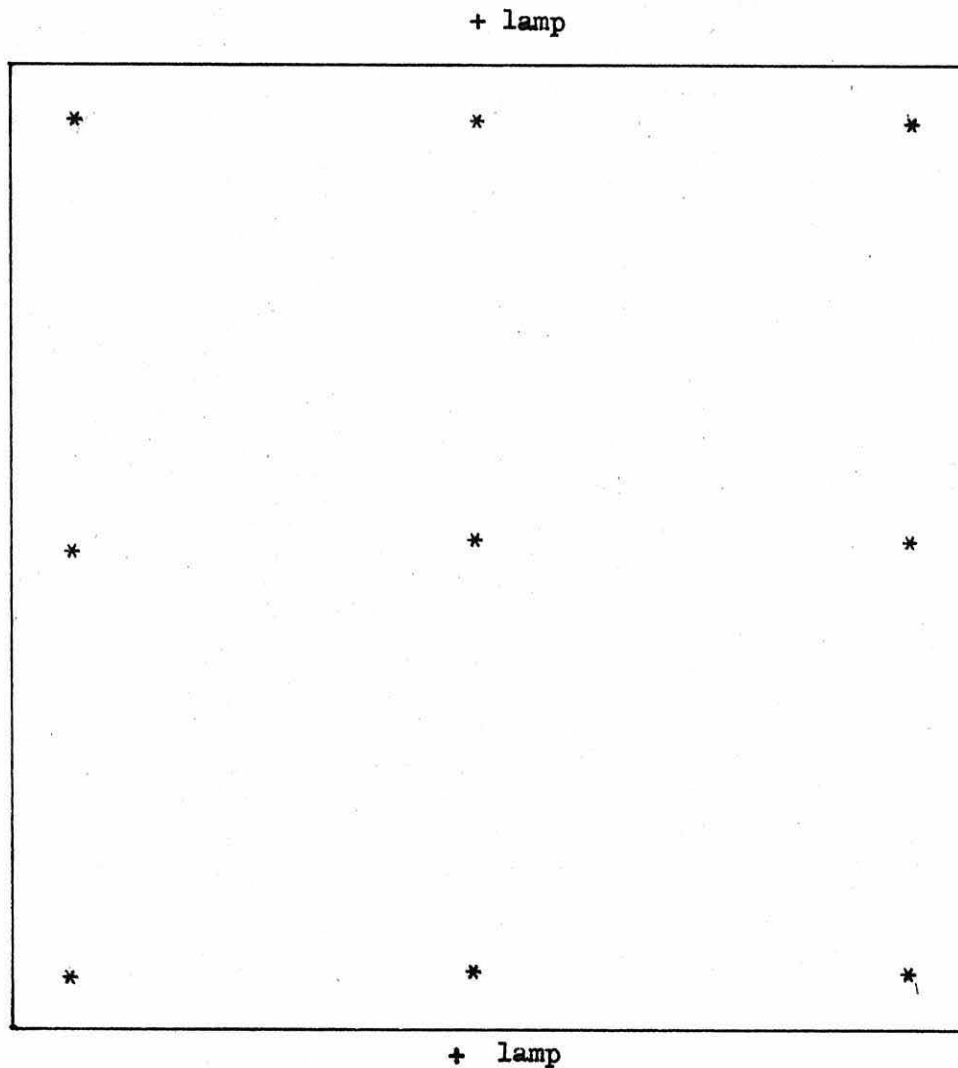
Diagram indicating points at which lighting was measured.
This was measured at 6" and 12" above the base at each of the
9 points indicated by a * . At each point the reading was
2.0, except that in the corners the open field was slightly
darker, the reading being 1.8. (See footnote on page 90).

* The light was directed at an angle through the
double layer of parachute nylon covering the top
of the open field. The light did not shine on the
experimenter.

tends to be crepuscular and to avoid bright light.   Each animal

had had experience of a higher level of lighting than that

encountered in the open field.   This would happen at feeding time,

when it was handled, and so on.

Recording of Data

The method of recording throughout has been that of observer

plus pencil and paper.   This has both advantages and disadvantages,

and will be discussed later in this chapter.

The method of scoring involved the observer recording the

behaviour on to prepared cyclostyled sheets.   The observer sat

outside the tent which covered the field and observed the animals

through a small gap in the tent curtain.   A stopwatch was used

for timing purposes.

In those experiments where several items of behaviour were

recorded the shorthand method described in Chapter 3 was used.

This is detailed on page 110 .   Also, as the data to be recorded

vary according to the experiment, these details will be given in

the appropriate chapters.

The great advantage of the human observer is flexibility.   For

example, if something occurs that has not been anticipated the

human observer is flexible enough to be able to take account of it.

Although this is not likely to happen where careful study has

enabled the experimenter to anticipate the forms of behaviour which

are likely to occur, the point is a valid one; something

unexpected may occur, and it may be important.   It should be

recorded.

Where there is only one observer there is the ever present

risk of human error.   It might be suggested that a check list

would demand less of the observer.   However, it is doubtful whether

this advantage would warrant the reduction in information obtained.
The check list permits recording of pre-determined items only;
it does not permit the recording of the animal's peregrinations
in the field, nor its position throughout the experimental session.
As Hutt and Hutt (1970) point out, a check list is not suitable
for recording the complete range of activities in a free field
situation.

Essentially the same argument applies to the use of an event
recorder. In the event of a new response occurring it would be
useless, and in some of the experiments to be described it was
possible to record more information than would be possible using
an event recorder. As with the check list the event recorder is
suitable for recording a selection of activities. It is not
adequate for recording the complete range of such activities.

The risk of human error in the methods under discussion can
be minimised by having two observers recording the same data.
Any significant difference in their data would have to be
investigated, but one would hope that if both were sufficiently
experienced and the behaviours clearly defined, there would be
no real difference. A high correspondence in their data would
increase the confidence one could place in the accuracy of their
recording.

In the present case this was not possible. It was necessary
for the experimenter to record all the data, and do all possible
to ensure a high level of accuracy and reliability. The period
of observation described in Chapter 3 provided practice in this.

It has been stated that the great advantage of the human
observer over a mechanised system is flexibility. It can be

argued that the use of Video or film would be the best method of
recording data.   All the behaviour emitted would be recorded
and it would not matter if a form of behaviour occurred which had
not been anticipated; it would be there, on tape or film.

An argument against the human observer in favour of videotape
would be hard to counter.   One might argue that videotape gives
one the best of both worlds; the flexibility of the human
observer, but with a permanent record of the behaviour obtained
mechanically and without error.   However, the behaviour still
has to be analysed.   This, in a sense, is similar to the method
of observer plus pencil and paper: the observer records from
the videotape onto paper.   There are important differences,
however.   The videotape can be run through again and again, and
if he wishes the observer can concentrate on one aspect of
behaviour at a time.   The precise duration of each activity and
the number of times it occurs can be checked and rechecked for
accuracy.   This would be easier than having to note everything
as it happens, and would reduce the risk of error.   It would be
possible to check for intra- and interobserver reliability.
However, it would be equally as important that the experimenter be
familiar with the animals' behaviour, and that the categories of
behaviour are clearly defined, as in the method of direct observation.

Nevertheless, the use of video does present problems.   Video
was used to record the experiment on exploratory behaviour
mentioned in Chapter 1.   When recording was carried out in a dim
light the picture obtained was of a poor quality, and at times it
was impossible to determine exactly what the animal was doing.

Also, when an animal moved quickly it virtually disappeared from the screen. There was also a degree of after-image which was confusing. It was not possible to obtain pictures in slow motion which might have been helpful in identifying some of those items of behaviour that were not clear.* As it was deemed advisable that there should be a low level of lighting for the experiments the problem of poor image would remain.

It is likely that ciné film would have the advantages of videotape without its disadvantages. With the use of a small camera the experimenter would have been able to film the experiments without help. The noise would not have presented a problem as it would be possible to accustom the animals to this prior to the experiment. A difficulty that would be harder to counter would be the likelihood of the experimenter's movements distracting the animals. A camera in a fixed position could be used, but it is possible that some aspects of behaviour which involved very little movement would be missed. Again, lighting would need to be low, but a suitable film could allow for this. If such a camera had been available it would have been used in a trial situation to see if it were suitable. However, as Hutt and Hutt (1970) point out: "It is a popular misconception that films are the most desirable of techniques for behaviour recording". What is often overlooked is the fact that all one has done is to make a two-dimensional replica of the behaviour. It still has to be analysed. But as with videotape, the film can be run through as many times as necessary to permit accurate recording of all the behaviour. It could be examined frame by frame if there was

* More recent developments allow slow motion replay.

doubt over any item of behaviour. And checks could be made of inter-observer reliability.

Yet another method with a lot to recommend it would be to record a spoken commentary onto magnetic tape. To watch and to speak is a considerably less demanding task than to watch and record by hand. At no time would it be necessary to move one's eyes from the open field. The duration of different items of behaviour could be determined subsequent to the experiment. The peregrinations of the animals could be recorded by using a system of coded squares on the floor of the field. The most obvious disadvantage of this method in the present instance would be the possibility of the animals being distracted by the sound of the experimenter's voice, which they had come to associate with the provision of food. This problem could be overcome by using a glass screen perhaps. The main argument against using it was the fact that a tape-recorder was not always available. It was decided, therefore, to use one method, rather than the tape-recorder on one occasion, pencil and paper on another.

Where appropriate the cyclostyled sheet was designed so as to permit recording of behaviour as it occurred during each minute of a five-or ten-minute session. (See diagram in Appendix 4.)

Recording of the behaviour:

This will be described in the appropriate chapters. Both the incidence and duration of the items of behaviour were recorded. The following shorthand notations were used :

sniffing	...	S
s-nosing	...	N
biting	...	B
defaecation	...	D
ano-genital dragging (trail laying)		T
urination associated with dragging	...	U͞
urination	...	U
pausing	...	P
freezing	...	F
grooming	...	G

If pilo-erection occurred its occurrence was noted, but it was not possible to time this behaviour; the same was true of tooth chattering.

pilo-erection	...	H
tooth chattering	...	ch.

Each occurrence of behaviour was timed with a stopwatch, and the time recorded in seconds.   Thus if an animal paused for 10 seconds, 10 would be written adjacent to the symbol for pausing, for example P 10.

It is not claimed that this method is without error, but it is claimed that this would not be in excess of plus or minus a second or so on each occasion, and that it is not significant.   Where the behaviour was of such short duration as to be impossible to time accurately it was arbitrarily counted as of 2 seconds' duration. Hutt and Hutt (1970) point out that Bridges (1934), when using this method, found that when accurate measurements were obtained the duration was approximately two seconds.

In those experiments where locomotion was recorded, this was done by pencilling the line followed by the animal in the open field.   This would be punctuated by other items of behaviour emitted.   Thus it was possible to record where the animal went, and where each item of behaviour occurred, as well as total distance, total time, and number of occurrences of behaviour (See Diagram in Appendix 4).   The peregrination was also recorded.   The diagrams were to scale (1 foot - 1 inch), and the distance was measured with

a map measurer.

In some of the experiments the only quantitative data recorded were the time spent by the subjects in either half of the open field. In another experiment time sampling was used. Both of these will be described in the appropriate chapter. Examples of the prepared sheets for the recording of data are given in Appendix 4.

The sample used was small. The reason for this was that it was not practicable to use large numbers: the accommodation was such that it was not possible to house more than ten guinea pigs at any one time. Therefore a large N would have entailed a regular influx of new animals and discarding of others. In view of the difficulties of working with guinea pigs and the time and effort required to accustom them to experimental procedures this would not be a viable proposition. Once one has a group of animals which do not become immobile at the least provocation they are valuable subjects, and should not be discarded unless the nature of the investigation demands naive animals. This point is discussed in greater detail on pages 114 - 116.

For the same reason the animals were used in more than one experiment. This is not unusual and whether or not it is a wise procedure depends on the nature of the investigation. For example, Harper (1966), Satinder (1969), Pearson (1970) Berryman (1974) and Landauer, Banks and Carter (1978) all, to a greater or lesser extent, used the same subjects more than once. Berryman (1974) reported that the behaviour of the subjects was unaffected. More specifically, Beauchamp (1974) reported that repeated testing did not alter the response of male guinea pigs to female urine.

Where subjects are used more than once it is customary to allow
a specified interval to elapse between experiments (Pearson,1970;
Berryman,1974; Landauer et al,1978).

It is not unusual for investigators to use a small N. Thus
Beauchamp, Criss and Wellington (1979), comparing two species of
cavy (domestic guinea pig and Cavia aperea) and a C. aperea x
C. porcellus hybrids had seven animals of each kind. Pearson (1970)
consistently used small numbers, and Berryman (1974) carried out an
informal experiment using two subjects. Nonetheless her findings
were unambiguous, and of considerable interest. Valenstein and
Goy (1957) comment that some of their groups contained only a
few animals, but added that "these are believed to be sufficient
in view of the unambiguous results and the long period that the
animals were followed". Gerall (1965) used a smaller number in
some of her groups than she had intended owing to the deaths of some
of her subjects.

The size of the sample and the type of statistical test to be
used was considered in relation to the nature of the subjects and
the type of behaviour being studied. This was taken into account
when designing the experiments.

The disadvantage of a small N is that there is a greater
likelihood of making a Type 1 error. The sensitivity of the
experiment would be increased with a larger N. Also, where N is
small a non-parametric test should perhaps be used, and again this
increases the probability that a real difference will be rejected
as not significant. However, where small numbers are used it is
possible to examine the data of each subject individually and it
may be that information can be obtained that normal statistical

procedures might overlook.   Sidman (1960) cites the type of research
experiment where two groups of subjects are exposed to a different
value of an independent variable.   Each group may display a
different mean value of the resulting behaviour but there will be
a spread around the means with possibly some overlap between the
two groups.   Where N is small it is possible to determine whether
or not this has occurred.   A large N is no substitute for good
experimental control;   where there is such control the possibility
of committing a Type 1 error is very small.   Fisher (1942) writes
"In order to assert that a phenomenon is experimentally demon-
stfable we need, not an isolated record, but a reliable method of
procedure.   In relation to the test of significance we may say
that a phenomenon is experimentally demonstrable when we know
how to conduct an experiment which will rarely fail to give us a
statistically significant result".

In the present series of experiments, where possible, the
method of identical subjects was used, each animal acting as its
own control.   This is a valuable method as it eliminates the
intersubject variability that occurs when two groups are used:
when the difference in behaviour is compared between a group
that has been exposed to an experimental variable, and a control
group which has not been so exposed.   This method increases the
sensitivity of the behavioural measurements.   Variables which
may be dismissed as having little or no effect when group compari-
sons are made may prove to be extremely powerful when evaluated
against an individual baseline.   As Sidman (1960) points out,
intersubject variability is not a feature of behavioural

processes in the individual organism, and when such variability
is included in the measurement of presumed individual processes,
the resolving power of the measures is reduced.   In other words,
intersubject variables contribute more to random error than do
within-subject variables.

In an identical subjects design each subject takes both
conditions and one condition must be taken before the other.
When this design is used it is important that a counterbalanced
design is used.   This is to balance the possible effect of order
of presentation of the two conditions, control and experimental.
As Underwood (1949) points out "Counterbalancing does not eliminate
(sequence) effects; counterbalancing only distributes these ...
effects equally over all conditions when the effects are considered
for all subjects combined."   He also recognises that "If the
experimenter has reason to believe that the effect of going from
A to B is quite different from the effect of going from B to A,
the method should not be used since it would give a distorted
picture of the experimental conditions as such."

In the present series of experiments therefore the identical
subjects design was used, with counterbalancing, or where more than
two conditions were involved order of presentation was varied.
Where this design was not appropriate matched pairs have been used.
The bases on which they were matched are described more fully
in the appropriate chapter, but care was taken that they were
matched on variables which seemed likely to correlate with the
dependent variable; for example, age but not colour.

Subjects:

Sidman writes "one of the most sacred restrictions imposed

on experimental design in psychology is the requirement that all
subjects in an investigation be treated alike except for the
independent variable in question".   Sidman implies that subjects
might be allowed to differ with respect (for example) to food
deprivation, previous history, age, genetic background, and
other such variables which have proved irrelevant in other
contexts.   If, in spite of these differences, the investigator
obtains similar orderliness from each of the subjects, the findings
will have greater generality than would otherwise be the case.

Of course, this would not be a wise procedure to adopt in
many cases, as if the experimenter fails to obtain such results
he will not know whether the failure was due to any one or a
combination of these variables, or whether the introduction of
the independent variable failed to produce the expected pattern
of behaviour.   In the present case no decision was made to vary
the history or age of the animals on the grounds that this would
give greater generality to the findings, but on account of the
constraints which determined that the sample be small, it was
decided that it would be possible to use subjects with some slight
variation in their previous histories.

In this context it is worthwhile to note that Beauchamp, Criss
and Wellington (1979) found no significant trends according to
age in the response of guinea pigs to chemical stimuli.

The animals in this study took part in several related
experiments.   It is not unusual for subjects to be used in this
way.   For example, Harper (1966), Pearson (1970), Satinder (1969),
Berryman (1974) and Landauer, Banks and Carter (1978) used the

same subjects on more than one occasion. Berryman (1974) reported

that the behaviour of the animals in question was unaffected. More

specifically, Beauchamp (1973) reported that repeated testing did

not seem to alter the response of male guinea pigs to female urine.

If learning or some form of behaviour modification were involved

in the investigation then it would have been necessary to use

naive animals.

With the exception of experiments I, Ia, III*, IX and X, the

order in which the subjects were exposed to the experimental

situations was varied. An interval of at least two weeks was

allowed to elapse between the different experiments.

All animals were of the tortoiseshell and white smooth-coated

variety, and all were obtained from the same source. They were

housed in one room where the temperature was 68°F. For the most

part they were kept individually** in cages measuring 24 inches

long, 14 inches wide, and 10 inches deep. The animals were kept

on woodchips and sawdust, and were provided with clean cages twice

weekly. At all times they were on food and water ad libitum, the

diet consisting of SG1 pellets and approximately five ounces of

carrots daily. The water was provided in plastic drinking bottles

with a plastic dispenser. There was a constant supply of hay.

When green food was available this was given to the animals, al-

though it was not given during experimentation. This was in case

diet affected olfactory stimuli, and in fact Beauchamp (1976)

found that guinea pigs are able to distinguish

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*Experiment III was carried out after the other experiments in view
 of the greater possibility of its affecting the behaviour of the
 animals in subsequent experiments.

**All the male guinea pigs were kept individually. Some females
 used in the subsequent experiments were kept in pairs.

between the urine of conspecifics given different diets.   Also,

Pearson (1970) suggested that factors related to diet may affect the

rate of defaecation.

The animals were kept on a 12 hour day night/night day schedule,

from 9 am to 9 pm.   They were fed at 5.15 pm.   Testing began

at approximately 6 pm.* and the interval between feeding and

testing was kept as uniform as possible.   Thus they were tested

at a time which naturalistic studies (King, 1956; Rood, 1972)

indicated would be a time of activity.

Acclimatisation:

Each experiment involved placing a single subject in the

apparatus on its own.   This necessitated removing it from its

conspecifics.   As the guinea pig's response to novelty is to

remain immobile, and previous experience had suggested that the

animals would remain immobile for the entire test period, it was

deemed necessary to accustom each animal to the experimental

room.   This was done by carrying each animal into the experi-

mental room in its home cage and placing it, still in the cage,

in the open field.   The lighting was the same as for the actual

experiment.   The animal was left for ten minutes, and this

procedure was carried out daily for the specified number of days

before the experimental session.

Procedure:

The experimental room was about 3 yards from the animal room.

When an animal was to be tested it was carried from the animal

room to the experimental room in its cage.   The animal was then

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* There was occasional variation due to extraneous noise beyond
  the experimenter's control.   They were also fed in the
  morning.

lifted out of the cage and placed in the open field.   The stop-
watch was started, and the behaviour of the animal was recorded.
At the end of the session the reverse procedure was carried out.

Providing the stimulus:

The majority of experiments to be described are concerned with
the effects of the scent of a conspecific on adult male guinea
pigs.   The method by which the scent was obtained will be
described in detail in the relevant chapters, but it will be
mentioned briefly here.   In all cases the scent was obtained from
a living animal placed in the apparatus and left there for long
enough to distribute his odour.   The disadvantage of the method
is that it is not possible to say that on each occasion the same
amount of odour is present.   However, it is the presence of
odour, or the lack of odour, which is being investigated.   It
has been emphasized how important it is to ensure that when the
experimental condition demands no odour, that this is in fact
the case.   On the basis of the observations made by the
experimenter it did not seem that the amount of odour present
was the significant factor.   What was significant was the
presence or absence of odour.

THE EXPERIMENTAL SECTION

Chapters 5-10

Introduction to the Experimental Section

Chapters 5 - 9 describe investigations into the behaviour
of male guinea pigs in response to the odours of

1) adult male conspecifics
2) the odour of another species
3) adult females
4) receptive females.

The behaviour emitted in response to male odour and to no
odour in Experiment I is compared with behaviour in response to
an adult female (Experiment VI) and to another species (Experiment
II).

Where appropriate identical subjects are used. Where it is
not possible to use a counterbalanced design the order of present-
ation is systematically varied. Some experiments involve a
two-choice preference situation where counterbalancing does not
apply, and one experiment was unsuitable for the identical subjects
design and matched pairs were used. This experiment involved
repeated exposure to the same situation and was, therefore, carried
out after completion of the other experiments. This experiment
(III) is described early in the experimental section: the
experiments are presented in the order which forms a logical
sequence. This is not always the same as the order in which
they were conducted.

Chapter 10 describes an investigation into relevant behaviour
in the female guinea pig. Observation and time-sampling were
used.

Where the data are presented in histogram form the scale is varied according to the level of behaviour emitted.

Chapter 5   Experiment I *

It was said in chapter 3 that observations of male guinea
pigs suggested that rump-dragging, s-nosing and defaecation
occurred in response to the odour of a male conspecific.   An
attempt to investigate this experimentally was inconclusive;
it seemed that this was due to a failure to remove all stimulus
odour in the control condition.   It was concluded that more
rigorous conditions were needed in the investigation of olfactory
stimuli and behaviour.

An open field was designed that would permit thorough washing.
It was constructed of materials that would not absorb odours.
This apparatus, and the method of cleansing, are described in
Chapter 4.

The present chapter describes the investigation into the
response of male guinea pigs to the odour of male conspecifics
using the new open field.

It was considered that the most suitable method of invest-
igating this behaviour would be a simple experimental design,
comparing a no scent condition with a scent present condition,
with each subject acting as his own control.

It was hypothesized that in response to odour of male con-
specifics the following items of behaviour would show an
increase in comparison with their occurrence in the control
condition where there was no odour.

The behaviours are as follows :

* This experiment formed part of a paper given to the Association
for the Study of Animal Behaviour in November, 1972

> ano-genital dragging
> urination associated with
>   ano-genital dragging
> defaecation
> s-nosing
> locomotion

The following behaviour was also recorded but no prediction was
made concerning its occurrence:

> sniffing
> grooming
> freezing
> pausing   ) immobility
> urination
>
> pilo-erection   ) noted but not timed.
> tooth chattering)

Subjects

Ten adult male guinea pigs acted as subjects.   They
initially consisted of two groups.

Group 1. comprised seven adult male guinea pigs aged approx-
imately 26 months at the start of Experiment I.   These animals
had been used for the experiment and observations described in
Chapter 3.   They had been in the laboratory for twenty-one
months.   There were initially ten animals but by the time the
present investigation began their numbers were reduced to seven.
Three additional males were purchased therefore in order to
restore the number of subjects to ten.   Thus Group 2 comprised
three animals of approximately 6 months.

The use of these younger animals fulfilled a dual purpose:
that of increasing N to ten subjects, and that of providing the
opportunity of replicating the original results, and thus
extending their generality.   Although it was intended to combine
the two groups into one, it would clearly be possible to do so
only if the findings were essentially the same for both groups,
with no real difference between the older, non-naive animals,
and the younger, naive animals.   Berryman (1974) had occasion

to use animals varying in age from three and a half months to three years, while Beauchamp, Criss and Wellington (1979) report that there were no apparent age trends between older and younger animals in response to chemical stimuli.

All animals were of the tortoiseshell and white, smooth-coated variety. They were housed in individual cages in one room. At all times they were on food and water ad libitum and there was a constant supply of hay. They were given carrots twice daily.

The animals were kept on a twelve-hour day-night, night-day schedule from 9 am to 9 pm. They were fed at 5.15 pm. Testing began at approximately 6 pm and the interval between feeding and testing was kept as uniform as possible.

Apparatus

The square open field described in Chapter 4 was used. The field was constructed of opaque grey perspex. As this is shiny the interior walls were buffed so as to eliminate reflection. The field was 3 feet 3 inches square, with 12 inch high walls. This stood on a formica base, which was covered with white cartridge paper. A drawing of the open field is given on page 100.

The stimulus scent of a conspecific was provided by a predecessor animal. Thus, one animal was placed in the open field for ten minutes. This was a subject undergoing the control condition, and at the same time providing the stimulus for the experimental condition. It was not possible to control for the amount of odour present, except in that it was consistently provided by an adult male guinea pig in the open field for a fixed

period of time (ten minutes).

The number of faecal boli' was controlled however, and kept at three. If the predecessor animal failed to defaecate during the control session the requisite number of fresh boli were taken from his cage and put in the open field before the experimental session commenced.

Procedure

For five days prior to each animal's first session in the open field each animal was carried in its home cage from the animal room to the experimental room. Here the cage was placed inside the open field and left for ten minutes. The curtains were in position and the lighting was the same as for the experimental sessions.

For several weeks prior to the experiment a stopwatch was used regularly in the presence of the animals.

The results were recorded by the experimenter using a pencil, cyclostyled sheets, and a stopwatch. As each session lasted for ten minutes it was considered necessary to have some idea of the incidence of behaviour over time. Thus the score sheets were designed in such a way as to permit this.

Two sheets were used, each providing 5 scale diagrams (one inch to one foot) of the open field, one for each minute of the session. As each item of behaviour occurred it was recorded on the appropriate diagram. This method also permitted the recording of where on the open field the particular item of behaviour occurred. The symbol was placed on the map in the position of the animal in the open field.

The peregrinations of the animal were drawn on the diagram, again in a position and direction corresponding to the actual position of the animal. These were later measured with a map measurer and translated into feet.

The apparatus was prepared and each subject was carried to the experimental room in the base of its home cage. This was placed in the corner of the room, and the animal lifted out and placed in the corner of the open field with its head towards the centre of the field and its rear towards the corner of the open field.

The experimenter then started the stopwatch and commenced recording the behaviour of the animal.

At the conclusion of the ten minute session the animal was lifted from the open field, put in its home cage, and returned to the animal room.

The first animal underwent the control session. The number of faecal boli in the field were adjusted if necessary, and the procedure was then repeated with a second animal undergoing the the experimental condition. The order in which subjects were exposed to the control and experimental situations was counter-balanced.

At the conclusion of the experimental session the apparatus was dismantled and washed. This process is described in detail in Chapter 3. The cartridge paper was discarded and the open field reassembled for the next session which would be carried out on the following or a subsequent day.

A Wilcoxon matched-pairs signed-ranks test was carried out in order to determine whether observed differences in the behaviour emitted in the experimental and control conditions

were significant (Siegel 1956).

The data for the two groups of animals (1 and 2) were compared. Where findings obtained with Group 1 were replicated by Group 2 the groups have been amalgamated for the purpose of statistical analysis. The two groups are distinguished in the raw data, which can be seen in Appendix 5.

RESULTS

Ano-genital dragging

There was considerably more of this in the experimental than in the control condition. Five animals did not emit this behaviour at all in the control condition, whereas all animals did so in the experimental condition.

The difference between the control and experimental conditions was in the same direction for each animal; that is to say, each animal showed a higher incidence of dragging in the experimental condition than in the control condition. This can be seen by inspecting Figure 5a. The difference is significant ($P < 0.005$, 1 tailed test. $T = 0$; $N = 10$).

The findings obtained with Group 2 replicated those obtained with Group 1. Groups 1 and 2 have been amalgamated, therefore.[*]

U-marking

Inspection of Figure 5b reveals that the incidence of this behaviour is low in the experimental condition, and that there is none at all in the control condition. Eight out of ten animals emitted this behaviour in the experimental condition. The difference is significant ($P < 0.005$, 1 tailed test. $T = 0$; $N = 10$).

Groups 1 and 2 have been amalgamated.

[*] In both histograms and tables the two groups may be distinguished: the data for the 7 subjects in Group 1 precede those for the group 2 animals.

Defaecation

The incidence of this was higher in the experimental condition, as can be seen by inspection of Figure 5c. The difference is significant ($P < 0.005$, 1 tailed test. $T = 0$; $N = 10$).

There was virtually no defaecation in the control condition: only two out of the ten animals defaecated in the control condition, whereas all animals defaecated in the experimental condition. Inspection of Figure 5c reveals that the direction of change between the experimental and control conditions was the same for each animal.

Groups 1 and 2 have been amalgamated.

S-nosing

There was very much more of this in the experimental than in the control condition. Each animal showed more of this behaviour in the experimental condition than in the control condition. One animal showed none at all in the control condition (see Figure 5d). The difference is significant ($P < 0.005$, 1 tailed test. $T = 0$; $N = 10$).

Groups 1 and 2 have been amalgamated.

Figure 5a. Ano-genital dragging

(no. of instances)

Figure 5b U-marking
(no. of instances)
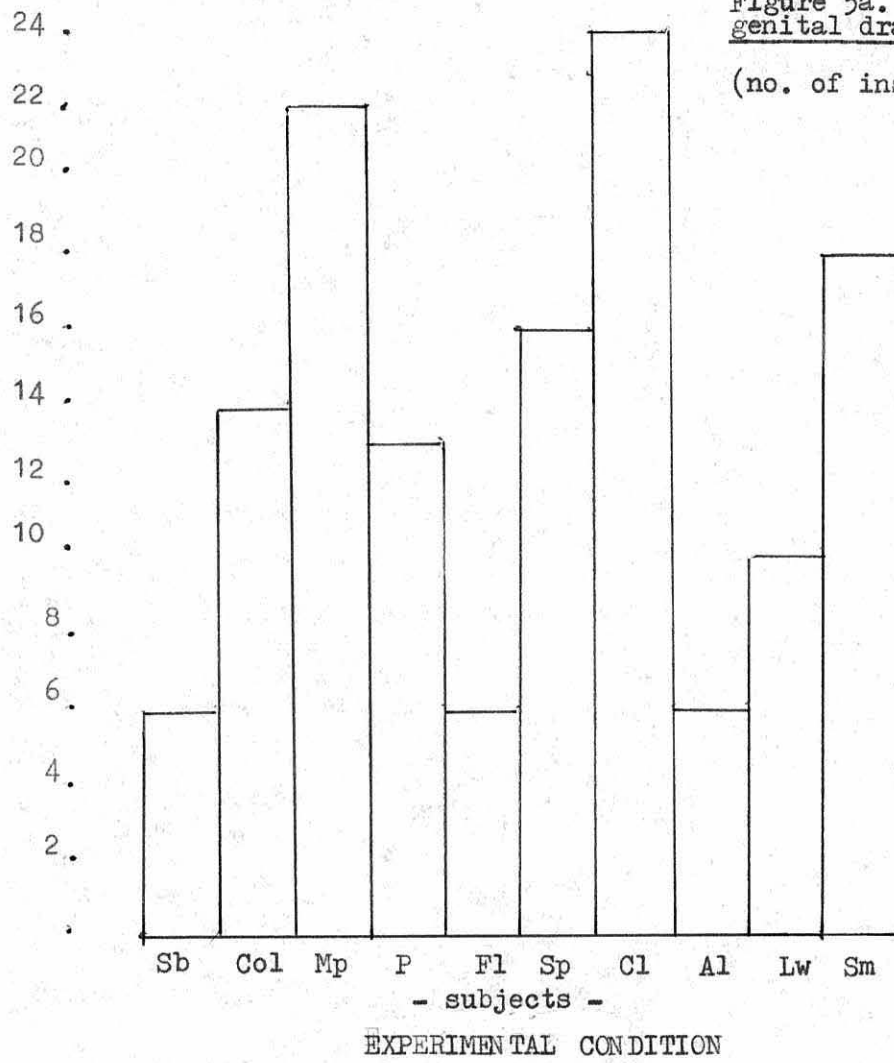
EXPERIMENTAL
CONDITION
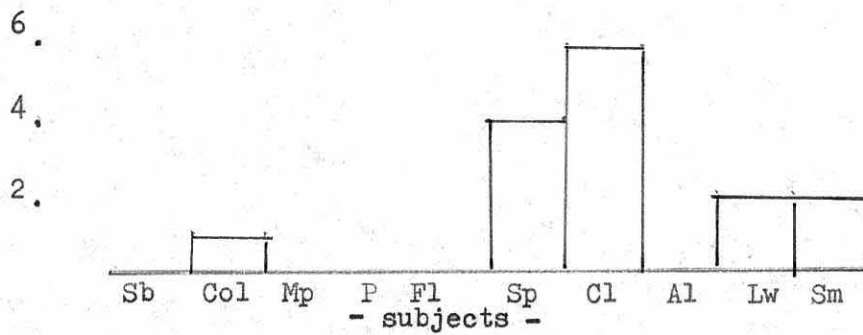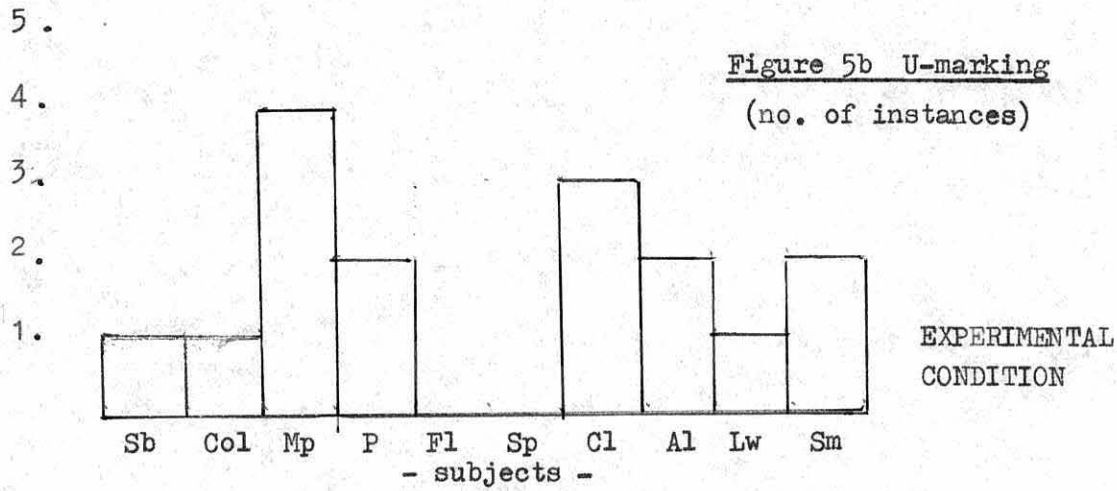
ZERO U-marking in the CONTROL CONDITION

Figure 5c Defaecation
(no. of pellets)

EXPERIMENTAL
CONDITION
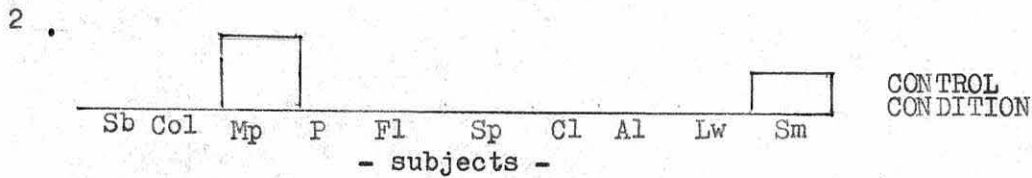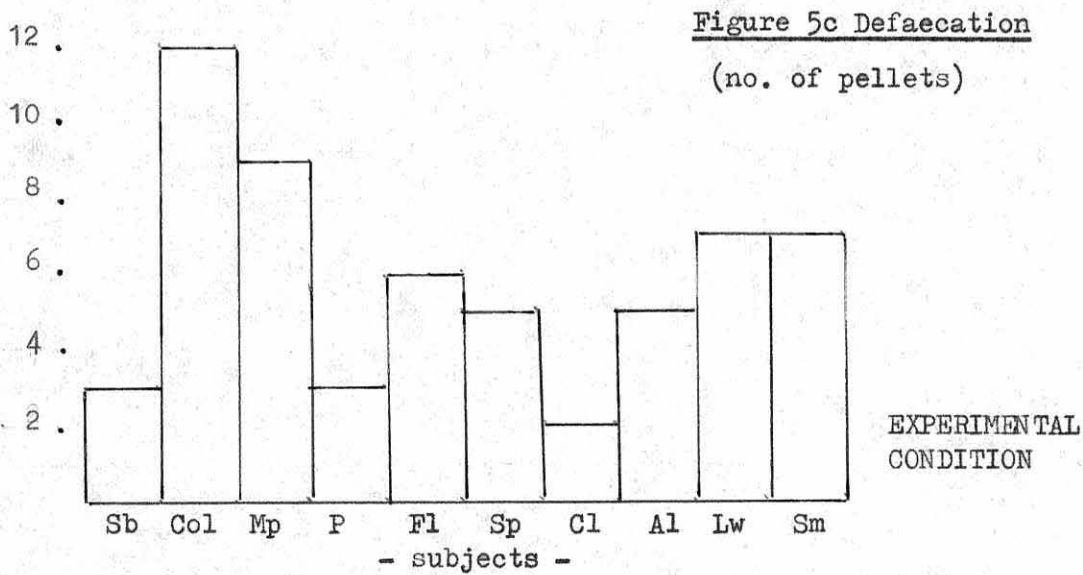
CONTROL
CONDITION

Figure 5d S-nosing (sec.)
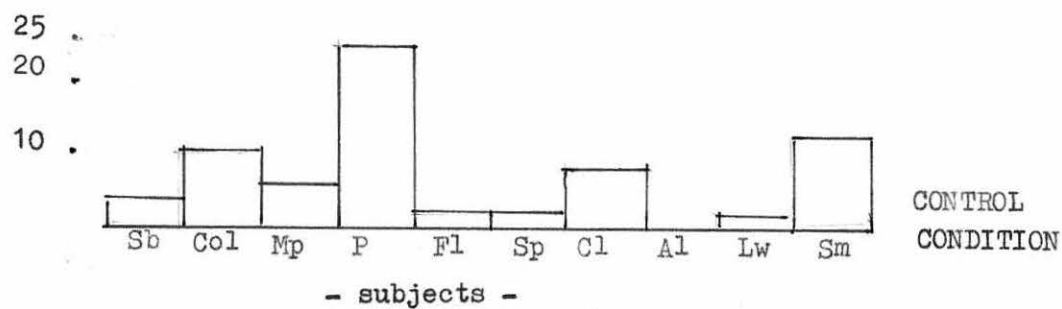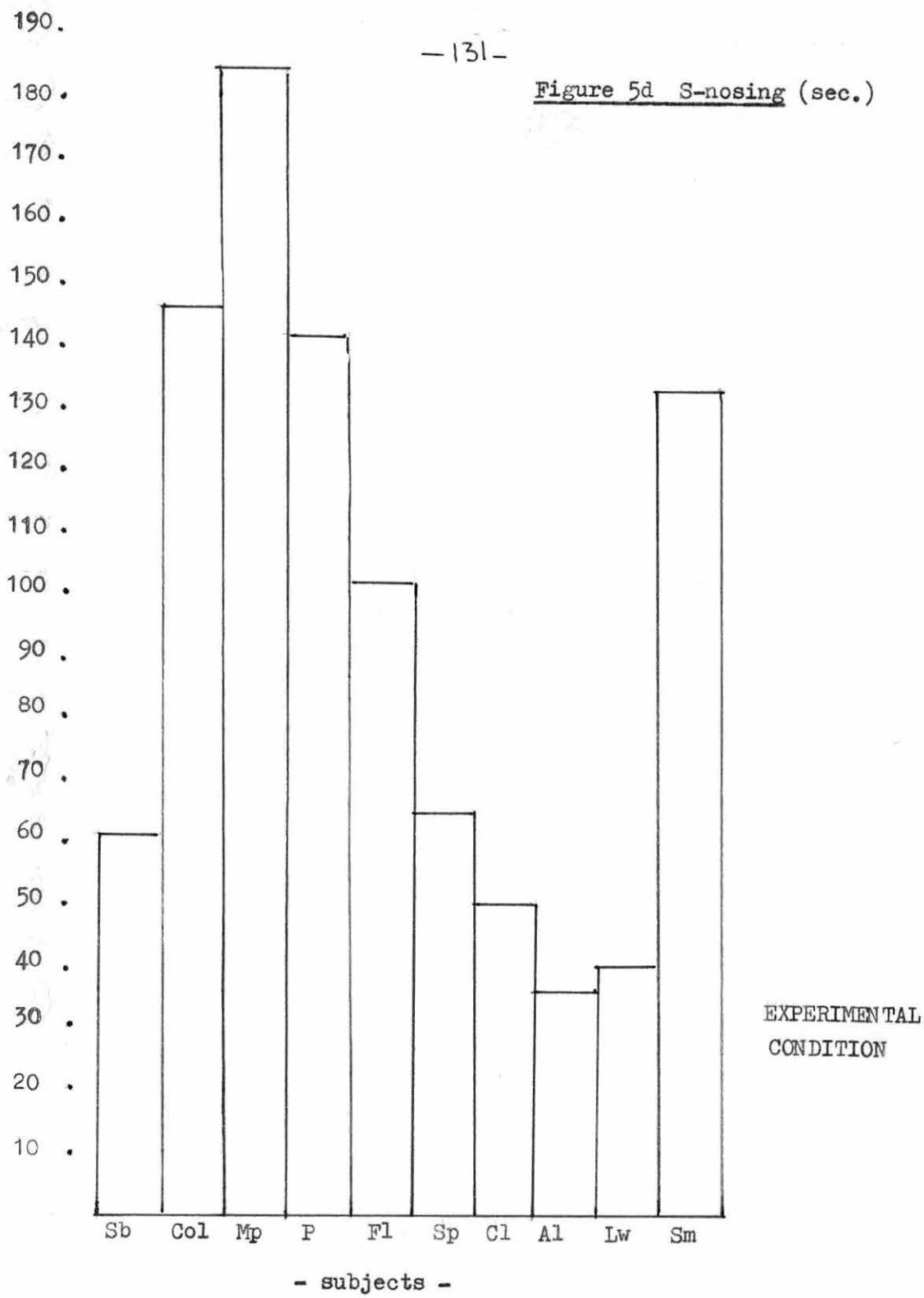
Locomotion

The distance traversed by the animals in the experimental session is higher than in the control situation. Eight out of ten animals behaved in this way, while two locomoted more in the control situation. With regard to these last however, the differences were very small, 52 and 53, and 46 and 50 feet respectively. This can be seen in Figure 5e. The difference in locomotion between the two conditions is significant ($P < 0.005$, 1 tailed test. $T = 3; N = 10$).

Groups 1 and 2 have been amalgamated.

Sniffing

As can be seen from Figure 5f sniffing varied little between the two conditions. No significant difference was found between them. ($T = 25.5; N = 10$).

Groups 1 and 2 have been amalgamated.

Grooming

As can be seen in Table 5i there was more grooming in the experimental condition than in the control condition. This difference is significant ($P < 0.01$, 2 tailed test. $T = 0; N = 10$).

Groups 1 and 2 have been amalgamated.

Figure 5e
<u>Locomotion</u> (in feet)

Figure 5f. Sniffing (sec.)

EXPERIMENTAL
CONDITION

- subjects -
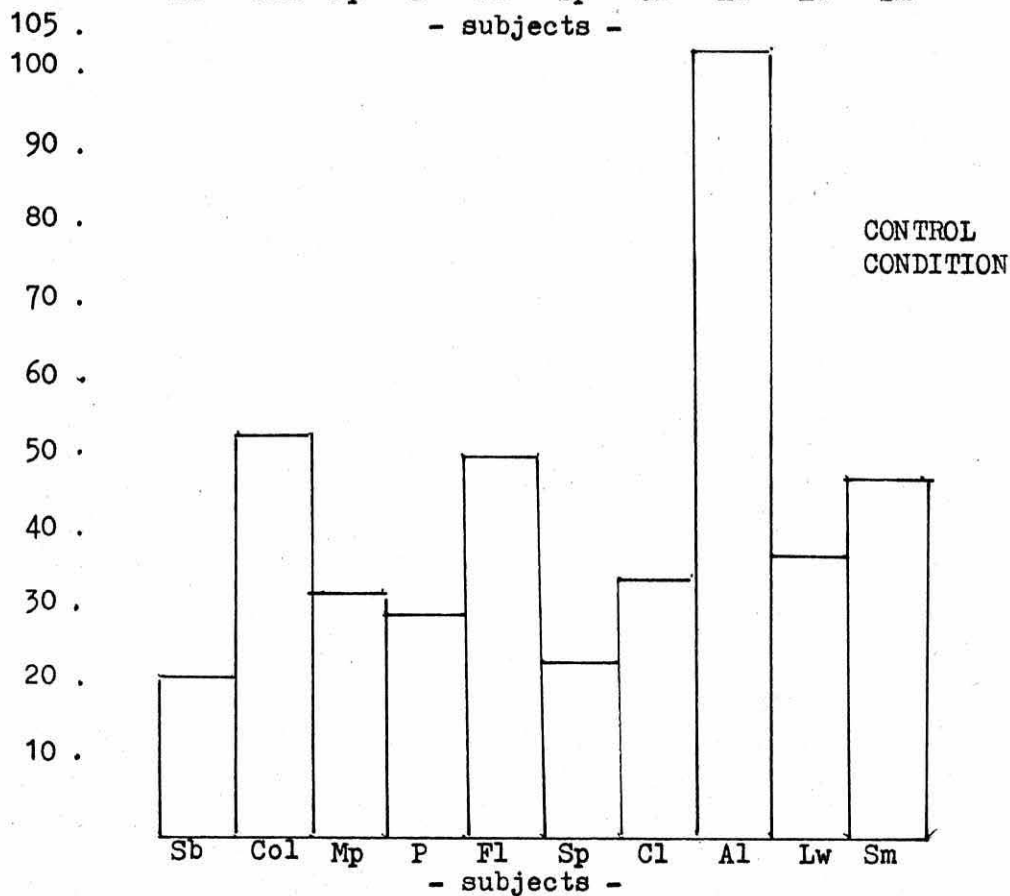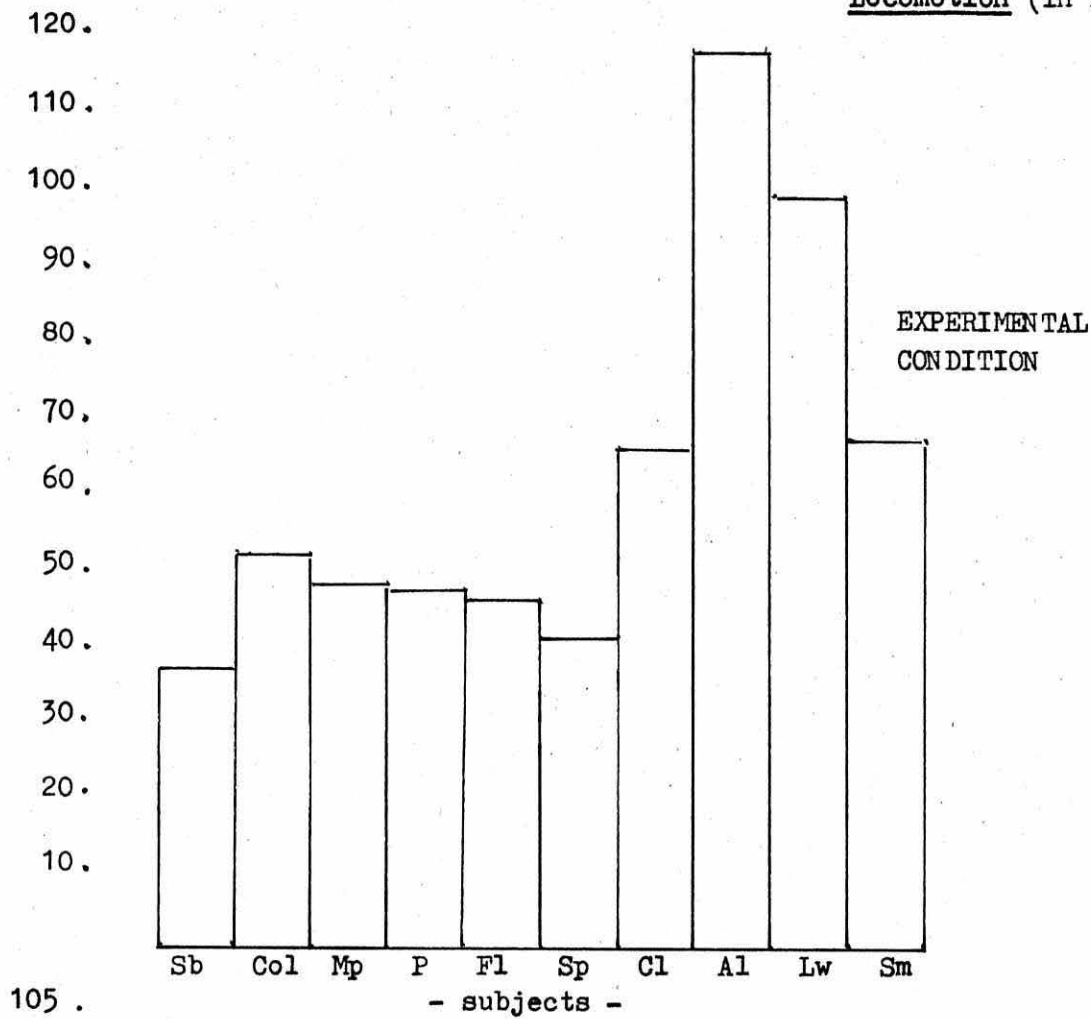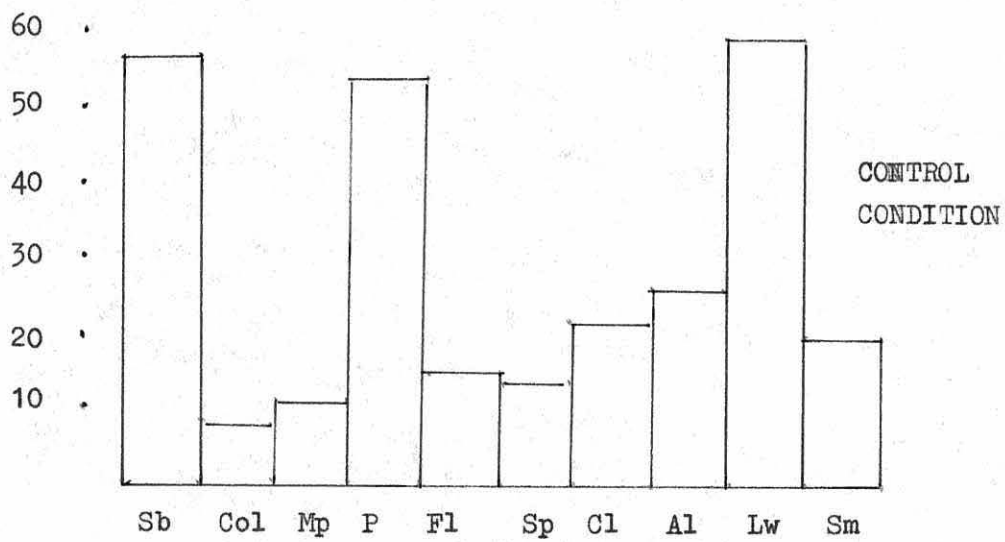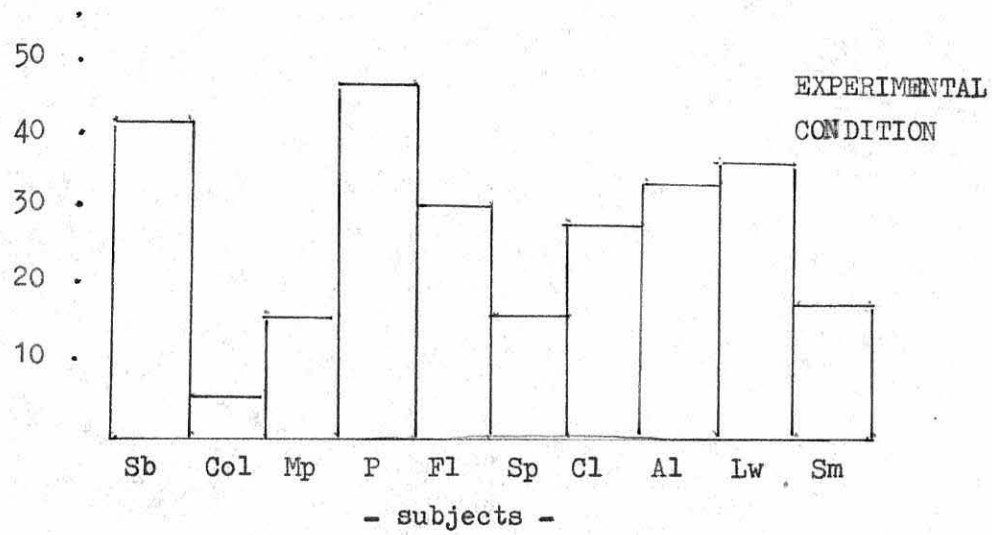
CONTROL
CONDITION

Immobility

As can be seen in Figure 5g there was more of this in the control condition. The difference is significant ($P < 0.005$, 1 tailed test. $\underset{T = 0; \; N = 10).}{\angle}$ Each animal showed more of this in the control condition than in the experimental condition. (see Figure 5h). Groups 1 and 2 were amalgamated.

Urination

As can be seen in Table 5ii the same three animals urinated in both conditions. The presence or absence of odour did not seem to affect this behaviour.

SUMMARY OF RESULTS

Behaviour which occurred at a significantly higher level in the Experimental Condition.

1. S-nosing
2. ano-genital dragging
3. u-marking
4. defaecation
5. locomotion

$P < 0.005$, 1 tailed test

6. grooming

$P < 0.01$, 2 tailed test

Behaviour which occurred more in the control condition

1. immobility

$P < 0.005$, 1 tailed test

No significant difference found

1. sniffing
2. urination

Table 5i　　　Grooming (sec.)

Subject	Experimental	Control
Sb	0	0
Col	20	2
MP	22	0
P	6	0
Fl	4	0
Sp	4	3
Cl	4	0
Al	8	0
Lw	4	2
Sm	0	0
TOTAL	72	7

Table 5ii

Urination (instances)

Subject	Experimental	Control
Sb	0	0
Col	1	1
MP	0	0
P	0	0
Fl	1	1
Sp	0	0
Cl	1	1
Al	0	0
Lw	0	0
Sm	0	0
	3	3

Figure 5g. Immobility (sec.)
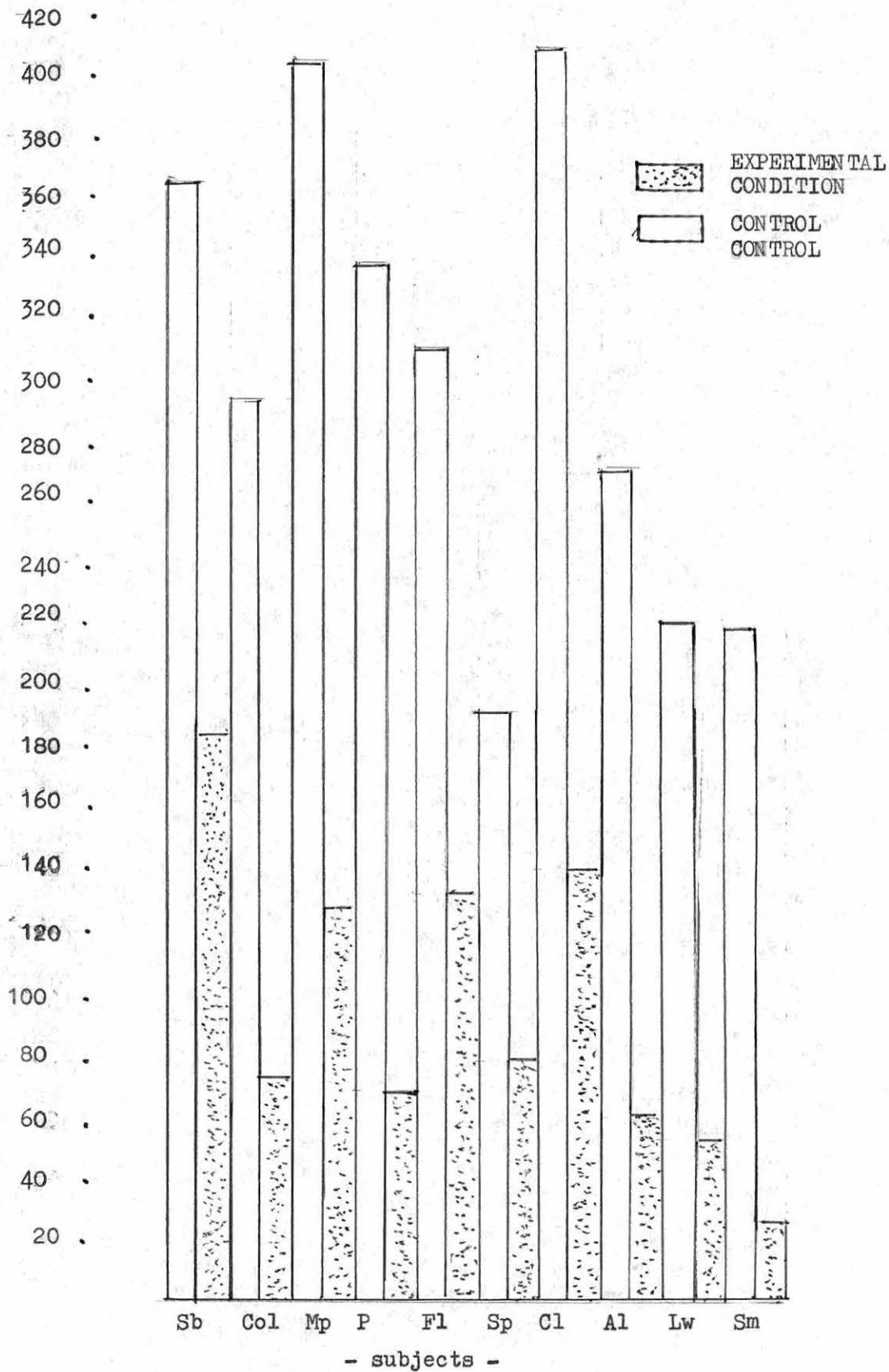
Figure 5h. Immobility over time

N = 10

- minutes -

EXPERIMENTAL CONDITION ————
CONTROL CONDITION — — — — — —
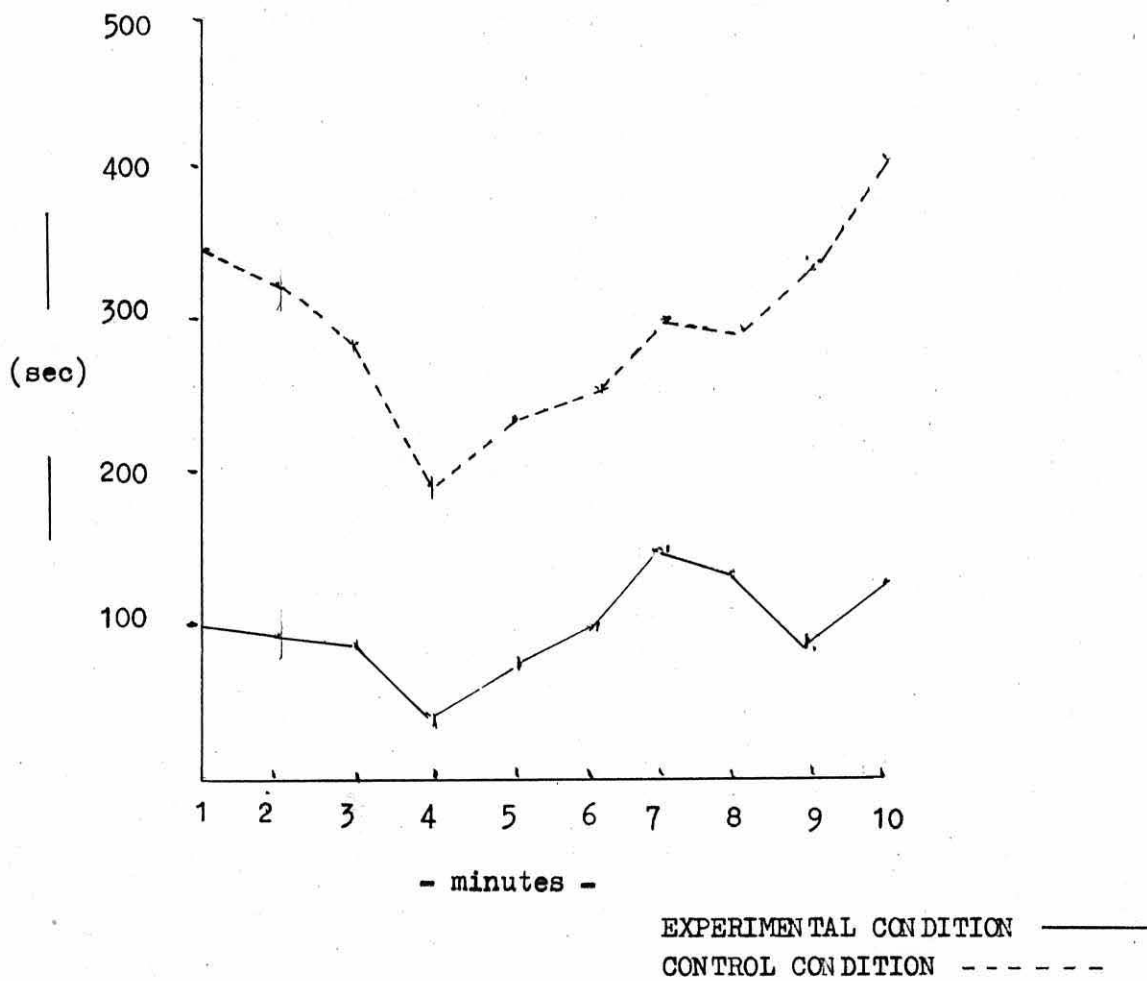
Qualitative Data

At the beginning of each session the guinea pigs tended to move cautiously, with the head extended and the body held low. Forward progress would be interrupted by brief pauses.

There was more immobility in the control session. However, for much of the time the animals did not appear to be freezing, but seemed to be uninterested, especially towards the latter end of the session. The animal stops moving around and simply appears to be waiting. Small movements occur from time to time. When an animal is freezing it is tensed, and there is no vibrissal movement.

This sort of behaviour was also observed in the experimental session, but to a lesser extent.

It could be seen that the s-nosing occurred over areas where a predecessor animal had defaecated, urinated, or even sat for a while.

Ano-genital dragging tended to follow s-nosing. Thus the animal would drag its ano-genital region over an area which it had been s-nosing, thus seeming to lay its own scent over the scent of the preceding animal. It is suggested on page 145 that s-nosing occurs in response to conspecific odour. Defaecation seemed to follow a similar pattern, although the pattern was not so clear.

The interest (as indicated by s-nosing) manifest by the guinea pigs in urination, defaecation and (when appropriate) glandular secretions was considerable. It was not possible to detect a preference for any one of these.

The guinea pigs showed pilo-erection and tooth-chattering in the experimental sessions. This occurred in close conjunction with ano-genital dragging.

The sniffing did not appear to indicate interest. It was cursory and was not pursued. When the guinea pigs were immobile they sniffed the air from time to time.

Although grooming was recorded and indeed shows a significant increase in the experimental condition, it did not seem to be of importance. What grooming there was occurred mainly in the experimental situation. Much of it appeared to be due to the animal's getting urine from a predecessor on its face or body.

The data were examined to ascertain whether a significant order of presentation effect existed. No such pattern was revealed.*

DISCUSSION

The data in Experiment I indicate that adult male guinea pigs respond to the scent of male conspecifics with ano-genital dragging and s-nosing.

It would seem reasonable to describe ano-genital dragging in terms of its function, that is, as scent marking. Johnson (1973) defines scent marking as "behaviour by which glandular secretions are deposited on the ground or on to objects in an animal's environment". As the guinea pig drags it ano-genital region over the ground it can be seen that the perineal pouch is everted, and that the glandular secretions are distributed along the ground.

* A key indicating the order in which the subjects underwent the two conditions is given in Appendix 5, page X.

What has been described as "urination with ano-genital dragging"
also occurred at a significantly higher rate in the experimental
condition.   This form of urination is very reminiscent of scent-
marking: small drops of urine are deposited in a line as the
guinea pig moves forward with the back legs flexed.   This form
of urination is markedly different from eliminative urination.
Urine is commonly used in scent marking.   Thus the Bahaman hutia
(Howe, 1974) marks in two ways, one of which involves moving slowly
forward depositing a trail of urine.   The Felidae mark with
urine (Kleiman and Eisenberg, 1973).

Urine would seem to have communicatory significance to the
guinea pig.   Guinea pigs have frequently been seen to pause and
sniff at a spot where another has recently urinated (Rood 1972).
Guinea pigs and C. aperea males often spray the female they are
courting with urine (Rood 1972; Beauchamp, Magnus, Shmunes &
Durham, 1977).   Females may squirt urine to repulse an approaching
female or male (Pearson 1970; Rood 1972; personal observation).

Thus it is concluded that the urination described in the
present investigation represents a form of marking behaviour.
To distinguish it from scent marking by ano-genital dragging it
will be called U-marking.   U-marking differs from normal
urination in the two ways suggested by Kleiman in his definition
of scent marking.   Thus Kleiman (1966) suggested "a definition of
scent marking which stated that odour can be dispersed by
urination, defaecation, and the secretion of glandular material ...
In all cases marking should be distinct from normal actions such
as grooming or elimination by virtue of qualitative and quantitative
changes in the behaviour".

It is possible that the defaecation observed in the present study is also a form of scent marking: as did marking and U-marking, defaecation occurred at a significantly higher rate in the experimental condition.

Barrette (1970) states that urination and defaecation occur consistently in association with marking with the facial glands in the muntjac. She defines marking as "the deposition of scented secretions and excretions in the environment". This definition is broader than that of Johnson (1973), and while many species do have specialized scent glands (for example the gerbil, the hamster, the muntjac, the lemur) it would seem to be equally true that many use eliminative products in scent marking, or a combination of the two.

The Canidae (for example the dog, the wolf, the jackal) use urine and faeces in scent marking (Kleiman and Eisenberg, 1973; Fiennes and Fiennes, 1968; van Lawick-Goodall and van Lawick, 1970). Many of these have anal scent glands; thus the golden jackal has two anal scent glands which may add secretions to the faeces.

Mykytowycz (1968) showed that the Australian wild rabbit marks its territory with faecal pellets. Secretions from the anal glands coat the faecal pellets passing out of the anus. It may be, therefore, that the guinea pig also uses faecal pellets in scent marking.

The results obtained in this study indicate that defaecation in response to odour of male conspecifics is distinct from normal elimination in that it increases in response to odour, and thus

fulfils one of Kleiman's (1966) criteria. It does not differ from elimination in the qualitative sense that U-marking differs from eliminative urination.

Although the data obtained in the present experiment suggest that defaecation may be a form of scent-marking, additional information is needed. One might expect to find a correlation between marking and defaecation, that is to say, those animals which showed a relatively high level of marking may also show a relatively high level of defaecation. Inspection of the data does not indicate a correlation. The Spearman Rank Correlation Coefficient confirms that there is no correlation between marking and defaecation, $r_S = 0.124$ (Siegel, 1956).

Nonetheless defaecation followed the same pattern as marking in that there was more of it in the experimental situation. If it is not a form of scent marking then there must be another reason why it was found to occur at a significantly higher rate in the experimental condition. A possible explanation is that emotionality was responsible for the raised incidence of defaecation. However, unlike Broadhurst's (1957) rats, the evidence available indicates that in a novel or "fearful" situation defaecation is inhibited in guinea pigs. Tobach and Gold (1966) report that the guinea pigs in their study showed the immobility response, and so little eliminative behaviour as not to permit analysis. Pearson (1970) suggests that evocation of the immobility response leads to the inhibition of eliminative behaviour. The writer, too, has observed that while a guinea pig may be immobile for extended periods of time in an unfamiliar situation, elimination very rarely occurs.

This shows beyond all reasonable doubt that the higher rate of defaecation in the experimental situation was not due to emotionality, but suggests the possibility that defaecation was inhibited in the control situation, while occurring at a relatively normal rate in the experimental situation. This must be considered as a possibility, especially as the reduction in defaecation is associated with an increase in immobility.

A supplementary experiment (Ia) was carried out to investigate this. The details of this are given on pages 157 to 159. While not conclusive the data obtained in this supplementary study indicate that the difference observed in Experiment I between defaecation in the control and experimental conditions, was not due to inhibition of defaecation in the control situation, but that the rate in the experimental situation was accelerated. Thus it is possible to conclude tentatively that defaecation increased in response to the scent of male conspecifics. It is therefore possible that defaecation in the guinea pig is used in scent marking. This is supported by the observation that the guinea pigs showed apparently equal interest in faecal pellets, urine, and ano-genital secretions. It has not been established however, and is offered here as a possibility.

S-nosing clearly occurred in response to the scent of a conspecific. The occurrence of s-nosing in the control condition was insignificant. The fact that nosing was seen to occur over areas where the predecessor animal had been suggests that it occurs solely in response to the odour of a conspecific. The stereotyped nature of the behaviour supports this view. If

this is so, then it would not be expected to occur during the control condition. What s-nosing did occur in the control condition seemed to be in response to traces of the subject's own odour. Pearson (1970) has reported that animals often pause during locomotion to invesitgate their own faecal boli. They are also interested in their own urine.

S-nosing has been described by other workers. Avery (1925) describes "sniffing and licking excretions". Pearson (1970) writes that Avery was mistaken in this, and suggests that he was misled by the fact that the guinea pig often gets so close to a faecal bolus that he moves it with his nose. However, licking does occur during s-nosing, although not always. The writer has observed it on many occasions.

Kunkel and Kunkel (1964) defined nosing as "sexual smelling". When females were seen to perform it they concluded that it was non-sexual. However, it would seem that, sexual or not, it is a social activity, and perhaps could be described as social sniffing. Beauchamp (1973) suggested that this behaviour might be related to sexual arousal.

There is a difficulty in terminology here. The writer initially referred to this behaviour as "nosing". However, other investigators use the term nosing to mean different things. Thus Rood (1972) uses nosing to refer to a form of grooming when the nose is rubbed through the hair. Harper (1966) terms contacting another animal with the snout as nosing, and Pearson uses the term when an animal slides the side of the nose along the length of another animal.

Pearson (1970) refers to the activity under discussion as "nodding movements", but although this has descriptive veracity in that the head does seem to nod back and forth, this term does not convey the essential nature of the behaviour. The same is true of the term "head bobbing" used by Beauchamp (1973). The common use of "nosing" (defined in the Oxford Dictionary as "sniffing or investigating with the nose") seems to describe the behaviour well. However, in order to avoid confusion, it was decided to term this behaviour scent-nosing, thus the more convenient s-nosing.

It has been shown that marking, defaecation and s-nosing increase in response to the scent of a conspecific. It is not possible on the basis of the data so far obtained to indicate what function the behaviours serve. It is clear, however, that they are social, involving communication through olfactory stimuli. This can be inferred from the observed behaviour of the animals. Communication can be defined as behaviour which transmits stimuli from one social source which alters the behaviour of the recipient. Scott (1968) defines communication as including any stimulus arising from one animal and eliciting a response in another.

The behaviour discussed thus far has had a social content involving chemical stimuli and responses to this. However, locomotion also occurred at a higher rate in the experimental situation. Although locomotion itself is not a social behaviour, in view of the high social content of the responses emitted in the experimental situation, it is possible that social factors contributed to the increase in locomotion; that

a higher level of arousal in the experimental condition resulted in greater locomotion.

However, in discussing this, a problem due to the experimental design intrudes. The independent variable was odour. All other stimuli of conspecifics were absent. Thus in the control condition there were no stimuli from conspecifics. Therefore it could be said that the control condition was more novel than the experimental condition. The novelty in this condition is an unwanted variable. However, every attempt was made to control for this by giving the animals acclimatisation sessions. If this successfully reduced the novelty of the situation, then it would be expected that locomotion would not differ significantly from locomotion emitted in the experimental situation except in response to the independent variable. However, if the acclimatisation sessions were inadequate to reduce the novelty, and if as a result novelty occurred differentially between the two conditions, then this would affect the findings.

This problem has already been encountered with regard to defaecation. The supplementary study provided additional data to clarify the situation. With regard to locomotion the graph (Figure 5j) is of interest. As can be seen, locomotion in both control and experimental conditions is approximately the same during the first minute of the ten minute session, but behaves differently over the remaining minutes of the session. The pattern in the control condition resembles that found in studies investigating exploratory behaviour where activity declines over time (Berlyne, 1955; Kumar, 1970). The pattern in the experimental condition shows less evidence of declining. If

Figure 5j. Locomotion over time
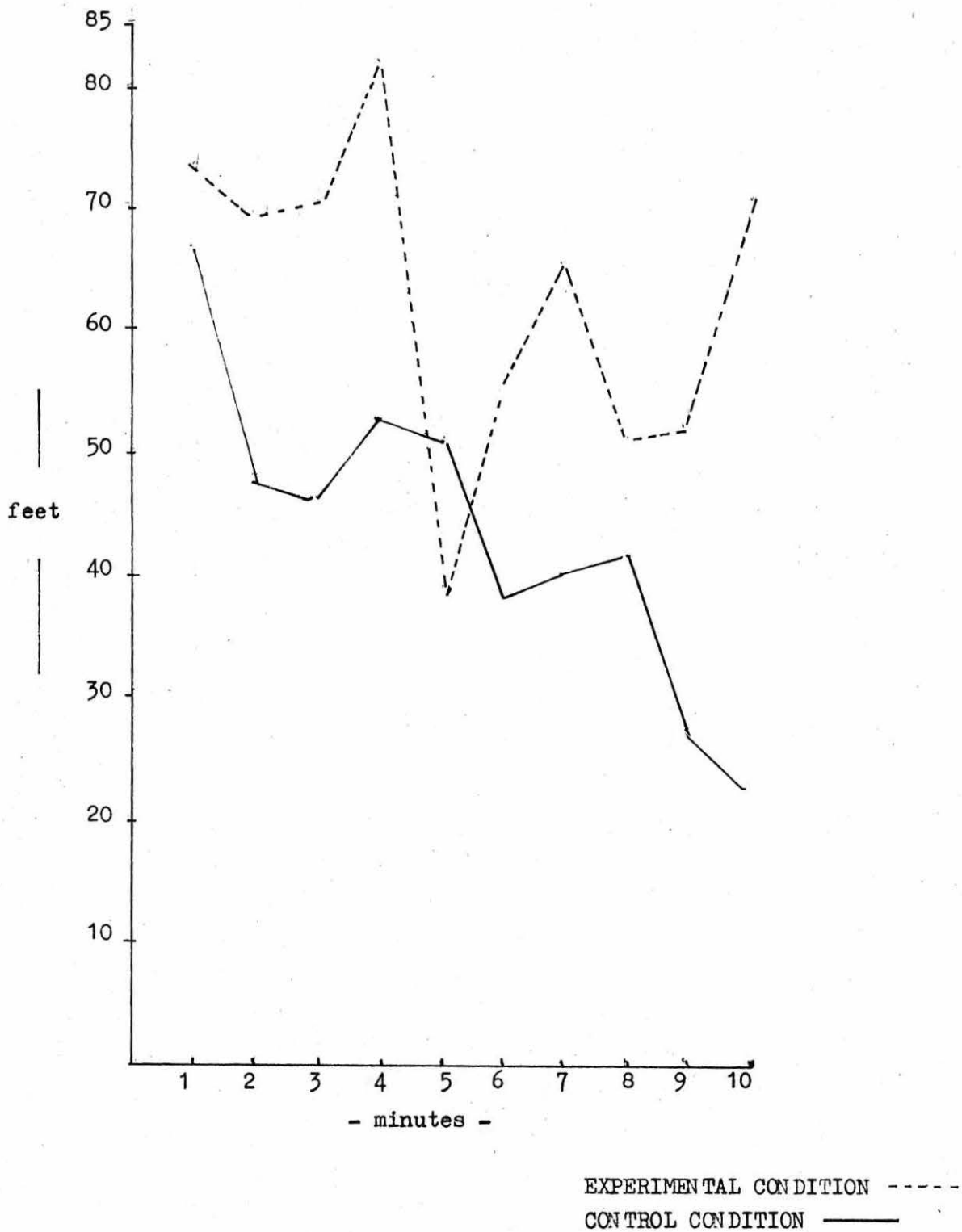
novelty were responsible for the lower level of locomotion and increase in immobility then a different pattern would have been expected. It is not possible to draw any conclusion on the basis of these data, but they seem to indicate that locomotion in the control condition is behaving in a similar way to exploration*, but that it is not doing so in the experimental condition. For the present it can be said that it is possible that the increase in locomotion in the experimental condition may in part be due to social factors. This will be investigated in the next chapter.

There is also some evidence that some animals are more active than others. Thus, the animal with the highest score in the experimental condition also locomoted most in the control condition. Those with a low locomotion score in the experimental condition, locomoted relatively little in the control condition.

Inspection of the data for the older and younger animals (groups 1 and 2) is of interest (see Table 5iii). Generally speaking the younger animals emitted the same or a lower level of behaviour than the older animals. However, as can be seen from the locomotion data they were almost twice as active as the older animals. This is in accordance with what would be expected. The writer has observed that young animals are more active than older ones. Experiments have shown that maximum activity in the rat occurs between fifty-one and one hundred-and-sixteen days of age (Williams, Carr and Peterson, 1966). Goodrick (1967) obtained data which show that after reaching maturity exploration decreases with increasing age.

* locomotion is used as an indice of exploration in many studies.

Table 5iii

Comparison of the mean scores for the younger animals (Group 2) with the scores for the older animals (Group 1).

Behaviour	Animals (Group)	Experimental condition	Control Condition	
S-nosing	1	107.0	10.0)	seconds
	2	60.0	4.0)	
Ano-genital dragging	1	14.5	1.5)	instances
	2	11.0	1.0)	
urination associated with dragging	1	1.6	none)	instances
	2	1.7	none)	
Defaecation	1	5.7	0.29)	faecal
	2	6.3	0.33)	pellets
Locomotion	1	48.3 *	34.8)	feet
	2	95.0	62.5)	
Sniffing	1	26.4	25.1)	seconds
	2	29.3	34.0)	
Immobility	1	115.7	332.1)	seconds
	2	48.0	238.6)	
Grooming	1	8.6	0.7)	seconds
	2	4.0	0.7)	

As can be seen in Table 5iii, with the exception of locomotion, the Group 2 animals tended to emit less behaviour in the experimental and control conditions than did the Group 1 animals. The direction of change from one condition to another was the same in both groups.

Nonetheless, despite the higher level of locomotion shown by the younger animals, the direction of change between the experimental and control conditions is the same as for the older animals. This can be seen in Table 5iii. The results are confirmed by those of Beauchamp Criss & Wellington (1979) who found no age trends in guinea pigs' response to chemical stimuli.

It is interesting that no significant difference was found between the two situations in respect of sniffing. As defined in the present study it is not a social activity, therefore it would not be expected to increase in the experimental situation in response to the odour of guinea pigs. Nonetheless, in view of the increase in activity, it might have been expected that more sniffing would occur in the experimental condition. However, the low incidence of sniffing in the experimental condition is probably due to the high incidence of snosing, which can be described as a stereotyped form of sniffing. Inspection of Figure 5k reveals a considerable degree of correspondence between subjects' individual scores in both conditions.

The incidence of grooming was also low; although there was significantly more of this in the experimental situation (there was virtually none in the control) only 1.2% of the time was spent in grooming. This suggests that it is of little significance. This view is supported by the observations recorded in the section on qualitative data where it was said that some of the grooming seemed to take place when an animal was contaminated with the urine of a predecessor. However, it is possible that grooming does have some significance, and if this is so then the

Figure 5k. Sniffing   (sec)
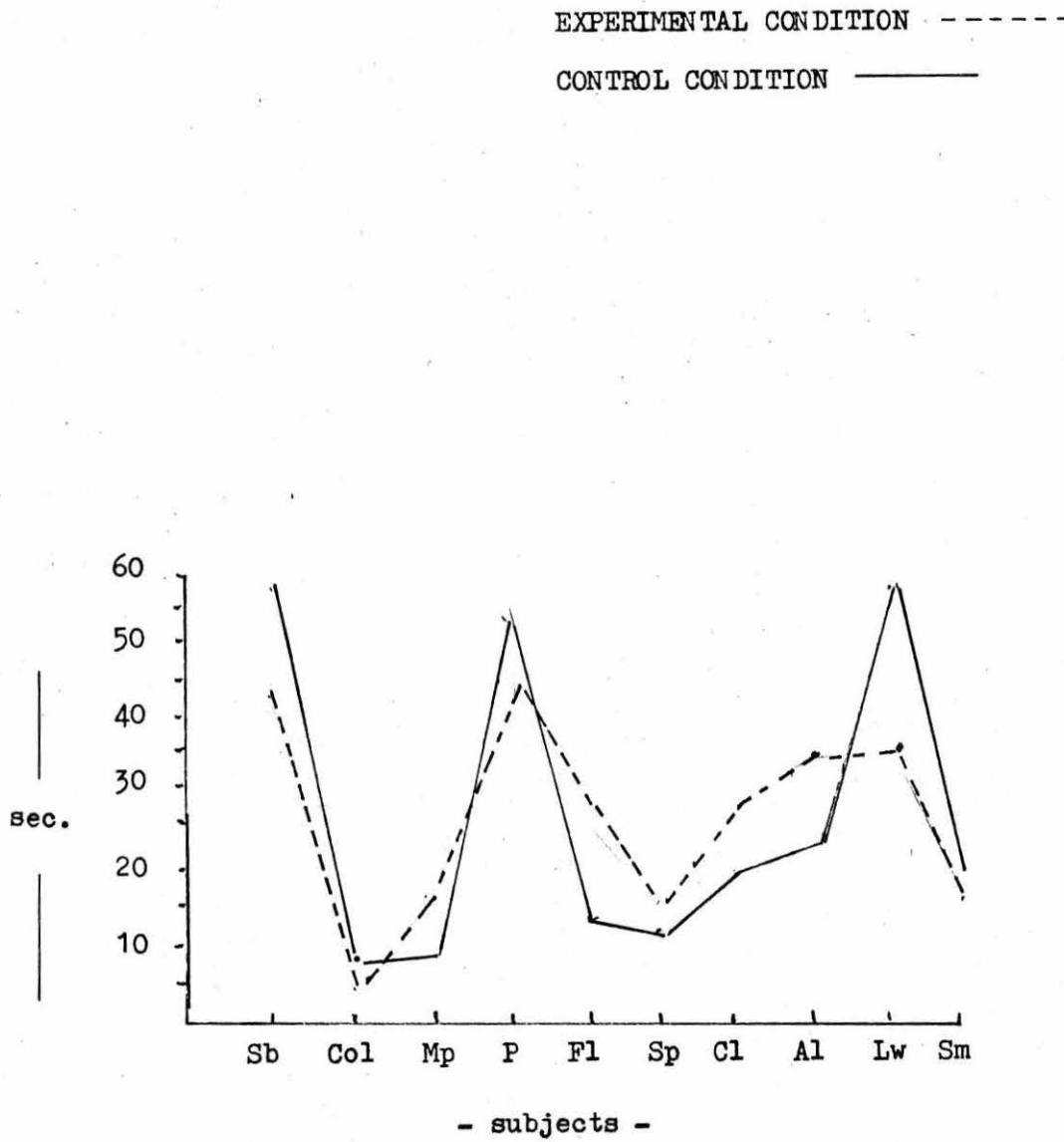
pattern of its occurrence in forthcoming experiments might indicate what this is.

There was significantly more immobility in the control condition. In the control condition no sight, sound, nor odour of conspecifics was present, and as has been said the guinea pig is likely to remain immobile in such a situation. This was countered by the acclimatisation trials but it is possible that the greater immobility in the control situation was due to increased novelty.

Here it is pertinent to point out that there is some question concerning the nature of the immobility. In the beginning of the present investigation a distinction was made between freezing and a behaviour described as pausing. Here the animal is not engaged in any obvious ongoing activity, but the characteristics of freezing are not present. Freezing and pausing were recorded separately. However in view of the fact that they are at times difficult to distinguish, they have been combined as one response, namely immobility.

Pearson (1970) writes that "it is impossible to determine by observation alone whether or not any animal is frozen". In their investigation into the guinea pig's immobility response to sound, Miller and Murray (1966) comment that this response "varies from a brief pause in ongoing activity to a full-blown response with a characteristic posture in which the back is arched, the head is up, and the front legs are extended;". Such an extreme response was not seen in the present study, but there was a considerable degree of variation in the severity of the response which suggests that further investigation would be helpful.

A suitable means of investigating this behaviour would be to monitor the heart rate of the guinea pig in various situations which are likely to result in immobility, and record those changes in behaviour which occur, however slight, in conjunction with changes in heart rate. The investigation by Fara and Catlett (1971) is of particular interest in this context.

It is perhaps of interest here to refer to the comments on immobility in the qualitative results section. For much of the time recorded as immobile the animals did not seem to be freezing; they simply were not active and appeared to be uninterested. However, this is a subjective comment.

It is clearly futile to speculate on the relationship between immobility and activity. Clearly, if an animal is active it is not immobile, and vice versa. If it were possible to discriminate accurately between freezing and pausing, then it might be possible to draw some conclusions concerning its incidence in the control and experimental conditions. It is possible that the investigation to be carried out in the following chapter will clarify the picture with regard to immobility.

Conclusion

The guinea pig emits behaviour in response to the odour of a male conspecific. Marking includes ano-genital dragging and U-marking. It is possible that defaecation is also used in scent marking.

S-nosing occurs in response to the odour of male conspecifics. It is a stereotyped response, and it is possible that it occurs only in response to the odour of conspecifics.

Pilo-erection and tooth chattering occur in conjunction with marking.

Locomotion would seem to increase in the presence of the odour of male conspecifics, but whether this is a genuine increase (rather than representing a reduction in the control condition) is not clear, and will be further investigated.

It is suggested that marking and s-nosing are social responses, involved in the chemical communication of information.

The fact that findings initially obtained with older animals which had been used in previous experiments were replicated with younger, naive animals, increases the generality of the findings.

The following chapter describes two experiments carried out to clarify the results obtained in the present investigation.

The first is to ascertain whether the behaviour recorded in the present study represents a specific response to conspecific odour or a generalized response to olfactory stimuli.

The second seeks to clarify the pattern of locomotor activity emitted in Experiment I, and in so doing to ascertain whether the novelty in the control condition significantly affected the data.

Experiment Ia

A supplementary experiment was carried out to compare the rate of defaecation emitted in Experiment I with the rate in the home cage.   The experiment was designed as follows:

Defaecation was measured over periods of (a) ten minutes, (b) one hour and (c) twenty-four hours.

(a)   A guinea pig was placed in a fresh cage for ten minutes.   This took place at the normal experimental time, and resembled the conditions of Experiment I in that it took place at the same time of day and for the same duration.   Faecal boli were counted at the end of the ten minutes.

(b)   A guinea pig was left for one hour in a fresh cage.   Defaecation was again measured.

(c)   A guinea pig was left in a fresh cage for twenty-four hours, at the end of which an approximate measure of the number of faecal boli was obtained.

Six of the animals used in Experiment I were used as subjects. This study was carried out shortly after the conclusion of that part of Experiment I using the Group 1 subjects.

RESULTS

Defaecation (number of faecal boli)

Subject	a	b	c	mean defaecation per hour over twenty-four hours.
Sb	4	8	80	3.3
Col	0	12	70	2.9
Mp	1	4	130	5.4
Fl	1	5	102	4.2
Sp	0	11	127	5.3
Cl	1	21	130	5.4

Table 5iv   Defaecation in the home cage during periods a, b, and c.

Defaecation (number of faecal boli)

Subject	Experimental condition	Home cage (a)	Control Condition
Sb	3	4	0
Col	12	0	0
Mp	9	1	2
Fl	6	1	0
Sp	5	0	0
Cl	2	1	0

Table 5v : Defaecation in Experiment I compared with defaecation in home cage (a).

Defaecation in the home cage during ten minutes was considerably lower than that emitted during the ten minutes of the experimental session in Experiment I, and very similar to that emitted in the control condition.

If the rates of defaecation emitted over the three periods spent in the home cage are compared with the rate in the experimental condition in Experiment I, it can be seen that it occurred at a considerably higher rate in the latter.

———————

Chapter 6

At the end of Chapter 5 it was concluded that marking and s-nosing occur in response to the scent of a male conspecific. Locomotor activity also shows an increase in response to this stimulus.   It is perhaps possible that while the guinea pigs' level of arousal was increased by this odour the behaviour emitted represented a generalized response to novel odour, rather than a specific response to conspecific odour.   Before investigating the function of scent marking in the guinea pig it would seem advisable to clarify this point, and to this end the following experiment was carried out.

Experiment II

The investigation required provision of the odour of another species, with care taken to ensure that this could in no way be considered as a predator.   There is some evidence that rats freeze in response to the odour of a cat (Griffith, 1920; Curti, 1935).   It was decided to use hamsters to provide the stimulus both for this reason, and because they were available in the laboratory at the time.

METHOD

Subjects

Six subjects which had taken part in Experiment I were used. They were maintained in the same conditions as described in Experiment I and were tested at the same time of day.

Apparatus

The grey open field as described in Experiment I was used, with the base covered with white cartridge paper.   The stimulus

odour was provided by placing a male hamster in the open field
for ten minutes.

Procedure

The subjects were given 5 10-minute acclimatisation sessions
prior to taking part in the experiment. The apparatus was
prepared and the subjects were carried into the experimental room
in the base of the home cage. They were placed in the open
field for 10 minutes, following the same procedure as in Experiment I.

The behaviour emitted was compared with that emitted by the
same animals in the control (no odour) condition in Experiment I.
The Wilcoxon Matched-Pairs Signed-Ranks test was used to determine
whether observed differences between the no odour and hamster odour
were significant.

RESULTS

Scent-marking and defaecation

Only one animal showed any marking or defaecation in the hamster
odour condition. These were both emitted by the same animal during
the first minute of the session (two instances of marking, two of
defaecation).

S-nosing

There was very little emitted in the hamster odour condition,
less than in the no-scent condition in Experiment I. The
difference is not significant ($T = 5; N = 6$). These data are given in Table 6i.

Locomotion

There was very little of this behaviour in the odour condition,
and considerably less than in the no-scent condition. The
difference is significant ($P < 0.05$; 2 tailed test. $T = 0; N = 6$). These
data are given in Table 6ii.

Sniffing

Although there was slightly less in response to the odour than

in the no scent condition the difference was not significant
(see Table 6iii) $(T=7.5; N=10)$.

Immobility

All subjects showed more immobility in response to the scent
of another species than in the no scent condition.   Eighty seven
per cent of the experimental session was spent immobile compared
with fifty-two per cent of the time in the no scent condition.
The difference is significant $(P < 0.05$;   2 tailed test, $T=0; N=6)$.   These
data are given in Table 6iv.

Qualitative Data

The most noticeable aspect of the behaviour of the animals
was the marked tendency to become immobile.   During immobility
an animal would show foot movements.   Thus the right foot might
be lifted and replaced, or the left.   Sometimes both, with one
following quickly on the other.

When the animals locomoted the behaviour was noted as "very
hesitant and slow".   The head was held near the ground, and
stretched forward.

It was recorded that one animal (MP) was s-nosing his own
scent.   There was no grooming.

Table 6i
S-nosing (in seconds)

Subject	No scent	Hamster scent
MP	6	6
Cl	8	5
Seh	4	0
Sam	12	0
Col	10	12
Sp	2	9
	42	32

Table 6ii

Locomotion (in feet)

Subject	No scent	Hamster scent
Mp	$32\frac{1}{2}$	2
Cl	34	$9\frac{1}{2}$
Sb	$21\frac{1}{2}$	0
Sm	47	0
Col	53	15
Sp	$23\frac{1}{2}$	$18\frac{1}{2}$
	$211\frac{1}{2}$	43

Table 6iii

Sniffing (in seconds)

Subject	No scent	Hamster scent
Mp	11	4
Cl	21	18
Sb	56	16
Sm	19	27
Col	8	0
Sp	13	22
	128	87

Table 6iv

Immobility (in seconds)

Subjects	No scent	Hamster scent
Mp	406	580
Cl	411	473
Sb	367	585
Sm	221	535
Col	295	540
Sp	193	443
	1893	3156

DISCUSSION

All activity was depressed in response to the scent of another species, with a considerable increase in immobility. This suggests that the scent of the hamster was aversive. Although the hamster is in no way a predator with regard to the guinea pig, nonetheless the scent of an unknown animal could be that of a predator, in which case defensive behaviour would be an appropriate response. Freezing in the guinea pig would seem to represent a form of defense, with flight as its only alternative. Both behaviours occur in the natural environment (Rood, 1972). Miller and Murray (1966) point out the adaptivity of immobility. The immobile guinea pig offers fewer stimuli to predators, and it may increase his own ability to observe the environment.

Very little research has been carried out into the response of animals to odours of another species. This is perhaps not surprising, as it is unlikely to be relevant to the complex within species social relations of a given species. However, such odours could possibly be used in defensive or avoidance behaviour. Jones and Nowell (1974) included urine from rats and hamsters in their investigation into urinary aversive pheromones in mice. No preference for a clean or urine treated half of an open field was found for the rat or hamster urine. Beauchamp (1973) found that adult male guinea pigs virtually ignored the odour of human male urine and that of Galea musteloides (Caviinae). However, Beauchamp's experiment was not designed so as to indicate the nature of the animal's response to the urine, apart from interest or lack of interest. It is not known, therefore, whether the guinea pigs used in his study would have shown similar levels of

immobility to human or _Galea_ urine as the guinea pigs in the
present investigation showed in response to the odour of a hamster.

While it is not possible to draw firm conclusions from the
foregoing experiment it would seem reasonable to conclude that
the above findings support the conclusion drawn from the data
obtained in Experiment I that the animals were responding
specifically to the scent of their own species, and that their
behaviour was not a generalized response to a strange odour.

Part II

Experiment I revealed that the male guinea pig responds with more s-nosing, marking, defaecation and locomotion to the scent of a conspecific in comparison with a no-scent condition. It was suggested that s-nosing and marking are social responses, occurring in response to olfactory stimuli of an adult male guinea pig. It was suggested that the increase in locomotion might also be related to social factors. It was also pointed out that a greater tendency to immobility in the control condition might have been the reason for the reduced level of locomotion, rather than the dependent variable giving rise to an increase. However, the pattern of locomotion suggested that this was not wholly the case. Whereas in the experimental condition there was no marked decline over time (see Figure 5x) in the control condition loco- motion declined over the ten minutes. Thus as the novelty of the situation is presumed to have waned locomotion decreased rather than increased. Thus it does not seem likely that novelty, resulting in greater immobility, can wholly account for the lower level of locomotion in the control condition. In parallel with the drop in locomotion immobility increased over time in this condition.

It was decided to investigate the problem. The rationale of this experiment is based on the fact that exploratory behaviour is known to decline with repeated exposures to a stimulus situation, and that locomotion is widely accepted as an indicator of exploratory activity (Berlyne, 1955; Montgomery 1953; Broadhurst, 1957; Adlerstein & Fehrer, 1955).

The experiment involves comparing the response of guinea pigs over five successive trials to the open field when it contained

odour with when it did not.   So as to avoid confusion with
Experiment I the experimental conditions will be described as
scent absent and scent present.

The following predictions were made:

A.   If locomotion increased in response to social stimuli
     (odour) it is expected that it will differ both
     qualitatively and quantitatively in the two conditions,
     thus 1.   In the scent absent condition it would show
               a decline over the five sessions, while the
               level would be maintained in the scent present
     and 2.   There would be more locomotion in the scent
               present condition.

B.   If s-nosing is a social response then it will occur
     significantly more in the experimental condition and
     (2) the level will be maintained in the scent present
     condition.

C.   Marking and defaecation, if social behaviour, would be
     expected to follow a similar pattern to s-nosing.

It was not, of course, possible to use each subject as his
own control, therefore matched pairs were used.   The subjects
were matched according to those variables which might be expected
to influence their behaviour, such as age, previous experimental
experience, and size.   Thus two rather large animals which moved
slowly and ponderously were paired, with one assigned to each
condition.   With regard to one pair it was not possible to match
for age, as there were three animals younger than the remainder.
In case there was an effect due to greater activity in younger
animals the odd young animal was included in the scent absent

group where activity was expected to be relatively low;   this was
so as not to bias the findings in the direction of the prediction.

Experiment III

The purpose of this experiment was to investigate the pattern
of the response of male guinea pigs to olfactory stimuli of male
conspecifics compared with a no-scent condition during five
sessions in an open field.*

METHOD

Subjects

Eight male guinea pigs acted as subjects.   They had been used
in previous investigations.   The conditions under which they were
maintained were identical to those described in Chapter 5, and
they were tested at approximately the same time of day as in the
previously described experiments.   They were divided into two
matched groups.

Apparatus

The square open field constructed of grey perspex was used.
The base was covered with white cartridge paper.   The conditions
were the same as those described in Chapter 5.   The scent of a
conspecific was provided by the preceding animal undergoing the
scent absent condition.

Procedure

The subjects were each given one acclimatisation session of
5 minutes.   The apparatus was prepared and each subject was carried
to the experimental room in the base of its home cage.   It was

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* This experiment was planned after completion of Experiment I
but was carried out at the end of the series because it
involved five successive exposures to the open field.   Six
weeks were allowed to elapse before conducting this experiment.

lifted from its cage and placed into the corner of the field,
with its face towards the centre of the field.

At the conclusion of each session the animal was returned to
its cage and the animal room.   The behaviour was recorded on
cyclostyled sheets as described in Chapter 4.   The behaviour
recorded was as follows: locomotion, s-nosing, marking,
defaecation and immobility.   The trials were carried out on five
successive days.

Statistical tests were not employed to evaluate the data
in view of the small N.   The data will be presented graphically.
The numerical data can be seen in Appendix 6.

RÉSULTS

S-nosing

The histogram (Figure 6a) shows that the pattern of s-nosing
in the scent present and scent absent conditions does not differ
markedly.   The difference lies in the amount of s-nosing with
very much more in the scent condition (16.7% compared with 2.0%).

Marking (including ∨ marking)

Marking occurs at a considerably higher level in the scent
present condition, and very little occurs in the scent absent
condition.   This can be seen in Figure 6b.   Marking shows a
tendency to increase over the five sessions of the scent present
condition.

Defaecation

It can be seen in Figure 6c that there was considerably more
of this in the scent present condition where it increased daily
over the five sessions.   It occurred at a low level in the
scent absent condition.
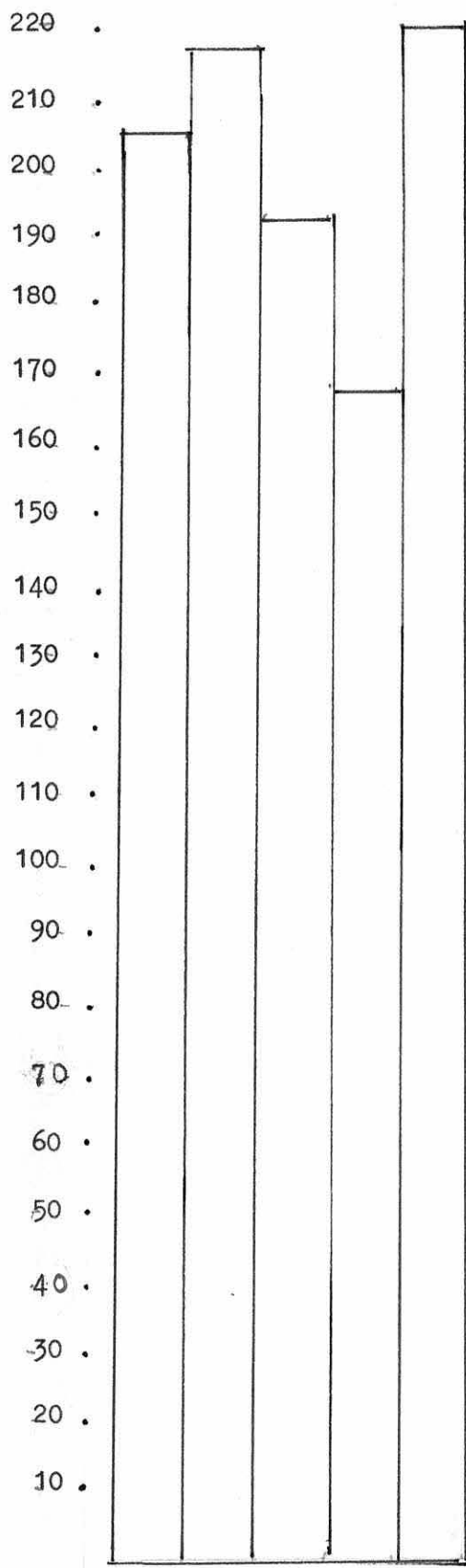
Figure 6a. S-nosing
(sec)
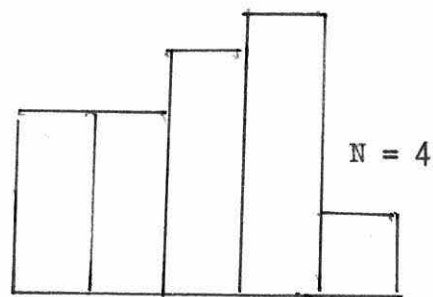
- Days -

Scent present   N = 4

Scent absent   N = 4

N = 4

Figure 6b Marking, including U-marking

Scent present   N = 4
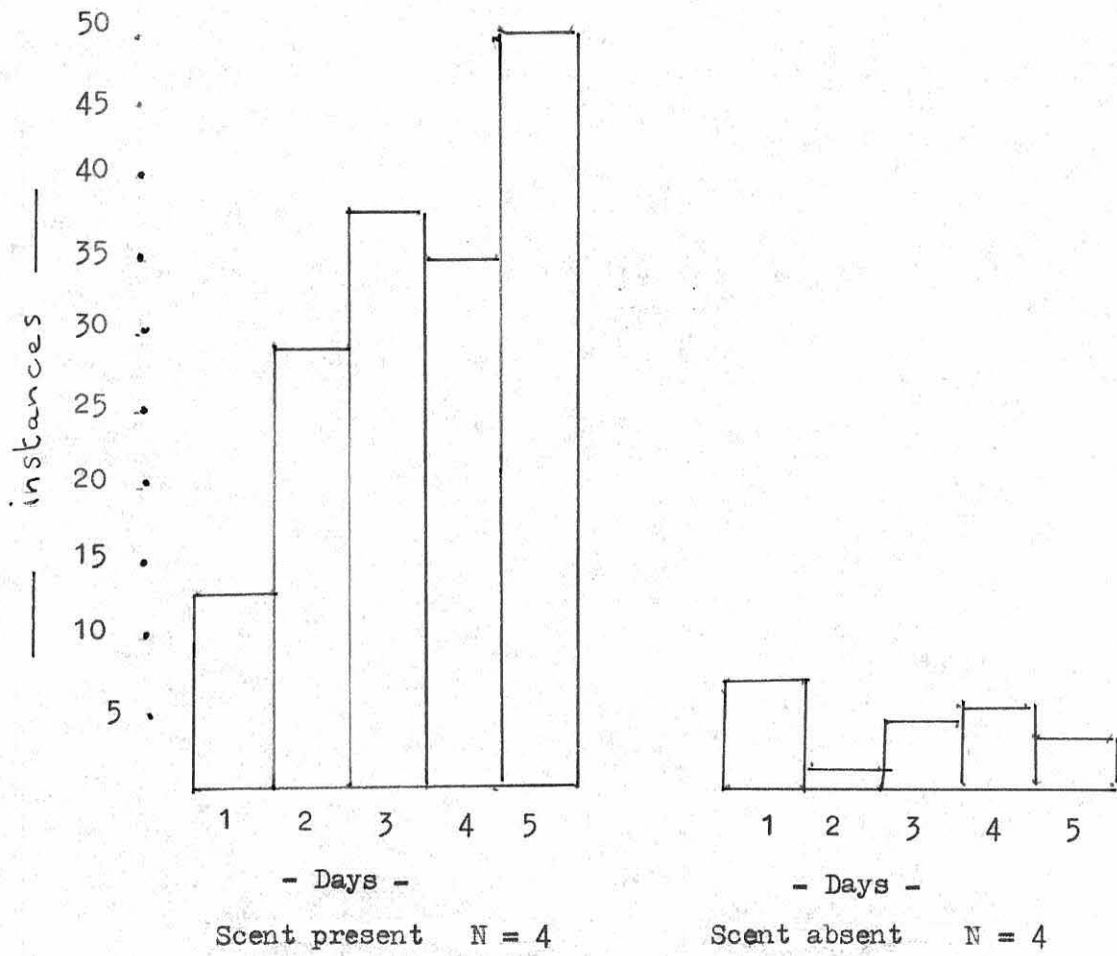
Scent absent   N = 4

Figure 6c. Defaecation (no. of pellets)

– Days –

Scent present   N = 4

– Days –
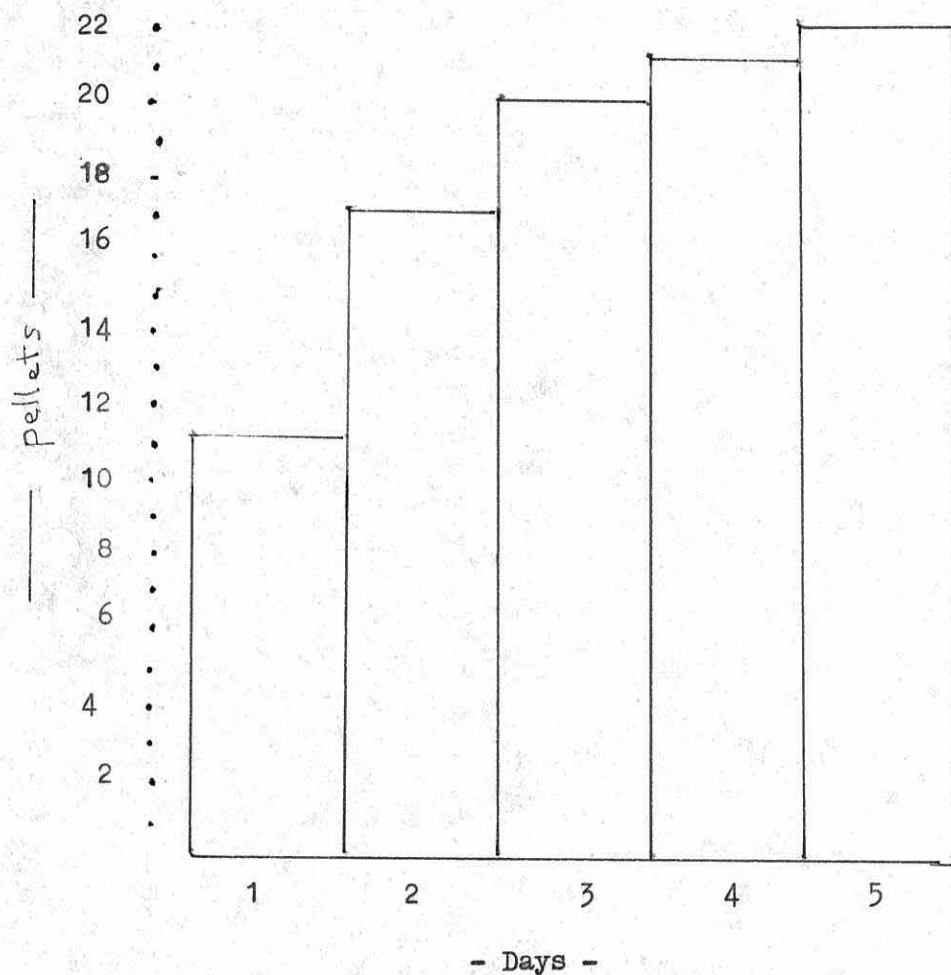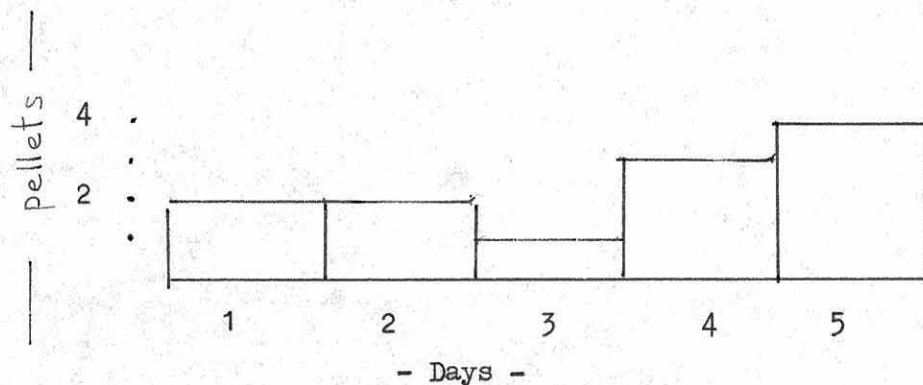
Scent absent   N = 4

Locomotion: scent present

There was more locomotion in this condition.   Figure 6d reveals that despite this overall difference there was less locomotion during Trial 1 of this condition than in the scent absent condition.   However, over the five days locomotion increases from $105\frac{1}{2}$ feet to $216\frac{1}{2}$ in this condition.   There is a slight drop in session 4, but overall a decided increase.

Locomotion: scent absent

Over the five trials locomotion drops from $145\frac{1}{2}$ feet to 57 feet.   As can be seen in Figure 6d it drops steadily over the five sessions.   It can be seen in Appendix 6 (p. xxxi) that one animal shows a particularly high level of locomotor activity in this condition.   This was one of the younger animals.   It accounts for the fact that locomotion on Trial 1 is higher in the scent absent condition than in the scent present.   This animal's locomotion declines over sessions 4 and 5.   This animal was also very active in both Control and Experimental conditions in Experiment 1.

Sniffing

Little sniffing occurred in either condition, but there was slightly more in the scent absent condition (see Figure 6e).

Immobility

Figure 6f reveals that the pattern is different in the two conditions.   In the scent present condition immobility declines, whereas in the scent absent condition it increases over the five sessions.   There is considerably more time spent immobile in the scent absent condition (64 per cent compared with 19 per cent).

Figure 6d.
Locomotion (feet)

scent present: N = 4

scent absent: N = 4

Figure 6e   Sniffing (sec.)

Days
Scent present; N = 4

Days
Scent absent; N = 4
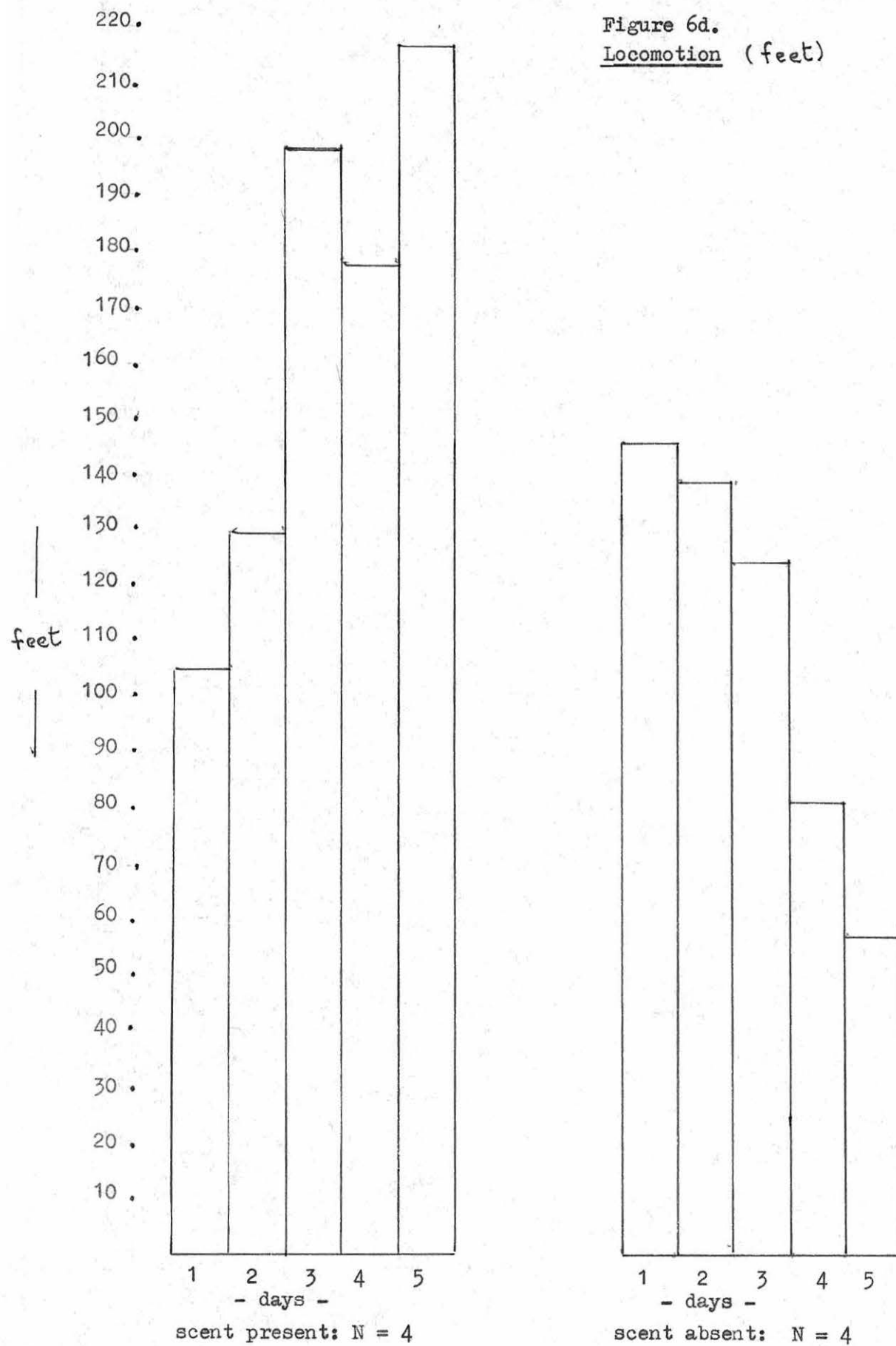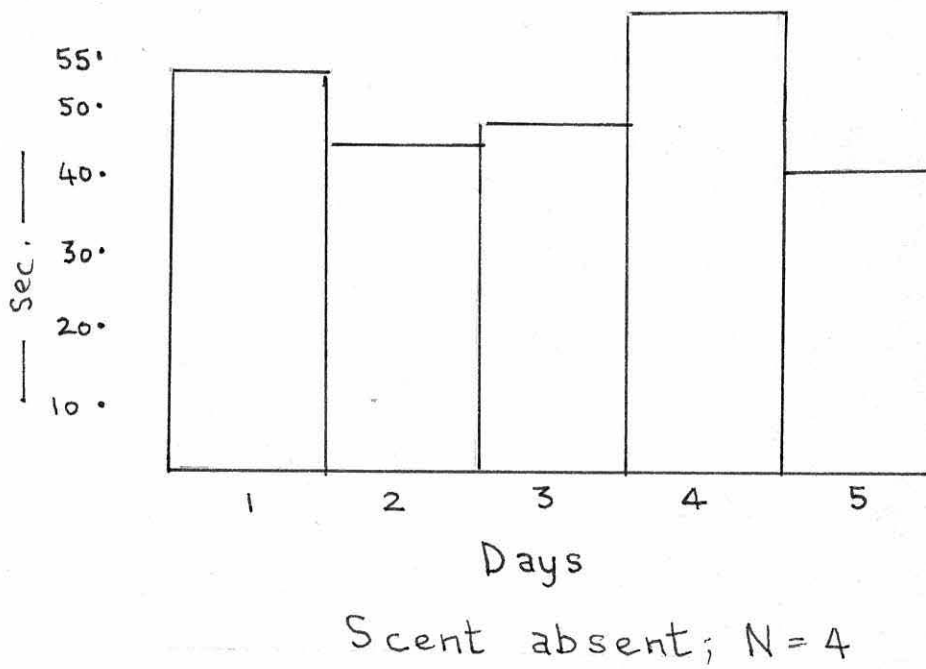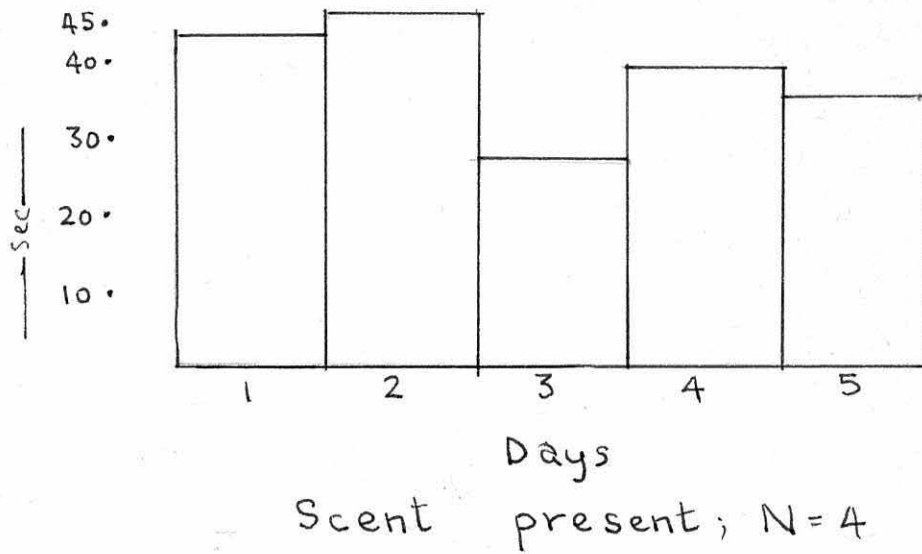
Figure 6f. Immobility (sec)
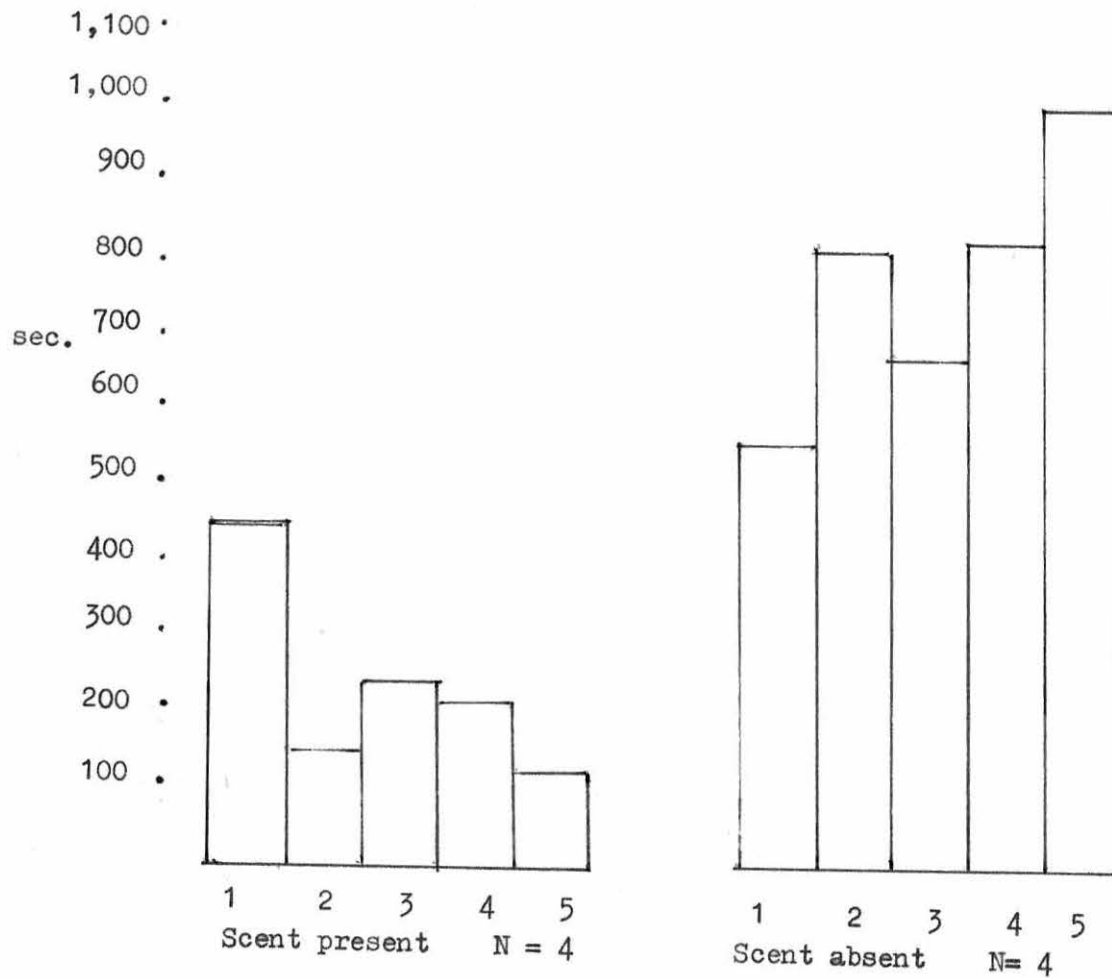
QUALITATIVE DATA

Scent present

When immobile the animals showed head movements and sniffing
of the air.   Animals sniffed intermittently as they moved forward.
Marking followed s-nosing.   There was pilo-erection and tooth-
chattering.

Scent absent

Sniffing of the air occurred during periods of immobility,
as did head and foot movements.   Sniffing occurred intermittently
as they progressed forward.   This behaviour looks as though the
animals are making sure it is safe to progress (this is intended
in a descriptive sense only).

DISCUSSION

It is clear that the animals are responding differentially
to the two conditions.   The differences are even more marked on
Day 5 than on Day 1.   This is a strong indication that the higher
levels of activity emitted in the scent condition in both
Experiment I and the present experiment are not due to the no-
scent condition inhibiting behaviour.

The results confirm the predictions made on page 167, except
for the tendency of locomotion, marking and defaecation to increase
over the five sessions of the scent present condition.

What is of particular interest in the present experiment is
the pattern of locomotion in response to the two conditions.   In
the scent absent condition locomotion is at its highest on Day 1
when novelty is at its greatest, and declines steadily thereafter.

Berlyne (1950, 1955) writes that it is stimulus novelty which evokes exploratory behaviour. With continued exposure to these stimuli curiosity will diminish. Thus an organism will respond to a curiosity arousing stimulus with an activity which after a while will cease. In the present experiment locomotion in the scent absent condition shows the pattern described by Berlyne. In the scent present condition it shows the reverse pattern.

In view of the fact that locomotor activity is frequently accepted as a measure of exploration, and in view of the fact that in this condition it conforms to the pattern described by Berlyne (1950; 1955), it would seem possible that in the scent absent condition it is essentially exploratory in nature. In the scent present condition it is suggested that the odour of conspecifics gives rise to responses which take precedence over exploration, for example, marking and s-nosing. The increase in locomotion represents an increase in the general level of arousal in response to the olfactory stimuli of conspecifics. Locomotion therefore is affected by social stimuli. The novelty in the scent absent condition is not responsible for the lower level of activity in this condition.

The pattern of immobility further supports this conclusion. As activity declines over time in the scent absent condition, so immobility increases. In view of the fact that immobility in the guinea pig occurs in response to novelty, immobility would be expected to decrease over the five sessions. That it does not do so indicates that the novelty of the situation is not a

significant factor in the occurrence of this behaviour.

Thus it is concluded that neither in Experiment I or III did novelty pay more than a minor role in the reduced level of behaviour in the no scent conditions, and that the increase in response to odour was a real increase. It would seem that the acclimatisation procedure was sufficient to reduce the novelty of the open field.

Defaecation is again higher in response to the scent of conspecifics. It would seem clear that it was not inhibited to any significant extent in either of the control conditions in Experiments I and III as indicated by Experiment Ia and the present experiment. With each trial the novelty of the open field decreased, yet defaecation in the scent absent condition showed no real increase to parallel this: it remained at a very low level. Experiment III in conjunction with Ic confirms that the rate of defaecation increases in response to conspecific odour. In view of this it would seem possible that it is a form of scent marking. It would seem to conform to the definition where "the deposition of urine and faeces, carrying secretions of the sex accessory glands or anal glands can.... constitute marking behaviour" (Johnson, 1973). However, the evidence is circumstantial, and further data are needed before it can be concluded that defaecation in the guinea pig is a form of scent-marking.

It is not clear why locomotion, marking and defaecation should increase over the five sessions. Examination of the raw data reveals no pattern to suggest why this should be so. However, it is not considered necessary to the present study that an explanation be found at this time, and the matter will not be

pursued further.

These experiments also indicate how important it is that apparatus used in investigating behaviour in animals be thoroughly cleansed. Experiments I and III reveal that guinea pigs behave in a different way in apparatus which contains odour and apparatus which does not, and not only with regard to species specific social behaviour. (It is not likely that this sort of effect is confined to guinea pigs. Thus Ropartz (1967) found that urine from male mice increased locomotor activity in male mice). It has also been shown that the effect persists over repeated sessions, and this must have implications for studies of activity or exploratory behaviour. These experiments, in conjunction with the experiment described in Chapter 3 indicate that it can be very difficult to remove odour. Thus Cheal and Sprott (1971) write that "the implications of social olfaction to experimental error should make every E aware of the necessity for controlling both for odors left by Ss and for other odors which might affect his behavior, such as food".

CONCLUSION

It is suggested that the data obtained in Experiment III confirm that scent marking and s-nosing are social responses, occurring in response to the scent of a male conspecific, and extend the generality of these findings. The rate of defaecation increases in response to conspecific odour, and it would seem possible that it is a form of scent marking. It is suggested that locomotion increases in response to olfactory stimuli as a result of increased arousal. The relative novelty of the control condition is not considered likely to affect the results to any significant extent.

It is important that apparatus involved in this sort of work be adequately cleaned.

In view of the fact that the male guinea pig responds to the odour of male conspecifics with scent marking, defaecation and raised locomotion, it would clearly be of interest to investigate the function of scent marking in the guinea pig. The following chapter describes two experiments designed to do this.

Addendum to Chapters 5 and 6

When a guinea pig is immobile it sniffs the air from time to time.   If an animal encounters an object it will sniff at it briefly.   It will either then move on or, if the object smells (for example) of a conspecific, it will s-nose it.   Sniffing in this sense occurs at a low level in this investigation.   It is perhaps not helpful to measure the incidence of sniffing in this study, as it would not seem to be a social activity.   Nevertheless, one of the guinea pig's means of finding out about the environment is certainly based on olfaction;   it is certain that he is continually aware of the olfactory environment about him;   he will respond, for example, with s-nosing or freezing according to the nature of the olfactory stimuli he encounters.   Thus to attempt to measure sniffing in terms of what is visible to the observer, as defined in the glossary, is perhaps misleading.

From now on sniffing will not be discussed as its incidence is low and because of the foregoing comments.   Data concerning sniffing will continue to be included in the Appendices, but it will not be further discussed unless the pattern of its occurrence suggests that this would be relevant.   Similarly, grooming occurs at such a low level that it would seem to serve no useful function to discuss it further.   Grooming as reported in Chapter 5 occurred in part in response to an animal being contaminated by urine, and does not seem to be an item of behaviour relevant to the present enquiry.   Should there be any cause to reconsider the matter, grooming will be further examined.

In view of the difficulty of distinguishing between pausing
and freezing the category of immobility has been used; thus
all "non-behaviour" tends to be recorded as immobility. In
view of this it might be sensible to omit this category from
further discussion, and concentrate on that behaviour which is
emitted.

It is extremely likely that immobility includes freezing
behaviour, and it is desirable that a reliable way be found
to distinguish between freezing and pausing as suggested in
Chapter 5.

Chapter 7.

Chapter 7

There is some evidence for rodent species that scent is involved in aggression. Archer (1968) found that if male mice were placed in a cage which had been used by other males this produced more aggression than placing them in a clean cage. Mackintosh and Grant (1966) found that aggression between male cagemates increased if the mice were rubbed with urine from strange males. Beauchamp, Magnus, Shmunes and Durham (1977) reported that after olfactory bulbectomy guinea pigs showed virtually no inter-male aggressive activity.

Rood (1972) observed that marking frequently occurs during bouts of stand-threats. These take place between males in an unstable dominance situation. Ralls (1971) points out that those species which have been studied experimentally tend to mark frequently in a situation where they are likely to show aggression to another animal.

It was noted during Experiment I that the guinea pigs showed both pilo-erection and tooth-chattering. Avery (1925) reports the occurrence of tooth-chattering during fierce fighting. Pearson (1970) reports that tooth-chattering was seen during fighting between males. He also noted that pilo-erection was most noticeable when purring and tooth-chattering were emitted. Berryman (1974) observed that tooth-chattering is emitted in threat behaviour during aggressive encounters between animals of the same sex, and Coulon (1975a) reports aggressive behaviour in male guinea pigs as accompanied by pilo-erection and tooth-chattering. Rood (1972) recorded tooth-chattering more frequently for the dominant animal of a pair.

Thus, although by no means conclusive, there is some evidence to suggest that the scent of a male conspecific evokes not only s-nosing, but also a tendency to aggressive behaviour, as evidenced by a raised level of scent marking and the occurrence of pilo-erection and tooth-chattering. This suggests that the behaviour may be territorial, where an intruder into an existing territory might be met with aggression. Marking has often been described as territorial marking. This has been reported for example in the gerbil (Thiessen, Owen and Lindzey 1971; Yahr, 1977) in the rabbit (Mykytowycz, 1968) in the rat (Barnett, 1963) and in the mouse (Mackintosh, 1973).

Lorenz (1966), and Hediger (1955; cited in Baran and Glickman, 1970) suggest that the function of territorial demarcation is to deter an intruder or stranger. Barnett (1963) writes that Hediger (1950) suggests that scent marks left by many mammals at fixed points in their territory deter other members of the species in a way comparable, for example, to bird song. However, experimental evidence of marking as serving to define a territory is sparse.

King (1956) concluded that guinea pigs were territorial, although the animals in his study did not actually develop terri-tories. If the male guinea pig uses marking to denote a territorial boundary then one might expect the scent of an adult male guinea pig to deter a male conspecific, on the grounds that territorial scent marking would serve to warn other males away from a territory without a conflict actually taking place.

The following experiment was designed to ascertain whether male scent deposited during scent-marking was aversive to adult male conspecifics.

Experiment IV

The problem was to determine the response of male guinea pigs to the secretions laid down during marking behaviour by adult male conspecifics. It is important here that a distinction be made between the smell of an adult male, and the smell deposited during marking by an adult male. The object of the experiment was to determine whether the subjects spent more time in one half of an open field than in the other half. One half had been marked by an adult male guinea pig.

No prediction was made as to which half the subjects would prefer.

METHOD

Subjects

The subjects comprised eight adult male guinea pigs which had taken part in Experiment I.

Apparatus

The apparatus is described in Chapter 4. It consisted of a 3'3" square open field, 12" in height. The walls were of buffed grey perspex, and the whole stood on a formica base covered with white cartridge paper. A perspex barrier divided the field into two halves, and a pencil line on the paper base marked the position of the barrier. The barrier was removed prior to the experimental session.

One side of the open field contained the secretions distributed during scent-marking by an adult male guinea pig.

The stimulus was obtained by using two adult male guinea pigs. First, stimulus animal 1 was placed into one half of the field. After 5 minutes it was removed and replaced by stimulus animal 2.

This animal was removed after 5 minutes.

The purpose of using two animals in this way was to ensure that the experimental side of the field was scent-marked.   It was found in Experiment I that relatively little marking occurred in the control (no scent) condition, but that it increased significantly in the experimental condition apparently in response to the scent of the preceding animal.

The barrier was then removed, the pencil line indicating the erstwhile position of the barrier.

To control for a possible position preference, for half the subjects the scent-marked side was on the left, and for the remaining four it was on the right side of the open field.

Procedure

Prior to taking part in the experiment the subjects and stimulus animals were each given one acclimatisation session. This involved placing them in the home cage in the open field for five minutes.

The animal to be tested was placed directly into the field with his rear to the wall nearest the experimenter and the midline of his body extending along the pencil line marking the erstwhile position of the barrier.   The animal was left in the field for five minutes.   The time spent in each half of the field and the number and direction of crossings from one side to another were recorded by means of a stopwatch and a cyclostyled sheet.

Preference for either half of the field was measured by the total time spent in each half.   The number of crossings from

one half to another provided an approximate measure of activity.
A crossing was recorded when the head and shoulders of the
animal were over the midline.

A two-tailed Wilcoxon matched-pairs signed ranks test was
used to determine whether a significant preference was shown for
either side of the field.

The field was dismantled and thoroughly washed between each
session.

RESULTS

Table 7a shows the responses of the animals in the test
situation. As can be seen, all animals spent considerably more
time in the scent marked half of the field, approximately three
times as much as in the no scent half. (77.4 per cent and 22.6
per cent of the total time respectively). This difference is
significant ($P < 0.01$, 2 tailed test. $T = 0; N = 8$) All animals were on the
scent marked half at the end of the session.

Although some animals were more active than others as measured
by the number of crossings, this showed no pattern in relation to
preference shown.

Qualitative Data

Additional notes were recorded on the behaviour of the animals.

No s-nosing or marking was observed in the no scent half.
Both occurred in the scent marked half, plus marking and defaecation.
There was a tendency for an animal when on the no scent half to
sniff at it briefly, and return to the scent side.

Tooth-chattering occurred on the scent half, also pilo-erection.

It would seem clear that the secretion deposited during
scent-marking is a positive stimulus. The guinea pigs were

clearly attracted to it, and were not deterred by it.

A point of interest is the occurrence of tooth-chattering and pilo-erection in response to the scent marks. This and the other data suggest that a male guinea pig is attracted to the scent of another male guinea pig, but that when the two encounter one another it is likely that they will fight or show threat behaviour.

Before these findings are discussed further a second study will be described. As the stimulus animals had been in the laboratory for some time it seemed that a possible explanation of the findings was the fact that their scent was familiar to the subjects. It was decided to repeat the experiment using fresh guinea pigs to provide the stimulus odour. Two male guinea pigs were purchased and kept in a separate room until they were used to provide the stimulus. Experiment V was identical to Experiment IV except that the stimulus animals were strangers to the subjects.

Experiment V

Subjects, methods and procedure were identical to those followed in Experiment IV The olfactory stimuli were obtained from the new animals.

RESULTS

As can be seen from Table 7b the results are similar to those obtained in the previous experiment. All subjects spent more time in the scent marked half than in the no scent half of the open field. The total time in the scent half was approximately four times that spent on the no scent half (80.7 per cent and 19.3 per cent respectively). The difference is significant ($P < 0.01$, 2 tailed test. $T = 0; N = 8$).

Table 7a.

Half Open Field.   Experiment IV

Subject	Marked Half (in seconds)	No scent	Grossings
Mp	224	76	5)
Sb	270	30	5)
Cl	278	22	4)
Lw	216	84	8)
Sm	220	80	7)
Sp	180	120	4)
Col	214	86	4)
Al	256	44	18)
TOTAL	1858	542	

Six out of the eight animals were in the experimental half at the end of the sessions. These findings replicate those obtained in Experiment IV.

Qualitative Data

The Subjects showed the same behaviour as in Experiment IV. Marking, defaecation, pilo-erection and tooth-chattering occurred in the experimental half of the field.

The advantage of the design of this experiment is that it is simple, easy to record, and involves no need for judgment on the part of the experimenter. It does have a fault, however, in that it is possible for scent from the experimental half to be transmitted to the control half on the feet of the animals. However, in view of the unequivocal nature of the findings, this would not seem to be of great importance.

Experiment V reveals beyond all reasonable doubt that when the stimulus odour is from a strange animal it is nonetheless an attractant. Experiments IV and V reveal conclusively that secretions deposited by an adult male during scent-marking attracts other male guinea pigs. They respond with s-nosing, scent-marking and defaecation, pilo-erection and tooth-chattering.

Table 7b

Half Open Field.   Experiment V

Subject	Marked Half (in seconds)	No scent	Crossings
Mp	284	16	6)
Sb	261	39	7)
Lw	239	61	10)
Sp	211	89	6)
Cl	222	78	7)
Sm	212	88	6)
Col	286	14	2)
Al	221	79	10)
TOTAL	1936	464	

Discussion

At first sight the findings obtained in Experiments IV and V
suggest that the guinea pig is not a territorial species: the
male guinea pig is not deterred by the scent of an unknown male
conspecific. The data might also be taken as indicating that
any deterrent effect which the scent of an adult male might
possess is acquired through experience, experience of defeat in
agonistic encounters. The subjects used in this study were all
kept singly, and had had no opportunity for social interaction.
There are three questions which need to be considered.

If the guinea pig is territorial would this reveal
itself as avoiding the odour of a male conspecific?
Are there circumstances in which the scent of an adult
male acts as a deterrent?
If so, how is the aversive quality acquired?
These three points will be considered in turn.

Territorial marking does not necessarily deter an animal.
Ralls (1971) defines a territory as "a fixed area of land which
the marking individual will defend against rivals of the same
species". If one considers the implications of this it is clear
that a territorial animal who encounters the scent of a strange
animal will not retreat from that scent. He is likely to seek
out and attack or drive away the intruder. Therefore the response
of a territorial animal to the scent of a conspecific would vary
according to where that scent is encountered. If he is at some
distance from his own territory he might be deterred from the
scent of male conspecifics.

However, the evidence available suggests that this is not
the case. Mykytowycz (1965, 1968) reports that the rabbit will
visit neighbouring territories. He describes the behaviour of
a rabbit entering an alien territory. Its posture changes, it
becomes more alert and ceases to feed. If it meets an occupant
of that territory it will flee, whatever its position in its own
colony.

Eibl-Eibesfeldt (1953) is cited in Johnson (1973) as
reporting that male hamsters were not frightened away from a
marking point. Scott (1967) points out that the domestic dog
does not retreat from an area scent-marked by another dog.
Barnett (1963) states that scent marks do not act as deterrents
to wild rats. He points out that Reiff (1952) found that odour
trails always have an attractive effect, even to a newcomer to the
colony.

Baran and Glickman (1970) found that male gerbils were
attracted to the scent marks of conspecifics rather than deterred
by them, and suggest that "any aversive characteristics of
specialized gland odors are acquired through specific social
encounters".

It is unlikely, therefore, that scent marks deter guinea pigs
from an area. It is more likely that they would function as
a warning informing an animal that he is in another animal's
territory. The data obtained in this study are not inconsistent
with this view. It is not possible to determine the relation
of the open field used in the present study to the guinea pig's
"home area". It would seem unlikely that it would be recognized
as home territory, owing to the lack of the individual's or a

colony odour. But neither would it seem likely to resemble the
territory of another colony, due to the small amount of odour.
Mykytowycz (1965) suggests that the marking behaviour of the
rabbit saturates the territory with smell. The marking and
eliminative behaviour of the guinea pig would probably have a
similar effect: marking, urination and defaecation are not
confined to given areas (Rood 1972; personal observation).

Thus it can be concluded that the fact that the odour was
an attractant does not of itself indicate that the guinea pig
is not territorial. Nor does this finding necessarily suggest
that scent-marking in the guinea pig never has a deterrent
function.

There is some evidence that urine may have a deterrent
effect; this effect may be enhanced by experience. Thus
Jones and Nowell (1973) reported that male mice are discouraged
from investigating an area marked with male urine. This effect
increased in mice when the area was marked with the urine of a
male which had defeated them.

Nyby, Thiessen and Wallace (1970) found that if high marking
Mougolian gerbils are exposed to aggressive interactions in the
territory of other males their level of marking in that territory
is significantly reduced. Thiessen, Owen and Lindzey (1971)
stress that the effect is due to olfactory cues in the territory
and cannot be attributed to visual or auditory cues.

Rood (1972) reports that subordinate Cavia aperea males
will often avoid a dominant male before they encounter it.
This suggests that olfactory stimuli may communicate the necessary
information.

It is known that male guinea pigs fight fiercely (Avery, 1925; Kunkel and Kunkel, 1964; Pearson, 1970, and Rood, 1972). It is possible that a fight or a series of fights with one animal consistently defeating the other might result in the odour of the victor having a deterrent effect on the defeated animal. This would involve individual recognition. Berüter, Beauchamp and Muetterties (1974) write that "individual recognition is, of course, a prerequisite for a social hierarchy if direct conflict is to be minimized". They report that the chemical complexity of secretions from the guinea pig perineal gland, as established by chemical analysis "is more than sufficient for the secretion to serve the function of individual recognition". Pearson (1970) obtained data which he suggested denoted individual recognition between two males, and Coulon (1975a) suggests that each male is aware of the position of the other males in the dominance hierarchy. Ruddy (1980) found that four male and four female guinea pigs were able to discriminate between individual animals on the basis of olfactory stimuli contained in ano-genital swabbings.

It has been established that guinea pigs form dominance hierarchies, thus it is possible that a subordinated guinea pig may be deterred by the scent of the alpha male. This has not been shown to be the case, but the finding that bulbectomized male guinea pigs showed no evidence of dominance-submission relationships (Beauchamp, Magnus, Shmunes and Durham, 1977) is perhaps significant.

The above paragraphs suggest that fighting may result in the scent of a dominant animal acquiring deterrent qualities for subordinated animals. This would involve individual recognition. However, it is possible that the scent mark of a dominant animal might have this deterrent quality without the need for individual recognition.

It has been reported that the odour of a dominant animal can be distinguished from that of a subordinate. Thus Krames, Carr and Bergman (1969) report that rats are able to differentiate between subordinate and dominant animals on the basis of olfactory cues. In their review on social olfaction Cheal and Sprott (1971) report that Kalkowski (1967, 1968) found that mice were able to use olfactory stimuli to distinguish between antagonistic and other males.

Schultz and Tapp (1973) point out that a number of rodents have externally ducted glands. These are frequently used in marking and there is a body of evidence indicating that dominance and aggression correlates with the size and activity of the scent producing glands. The glands would seem to change in response to the level of circulating androgen.

Mykytowycz (1968) reports that the secretory activity and size of the anal gland is greatest in dominant rabbits. Beauchamp (1974) cites the work of Mykytowycz and Dudzinski (1966) who found that the weights of the anal and inguinal glands correlated with the position of the rabbit in the dominance hierarchy. Drickamer, Vandenburgh and Colby (1973) found that the size and pigmentation of the flank gland in the male golden hamster varied according to social rank.

There is evidence that the increase in the size of scent glands associated with dominance is the result of increased levels of androgen. Jones and Nowell (1974) report that the aversive factor in the urine of male mice is androgen dependent. Drickamer, Vandenburgh and Colby (1973) write that size and pigmentation

of the flank gland in the hamster is related to androgen levels.

Thiessen, Lindzey, Blum and Wallace (1971) report that marking and androgen levels are positively correlated. Thiessen, Friend and Lindzey (1968) found a positive correlation between androgen titre and marking.

Beauchamp (1973) obtained data which suggest that the character of male guinea pig urine is androgen dependent.

A positive correlation between marking and dominance would seem to occur in several mammalian species. Ralls (1971) writes that the correlation between the two is striking. She cites Johnston (1970) who found that dominant male hamsters marked much more frequently than did the subordinate males and Epple (1970), who found that dominant marmosets marked more than the other group members.

Similar findings have been obtained with guinea pigs. Beauchamp (1974) found that the frequency of marking in male guinea pigs was greater in the higher ranked animals.

Thus there is a relationship between androgen titre, dominance, and marking behaviour. Johnson (1973) points out that aggression, marking and sexual behaviour have a common physiological basis in that they are dependent on the sex hormones.

It is possible that a difference in androgen titre between dominant and subordinate males is responsible for the ability of other males of the species to distinguish between the two; also for the aversive factor in the urine of dominant mice, as suggested by Jones and Nowell (1974). This could apply to the guinea pig.

Thus, a deterrent factor (if any) in the urine of a dominant male guinea pig might be due to experience and the subordinated animal recognising the scent of the victor. Or the odour of

dominant animals might serve to deter an animal lower in a hierarchy without the need for experience or individual recognition due to a factor dependent on androgen titre.

It is clear that there is room for research in this area. It is possible that odour is more likely to have a deterrent effect in relation to dominance than in territorial behaviour. Beruter, Beauchamp and Muetterties (1974) suggest that individual recognition is a prerequisite for a social hierarchy if direct conflict is to be avoided. Scent marking may be the means of avoiding conflict, although it is possible that threat postures on the part of the alpha male may avoid direct conflict. Coulon (1975b) suggests that agonistic displays in the guinea pig function as a means of re-solving conflict and establishing dominance relations. In this context, it is of interest that Rood (1972) reports that subordinate animals avoided the dominant male without an encounter taking place. Ralls (1971) suggests that scent marking may help to maintain dominance by acting as a threat.

The fact that high marking correlates with dominance is not inconsistent with the hypothesis that the odour of a dominant male guinea pig deters a subordinate. This is amenable to research.

It should, however, be pointed out that high marking in a dominant male may have an alternative function. Ralls (1971) suggests that marking by one animal may keep the other males in the group in an under-developed physiological condition by distributing primer pheromones *

* Pheromones affect the development, reproduction, or behaviour of other animals. A primer pheromone affects behaviour over time; prolonged release is necessary. Bruce (1970).

Conclusion

The results of Experiments IV and V suggest that the guinea pigs were attracted to conspecific odour. This is supported by the fact that male guinea pigs have been observed to voluntarily enter the recently vacated cage of another male where they emitted the same behaviour as in the open field (Chapter 3).

The fact that they show aggression-related behaviour and are more active suggests behaviour similar to that of the male *Cavia aperea* described by Rood (1972) and that the guinea pig is emitting behaviour appropriate to the pursuit and attack of a strange animal.

It is concluded that the response of the guinea pigs to the scent of an adult male is not inconsistent with territorial behaviour. However, the behaviour of the guinea pig is equally consistent with the establishment and maintenance of dominance, and it has been established that guinea pigs form dominance hierarchies. However, *Cavia aperea* has a home range, and it would be of interest to investigate the possibility that the guinea pig is territorial. Ralls (1971) writes that the degree of crowding may affect the type of dominance within a species; territorial dominance at low densities, individual at high densities. This should perhaps be taken into account when investigating territorial behaviour.

It would seem likely that territorial scent marking does not function as a deterrent and that Ralls'(1971) description of a territory is more likely to be generally applicable than that of Hediger (1955) and Lorenz (1967).

The relationship between scent marking, aggression, dominance and territorial behaviour is clearly an area where there is a great deal of scope for further research.   As Schultz and Tapp (1973) write "Convincing research on territorial marking is conspicuously lacking.   A large number of investigators have observed behaviour resembling the marking of territory with odorants, and others have observed behaviour that seems consistent with the existence of territorial marks, but much remains to be tied together."

The following chapters investigate the response of the male guinea pig to the scent of female guinea pigs, and Chapter 10 is concerned with the behaviour of the female.

Chapter 8.

Chapter 8

Part I

It has been said that the male guinea pig is unable to distinguish between the sexes on the basis of smell (Ibsen 1950). Pearson (1970) found that the behaviour of male guinea pigs to another guinea pig did not vary according to the sexual or hormonal status of the other. "Variations which did arise in this respect were shown rather later in the encounters."

Rood (1972) found that male guinea pigs were more likely to court young male conspecifics than were Cavia aperea. He also found that Cavia aperea responded sexually to C. porcellus males and that homosexual mounting was more frequent in domestic males. Rood (1972) suggested that some of these differences between C. aperea and C. porcellus might be due to the loss of distinctive male and female odours during the process of domestication.

Pearson (1970) carried out an experiment to investigate whether male guinea pigs can distinguish between male and female animals on the basis of odour. He compared the response of male guinea pigs to

    a)   a ball of cotton wool

    b)   a ball of cotton wool rubbed over the ano-genital area and soaked in the urine of a male

and c)   cotton wool soaked in female urine.

Pearson found that the addition of stimuli of urinary and ano-genital origin increased the span over which attention was paid to the cotton wool, but found no apparent difference in responsiveness to the male and female odours.

The present experiment is designed to ascertain whether or not the male guinea pig is able to distinguish the sexes by smell.* It is hypothesized that they are able to do so.

Experiment VI **

The purpose of this experiment is to determine whether adult male guinea pigs will spend more time in one half of an open field than in the other.

Method

Subjects

Eight male guinea pigs which had taken part in Experiment I acted as subjects. The conditions under which they were maintained were identical to those described for Experiment I. They were sexually naive.

Apparatus

This was the same as described in Chapter 7 with the open field of grey perspex divided by a perspex barrier. A pencil line on the paper marked the erstwhile position of the barrier.

One half of the field contained the scent of an adult male guinea pig. The other contained the scent of an adult female guinea pig. For the sake of convenience the two halves will be referred to as "male" and "female". To control for a possible position preference for half the subjects the female side was on the right, the male on the left. For the remaining four this was

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* This has also been investigated by Beauchamp (1973) whose work is discussed on pages 217-218.

** This experiment was published in The Guinea Pig Newsletter in November 1972.

reversed.

Procedure

The olfactory stimuli were obtained by placing an animal in one half of the open field for approximately 5 minutes, followed by one of the opposing sex in the other half of the field. Care was taken that the quantity of urine and faecal boli was approximately the same in each half.

The barrier was then removed.

Prior to taking part in the experiment each subject was given one 5-minute acclimatisation session. The male stimulus animal was given one acclimatisation session, and the female ten, including 3 where she was placed directly into the half-field, rather than being put there while still in her cage.*

Each subject was placed directly into the field with his rear to the side nearest the experimenter and the midline of his body along the pencil line marking the division between the two halves.

The time spent in each half of the field was recorded using a stopwatch and a cyclostyled sheet. Preference for one half of the field over the other was measured in terms of the accumulated time spent in each half of the field. The number of crossings from one side to another provided an approximate measure of activity (an animal was considered to have crossed the central line when both head and shoulders were over the line).

A Wilcoxon matched-pairs signed-ranks test was used to determine whether a significant preference was shown for either half of the field.

* This was necessary as the female animals had only been in the laboratory for a few weeks and readily became immobile.

RESULTS

As can be seen in Table 8i six of the eight subjects spent considerably more time in the female side of the field. One animal showed a preference for the male side, and one showed no preference, although he spent slightly longer in the female half of the field. The difference is significant ($P < 0.025$, 1 tailed test. $T = 2$; $N = 8$).

Qualitative Data

It was recorded that an animal on crossing to the male side of the field would turn and move rapidly back to the female side. This was noted in the more active animals. Pilo-erection and tooth chattering were not observed.

Comment

These findings show that the male guinea pig can indeed distinguish between the sexes by smell. Beauchamp (1973) obtained similar findings. He found that adult male guinea pigs show a very decided preference for female urine over their own and that of unfamiliar males. This preference was measured in terms of the length of time that the male subjects' heads "bobbed" in response to male and female urine. Sexual experience is not necessary for this preference, as evidenced by the present experiment (Experiment VI) and by the work of Beauchamp, Magnus, Shmunes and Durham, (1977). Thus it is clear that domestication has not resulted in the loss of distinctive male and female odour in guinea pigs. Before this is discussed further a second experiment will be described. This was carried out to investigate the response of male guinea pigs to the odour of a female. Although the two choice preference test reveals that the guinea pig is able to distinguish between the two sexes by smell, the

Table 8i

Open field.

Time in seconds

Subject	Female half	Male half	Number of Crossings
Sm	209	91	12
Sb	153	147	6
Al	217	83	14
Lw	209	91	12
Sp	184	116	3
Col	232	68	9
Mp	207	93	17
Cl	118	182	8
TOTAL:	1529	871	

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only information it provides is that the animals spend longer investigating female odour than male odour.

Part II

The experiment to be described was carried out to compare the response of adult male guinea pigs to the scent of a female with the scent of a male. It differs with regard to the previous experiment in that the two odours are not presented concurrently and no "choice" is required.

The rationale of this experiment was that the male will respond differentially to male and female odour. As marking

would seem to be associated with aggression in the guinea pig, and as aggression is not usually directed towards the female of the species, it was predicted that there would be significantly less marking in response to female odour than to male odour.

In this experiment the response of the animals to the scent of a female was compared with their response to the male odour in Experiment I. The conditions pertaining in the present experiment were identical to those of Experiment I which makes the comparison a valid one. The only way in which this experiment does not replicate the conditions of Experiment I is that it was not possible to counterbalance the order of presentation. However as has been indicated, the order of presentation did not affect the results in Experiment I, and a time interval of several weeks elapsed between exposure to male and female odours.*

This was considered preferable to exposing the animals to an identical experimental treatment on two occasions; it was also considered desirable to limit the number of times the animals were exposed to the open field.

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* The increase in age of the animals would not be enough to affect their behaviour. The guinea pig is a relatively long-lived species. Beauchamp (1979) reports that no age trends were found in response to olfactory stimuli.

Experiment VII

The purpose of this experiment was to investigate the
response of adult male guinea pigs to the scent of a female, and
to compare it with their response to the odour of an adult
male conspecific.   The data were compared with those obtained
in the male scent condition of Experiment I.

Subjects

Eight of the ten male guinea pigs which took part in
Experiment I acted as subjects.   They were maintained under the
same conditions as in Experiment I.

Apparatus

The grey open field was used.   The base was covered with
white cartridge paper.

The stimulus odour was provided by placing a female predecessor
in the open field for 10 minutes.

Procedure

The subjects were given 1 5-minute acclimatisation session,
and the female stimulus animals were given 10 sessions of which
three involved placing her directly into the open field.

The apparatus was prepared and a stimulus female was placed
in the field.   After 10 minutes she was removed.

Each subject was carried to the experimental room in the
base of his home cage.   This was placed on the floor, the animal
lifted out and placed in the corner of the open field.   Each
session lasted for ten minutes.

The stopwatch was started and the behaviour of the animal
recorded.

At the conclusion of the session the animal was replaced in its cage and returned to the animal room.

The following behaviour* was recorded:

> S-nosing
> defaecation
> marking
> U-marking
> (Sniffing)
> (grooming)
> (immobility).

The behaviour was recorded on the cyclostyled sheets described in Chapter 4.

Wilcoxon matched-pairs signed ranks tests were used to determine whether differences between the subjects' response to the two odours were significant.

RESULTS

S-nosing

As can be seen from Table 8a there was nearly twice as much s-nosing in response to the scent of a female conspecific compared to the scent of a male. All animals showed more s-nosing in the female scent condition. 28 per cent of the total time was spent s-nosing in response to female odour compared with 15 per cent to male odour. This difference is significant ($P < 0.01$, 2 tailed test . $T = 0; N = 8$).

Marking (including U-marking) **

Table 8b reveals that there was less marking in response to the female odour, 84 instances compared with 131 in the male condition. This difference is significant ($P < 0.025$, 1 tailed test . $T = 3; N = 8$).

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* Grooming, sniffing and immobility are not discussed. See page 182.

** Marking and U-marking data are included separately in Appendix 8.

Table 8a

S-nosing (in seconds)

Subject	Male odour	Female odour
Sb	61	129
Col	146	292
Mp	185	218
Al	36	194
Lw	40	191
Sp	65	70
Cl	50	58
Sm	133	181
	716	1333

Table 8b

Marking (No. of instances)   (includes ♂ marking)

	Male odour	Female odour
Sb	7	13
Col	15	8
Mp	27	19
Al	8	12
L	11	3
Sp	16	5
Cl	27	14
Sm	20	10
	131	84

Defaecation

There was over twice as much defaecation in the male scent condition as in the female scent condition (Table 8c). Six out of eight animals defaecated more in the male scent condition than in the female scent condition. This difference is significant ($P < 0.05$, 2 tailed test. $T = 1.5$; $N = 8$).

Locomotion

Although a greater total distance was covered in the female scent condition, the difference is not significant ($T = 10.5$; $N = 8$). Inspection of Table 8d reveals individual differences. Thus while four animals covered more ground in the female scent condition, three locomoted more in the male scent condition.

Qualitative Data

It was noticed that the animals tended to show considerable vocalisation in response to female odour. Pilo-erection and tooth chattering were not observed to occur.

Table 8c

Defaecation (No. of pellets)

Subject	Male scent	Female scent
SBb	3	4
Col	12	5
Mp	9	0
Al	5	4
Lw	7	3
Sp	5	5
Cl	2	0
Sm	7	0
	50	21

Table 8d

Locomotion (in feet)

Subject	Male scent	Female scent
Sb	37	50
Col	52	53
Mp	$48\frac{1}{2}$	114
Al	118	156
Lw	$102\frac{1}{2}$	$70\frac{1}{2}$
Sp	$41\frac{1}{2}$	$30\frac{1}{2}$
Cl	$66\frac{1}{2}$	53
Sm	$67\frac{1}{2}$	103
	$533\frac{1}{2}$	630

Discussion

The results obtained in Experiment VII provide additional evidence of the male guinea pig's ability to distinguish between the sexes on the basis of odour.

Beauchamp (1973) investigated the response of male guinea pigs to male and female conspecific urine. The present investigation used olfactory stimuli left by an animal moving about in an area. This indicates that urine is not the only means by which the male may identify the female. Although the female stimulus animals urinated in the open field this was by no means always the case. Unfortunately quantitative data are not available concerning urination by the stimulus females in the open field.

The fact that male guinea pigs are able to make this distinction suggests that domestication has not resulted in male and female guinea pigs losing distinctive odours. Beauchamp, Criss and Wellington (1979) investigated the response of Cavia aperea, C. porcellus and F. aperea x porcellus hybrids. While they found that all the males preferred female urine of each type, both C. porcellus and C. aperea preferred urine, both male and female, from animals of their own type. Beauchamp et al (1979) suggest that the odours of C. aperea and C. porcellus have diverged. Thus the C. aperea males may perceive less difference between C. porcellus male and female urine than between C. aperea male and female urine.

It would seem that the homosexual behaviour observed in the guinea pig is not due to an inability to distinguish between the sexes. Beauchamp, Magnus, Shmunes and Durham (1977) suggest that

the novelty of an animal is an extremely important stimulus in
eliciting mounting behaviour in guinea pigs. It has been ob-
served that a male guinea pig will mount indiscriminately a
male or female when these animals are first introduced into the
male's home cage (Louttit, 1927). However, Beauchamp et al (1977)
report that males living in social groups usually confine mounting
to receptive females.

The guinea pigs used in this study marked significantly less
in response to female odour than to male odour. This is of
interest in view of the relationship between aggression and marking.
Ralls (1971) reports that a dominant male marmoset increases his
marking in response to a strange male, but there is no increase,
or a smaller one, in response to a strange female.

Marking occurs during courtship in the guinea pig (Louttit,
1927; Pearson, 1970; Rood, 1972; and Jacobs, 1976). It would seem
therefore that it has some function related to sexual activity. It
is not clear to what extent the male guinea pig is able to distin-
guish between receptive and non-receptive females.* He frequently
courts non-receptive females (Avery, 1925; Louttit, 1927; Pearson,
1970). Jacobs (1976) reports that courtship of non-receptive
females is a normal aspect of guinea pig behaviour. The marking
shown by the male guinea pigs in response to female odour in the
present study is perhaps conparable to that emitted by a male
during courtship. Ano-genital dragging is not the only form
of marking shown by the guinea pig during courtship: during
courtship the male typically rumps the female and this
is frequently accompanied by urine spraying. This

* This is investigated in the following chapter.

marks the female and Rood (1972) suggests that this may cause
the subordinate males to avoid her. The ano-genital dragging
may serve a similar function. Thus by marking the area in
which he is courting the female the alpha male may deter sub-
ordinate animals from attempting to copulate with her. Rood
(1972) reports that the alpha male chases away subordinates
who attempt to approach the female. He usually succeeds and
will copulate first. However, it has yet to be shown that the
scent of an alpha male is aversive to subordinate males.

It is possible that the scent of the male affects the
receptivity of the female. Female guinea pigs with ablated
olfactory lobes develop disturbances of receptivity, despite
apparently normal oestrous cycles (Bruce, 1970).

It is possible, also, that male scent marking in response to
female odour may serve to attract oestrous females to him. The
female may be more sensitive to odour during oestrus, and would
be attracted to the male at the appropriate time.* Jacobs (1976)
reports that observations of females following their associating
males after courtship suggest that their role is not entirely
passive.

The fact that the pattern of defaecation resembled that of
marking is of interest. It was significantly lower in response
to female odour than to the male odour. This lends support to
the possibility that it may be a form of scent marking. If the
raised level of defaecation in response to male odour were
due to increased arousal, it would be expected to occur at a

* This is discussed in Chapters 10 and 11.

at a similar level in response to female odour.   This was not the case.*

The data obtained in Experiment VI suggest that the scent of the female is a powerful attractant.   However this may be due in part to the novelty of the female scent in this study.   The males were kept singly and were sexually naive.

Conclusion

The male guinea pig is able to distinguish between the sexes on the basis of olfactory stimuli.   These may be contained in the urine or in the odour trails left as an animal moves about. It would seem therefore that the guinea pig has not lost distinctive sex odours as a result of domestication.   It is possible that the odours of the wild and domestic species have diverged.

The male guinea pig marks less in response to female odour than to male odour.   This is consistent with Ralls' (1971) statement that those species which have been studied tend to mark most frequently in an agonistic context.

It is possible that the marking in response to female odour recorded in this study is related to marking observed during courtship.   It has been suggested that this might function to keep subordinate males from the receptive female.   It may also function as a sexual attractant to the oestrous female.

It is possible that scent marking in the guinea pig has several functions, and these will be discussed in Chapter 11.

* The data obtained in this study do not confirm that defaecation
  is a form os scent marking. It would be interesting to investi-
  gate this further using methods similar to those of Hesterman
  and Mykytowycz, 1968 (cited in Johnson, 1973).

Chapter 9

Chapter 9

It is clearly of importance that the male of the species be able to identify the female in oestrus. This can be communicated by olfactory cues. In the _Felidae_ the male locates the receptive female by means of odour (Kleiman and Eisenberg, 1973). Beach and Gilmore (1949) report that the female domestic dog indicates her oestrous status to the dog by means of urine marks. Rats use olfactory cues to communicate the oestrous state of the female to the male (Le Magnen, 1952). Carr and Caul (1962) found that male rats preferred the odour of receptive females to that of non-receptive females. Birke (1978) found that oestrous rats marked more often than dioestrous animals. Urinary and sebaceous odour from oestrous rats is highly attractive to the male rat (Pfaff, Lewis, Diakow and Keiner, 1973).

Male mice showed significantly more social investigation and sexual behaviour in response to urine from oestrous than from non-oestrous animals (Dixon and Mackintosh, 1975). The Bahaman hutia showed more intense olfactory investigation and marking in the presence of the scent of an oestrous female than at other times, thus indicating that he is able to distinguish between oestrous and non-oestrous odour (Howe, 1974).

There is some evidence that experience is relevant. Carr, Loeb and Dissinger (1965) found that sexually experienced male rats preferred receptive female odour, whereas castrates and naive males showed no such preference.

In contrast, it has been reported that male hamsters show no differential response to vaginal secretions from oestrous and

post-oestrous females (Johnston, 1974). Landauer, Banks and
Carter (1978) found that although male hamsters demonstrated
a significant preference for female over male odour, they did
not show a preference for either oestrous or dioestrous female
odour.

There is evidence which suggests that the guinea pig, too,
is unable to distinguish between oestrous and non-oestrous females.
Thus Avery (1925) writes that his experiments revealed that male
guinea pigs show "a minimum of discrimination between receptive
and non-receptive females and a maximum of trial and error
mounting". Avery (1925) also reported that anosmic males (with
transected olfactory bulbs) did not seem to be handicapped in
the performance of sexual behaviour, once the shock effects of
the operation had passed.

Louttit (1927) writes "The differences between the mating
behaviour of guinea pigs when the female is receptive is one
of degree and not of kind", and suggests that the behaviour of
the female is the determining factor. Louttit cites the work
of Loeb and Lathrop (1914) who suggest that when a male loses
a receptive female among a group of animals he has no way of
finding her again except by trial and error.

Beauchamp (1976) reported that he and his fellow workers
have failed to find any attractiveness of female guinea pig urine
as a function of the stage of oestrus. However, courtship be-
haviour is guinea pigs is depressed after olfactory bulbectomy,
suggesting that olfaction is of importance in sexual behaviour

(Beauchamp, Magnus, Shmunes and Durham, 1977). But again, Beauchamp, Criss and Wellington (1979) found no difference in the response of male guinea pigs to oestrous and non-oestrous urine.

Thus it would seem that there is some question concerning the guinea pig's responsiveness to olfactory stimuli associated with the oestrous cycle of the female. This is surprising as the guinea pig is a social species, and olfaction would seem to be important in its social behaviour.

There is evidence which suggests that the male guinea pig is able to distinguish the oestrous female, or a female shortly to come into oestrus. Thus King (1956) observed that males tended to remain only with females in oestrus. Beauchamp (1973) suggested that males can discriminate between females soon to be in oestrus from those in oestrus, and those not near oestrus. Rood (1972) observed that the alpha male courts the female with increasing frequency as parturition (and the post-partum oestrus) approaches.

Jacobs (1976) noted that associating male guinea pigs became more aggressive as parturition approached. Kunkel and Kunkel (1964) report that high ranking males only mounted oestrous females, although the younger males were less selective. Male guinea pigs living in social groups usually confine mounting behaviour to receptive females (Beauchamp, Magnus, Shmunes and Durham 1977).

It is possible that olfactory stimuli enable the guinea pig to determine the female in oestrus, or about to come into oestrus. Urinary excretion of steroids and their metabolites is likely to change with the oestrous cycle (Birke, 1978). Similar changes

would be associated with the onset of parturition. Yet only the study of Beauchamp et al (1977) on the effects of olfactory bulbectomy indicate that olfaction is important in the sexual behaviour of the guinea pig, and Avery (1925) obtained contrary data with his anosmic animals. However, it is possible that changes in surgical techniques are responsible for the different findings.

It is also possible that the behaviour of the female provides the necessary stimuli. It is known that shortly before oestrus she is likely to pursue and mount other animals, and this stimulates the male into sexual activity. However, there is no information concerning the behaviour of the female during the days preceding parturition and oestrus.*

The investigation reported in this chapter was carried out in order to determine whether the male guinea pig is able to distinguish a female in oestrus from a non-oestrous female on the basis of olfactory cues. It is suggested that if he is able to make this discrimination he will spend longer investigating odour from an oestrous than from a non-oestrous female.

It was decided to use urine as the stimulus odour for two reasons. First, the female guinea pigs had only been in the laboratory for a few weeks and showed a tendency to become immobile in the open field. Second, the method employed in the present investigation was far less time consuming than testing the animals in the open field. This was important as only two females were in the laboratory at any one time, and came into oestrus only every 17 - 18 days.

* This is discussed in Chapter 10.

It was also decided to present one stimulus at a time. It was considered that if the stimuli were presented concurrently the male might concentrate on whichever he happened to sniff at first. His first choice may be random. Personal observation suggests that guinea pigs are inefficient at locating odours to which they are not in close proximity.

The olfactory stimuli consisted of urine from oestrous and non-oestrous females; this was never more than 90 minutes old. It was obtained by placing the females in a clean plastic bowl for the necessary length of time. Urine contaminated by faecal pellets was not used.

The condition of the female was determined by her behaviour and the assumption of lordosis in response to the appropriate stimulation. The time of testing varied, but was between 6 and 8 pm.

Each subject underwent both conditions, using a counter-balanced design. They were not sexually experienced, but all had had a brief encounter with both a receptive and a non-receptive female. They were not permitted to copulate.

The dependent variable was the time spent investigating the olfactory stimulus.

The Wilcoxon matched-pairs signed-ranks test was used to compare the response of the animals to the olfactory stimuli.

Experiment VIII

METHOD

Subjects

The eight male guinea pigs used in Experiments VI and VII acted as subjects. They were maintained under the same conditions as the earlier experiments.

Apparatus

Each animal was tested in his home cage. The equipment used consisted of Q-sticks, two plastic bowls, and glass jars. The experimenter wore rubber gloves.

Procedure

Urine was obtained by placing the female in a clean plastic bowl for the required length of time. The urine produced was transferred to a clean glass jar, and was kept under refrigeration until used.

A Q-stick was dipped into the urine, and offered to the subject. The time spent s-nosing the stick was recorded by means of a stopwatch; each instance of biting was noted.

When the subject stopped investigating the stick it was withdrawn and offered again in 10 seconds. This was repeated until presentation failed to elicit investigation. The periods spent s-nosing were summed; the 10-second intervals were not included.

Subjective observations were written down at the end of each session.

RESULTS

Table 9i gives the time the animals spent s-nosing the oestrous and non-oestrous urine. Although two animals spent longer investigating non-oestrous urine, altogether more time was spent investigating oestrous urine. The difference is significant ($P < 0.05$, 2

tailed test. T=4; N=8). (However two of the scores are very similar.
If these are considered as ties then the finding is not significant).

Table 9i

Subject	Oestrous	Non-oestrous
Al	210	67
Sb	60	114
Cl	208	117
L	125	51
Mp	376	196
Sp	213	136
Col	96	107
Sm	58	46
T.	1346	834

Time spent by male guinea pigs s-nosing urine of
oestrous and non-oestrous females (in seconds)

Table 9ii gives the number of incidents of biting during the
investigation of female urine. It can be seen that seven of the
eight animals showed more biting in response to oestrous than to
non-oestrous urine. The difference is significant ($P < 0.02$,
2 tailed test; $T = 4$; $N = 8$).

Table 9ii

Subject	Oestrous	Non-oestrous
Al	19	7
Sb	3	5
Cl	15	8
L	7	3
Mp	35	17
Sp	29	9
Col	7	6
Sm	5	1
T.	120	56

Incidence of bitng by male guinea pigs during in-
vestigation of urine from oestrous and non-oestrous
females

Qualitative Data

The initial response to both odours appeared to be identical.
There was a great deal of licking and biting of the stick, and
occasionally a piece of cotton wool would be bitten off the stick
and apparently swallowed. There was more biting in response to
oestrous urine.

The time spent s-nosing the stick after each 10-second inter-
val grew progressively shorter. Finally, the animal ignored the
stick. There was very little vocalisation.

This experiment provides some evidence to suggest that the
male guinea pig is able to distinguish between urine from recep-
tive and non-receptive females, as manifest in the greater inci-
dence of biting, and greater total time spent s-nosing, in response
to oestrus urine. Ruddy (1980) has demonstrated that both male
and female guinea pigs are able to make the discrimination be-
tween oestrous and non-oestrous odours. Ruddy used an aversion-
motivated situation, with ano-genital swabbings providing the
olfactory stimuli.

Ruddy (1980) writes that her study indicated that information
from the entire ano-genital region is necessary for the animals
to make the discrimination. This might explain why earlier
studies using urine as the stimulus (Beauchamp, 1976; Beauchamp,
Criss and Wellington, 1979) have failed to reveal a preference
for oestrous as opposed to non-oestrous urine. However, as Ruddy
(1980) points out, previous attempts to investigate the response
of guinea pigs to oestrous and non-oestrous stimuli have used
preference tests, and this method may not be appro-
riate to provide the answer to the question of olfactory

discrimination of physiological oestrus. The present investigation (Experiment VIII) has revealed a degree of preference for urine from a receptive female; it differs from previous investigations (Beauchamp, 1976; Beauchamp, Criss and Wellington, 1979), in that it presents one stimulus at a time, and tests for a re-awakening of interest in the stimulus after a brief interval. The initial response to the stimuli seemed identical. Ruddy (1980) comments that urine should not be discounted as a sufficient stimulus, and the data obtained in Experiment VIII suggest that urine is a sufficient stimulus to enable male guinea pigs to distinguish receptive from non-receptive animals. The finding of Jesel and Aron (1976) that urine collected from guinea pigs during the period of vaginal opening shortened the period of vaginal closure in subject guinea pigs also indicates that urine may vary according to the stage of the oestrous cycle of the donor. It is likely that urinary excretion of steroids and their metabolites would vary according to the stage of the oestrous cycle (Birke, 1978). It would seem likely that the male guinea pig is able to use both urine and stimuli from the ano-genital area to distinguish the receptive female.

If the data obtained in Experiment VIII and Ruddy's (1980) findings are considered together, it would seem clear that the male guinea pig is able to distinguish the receptive female on the basis of olfactory stimuli, and that he is likely to show a preference for the odour of a receptive (or oestrous) female. As Ruddy (1980) points out, her findings do not indicate that in a natural setting odour cues are used by guinea pigs to detect oestrous from non-oestrous animals. The slight preference shown for oestrus urine shown in Experiment VIII suggests that they

may be so used, and it is possible that olfactory stimuli asso-
ciated with hormonal changes are responsible for the males' be-
haviour towards females soon to give birth or to come into
oestrus.

The propensity of the male guinea pig to court non-receptive
females would not seem to be due to the inability of the guinea
pig to distinguish the oestrous female. In the sort of experiment
where another guinea pig is put into a male's cage the behaviour
emitted is very likely due to the novelty of the second animal,
as suggested by Beauchamp, Magnus, Shmunes and Durham (1977).
They point out that when living in social groups the male usually
confines his mounting to oestrous females. This exemplifies the
unsuitability of laboratory techniques for investigating some
forms of behaviour. However, it is possible to simulate some
aspects of the natural environment in the laboratory. Kunkel and
Kunkel (1964) in their observations of groups of guinea pigs main-
tained in the laboratory, report that high ranking males only
mount oestrous females, although the younger animals are less select-
ive. It is possible that courtship of non-receptive females occurs
mainly in the subordinate males, especially if the alpha male is
successful in keeping them from the oestrous females.

The observation that the male guinea pig seems to find his
receptive female on the basis of trial and error, is perhaps due
to the fact that the male guinea pig is not efficient at locating
olfactory stimuli. Beauchamp (1973) notes that the guinea pigs in
his study could not discriminate male and female urine at a
distance greater than a few centimetres. This suggests that if

the male is to locate the female he may need some assistance.
It has already been said that the female shows male-like
mounting behaviour immediately prior to oestrus. It is also
possible that she uses olfactory stimuli to scent mark the
environment. This possibility is investigated in the following
chapter.

It is possible that the apparent insensitivity to female
odours frequently shown by the male guinea pig is due to the
effects of domestication. It would be illuminating to investi-
gate the response of Cavia aperea to urine from oestrous and non-
oestrous females. It might also be of interest to compare scent
marking in the male guinea pig in response to oestrous and non-
oestrous odour.

It is possible that sexual experience may enhance the ability
of the male to distinguish oestrous from non-oestrous urine, and
this could be investigated.

It would also be of interest to investigate the possibility
that low ranking males mount non-receptive females significantly
more often than do high ranking males.

Conclusion

The data obtained in the present experiment, together with
Ruddy's (1980) findings, indicate that the male guinea pig is able
to distinguish between oestrous and non-oestrous females on the basis
of odour; the present data also suggest that he may prefer oestrous
to non-oestrous odour. Further research is needed to confirm this,
and whether urine alone is a sufficient stimulus for the discrim-
ination to be made, also to determine whether the male guinea pig
discriminates between oestrous and non-oestrous odour in a natural

environment. That the male guinea pig makes this. distinction is consistent with his behaviour towards females soon to be in oestrus.

Suggestions to account for the observed mounting of non-receptive females are made, also for the male's apparent difficulty in locating the receptive female in a group of animals. The behaviour of the female is perhaps of importance in this context.

Chapter 10.

Chapter 10

With the exception of those patterns morphologically confined to the male, guinea pigs of both sexes display the range of responses available to the guinea pig (Pearson, 1970). Variation in the frequency with which the patterns occur is affected by factors such as the sexual and hormonal status of the animal and of its partner.

Several investigators have described the male-like behaviour of the female at oestrus, for example Avery (1925); Louttit, (1927); Young, (1969); Pearson (1970); Beauchamp, Magnus, Shmunes and Durham (1977).

Pearson (1970) describes the responses shown by a receptive female to another. They include purring and circling behaviour, ano-genital nuzzling, rump dragging, mounting and pelvic thrusts.

Male and female animals also show a similar form of marking behaviour in urine-spraying. It occurs in different contexts, however. The female uses it to repulse the attentions of a male (or female), whereas the male may spray the female during courtship.

Both male and female guinea pigs drag the ano-genital region over the ground. This occurs in response to an alteration in the environment such as clean bedding, as well as in sexual and aggressive encounters (Beauchamp 1973). The male also shows this behaviour in response to the odours of male and female conspecifics, as shown in this investigation.

However, apart from the fact that it occurs during sexual behaviour, little is known about marking behaviour in the female

guinea pig. Several mammalian species use scent to communicate their reproductive condition to the male (Le Magnen, 1962; Carr and Caul, 1962; Beach and Gilmore, 1949; Kleiman and Eisenberg, 1973; Howe, 1974).

It might be expected, therefore, that "cyclic variation in the marking activity of the females, related to their oestrous cycle, might occur " (Johnson, 1973). Calhoun (1962; cited in Birke, 1978) reports that on the night of pro-oestrous the female Norway rat kept in semi-wild conditions, wanders about, marking both objects and the soil. Birke (1978) found that oestrous rats mark novel objects more frequently than dioestrous rats. She suggests that increased marking at oestrus serves to attract males, which follow the characteristic scent of the oestrous female.

The present study investigates the possibility that the frequency of scent marking increases in relation to the oestrous cycle of the female guinea pig. It is also considered whether additional behaviour on the part of the female may facilitate her location by the male.

The animals used in this study were four female guinea pigs, originally used to provide stimulus odours. Only two were in the laboratory at any one time; the first two died, and were replaced with a second two females. None of the females had been long in the laboratory and it was found that they were prone to become immobile. It seemed advisable to investigate their behaviour in a familiar environment.

It had been observed that the females would jump into the empty cage of a male, where they would drag the ano-genital

region over the bedding. Generally, marking was observed to occur only rarely in these animals, although the females would mark occasionally during their normal daily activity. It was also noticed that a female tended to urinate where the other female had recently urinated.

To avoid the tendency to immobility associated with novelty, it was decided to use a cage which had held a male for a short while in which to test the females for marking behaviour. This would remove problems associated with novelty, and seemed more likely to elicit marking than a clean cage.

The following experiment compared the frequency of marking in female guinea pigs during (a) pro-oestrus and oestrus, and (b) during dioestrus.

Experiment IX

METHOD

Subjects

The guinea pigs used were four tortoiseshell and white smooth-coated females. They were aged approximately six months. They were kept in pairs in the same cages and under the same general conditions as the male guinea pigs used in this study. They were on food and water ad libitum and were given carrots twice daily. They were accustomed to being handled by the experimenter.

Apparatus

This consisted solely of a cage recently vacated by a male guinea pig and containing his slightly soiled bedding. It was placed in a corner of the animal room.

Procedure

The cycle of the guinea pigs was estimated by recording the dates at which the animals came into oestrus. The cycles were

from 17 to 18 days in length. Oestrus was determined (i) by
the mounting and associated behaviour of the animals, (ii) by
inspection of the vaginal membrane, and (iii) by the elicit-
ation of lordosis.

Marking was recorded over 4 days at oestrus and dioestrus.
Testing began 2 days before the estimated date of the receptive
period. This would provide data on marking on the two days
preceding oestrus, the oestrous day and the day after.

When animals did not come into oestrus on the expected day
it was necessary to repeat the procedure on the fifth day. When
this occurred the first day's data were excluded. The dioestrous
data were obtained during days 7 to 10 of the cycle. Thus the
periods compared were days -2, -1,* 1 and 2; days 7,8,9 and 10.

The animal to be tested was carried to the male cage by hand
and placed into it at one end. The number of marks emitted during
two minutes was recorded. After two minutes the animal was re-
moved and returned to her home cage.

Each session was timed with a stopwatch. The raw data can be
seen in Appendix 10.

RESULTS

As can be seen in Table 10 three guinea pigs increased their
frequency of marking during the oestrous period. 68.3 per cent
of the total marks were emitted over the four days including
oestrus. 31.7 per cent were emitted during dioestrus.

There is some variation in the pattern of marking over days
-2,-1, 1 and 2 which can be seen more clearly in Figure 10a.

---

* days -2 and -1 being the last two days before oestrus: 16 and
   17, or 18 and 19, depending on the length of the cycle

Table 10.

Frequency of marking in relation to the oestrous cycle (mean score for cycles observed).

	Days				
Subject	-2	-1	1	2	
G	4.0	4.0	2.0	1.5	(2 cycles)
P	1.7	6.3	2.7	2.0	(3 cycles)
B	9.0	5.0	9.0	2.5	(2 cycles)

	Days				
	7	8	9	10	
G	1.0	2.0	1.5	1.0	(2 cycles)
P	2.0	1.0	2.3	3.0	(3 cycles)
B	1.5	3.0	1.0	2.5	(2 cycles)

Figure 10a
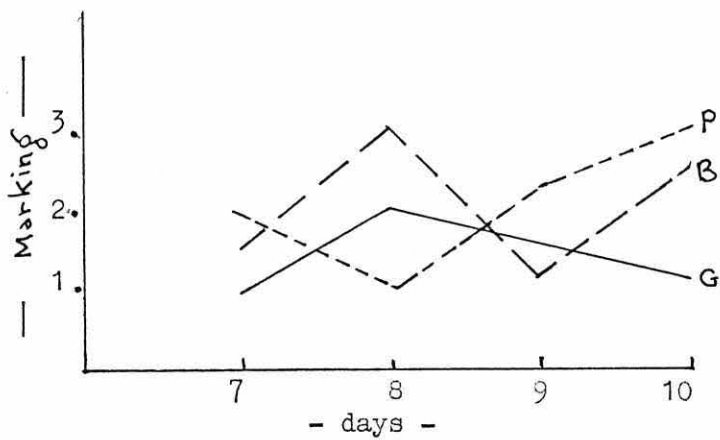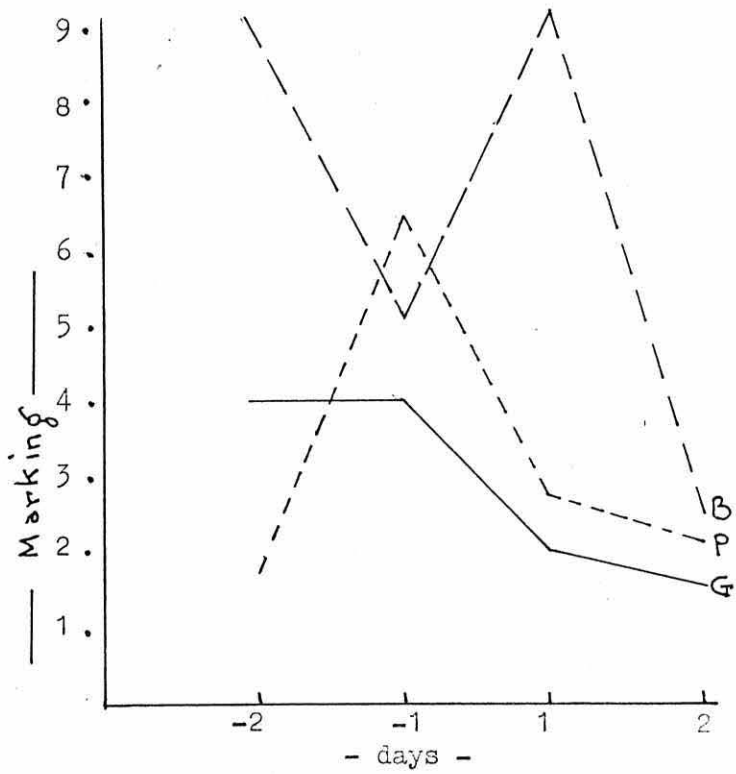
Frequency of marking in relation to the oestrous cycle

There was variation in the frequency of marking by different animals. One showed a tendency to mark more often than the others; she also marked more on Day 1.

The fourth female was to have been included in this study, but during the testing period no signs of receptivity could be found; she frequently showed chasing and mounting behaviour, but it was not possible to elicit lordosis. She was rarely seen to mark.

Qualitative Data

The females frequently urinated immediately on being placed in the test cage. There was little s-nosing in the cage, but what there was occurred mainly during the pro-oestrous period for periods of between 15 - 60 seconds. The onset of male-like chasing and mounting behaviour varied, commencing from 3 to 12 hours before the female was receptive. During one cycle Subject P became receptive at 6.0 p.m.; the following cycle, at midnight.

Observations of the daily activity of the animals indicated a considerable increase in marking at or preceding oestrus. S-nosing did not occur frequently, but, as in the test cage, increased during the oestrous period.

Discussion

Although data pertaining to three animals only are available, the present experiment suggests that the female guinea pig increases her rate of marking in the pro-oestrous period. In connection with this finding Birke's (1981) data are of particular interest. Birke found that marking, along with locomotion, approaching a companion, and sniffing, showed a significant increase on the day of oestrus. Birke's method differed from the present investigation in that each subject was placed alone in a small area, then a stranger stimulus animal was introduced, and the experimental animal's behaviour was recorded for ten minutes. In the present experiment the response of the subject animals to

the empty cage of a male was recorded for two minutes. Nor do
the two sets of data alltogether parallel one another. The
animals in the present investigation tended to increase their
rate of marking on the two days preceding oestrus, although one
animal maintained a higher rate of marking on the day of oestrus.
It is possible that the larger N used by Birke (N = 6), and the
longer test period, provided a more accurate indication of the
changes in behaviour. However, the data with regard to marking
and s-nosing (nodding) are broadly the same; in both studies they
increased at or around the time of oestrus (see Birke, 1981).

In view of the increase in marking behaviour by the oestrous
female it would seem surprising if the male were insensitive to
olfactory stimuli emanating from oestrous and non-oestrous females.
As suggested in the previous chapter (Chapter 9) the male's
apparent insensitivity to oestrous and non-oestrous odours is
possibly due to inappropriate experimental methodology. Experi-
ment VIII and Ruddy's (1980) findings indicate that the male
guinea pig can distinguish olfactory stimuli from oestrous and
non-oestrous animals, but it is not clear to what extent he
responds to the olfactory cues in a natural environment; nor is
it certain that urine is a sufficient stimulus for the distinction
between oestrous and non-oestrous females to be made. It is possible
that during marking the female spreads secretions other than urine
which attract the male. However, as Reynolds (1971) points out,
it is likely that urine is of particular importance in the trans-
mission of information in those species which urinate in specific
social and territorial situations. Both male and female guinea
pigs deposit urine during marking and, as has been indicated,
odour is a potential source of information concerning the sex,

reproductive condition, and individuality of an animal. The
finding of Jesel and Aron (1976) that the odour of urine coll-
ected from female guinea pigs during the period of vaginal
opening resulted in a shortening of the oestrous cycle of subject
guinea pigs indicates that urine can convey the reproductive
status of an animal. Urine collected during the first seven
days of vaginal closure did not have the effect. It is desirable
that the response of the male guinea pig to both sebaceous
secretions and urine from an oestrous female, presented indepen-
dently, are investigated. It would seem likely that both are pot-
ential sources of information as to the reproductive status of the
female.

Birke (1979) found that investigation of objects increased in
female guinea pigs at oestrus. The present experiment (Experiment
IX) and Birke's (1981) investigation indicate that she marks at
oestrus. Observation suggests that the female is more active
during pro-oestrus, and Birke (1981) reports that locomotion in-
creases at oestrus. As Birke (1979) points out, guinea pigs are
very social animals, and rarely wander off alone (Rood, 1972).
There is less need, therefore, for this species to wander more
widely at oestrus. She makes a similar comment in her (1981) re-
port: while the advantage of marking by the oestrous animal is
clear for solitary species, the advantage is less clear in a
gregarious species such as the guinea pig.

It is possible that increased marking by the female guinea pig
at oestrus functions to attract the male. Birke (1978) writes that
marking in the oestrous rat "presumably serves to attract males
which follow the characteristic scent of the oestrous female."

Unlike the rat, there are no data which indicate that the urinary
and sebaceous odour of the oestrous guinea pig is attractive to
the male, although Experiment VIII suggests that he may prefer
oestrous to non-oestrous urine. It would be of interest to com-
pare the response of male guinea pigs to the scent left during
marking by oestrous and non-oestrous females in a semi-natural en-
vironment. Certainly the oestrous female produces an odour readily
detectable to the human nose and Ruddy (1980) has shown that the
male guinea pig can discriminate between oestrous and non-oestrous
odours in an aversion-motivated situation.

It is also possible that scent marking in the female may
affect the sexual behaviour of the male by acting as a releaser
pheromone.* This, of course, would involve a differential res-
ponse to oestrous and non-oestrous odours.

Even if a male does not distinguish between the oestrous and
non-oestrous females in a natural, or semi-natural environment,
her marking may still have the effect of attracting the alpha
male. Beauchamp and Berüter (1973) found that the attraction of
female guinea pig urine waned fast. "If urine functions to attract
conspecifics, it is reasonable that the attractiveness should not
remain long since the environment would soon become saturated
with the attractant making localization difficult." It has been
demonstrated in the course of this investigation (Experiment VI)
that male guinea pigs are attracted to the scent of a female.
Thus a significant increase in marking by one female would possibly
cause her scent to become the pre-dominant female odour in the

* releaser pheromone: a pheromone which causes an immediate and
  reversible response operated directly through the central
  nervous system.

group. If the scent of a particular female becomes the dominant odour this represents a change in the background odour. This change will alert the alpha male, and he will increase his level of activity and seek out the source of the odour. (That he does so in respect of strange males has been observed by Rood, 1972). This would require that the male guinea pig be capable of individual recognition, and available data indicate that this is indeed the case (Pearson, 1970; Beauchamp and Berüter, 1973; Coulon, 1975a; Berüter, Beauchamp and Muetterties, 1974; Ruddy, 1980). Guinea pigs frequently stop and sniff at a spot where another has recently urinated (Rood, 1972; Beauchamp, 1973). Thus the alpha guinea pig would soon be aware of any change in the olfactory environment.

The observed behaviour of male guinea pigs courting or guarding a female guinea pig shortly before oestrus (Rood, 1972; Beauchamp, 1973) is most likely mediated by olfactory stimuli. However, activity on the part of the female may be a relevant factor, apart from the male-like behaviour which precedes the receptive phase. It was noted in the present study that the female guinea pigs spent longer s-nosing male odour during pro-oestrus than in dioestrus. Birke (1981) reports that during the oestrous period nodding (s-nosing) increased, and that it generally preceded marking; also, marking was often preceded by sniffing. Carter (1972) suggests that the female guinea pig is less sensitive to odour than the male. However, Pietras and Moulton (1974) report that the oestrous cycle in the rat is characterized by a lowered olfactory threshold. Birke (1981) suggests that the increase in nodding at oestrus (and the fact that it precedes marking) may be due to increased olfactory sensitivity. There is some evidence which suggests that scent is important to the female guinea pig. Female guinea pigs show disturbances of recep-

tivity when the olfactory lobes are ablated, despite seemingly
normal oestrous cycles (Donovan and Kopriva, 1965).

The increased s-nosing of the pro-oestrous females in the test
cage* (apparently in response to the male odour) suggests that this
scent is an attractant to the female at this time. During the
cycle of one of the guinea pigs it was noticed that she showed a
marked tendency to approach a male in his cage. This was investi-
gated during the following cycle. (This supplementary experiment is
described at the end of this chapter, pages 249-252. It revealed
that the guinea pig spent significantly more time near the cage of
a male during the day of oestrus than the three days following
oestrus).

No general conclusions may be drawn on the basis of the behaviour
of one animal on one occasion. However, the fact that the female
interacts more with conspecifics at oestrus (Birke, 1981) perhaps
lends some indirect support to this finding. A lowered olfactory
threshold (if this is found to be the case) might also support the
finding, as this would render her more susceptible to the scent of
the male. Although there are some data which indicate that the
sense of smell is unimportant with regard to the oestrous cycle,
Donovan and Kopriva (1965) suggest that the role of the sense of
smell in mediating oestrous behaviour merits further study, especially
in view of the odoriferous glands of the male guinea pig, the fact
that they are reduced in size by castration, and restored by
androgen injection, together with the use of the nose prior to
coitus. An investigation into the response of oestrous and non-

* numerical data for s-nosing were not obtained in Experiment IX

oestrous females to male odour is desirable. It is possible that at oestrus, olfactory sensitivity is increased in the female, and she may be attracted to the odour of the male. This does not necessarily imply that she seeks out the male, but it would be consistent with this behaviour. As Jacobs (1976) writes, the role of the female may not be entirely passive.

It is clear that there is a great deal of scope for further investigation into the marking behaviour of the female guinea pig, her response to male odour at oestrus, and into the response of the male guinea pig to olfactory stimuli from oestrous and non-oestrous animals. It would also be of interest to investigate the behaviour of Cavia aperea females, to determine whether they increase their rate of marking at oestrus. It is of considerable interest that according to Rood (1972) the C. aperea female does not emit the characteristic male-like mounting behaviour of the female C. porcellus.

Conclusion

The present data suggest that the female guinea pig increases her frequency of marking at the time of oestrus; this is supported by the investigation of Birke (1981). It is possible that female guinea pigs are more sensitive to odour during oestrus and pro-oestrus, and that this may affect their behaviour at this time. The female guinea pig may play an active role in approaching the male.

The female guinea pig's increased rate of marking may attract the male to her, either through oestrus-related odours, or by her odour becoming the prevailing female odour and attracting the male. It is also possible that scent deposited during marking by the oestrous female may contain a releaser pheromone.

The issue is still unclear in the absence of sure information
as to whether the male guinea pig discriminates between olfactory
stimuli from oestrous and non-oestrous females in group or natural
conditions. It is suggested that there is room for further research.

Experiment X

The two females were removed from their cage and housed for eight days in a 3 feet square enclosure on the laboratory floor. The floor was covered with a thick layer of newspaper and some hay. Two cardboard boxes with holes cut in the sides served as shelters for the guinea pigs. These contained woodchips and hay. A normal laboratory cage was placed so that it formed part of the boundary wall (a diagram is given on page 250). This contained a male guinea pig.

Beginning on day 17 of an 18 day cycle the behaviour of the guinea pigs was observed for half an hour in the mornings and evenings (9.30 to 10.00 am; 5.30 to 6 pm). On days -1 and 1 the position of the subject animal was monitored every 60 to 90 minutes.

The position of the animal was recorded as "near" or "not near" the male. "Near" meant touching the male's cage or in very close proximity to it. "Not near" was recorded if she was a foot or more apart from the male. "I" was to have indicated an intermediate position but in fact this did not happen.

The results were as follows:

Day 17:

Morning watch	The subject was not seen to approach the male.
Evening watch	The subject went up to the male's cage twice. Both the male inside the cage and the female outside the cage reared up, and showed the "nose-nose" (Rood, 1972).

Figure 10b

cage containing male

box containing
bedding

box containing
bedding
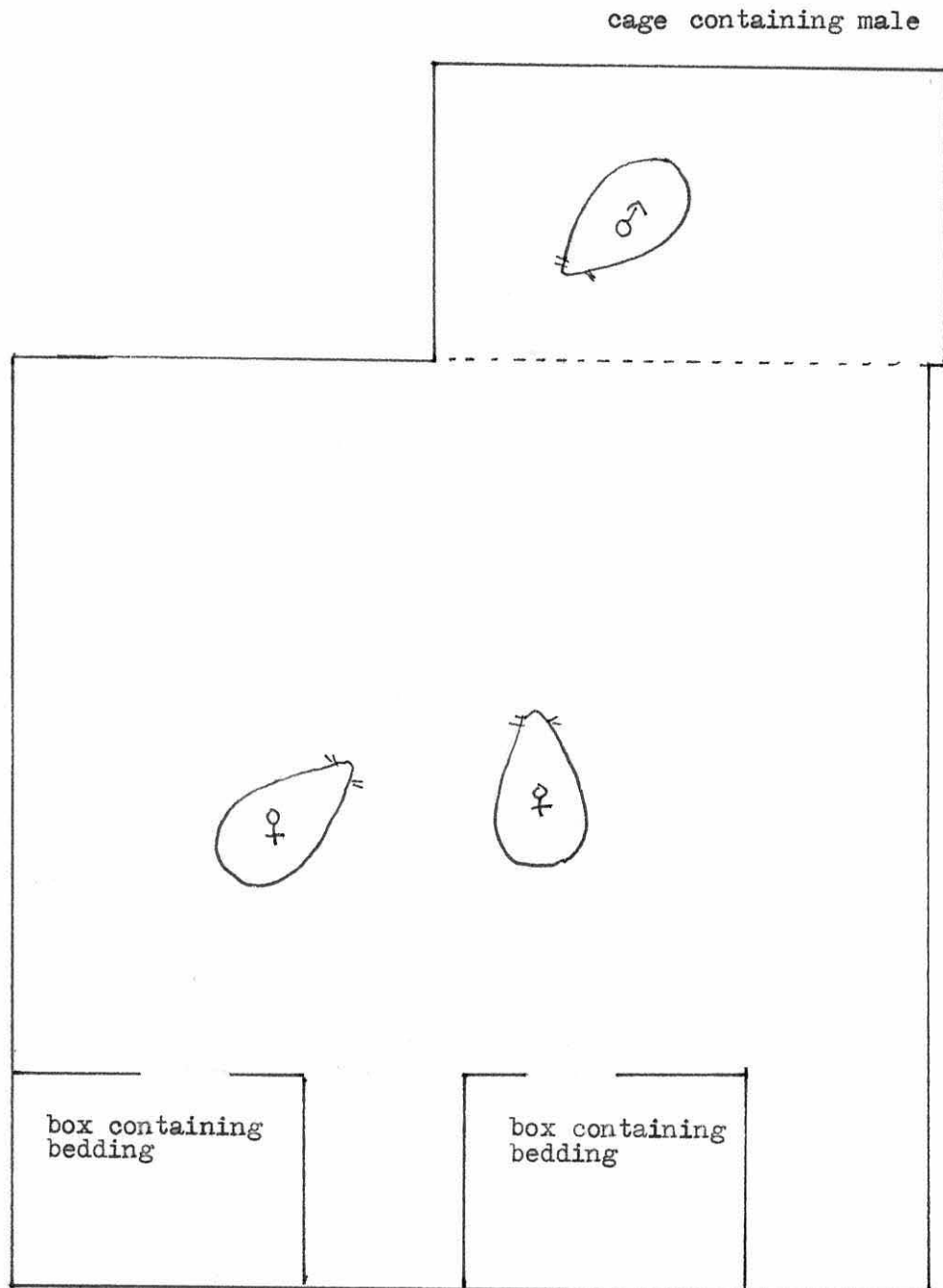
Day 18:

Morning watch   The subject went up to the male's cage;
                                 she remained leaning against it for
                                 approximately 3 minutes.

Time sampling was carried out subsequent to this observation.

Time	Position of S
10.30	Near
12.00	Near
1.00 pm	Near
2.30	Not near
3.30	Not near
4.30	Near
5.30	Not near
7.00	Near
8.00	Near

At 8.30 pm the subject was moving about. During 5 minutes she marked the substrate 4 times, chased the other female guinea pig and purred briefly.

Day 18-1:

Midnight   The subject was quiet and showed
                                 lordosis in response to stroking.

Day 1:

Time	Position of S
10.30 am	Near
12.00	Not near
1.00 pm	Not near
2.00	Not near
3.00	Not near
4.00	Not near
5.30	Not near
6.30	Not near
7.30	Not near

During Day 1 the female was observed to be near the male's cage for 66.7 per cent of the time sampled. On Day 2 this dropped to 11 per cent.

Observations were made at frequent intervals on the following 5 days, but at no time was the female lying near the cage of the male. On one occasion only she was approximately one foot away.

During the time sampling during Days 18 and 1 the female was either near the male's cage or well away from it.   There was no intermediate position recorded.

Unfortunately it was not possible to repeat this experiment with the other female.   Although she showed chasing and mounting behaviour, at no time did she prove to be receptive.

———————————

Chapter 11

Discussion

Introduction to Discussion

This chapter begins with some comments on factors associated with experimental design: the small N, the repeated use of subjects, and the lapse of time between Experiments I and VII.

This is followed by a summary of the findings obtained in this investigation, and suggestions as to the possible functions of scent marking.

These suggestions are then discussed in relation to the guinea pig, and in the context of data concerning other mammalian species. The areas covered include the effects of scent marking, dominance, the functions of dominance, information conveyed in scent marks, scent marking and sexual behaviour, group cohesion, and pheromones.

Finally, the role of scent marking in the guinea pig is summarized, and suggestions are made with regard to possible areas for future research.

_____

Discussion

The sample used in this investigation was small. The implications of this have been discussed in Chapter 4, where it was suggested that where there is good experimental control the possibility of committing a Type 1 error is very small.

For the experiments where the subjects were male guinea pigs (I - VIII) N ranged from 6 - 10 subjects with the exception of Experiment III where N = 4, and except for the latter it was possible to use the Wilcoxon Matched-Pairs Signed Ranks Test. Although this is a non-parametric test, compared with the t test its power efficiency is near 95 per cent for small samples (Siegel, 1956). With regard to Experiment III it was considered inappropriate to attempt a statistical analysis; however, the data are unambiguous, and there can be little doubt as to the validity of the findings.

Two experiments were carried out using female guinea pigs as subjects. In one of these there were three subjects, in the other only one. These experiments differ from those using male subjects in that they looked at the behaviour of the female in relation to the oestrus cycle; thus the behaviour was examined over a period of time. Three is too small a number of subjects to permit any firm conclusion. If it had been possible to record the behaviour of the subjects over a longer period of time this would have extended the generality of the findings. However, it has been possible to come to a firm conclusion concerning the hypothesis underlying this experiment owing to the recent work of Birke (1981), who obtained similar data.

The same is true of Experiments VI and VIII. Similar findings

have been reported by Beauchamp (1973) and by Ruddy (1980), respectively.

With regard to Experiment X where only one subject was used, no firm conclusions may be drawn. Again, if the one animal had been studied over several cycles rather than just one cycle, the finding would have greater validity. The data obtained suggest that further research might be worthwhile.

Where experimental control is good a small N would not seem to pose a problem. This would seem to be the view of other workers in the field. Thus Ruddy (1980) used four male and four female subjects. and Birke (1981) used six subjects. A small N may be just as suitable for asserting that a phenomenon is experimentally demonstrable as a large N. It is up to each worker to decide on the relative merits of small and large sample sizes in relation to the species being studied, and the experimental design. In the sort of experiment described in the present investigation it is suggested that N should not be less than 8, while as many as 10 - 12 subjects is preferable.

The subjects used in this study were used in more than one experiment. As pointed out in Chapter 4 this is not unusual, and whether it is or is not a wise procedure depends on the nature of the investigation. Beauchamp (1974) reported that repeated testing did not alter the response of male guinea pigs to female urine, and Berryman (1974) reported that the behaviour of guinea pigs used on more than one occasion was unaffected: Berryman was investigating vocalisation in infant and adult guinea pigs. Geissler and Melvin (1977) found that there was no decrease in aggression across six thirty-minute test sessions. No effect has been observed in the present study to suggest that several exposures to the open field

or to conspecific odour affected the behaviour of the subjects. Nevertheless, in line with other workers who have used the same subjects on more than one occasion (for example, Pearson, 1970; Berryman, 1974) an interval was allowed between experiments. Also, the order in which the animals underwent the experiments was varied to minimize any possible effects of the repeated exposures.

The counterbalanced design used in most experiments where subjects acted as their own controls did not affect the results, as reported on page 141 . The need for this design would seem to be emphasized by the comments of several workers as to the variability between guinea pigs, and the consistency of behaviour within each individual (Seward and Seward, 1940; Young, 1969; Willis, Levinson and Buchanan, 1977; Levinson, Buchanan and Willis, 1979).

Another detail which should be considered is the lapse of time between Experiment VII where the response to female odour was compared with the response to male odour in Experiment I. The greatest interval was eight weeks, but was less in most cases. The shortest interval was two weeks. The difference of eight weeks is not considered to be significant in the case of the older animals who were 26 months old (see Chapter 5). Guinea pigs may live for as long as 8 years (Festing, 1974). In this context the finding of Beauchamp, Criss and Wellington (1979) is relevant. They found no significant trend according to age in the response of guinea pigs to chemical stimuli. The data obtained in the present study, and the observations described in Chapter 3, do not suggest that the response of mature guinea pigs to olfactory stimuli is modified by a period of considerably

longer than eight weeks. However, this interval would not be advisable if the animals are not fully mature. In the case of the younger subjects (approximately six months old) the interval which elapsed was from 2 - 4 weeks.

It is concluded that neither the use of the same subjects on more than one occasion, nor the lapse of time involved in relation to Experiment VII affected the findings.

Finally, it should perhaps be pointed out that the series of Experiments I to V are interrelated, with each confirming and extending the data obtained. Experiments VI and VII are also related, and the data obtained in VI and VIII are extended and confirmed by the findings of Beauchamp (1973) and Ruddy (1980). It has been the policy throughout this thesis to consider the data obtained in conjunction with the work of other investigators. In this way a more complete picture may be obtained of the pattern of social behaviour in the guinea pig.

The preceding chapters have revealed that the male guinea pig marks vigorously in response to the scent of male conspecifics, and that he uses more than one source of odour in scent marking: secretions from the perineal gland distributed during ano-genital dragging, and urination. The pattern of defaecation in response to olfactory stimuli suggests that faeces may also be used in marking.

The male shows pilo-erection and tooth chattering in response to male conspecific odour, also increased locomotion. He is attracted to the odour of a male conspecific, even when it is that of a stranger.

The male guinea pig can distinguish the sexes by smell, and

would seem to be attracted to female odour. He spends signifi-
cantly more time s-nosing female than male odour. He marks in
response to female odour, but does not show pilo-erection or
tooth chattering, and marking is significantly less than in res-
ponse to male odour.

The male guinea pig is able to distinguish between urine from
oestrous and non-oestrous females, and would seem to prefer oestrous
urine: s-nosing and biting are more persistent in response to
oestrous urine.

The female guinea pig increases her rate of marking at oestrus,
and it is possible that the female guinea pig develops approach
behaviour towards the male at this time. As does the male, the
female deposits urine during scent marking.

Both male and female guinea pigs mark in response to a clean
cage or fresh bedding, and mark the substrate during their normal
daily activity. Both sexes tend to mark over the scent of a previous
animal.

It is probable that scent marking in the guinea pig serves
several functions. "Marking might play a part in any field of ol-
factory communication and there have been a number of .....
suggestions as to its communication value". (Johnson, 1973).
Ralls (1971) and Johnson (1973) list several functions   of marking
that have been proposed by various authors. These include the
following:

> a deterrent or substitute for aggression, to warn
> conspecifics away from occupied territory
>
> individual recognition, perhaps including in-
> formation on sexual status, dominance, age, and
> so on.
>
> a sex attractant or stimulus

labelling of the habitat for an animal's own
use in orientation; to maintain a sense of
familiarity with an area; to promote group
cohesion

to distribute primer pheromones influencing
reproductive processes

These suggestions will be considered in relation to the be-
haviour of the guinea pig on the basis of the data obtained in
this and other investigations. Work involving other mammalian
species will also be mentioned where it would seem relevant or
illuminating.

Effects of scent marking - location

Territorial behaviour has been defined frequently as a means
of territorial defence, to deter alien conspecifics from entering
the territory (Lorenz, 1966; Hediger, 1950). If this is the case
then it might be expected that the scent marks of a territorial
species would have deterrent qualities. However, it would seem
that this is not necessarily the case. Thus rabbits (Mykytowycz,
1965), the Norway rat (Barnett, 1963) and the black rat (Ewer,
1971) will enter alien territory. Lacher, Bouchardet, da Fonseca
and Alves (1981) found that although wild marmosets scent marked,
those scent marks did not deter conspecifics from using a marked
area. Lacher et al conclude that olfactory cues do not aid
marmosets to defend a home territory, but do not discount the
possibility that the marking has a territorial function.

In her study of the New Forest pony Tyler (1972) reports that
although stallions scent marked she found no evidence to suggest
that marking had a deterrent effect on rival stallions. Tyler
points out that the stallions did not have geographically de-
fined territories, but suggests that their harems constitute

moving territories. Scott (1967) points out the well known
observation that the domestic dog does not retreat from the
scent marks of another dog.

Thus, in investigating territorial behaviour, to seek for
a deterrent effect in scent marking may not be helpful. However,
there are some data which indicate that scent marks may have a
deterrent effect. Several canids have been reported as showing
avoidance responses to the scent marks of territory owners, the
red fox (Macdonald, 1977; cited in Barrette and Messier, 1980),
the wolf (Rothman and Mech, 1979) and the coyote (Barrette and
Messier, 1980). Rothman and Mech (1979) observed behaviour in
lone wolves which indicated a deterrent effect of the scent of
the resident pack. The territorial significance of scent marking
is further illustrated by the fact that lone wolves and coyotes
do not have territories and either generally do not mark (wolves:
Rothman and Mech, 1979) or mark significantly less than the terri-
torial animals (coyotes: Barrette and Messier, 1980).

It is possible that scent marking may serve to reduce en-
counters between resident and intruding animals. Thus Rothman
and Mech (1979) suggest that the scent marking of the pack to-
gether with the frequent investigation of olfactory stimuli shown
by a lone wolf, reduces the likelihood of a lone wolf encountering
a pack. Ewer (1971) reports that a black rat entering an alien
territory would often withdraw when it encountered the scent of
a dominant male.

Ewer (1971) reports that in an encounter between a home rat
and an intruder the advantage is always with the home rat. The
intruder is cautious and usually flees. Even a large male is
normally routed by a very much smaller animal. Mykytowycz (1968)

found that although a rabbit will enter an alien territory its behaviour will change; it ".... seems always on the alert. Its neck is stretched, the movement of its nostrils indicates that it is sniffing continuously, and it does not feed." Although an interloper may be dominant in its own territory, when challenged outside it by a rabbit permanently attached to the foreign territory it will offer no resistance, even if the challenger is half grown.

Thiessen, Blum and Lindzey (1970) suggest that the behaviour of the gerbil in the presence of an alien scent may be analogous to the marked hesitancy and caution shown by rabbits when entering an alien territory. This "cautious" behaviour might be in response to the scent of the residents of the territory.

Thus it would seem that while scent marks do not generally cause avoidance, as Johnson (1973) writes, they "may signal that an animal is in foreign territory and predispose withdrawal in the presence of the dominant animal." However, Johnson points out that the behaviour could be in response to any novel environment, or to the absence of the animal's own scent.

If an intruder into a territory is predisposed to flight, it is also true that a territory holder within his territory is more likely to initiate an attack than an animal with no territory (Ralls, 1971). The same is true of a dominant animal in a group with a social hierarchy. A stimulus which is especially effective in eliciting aggression from a territory holder or a dominant animal is the appearance of a strange conspecific of the same sex (Ralls, 1971). This, together with the predisposition of the intruder to flee suggests that the scent marks act as a threat; a deterrent, or substitute for aggression.

Rasa (1973) says that scent from the cheek glands of the
African dwarf mongoose seems to act as a threat. The scent of
a strange animal elicits reciprocal aggression, and seems to
cause unease. Macdonald (1979) in an investigation into marking
by the red fox reports that marks were most frequently made by
dominant animals and were observed in several contexts, in-
cluding aggression. Müller-Schwarze (1972) suggests that scent
rubbing in blacktailed deer might act as a means of agonistic
interaction. He cites Ralls (1971) who says that individuals
which mark frequently are likely to win an agonistic encounter.

A high rate of marking is associated with aggression in the
guinea pig. The present study demonstrates that vigorous marking
in response to male conspecific odour is accompanied by pilo-
erection and tooth chattering, both of which occur in agonistic
situations (Pearson, 1970; Rood, 1972). Also, a high rate of
marking in the guinea pig is associated with dominance: Beauchamp
and Berüter (1973) report that the frequency of perineal drag in
male guinea pigs is dependent on rank. Ralls (1971) points out
that high-frequency marking occurs when an animal is motivated to
aggression, and likely to win. Thus the scent of a male conspec-
ific would seem to prepare the male guinea pig for an agonistic
encounter. Certainly the results obtained in the present study
suggest this: as has been stated, he marks vigorously, increases
his rate of locomotion, and shows signs of aggression (pilo-
erection and tooth chattering). The data obtained in this in-
vestigation also reveal that he is attracted to the odour of a
strange conspecific, and this suggests that in more natural
conditions he would seek out the source of the odour and attack,
or chase the animal away. Such behaviour has been reported by

Rood (1972). Adult <u>Cavia aperea</u> males, when placed into a pen
containing <u>C. aperea</u> were attacked and killed. The same was true
of <u>C. porcellus</u> except that the introduced animal was not killed
and eventually became integrated into the group at the bottom of
the dominance hierarchy. The difference is possibly due to dom-
estication resulting in reduced aggression in the guinea pig.
This behaviour is consistent with territoriality, where an in-
truder is typically chased and/or attacked.

Berüter, Beauchamp and Muetterties (1974) write that the fact
that the male guinea pig marks when the environment is changed
suggests that it serves to mark the home range or territory. The
male's own scent would serve to identify an area as familiar,
whereas the mark of a strange male could serve to alert the male
to the presence of possible competitors.

The fact that scent marks appear to attract male guinea pigs
does not indicate that the guinea pig is not territorial. Work
with other species has shown that territorial scent marking does
not necessarily act as a deterrent, although there is considerable
evidence to suggest that it acts as a threat, modifying the be-
haviour of an intruder, and conferring an advantage, in the event
of an agonistic encounter, on the territory resident.

Moreover, there is some evidence which indicates that a
rabbit's response to alien scent marks may vary according to the
context in which they are encountered. If foreign faecal pellets
were distributed in the home area of rabbits, the rabbits responded
by marking vigorously. However, if the rabbits were placed in alien
territory they did not scent mark. That this was not due to novelty
is demonstrated by the fact that they would mark in a novel, but
neutral, area (Mykytowycz, 1968; Mykytowycz and Hesterman, 1970).

This has been discussed in Chapter 7. As Johnson (1973) points out, it "may be an important consideration for the interpretation of laboratory studies." It exemplifies the need for field or naturalistic as well as laboratory studies.

Further light may be thrown on the nature of scent marking by investigating the distribution of scent marks. If marking acts as a means of territorial defence it might be expected that marking would occur at the territorial boundaries. Hediger (1949; cited in Tinbergen, 1953) said that many species deposit scent where they are likely to meet rivals. This would tend to be near the edge of a territory. However, many animals do not confine marking to the territorial boundaries.

Thus Mykytowycz (1968) comments that the marking behaviour of the rabbit probably saturates the territory with odour, and Mykytowycz and Gambale (1969) have found as many marking points inside the territory as round it; however, the rabbits' marking points were most numerous in the direction of the neighbouring colony. The European beaver marks territorial boundaries but has marking points throughout the territory (Richards, 1967; cited in Johnson, 1973). Rasa (1973) reports that the mongoose marks at the centre rather than at the perimeter of the living area, and Goddard (1967) found that the rhinoceros deposits scent marks throughout the home range.

Kawamichi and Kawamichi (1979) describe "aggressive territorial" chases in the tree shrew, and conclude that the species is territorial. Both males and females scent marked inside and outside territories with frequent marking around home range boundaries. The European lynx and the wild cat bury urine and faeces within the territory, but leave them exposed near the boundaries

(Lindemann, 1955; cited in Ewer, 1968). Thompson's gazelle also distributes more scent at the boundaries of the range (Walther, 1978).

van Lawick Goodall and van Lawick (1970) report that spotted hyenas regularly patrol and scent mark territory boundaries. Peters and Mech (1975) in wolves, and Bowen (1978; cited in Barrette and Messier, 1980) in coyotes, report greater rates of marking at the edge of the territories where the presence of alien group scents elicited scent marking by the owners. However, Barrette and Messier (1980) challenge this, suggesting that the "spatial distribution of scent marks over an animal's territory is a function not only of the rate at which an animal marks when it travels on a trail, but of the rate with which it uses that given trail as well." Barrette and Messier conclude, therefore, that the spatial distribution of scent marks in canids is still unknown.

The guinea pig deposits urine and faeces throughout its environment (Rood, 1972; personal observation). However, it would be of interest to investigate the distribution of scent marks in the home range of Cavia aperea and in comparable conditions for the guinea pig.

Another factor which should perhaps be borne in mind in looking at the location of scent marks in relation to territory is that the territory of the animals may not correspond with the range. Mykytowycz (1968) points out that the area within which an animal confines its activties is not necessarily the same as its territory. In a strict sense of the term, "territory" refers to that part of an animal's home range which it protects, sometimes by fighting. Ewer (1971) observed that the area defended by the

black rat is relatively small in comparison with the range. Ewer points out the advantage to a species of familiarity with the environment beyond its immediate territory.

In conclusion, the evidence suggests that most species will enter foreign territory. Thus scent marks do not seem to act as a deterrent. But the behaviour of an intruder would seem to change in response to the alien odour, suggesting that this serves as a warning or threat. It also confers an advantage on the territory holder in that it clearly helps to defend a territory.

Scent marking may also serve to reduce encounters between resident and intruding animals. In given circumstances scent marks have a deterrent effect in canids.

The distribution of scent marks may be relevant in studying territorial behaviour, but while some species would seem to concentrate marking at the boundaries of a territory, this is by no means always the case.

The fact that the guinea pigs in the present study were attracted to the odour of comspecifics does not imply that they are not territorial. It is possible that the response of animals to alien scent marks varies according to where they are encountered. The response of the guinea pigs in the present study to conspecific odour (persistent s-nosing, a high rate of marking, behaviour associated with aggression and increased locomotion, together with the fact that they were attracted to the odour) is consistent with the behaviour of an animal in its own territory when it encounters the scent of an intruder. It is clearly necessary to extend this work, providing conditions where it is possible to investigate the response of the guinea pig to alien

conspecific odour encountered in the "territory" of another
animal.

Although further investigation is needed to establish
whether the guinea pig is territorial, it is concluded that the
behaviour reported in the present study suggests that the guinea
pig is a territorial species. King (1956) writes that the
sedentary and aggressive behaviour of the male guinea pigs
suggests that in natural conditions they have territories.

Dominance hierarchies - variable reports in guinea pigs - other
species. Factors which affect dominance - scent of dominant
animals - a threat?
_____

There is a great deal of evidence to suggest that guinea pigs
form dominance hierarchies. These are generally described as
linear (Rood, 1972; Bates, Langenes and Clark, 1973; Coulon,
1975a; Berryman, 1978) in the male population, although tri-
angular hierarchies have been reported (Kunkel and Kunkel, 1964).
Jacobs (1976) reports that male and female animals formed lasting
associations. Dominance shifts occurred frequently as the
different females became receptive. When the associating fe-
male came into oestrus the associating male assumed the alpha
position or moved up the hierarchy. The rank usually fell after
the oestrous period. These findings are at variance with those
of Kunkel and Kunkel (1964) and Rood (1972) who report stable
hierarchies, and of Berryman (1978) who reports a fairly stable
hierarchy. Rood (1972) reported that no permanent social re-
lationships were formed, and that mating was promiscuous.

Although Jacobs (1976) offers an explanation of the difference
between his and Rood's (1972) findings based on a comparison
of their respective observation methods, it does seem that the

animals in Jacobs' (1976) study behaved differently from those
in other studies with regard to the male-female associations.
However, shifts in dominance related to oestrus have been reported
by other workers. Thus Coulon (1975a) found that dominance
changes could occur during periods of sexual activity stimulated
by an oestrous female, and Beauchamp and Beruter (1973) reported
shifts in dominance which they suggest might be related to the
post-partum oestrous period of the females. The picture is
further complicated by the work of Fuchs (1980) who found that
guinea pigs kept outside in relatively large spaces did not form
hierarchies, although one male was dominant over all the other
males.

It is likely that dominance in the guinea pig is affected by
many variables which as yet are incompletely understood. Although
dominance hierarchies have been observed in many species they are
frequently variable and difficult to predict. Some indication
will be given of the variability in relation to dominance in other
species, and of the factors which seem to affect hierarchies.

Koupt, Law and Martinisi (1978) report linear hierarchies in
small groups of horses; in large groups triangular hierarchies
were observed. Tyler (1972) describes dominance hierarchies in
New Forest ponies. Hierarchies were mainly linear, but there
were some triangular relationships. However, when stallions were
included in assessing the rank order of a group the dominant-
subordinate relationship was not consistent. A stallion would be
dominant over the mare in one situation, while the mare was
dominant over him in another. Tyler suggests that the hierarchies
for mares and stallions be separated.

In a pack of Cape hunting dogs separate hierarchies were recorded for male and female animals (van Lawick Goodall and van Lawick, 1970). However, it was not possible to determine precisely the rank-order of the males. Two were high ranking, with the remaining animals below. Separate hierarchies were found for the male and female grey kangaroo (Grant, 1973). However, in a captive group consisting of one male and six females the male was dominant over the females. In a free-ranging group no aggressive interactions occurred between males and females.

Rowell (1974) points out that there is sometimes a low correlation between different types of behaviour used to measure dominance and subordinacy. Rowell (1966) found that no single criterion could be used throughout a group of baboons to assess rank orders. Deag (1977) accepts that there are sometimes poor correlations between different types of behaviour used to measure dominance and subordinacy, and suggests that the term hierarchy should be qualified according to the behaviour used to define it. Berryman (1978) suggests that it is not necessary to predict that all or many patterns of social interaction should reflect the same stable hierarchy.

Richards (1974) found that in stable groups of macaque monkeys different measures of dominance agreed with each other, and suggests that this correlation was due to the stability of the groups he was studying. Rowell (1967) was unable to determine the presence of a dominance hierarchy in wild baboons, but was able to do so in a captive group. This suggests that free and captive groups behave differently. However, the groups also differed in that there were several males in the wild groups,

and only one in the captive group. Richards (1974) suggests that a group of rhesus monkeys, consisting of one male with several females and their offspring, has a more rigid and linear social structure than a group where there is more than one male.

Richards (1974) suggests that results obtained with a captive group may not be typical of a wild group of the same species. In captivity feeding is condensed to one or two brief periods. The rest of the day is unoccupied and with individuals maintained in close proximity, behavioural changes would be expected to occur.

In the wild, agonistic interactions are less frequent and shorter than in captivity (Rowell, 1966). Escape is not possible in a captive group. Rowell (1967) notes that most hierarchies are reported in captive groups, and suggests that some animals respond to the stress of captivity with a syndrome of physiological and behavioural change (Rowell is referring mainly to primates).

Ewer (1971) comments that "studies on caged animals are not a reliable guide to the social organization of free living populations as has been shown particularly clearly for primates". Ralls (1971) points out that the degree of crowding may affect the type of dominance within a species; territorial dominance at low densities, individual at high densities. Leroy (1974) says that when the area available to a group of animals is reduced experimentally a territorial organization becomes a hierarchical one.

Odell (1977) studied the social structure of the Northern

elephant seal. Odell found that most of the dominant males became territorial, defending an area of beach containing app- roximately fifty females. While fourteen groups were territorial, one larger group was controlled by three males in a social hierarchy. Odell suggests that if space is limited the females may congregate in one large group: the same males would then be forced to co-exist in an area larger than one from which any one of them could exclude all the others. Thus, instead of being territorial, they form a dominance hierarchy.

Fuchs (1980) found that dominance hierarchies did not develop in guinea pigs. One male became dominant but the remaining males were subordinate to him, and did not form a hierarchy. Fuchs maintained six male and eight female guinea pigs in a $12 \times 12m^2$ outdoor "field". This is a large area relative to the number of animals, and Fuchs suggests that the dominance hierarchies ob- served by other investigators are due to the relatively high number of animals in a limited area; the animals had no option but to fight back as they could not escape.

Berryman (1978) makes a similar point, suggesting that the space available to each animal within a colony and the number of animals are likely to be critical: it might be less feasible for a single animal to defend a territory in a relatively small area due to the number of animals likely to intrude during random movements.

It is also possible that aggression by dominant animals may result in dpspersal. In captive animals in a small area this is not possible, and this is another factor which should be considered when investigating dominance hierarchies.

It is probable that dominance hierarchies are affected by several variables, including population density, which in turn

is related to the space available. It would also seem that captivity has a significant effect in several species.

Berryman (1978) found that dominance was consistent from group interaction to paired interactions. She also found that purring in the guinea pig indicated with quite a high degree of consistency the dominance status of an individual as it might be assessed in a sexual or aggressive conflict. Berryman concludes that dominance in the guinea pig is influenced by a variety of factors. Status is to some degree dependent on the situation, and may fluctuate with oestrus in females outside the aggressive context.

There is yet another factor which complicates the investigation of the formation of social hierarchies; thus in some species hierarchies occur only in one sex. In others each sex forms a separate hierarchy, and in some, notably the primates, a hierarchy will include animals of both sexes.

Mykytowycz (1968) observed that male rabbits establish a hierarchy at the start of the breeding season; the females did likewise. Ewer (1971) reports a hierarchy, linear among the top three black rats, but less clearly defined among the lower ranking animals. There was no hierarchy observed in the females, although one female was dominant. van Lawick Goodall and van Lawick (1970) describe a linear hierarchy in female Cape hunting dogs, and a hierarchy in the males where it was possible to rank the top three animals only.

Odell (1977) described dominance hierarchies occurring independently in male and female elephant seals. Tyler (1972) and Koupt, Law and Martinisi (1978) report male-female hierarchies in horses, with stallions generally dominant over females. In a captive group of one male and six female grey kangaroos a hier-

archy developed with the male dominant over the females (Grant, 1973). In a free ranging group no aggressive interactions occurred between males and females.

Rowell (1974) writes that in many primate species females may rank higher than the male. Keveme, Scruton and Young (1978) report that female Talapoin monkeys are frequently dominant over males. The situation is complex in the African dwarf mongoose where the social structure is described by Rasa (1973) as a matriarchy. The mongoose lives in groups of up to twelve animals consisting of a founding pair and offspring of several generations. The founding female is highest in rank followed by the founding male. The next highest in the hierarchy are the youngest members of the group. Wolf packs include a dominant adult male and female which Rothman and Mech (1979) describe as the alpha pair.

Hierarchies in guinea pigs are reported as developing in the males, although weak hierarchies have been reported occasionally in the females (see page 39). However, Bates, Langenes and Clark (1973) report that in unfamiliar juvenile guinea pigs females were dominant over males in competition for water. It would be of interest to carry out research into inter-sex aggression in the guinea pig in relation to appetitive behaviour (competition for food or water).

The possible threat or deterrent function of scent marks has been considered in relation to territorial behaviour. In view of the fact that guinea pigs form dominance hierarchies it is possible that odours deposited during scent marking have, or acquire, aversive properties. If marking can be shown to be

related to dominance then it suggests that it might act as a
threat. It has been reported that dominant animals mark more
than subordinates (Rood, 1972; Beauchamp and Berüter, 1973).
Beauchamp and Berüter (1973) have found that the perineal gland
of the dominant male guinea pig produces more sebum than the
gland of the subordinate males.

Mykytowycz (1968) reports similar data for the rabbit. He
found a significant relationship between the size of the anal
gland, the secretory activity of the gland, and the position of
the animal in the social hierarchy. The chin gland behaves like
the anal gland, being larger and secreting more in the dominant
animals. Chinning (marking with the chin glands) was highest in
the dominant rabbit.

Where there is such a clear association between scent marks
and dominance it is possible that the scent of the dominant male
acts as a threat. In the present investigation male guinea pigs
were not deterred by the scent of a strange adult male. In view
of the fact that the formation of a dominance hierarchy requires
individual recognition (Beauchamp, Berüter and Muetterties, 1974;
and Rowell, 1974) it would not be expected that the scent of a
strange male would have a deterrent effect. It would clearly be
of interest to determine whether the scent of an alpha male is
aversive to subordinated animals. Rood (1972) reports that a
subordinate male will avoid the alpha male before he encounters
it, implying that this is mediated by the scent of an alpha male.

To conclude this section on dominance, it is clear that in
several species dominance hierarchies are variable and difficult
to predict. Several factors would seem to affect the formation

of dominance hierarchies, such as the presence or absence of a
male, or the number of males in a group; and whether inter- or
intra-sex aggression is involved. The density of the population
and the amount of space are relevant. It is possible that the
behaviour of animals in captivity is not a reliable guide to
the behaviour of a free-living population with regard to dom-
inance. A territorial species may form dominance hierarchies
when dispersal is not possible. Different measures of dominance
in a species may not correlate.

The high rates of marking observed in dominant animals
suggest that the scent of a dominant animal may act as a threat
to subordinate animals. Factors which seem likely to be relevant
to the formation of a dominance hierarchy in guinea pigs include:

> the size of the living area
> the population density
> the number of males, and the ratio of
> males to females
> the occurrence of oestrus in females

It is suggested that the size of the area in which a given
number of animals is maintained is critical, and that the guinea
pig is probably a territorial species which forms dominance hier-
archies when the animals are obliged to remain in close proximity.
King (1956) at the conclusion of his semi-naturalistic study of
social behaviour in the guinea pig writes: "Under natural con-
ditions it is likely that territoriality develops because of
the sedentary and aggressive behavior of the males." Further
research is needed.

Functions of dominance - reduction of aggression - priority
of access - territoriality - population control

A discussion of dominance hierarchies would not be complete
without some reference to the possible functions served by a
hierarchy.

Rowell (1974) writes that it has been suggested that dom-
inance hierarchies may function to reduce aggression (Lorenz,
1966; Tinbergen, 1964) and this would seem to be a widely held
view. Rowell (1974) disputes it on the grounds that hierarchies
tend to be associated with high rates of aggression in primate
groups. However, she does add that in theory, where a high rate
of aggression is accompanied by a hierarchy an even higher
potential level of aggression is avoided.

Deag (1977) also is not happy with the assertion that the
function of a dominance hierarchy is to reduce aggression, and
suggests that it is necessary to concentrate on the function of
specific acts rather than the function of dominance and hierar-
chies. Deag says that there may be advantages for the winner
of an agonistic encounter and an advantage, therefore, to be of
high rank. These may include:

> access to water
> increased feeding efficiency due to receiving
> fewer threats
> priority of access to receptive females

Data obtained by Rasmussen and Rasmussen (1979) suggest that
high-ranking animals have access to superior food supplies; and
their data lend some support to the reduction of aggression
theory. In their study of twenty male Japanese macaques

Rasmussen and Rasmussen found that higher ranking males used the most preferred and least plentiful resting sites; they ate from the densest food patches. Low ranking males made detours to avoid other animals, thus rank correlated with consistency in the use of paths. Rasmussen and Rasmussen suggest that attachment to areas may reduce agonistic encounters since low-ranking males avoided areas used by the high ranking males.

Lacher, Bouchardet , da Fonseca and Alves (1981) report that dominant wild marmosets feed first, followed by lower ranking animals. Tyler (1972) reports that in competition for food the stallions were dominant over most of the mares. When hay was provided the most dominant animals generally remained near the hay until it was finished. Subordinate animals avoided threats by remaining at a distance from the hay and making little or no attempt to eat any. Koupt, Law and Martinisi (1978) also report data indicating that dominance in horses gives priority in feeding.

Grant (1973) writes that his data suggest that formation of a hierarchy in grey kangaroos may avoid contact between individuals, and therefore reduce aggression. Grant also notes that there was some evidence of high ranking animals gaining preference at feeding places in the enclosure. Chance (1956) suggested that "dominance gives priority of access".

Appleby (1980) obtained data which indicate that high rank in red deer stags increased their access to food. Richards (1974) notes that agonistic behaviour was less frequent in stable groups of rhesus macaques than in newer groups, especially at feeding times where a recognised priority of access

existed. Richards comments that this suggests that a recognized order of priority reduces the incidence of aggression.

van Lawick Goodall and van Lawick (1970) report that the high ranking spotted hyena female gets more, and better, food from the kill. As a consequence her cubs benefit. This would seem to confer a benefit on both mother and young. Mykytowycz (1968) observed that the young of high-ranking female rabbits have a much higher survival rate than young of subordinate females. Some subordinate females are chased away from the warren, and are forced to have their litters in isolated breeding "stops": shallow burrows which are vulnerable to predators.

A high rank in the female elephant seal would also seem to benefit the young. The pups of low-ranking females are frequently bitten, and this is a major cause of death in pups. The pups of dominant females were rarely bitten (Le Boeuf, Whiting and Gantt, 1972; Reiter, Panken and Le Boeuf, 1981).

There are data which suggest that high rank gives priority of access to females. The stallions in Tyler's (1972) study defended certain mare groups (harems) from rival males, thus preventing copulation with another male. Reiter, Panken and Le Boeuf (1981) note that only the most pugnacious northern elephant seal. males monopolized mating. Keverne, Leonard, Scruton and Young (1978) report that sexual behaviour was mainly the prerogative of the dominant male in groups of talapoin monkeys. Sexual behaviour in females was not so clearly related to rank, although the dominant female tended to be preferred sexually. This is also true of horses (Tyler, 1972). Harcourt (1979) observed that during oestrus, female mountain gorillas spent more time with the

dominant male which suggests that he might have priority of access. In wolves, where each sex forms a separate hierarchy, breeding is confined to the dominant pair.

In the guinea pig there are data which suggest that high rank gives some priority of access to females, but mating does not seem to be the sole prerogative of the dominant male. Although the dominant male guards the pre- and oestrous female, exclusive mating by the alpha male is dependent on his relative dominance and the number of subordinates. If many subordinates attempt to mount the female, the dominant male will be less successful in guarding her. However, he is typically the first to ejaculate (Rood, 1972). Berryman (1978) reports that the dominant male was responsible for 40 per cent of the courtship recorded; the eighth, and lowest ranking male, was never observed to court an adult female. Rowlands (1962) observed that only the dominant male copulated: however, the dominant male in this instance was one of two males only.

It would seem likely that dominant guinea pigs would have priority of access to a limited food or water source. Rood (1972) reports that female guinea pigs were occasionally seen to push a younger animal away from a food dish with a head thrust. Further research is needed into the behaviour of guinea pigs in response to a limited food or water supply. The finding of Berryman (1978) is of interest in this context. Berryman obtained data which indicate that the behaviour of guinea pigs at a single water source is governed by different factors than those pertaining in sexual and aggressive encounters.

In the guinea pig, therefore, it would seem that high rank

may give the male priority of access to an oestrous female, de-
pending to a large extent on the number of subordinate males.
It may not give priority of access to food or water; this is
not clear. In a natural environment it would seem that the
aggressive behaviour of the dominant male would lead to dis-
persal of some of the subordinates. In captivity, where dis-
persal is not possible, the formation of a hierarchy would
serve to limit conflict within the group. Thus dominance
leading to dispersal, or a dominance hierarchy serving to
limit conflict within the group, are clearly of benefit to
the species. Where dominant animals have priority of access
at a limited resource, this ensures that at a time of shortage
some animals are able to survive and reproduce. Dominance
hierarchies probably serve a species by encouraging dispersal.
This is clearly desirable to avoid over-utilization of an area;
it also encourages the development of new breeding groups in new
areas. Ewer (1971) comments on the value of the aggressive be-
haviour of dominant black rats in that it encouraged dispersal
before any food shortage developed.

Territorial behaviour serves a similar function. Lone wolves
must establish a pair-bond and a territory before they can re-
produce (Rothman and Mech, 1979). This ensures that no more
animals breed that can be supported by the environment. Myky-
towycz (1968) suggests that possession of a territory is im-
portant in regulating population density: possession of a
territory makes breeding possible for some animals and prevents
it in others.

Thus, broadly speaking, territorial and dominance behaviour

would seem to limit the growth of the population in relation to the environment, and aid dispersal. Dominance would also seem to ensure that in a time of shortage some animals survive to reproduce. It can also function to reduce conflict between members of a group.

However, if dominance results in the alpha male having priority of access to oestrous females, this would not benefit the species as it would result in inbreeding.* It would seem likely that in the guinea pig the alpha male will copulate first, but that subordinate males will copulate subsequently. Rood (1972) points out that Ishii (1920) found that more pregnancies resulted from copulations occurring near the end than at the onset of oestrus.

It would be of considerable interest to investigate the role of dominance hierarchies in the guinea pig in relation to priority of access to resources such as food and water, and to oestrous females. Also the effects of dominance on dispersal in guinea pigs and/or Cavia aperea, particularly in view of Fuchs' (1980) findings and comments.

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* this is assuming dominance to be stable, and not subject to reversals as described by Jacobs (1976)

Scent marking - dominance and individual recognition -
reproductive status

It has been said that one of the functions of dominance is
the reduction of aggression.   If a hierarchy is to be main-
tained without continual conflict then, as Rowell (1974) says
of primates, "... it seems obvious that individual recognition
.... is the basis of hierarchical organization." Beauchamp,
Berüter and Muetterties (1974) suggest that individual recog-
nition is a pre-requisite for a social hierarchy if direct
conflict is to be minimized.

Berüter et al (1974) have found that the perineal gland
secretion of the male guinea pig is sufficiently complex to
permit individual recognition, and Ruddy (1980) has demonstrated
that both sexes are able to discriminate individual guinea pigs
on the basis of olfactory stimuli of anogenital origin. This
capability appears to be widespread; several species of rodent
have been found capable of individual recognition on the basis
of odour. These include mice (Bowers and Alexander, 1967),
gerbils (Halpin, 1974), the Norway rat (Krames, 1970) and the
black rat (Ewer, 1971).

The canidae use olfactory stimuli for individual recognition
(Smythe, 1958; Fiennes and Fiennes, 1968). Rasa (1973) found
that secretions from the anal gland of the African dwarf mon-
goose serve both to identify the individual making the mark,
also to date it. Gorman (1976) also demonstrated that mon-
gooses can recognize individuals on the basis of olfactory
stimuli from the anal glands.

Barrette (1977) reports that the behaviour of the muntjac

suggests that they recognize each other as individuals, and that they do so by olfaction. Müller-Schwarze (1971) reports that one of four scents important in the blacktailed deer, the tarsal scent, is used for individual recognition.

Thus it would seem that individual recognition on the basis of olfactory stimuli is widespread among mammalian species. Information on social status can also be conveyed by odour. Barrette and Messier (1980) point out that urine can communicate sex, reproductive status and dominance status in coyotes. The muntjac advertises its social status through scent marking (Barrette, 1977). Rasa (1973) reports that the African dwarf mongoose is able to determine whether the scent mark was made by an actively threatening animal. Müller-Schwarze (1972) writes that scent marking in the blacktailed deer can be interpreted as a means of advertising the presence and possibly the physiological status of the male.

The observation that intruding black rats tended to withdraw from the scent of the dominant male (Ewer, 1971) suggests that dominance status is conveyed by olfactory stimuli in this species. Krames, Carr and Bergman (1969) report that rats are able to distinguish between dominant animals on the basis of olfactory cues, and Cheal and Sprott (1971) report that Kalkowski (1967, 1968) found the mice were able to use olfactory stimuli to distinguish between antagonistic and other males.

Increased rates of scent marking around the breeding season

suggest that scent is involved in communicating the repro-
ductive status of the animals. Such behaviour has been rep-
orted in several species, including the deer (Müller-Schwarze,
1972), mongooses (Rasa, 1973) several canids (Kleiman, 1966;
van Lawick Goodall and van Lawick, 1970) and the rat (Calhoun,
1962; cited in Schultz and Tapp, 1973. Birke, 1978).

The oestrous status of the female can be communicated by
olfactory cues. Beach and Gilmore (1949) report that the
oestrus domestic dog conveys her receptive state to the dog by
means of urine marks. Coyotes also use urine to convey repro-
ductive status (Barrette and Messier, 1980). In the Felidae
the male locates the receptive female by means of odour
(Kleiman and Eisenberg, 1973). Rats use olfactory stimuli to
convey the oestrous state of the female (Le Magnen, 1955; Carr
and Caul, 1962). The same is true of mice (Dixon and Mackin-
tosh, 1975).

Tyler (1972) reports that when stallions sniffed urine they
often urinated onto it. This marking was almost always directed
to the urine from the oestrous mare, and Asa, Goldfoot and
Gunther (1979) report that mares show increased urination at
oestrus. These data suggest that urine can convey the repro-
dictive status of the mare. Howe (1974) suggests that marking
in the Bahaman hutia communicates the state of oestrus: ol-
factory investigation and marking is more intense in the
presence of oestrous females or their scent.

Until relatively recently it seemed that the guinea pig
was not able to use olfactory cues to determine the repro-

ductive status of the oestrous female, as indicated in Chapter 1.
This seemed surprising in view of the propensity of this species
to investigate conspecific odour. However, it is now clear that
the male guinea pig is able to use olfactory stimuli to make
this discrimination. Experiment VIII indicates that males
respond differentially to urine from oestrous and non-oestrous
females, and the greater persistence of biting and s-nosing in
response to oestrous as opposed to non-oestrous urine, suggests
a preference for oestrous urine.

Ruddy (1980) obtained data revealing that the male guinea pig
is able to discriminate between anogenital stimuli from oestrous
and non-oestrous females. However, it is not known whether he
does so under natural or semi-natural conditions, and further
research is needed. The fact that the male guinea pig has not
responded differentially to oestrous and non-oestrous odour in
laboratory studies indicates that the experimental situations
failed to elicit the response. It is also possible that the
long period of domestication has resulted in reduced sensitivity
to the odours. It would clarify the situation if the response
of male Cavia aperea to oestrous and non-oestrous odours were in-
vestigated.

If male guinea pigs do distinguish between odour of oestrous
and non-oestrous females in natural conditions, then one might
expect this to be paralleled by increased marking in oestrous
females. This was investigated in the present study (Experiment
IX) and it was found that the female does increase her rate of
marking in association with the period of oestrus. N was small

(N = 3), but Birke (1981) also reports that female guinea pigs increase scent marking at oestrus, and there can be no real doubt that oestrus in the female guinea pig is accompanied by increased scent marking.

It would seem likely that the increase in marking associated with oestrus in many species is mediated by hormones. The oestrous cycle is accompanied by changes in the level of several hormones (Birke, 1979).

To conclude, both individual identity and dominance status may be conveyed by olfactory stimuli. The conveying of the reproductive status of the female by scent marks would seem to be widespread. Although it has been difficult to demonstrate that the guinea pig is able to distinguish the oestrous female on the basis of odour, it is now known that he can do so, although it remains to be determined whether he does so under natural conditions.

Scent marking - sex attractants - courtship

Much of the work indicating that animals are able to use olfactory stimuli to determine the oestrous female also reveal that the odour is an attractant. Thus Carr and Caul (1962) found that male rats preferred the odour of receptive females. Urinary and sebaceous odour from female rats is attractive to the male (Pfaff, Lewis, Diakow and Keiner, 1973). Urine from female dogs in oestrus was preferred by males to anoestrous urine (Beach and Gilmore, 1949).

Olfactory investigation in the Bahaman hutia is more

intense in response to oestrous females or their scent, suggest-
ing, perhaps, that the scent is an attractant (Howe, 1974).
Urine of the blacktailed deer attracts the male (Müller-
Schwarze, 1971). There is some evidence to suggest that the
male rhesus monkey is attracted to the odour produced in the
vagina of the female (Curtis, Ballantine, Keverne, Bonsall and
Michael, 1971).

While Ruddy (1980) demonstrated that male guinea pigs are
able to distinguish between odours of oestrous and non-oestrous
origin, the present investigation not only indicates that the
male guinea pig is able to distinguish between oestrous and non-
oestrous urine, but suggests that he prefers oestrous urine. More
certainly, Experiment VI in the present study demonstrates that
the male is attracted to the scent of a non-receptive female.
This suggests therefore, that if the male guinea pig fails to
differentiate between olfactory stimuli of oestrous and non-
oestrous females in natural conditions, increased scent marking
on the part of the oestrous female may still serve to attract
the male. It is clearly of importance that the ability of the
male to distinguish between oestrous and non-oestrous odours in
the natural environment is investigated.

Thus there is some evidence to suggest that scent marks may
serve as a sexual attractant in several species and may, there-
fore attract a mate. While the data generally suggest that the
scent of a receptive female is attractive to the male, it is
also possible that in some species the oestrous female is
attracted to the scent of the male. It is known that the period
of oestrus in the rat is characterized by a lowered olfactory

threshold (Pietras and Moulton, 1974). Tyler (1972) reports that at oestrus some mares left their group and sought out stallions, only returning after copulation had occurred. Asa, Goldfoot and Gunther (1979) report that pony mares in oestrus tend to increase following and approaching the stallion. Harcourt (1979) reports that female mountain gorillas were attracted to the dominant male, and during oestrus would spend more time with him.

If scent marking on the part of the male serves to attract the oestrous female then one would expect two behavioural consequences.

1. He would mark in response to an (oestrous) female
2. The oestrous female would be attracted to the odour of the male.

Results obtained in the present study (Experiment X) suggest that the oestrous female may be attracted to the male. Although no firm conclusion can be drawn on the basis of one animal, nevertheless it does suggest that further investigation might be fruitful.

The male guinea pig marks in the presence of the oestrous female, as he marks during courtship (Pearson, 1970; Jacobs, 1976). He also marks in response to the scent of a non-oestrous female, as demonstrated in the present investigation. It would be of considerable interest to determine whether the male guinea pig marks in response to olfactory stimuli from an oestrous female. It is possible that scent marking in the male in response to the oestrous female during courtship functions to deter subordinate animals from the oestrous female. Further research is needed

into the response of the male to oestrous odour, of the response of the oestrous female to male odour, and of the subordinate males to the scent marking of the male during courtship.

It is possible that marking in both male and female animals in relation to breeding facilitates courtship. Rothman and Mech (1979) suggest that marking by both male and female wolves of a newly formed pair (termed "double marking") is important in pair formation and courtship success, and aids reproductive synchronisation. Double marking has been reported in other canids such as the Cape hunting dog (van Lawick Goodall and van Lawick, 1970).

In conclusion it would seem likely that scent marking may serve to attract the male guinea pig to the oestrous female. Although there is some evidence in other species to suggest that the oestrous female is attracted to the male, the evidence for this in the guinea pig is very slight, as only one subject was used. However, this possibility is worthy of further investigation.

Although scent marking in several species would seem likely to attract a mate, Johnson (1973) points out that scent marks may not do so in a natural environment, suggesting that it would be more adaptive to attract a mate by a volatile signal rather than a scent mark, so that animals are directly attracted to one another, rather than to the area in which they are living. In response to this, it would seem possible that both scent marks and a volatile signal might serve to attract a mate. There is need for further research into the whole area of scent marking in relation to reproductive behaviour.

Scent marking - labelling the habitat - group cohesion -
marking points

Another function which may be served by scent marking is
labelling of the habitat. Johnson (1973) suggests that scent
marking in response to novelty with maximum marking at a
moderate level of novelty, lends support to the idea that
marking might serve to make an area familiar to an animal by
olfactory labelling. Ewer (1968a) suggests that animals mark
both to reassure themselves and to threaten others, with the
relative importance of the two varying according to the
situation.

Marking in response to moderate novelty or to a change in
the environment has been reported in several species, including
the Mongolian gerbil (Baran and Glickman, 1970; Thiessen, Blum
and Lindzey, 1970), the tree shrew (Martin, 1968) and the mar-
supial mouse (Ewer, 1968b). The guinea pig marks in response
to a change in the environment, such as fresh bedding (Berüter,
Beauchamp and Muetterties, 1974; personal observation). Berüter
et al suggest that this marking in response to a change in the
environment may serve to mark the home range, and serve the
function of familiarising a new environment.

Mykytowycz (1968) comments that the marking behaviour of
the rabbit probably saturates the territory with odour. This
could serve to label the territory with the group odour. Müller-
Schwarze (1971) says that in the blacktailed deer urine is used
for familiarisation with the environment.

Rasa (1973) obtained data which indicate that scent marking
is important as a bonding mechanism in the dwarf mongoose. The
mongooses mark one another, and newborn young are marked by

other group members. Rasa suggests that this allomarking serves as a bonding mechanism and indicator of group acceptance between individuals. Scent marking takes place in the centre rather than the perimeter of the living area and argues for the importance of group odour as an assurance to the animals. Rasa also suggests that one function of the marking at exits and entrances of nest boxes is to indicate to colony members that they are entering a known and therefore a non-dangerous place. Allomarking also occurs in rabbits; Mykytowycz (1968) observed that rabbits mark one another with urine; young rabbits marked by adult members of the group are identified with it.

It is possible that horses use scent to aid group cohesion. Both stallions and mares sniff faeces. Mares and stallions were seen to sniff faeces when separated from their companions (Tyler, 1973). Tyler suggests that this is to obtain olfactory cues about whether their companions had passed, and it would seem that this behaviour could help them to regain the group. Howe (1974) suggests that marking in the Bahaman hutia conveys several messages, including gregariousness and identifaction with the home range.

Guinea pigs do not mark only in response to an alteration in the environment, but mark the substrate during their normal daily activity (personal observation). This low level but sustained marking in all members of a group, combined with urination and defaecation, would imbue the home area with the group odour. This would make the area familiar to them and would aid group cohesion. This interpretation is supported by

the behaviour of <u>Cavia aperea</u> and <u>C. porcellus</u> observed by Rood
(1972): lone animals do not wander off; <u>C. aperea</u> has a home
range. Thus the animals in a group would probably eat the
same diet which would contribute to the group-typical odour.
Beauchamp (1976) found that guinea pigs preferred the scent of
urine from animals fed on the same diet as themselves to that
of guinea pigs fed on a different diet. This suggests an attract-
ion to the colony odour. There is experimental evidence in support
of this in the work of Carter (1972) who found that preference be-
haviour in adult guinea pigs was affected by their experience of
odours during rearing.

Beauchamp (1973) suggests that the preference shown by male
guinea pigs for urine of a related species may indicate that urine
from conspecifics aids sociality. It has been demonstrated in the
present study that male guinea pigs are attracted to the odour of
non-receptive females. Beauchamp (1973) also found that male
guinea pigs were attracted to the odour of non-receptive females,
and he suggests that this may serve to maintain group structure.
Beauchamp (1973) points out that in normal conditions females
are receptive for a few days only every 66 to 70 days. Thus
female scent may aid social cohesion when stimuli from sexually
receptive females are absent. It was also found in the present
study that male guinea pigs scent mark in response to non-
receptive female odour. This, too, could aid group cohesion.

Thus it would seem likely that olfactory stimuli deposited
by both male and female guinea pigs are important in maintaining
the social structure and cohesion of a group.

Johnson (1973) writes that when animals scent mark over the

scent of a previous animal may indicate that they use marking points. These include the dwarf mongoose (Rasa, 1973) and the tree shrew (Kawamichi and Kawamichi, 1979). The red fox urinates frequently on conspicuous sites (Macdonald, 1979), and Northern wolves use scent posts along their runways (Fiennes and Fiennes, 1968). Here wolves might urinate, defaecate, or both. Müller-Schwarze (1972) observed that the scent marking sites of the blacktailed deer ("rubbing" sites) might be communal or otherwise.

Johnson (1973) writes that marking sites occur in many species. Common marking sites may be used by several animals, and marking points may be sought out, and appear to elicit marking behaviour. This might be interpreted as indicating that scent marks act as sites for a general exchange of information. It was observed in the present investigation that male guinea pigs mark over the scent of a previous animal, and that females urinate where another has recently urinated; the possibility that guinea pigs use marking points could be investigated.

Thus scent marking would seem to contribute to group cohesion in several species, including the guinea pig. The scent of both male and female animals contribute to this.

Although some species use marking points there is no real evidence to imply that guinea pigs do likewise. However, guinea pigs may mark or urinate over the scent of a previous animal, which suggests that this point should be investigated.

Pheromones – their role in reproduction, aggression,
territoriality etc. Evolution of pheromones and
<u>functional odours.</u>

The obvious importance of chemical communication in the
guinea pig suggests that pheromones may be involved. It was
suggested in Chapter 7 that a high rate of marking in a dom-
inant male might serve to distribute a primer pheromone. This
may keep the subordinate males in an under-developed physio-
logical condition, thus aiding the alpha male to maintain his
dominant position. It has also been suggested (in Chapter 10)
that scent marking in the oestrous female may affect the sexual
behaviour of the male by acting as a releaser pheromone.

Pheromones were originally termed <u>ecto-hormones</u> "external
hormones" (Rogel, 1978). Karlson and Luscher (1959) coined
the term "pheromone" from Greek <u>pherein</u> "to transfer" and
<u>hormon</u> "to excite". They define pheromones as "substances
which are secreted to the outside by an individual, and re-
ceived by a second individual of the same species, in which
they release a specific reaction, for example, a definite be-
haviour or a developmental process." Rogel (1978) points out
that a stimulus need not be olfactory in order to be a phero-
mone; they may be ingested or absorbed.

Insect pheromones were the first to be discovered, and
much of the research into pheromones has been done with insects.
Many insect pheromones have been artificially made (Rogel, 1978;
Gleason and Reynierse, 1969).

Pheromones differ from hormones in that they are 1) secreted
or excreted to the external environment, while hormones are
secreted to the internal environment, and 2) pheromones

function as vehicles for intra-specific communication while
hormones do not (Gleason and Reynierse, 1969). Thus as Bruce
(1970) points out, pheromones differ fundamentally from hor-
mones. "Pheromones, like hormones, affect the development,
reproduction or behaviour of other individuals. Unlike hor-
mones, which may be active and chemically similar in several
species, pheromones appear to be mainly species-specific".
Bruce adds that there is some overlap between closely related
species.

A pheromone may act on the recipient by olfaction, by
ingestion or by absorption (Bruce, 1970).

Pheromones can be divided into two classes:

1. Primer pheromones
2. Releaser pheromones

Primer pheromones are slow to act, and prolonged stimulation
is required. This initiates a chain of physiological events in
the recipient (Bruce, 1970). Releaser pheromones produce an
immediate and reversible change in the behaviour of the recipient
(Bruce, 1970).

Bruce (1970) points out that releaser pheromones may be in-
volved in several forms of behaviour, including territory marking,
homing, recognition of status, sexual behaviour and aggression.
Thus a releaser pheromone might be involved in the receptive
behaviour of the female guinea pig. Female guinea pigs developed
disturbances of receptive behaviour when their olfactory lobes
were ablated, despite apparently normal oestrous cycles (Donovan
and Kopriva, 1965). Donovan (1969) reports that the anal gland
secretion from an oestrous bitch stimulates mounting in the dog.

The studies indicating the attractant quality of olfactory
stimuli from oestrous females of various species cited earlier
in this chapter, also suggest the action of releaser phero-
mones.

Releaser pheromones would also seem to be involved in
aggressive and territorial behaviour. This has been shown to
be the case in mice. Jones and Nowell (1973) refer to the
presence of a pheromone in male mice urine which discourages
investigation by male conspecifics. The deterrent function
of the scent marks of territorial wolves on lone wolves (Rothman
and Mech, 1979) would suggest the involvement of releaser phero-
mones. Rasa (1973) says that the scent from the cheek gland of
the mongoose seems to act as a threat. The scent of a strange
animal elicits aggression and seems to cause unease. The
vigorous marking of some species in response to scent marks
also suggests the involvement of releaser pheromones. This has
bee reported in the dwarf mongoose (Rasa, 1973) and occurs in
the guinea pig, as demonstrated in the present study. The high
frequency of marking characteristic of dominant animals also
suggests that a releaser pheromone is being distributed. More
research is needed into the response of subordinate guinea pigs
to the scent marks of a dominant male.

The effect of primer pheromones might be seen in the oestr
cycle of some species. Bruce (1970) writes that in some species
the male exerts a controlling influence over oestrus. This is
particularly well-documented in the mouse. When female mice are
grouped and no male is present, oestrus is suppressed. The

introduction of a male results in the commencement of a new
cycle, with the oestrous cycles of the group becoming syn-
chronized (Whitten, 1966; Bruce, 1970). Bruce (1970) reports
that in sheep and goats the introduction of the male shortly
before the start of the breeding season stimulates ovulation
and heat in the female, thus ending the period of non-oestrus.
Some synchronization of oestrus has been reported in the guinea
pig when the females are kept in groups (Donovan and Kopriva,
1965; Harrison, 1977). Female guinea pigs exposed to the odour
of female urine collected during the period of vaginal opening
showed a shortening of the oestrous cycle. The same effect
occurred in response to male urine, but did not occur in bulb-
ectomized females exposed to male urine (Jesel and Aron, 1976).
Jesel and Aron conclude that urine contains a pheromone capable
of shortening the oestrous cycle.

It was suggested at the start of this section (page 295) that
the dominant male guinea pig may secrete a primer pheromone
which serves to keep the subordinate males in a physiologically
immature condition. This receives some support from an experi-
mental manipulation carried out by Rood (1972). He removed the
alpha male from a group of animals; he concluded that the
presence of the alpha male suppresses aggression in subordinate
males, and may also inhibit the incidence of rumbas to adult
females. Some inhibition of rumbas to females appears to persist
even after the alpha male is removed. The inhibition gradually
fades.

Perusal of the current literature on chemical communication
reveals that the term "pheromone" is rarely used, except with
regard to insect pheromones. There has been a tendency to use

the term incorrectly (especially in the popular media), using
it to refer generally to olfactory or chemical communication.
That a species is macrosmatic and, for example, may use ol-
factory stimuli for individual recognition, as an alarm sub-
stance, a sexual attractant, or in territoriality, does not
necessarily mean that pheromones are involved. Pheromones
are not examples of olfactory sensitivity.

Scent marking generally involves the deposition of olfactory
stimuli from more than one source, as shown in the present in-
vestigation, and generally responses to scent marks are not
clearly defined. Also, as pointed out in the present investi-
gation, the response to conspecific odour may vary according to
where the scent is encountered. The term pheromone should only
be used when it can be shown that a single substance brings
about a specific effect in the recipient. As Gleason and
Reynierse (1969) point out, it is necessary to distinguish
pheromones from olfactory cues which function in a manner analo-
gous to pheromones, but which are varied or are affected by both
the quantity and combination of hormones in the organism. For
example, discrimination of oestrous and non-oestrous females by
males may be made on the basis of a pheromone, but may be based
on the hormones present in the female. Several hormones are
known to vary according to the stage of the oestrous cycle (Birke,
1979).

It is perhaps due to the difficulty in determining when it
is reasonable to infer that a pheromone is involved that so many
workers now avoid using the term; it is used extensively only in
relation to insects. This is appropriate as it is in insects
where most of the research into pheromones has been carried out,

and where the action and composition of the pheromones is well
understood. However, further research into mammalian chemical
communication may reveal the action of pheromones. Rasa (1973)
in the mongoose, and Müller-Schwarze (1972) in the blacktailed
deer have demonstrated that separate scent-producing glands
serve different functions.

The situation is less complex with regard to primer phero-
mones, the action of which may be inferred from their effect
on physiological processes in conspecifics.

Wynne-Edwards (1962) suggests that pheromones and functional
odours have resulted from natural selection of metabolites
originally secreted for another function. Gorman (1978) suggests
that such odours as pheromones have derived from the secretion of
sebum originally serving another function. Gorman analysed the
sebum contained in the anal pocket of the mongoose, and found
that it contained six short-chain odorous carboxylic acids. The
mongooses were able to distinguish the secretions of different
individuals, and when presented with synthetic mixtures of car-
boxylic acids were able to distinguish as effectively as between
the natural secretions. Gorman (1978) points out that carboxylic
acids form part of the scents of many mammals. They have been
found, for example, in the scent glands of the red fox (Albone
and Fox, 1971); the weasel (Gorman, 1976; unpublished observation),
in the vagina of the rhesus monkey (Curtis, Ballantine, Keverne,
Bonsall and Michael, 1971), and in the perineal gland of the
guinea pig (Berüter, Beauchamp and Muetterties, 1974).

Gorman (1978) writes that the carboxylic acids are produced
from sebum and apocrine secretions by bacterial action. The

relative concentrations of the acids vary from one individual
to another, giving each a different odour. Gorman adds that
the involvement of bacteria in the production of these acids
has been found in several species, including the guinea pig
Gorman, 1976; unpublished observation). This then would
seem to be the mechanism permitting individual recognition in
the guinea pig. Rasa (1973) reports that the African dwarf
mongoose is able to distinguish between secretions varying in
age as well as between secretions of individuals. Gorman
(1978) suggests that a chemical change occurs when the secre-
tion is exposed to the air.

Thus it is possible that in other species too, including
the guinea pig, an animal may be able to determine the age of
a scent mark. This might be important in a species where scent
marks function to prevent low ranking animals from encountering
dominant animals, or a lone wolf from encountering the pack
(Rothman and Mech, 1979). If the scent marks were not fresh
it would not be necessary to avoid that area.

It is clear that olfactory stimuli play an important role in
the social organization of the guinea pig. Further research is
needed into the extent to which pheromones might control be-
haviour in this species. It would seem that both releaser and
primer pheromones could be involved in the behaviour of the
guinea pig. Further investigation is needed into whether the
scent of the oestrous female is an attractant to the male guinea
pig, his response to it in natural or semi-natural conditions,
and the role of olfactory stimuli in sexual behaviour. Also
into the effects (if any) of male and female primer pheromones

on the oestrous cycle, and on the possibility that dominant male guinea pigs secrete a primer pheromone.

It would also be of interest to examine the possibility that the guinea pig is able to differentiate between scent marks varying in age.

Conclusion

This investigation has revealed that the male guinea pig scent marks in response to the odour of a male conspecific, and that he uses more than one odour source. Scent marking includes anogenital dragging and urination, and the data also suggest that defaecation is involved in scent marking. The male shows pilo-erection and tooth chattering in response to male conspecific odour, also increased locomotion. He is attracted to the odour of a male conspecific, even when it is that of a stranger.

The male guinea pig can distinguish the sexes by odour, and prefers female to male odour. He spends significantly more time s-nosing female than male olfactory stimuli, and is attracted to female odour. Although he scent marks in response to female odour this is significantly les than in response to male odour, and he does not show pilo-erection or tooth chattering. The data indicate that the male guinea pig is able to distinguish between urine from oestrous and non-oestrous females, and suggest that he may prefer oestrous urine.

The female guinea pig increases her rate of marking at oestrus, and it is possible that she develops approach behaviour towards

the male at this time. As in the male, urine is frequently deposited during scent marking.

Both male and female guinea pigs mark in response to clean bedding, also mark the substrate during their normal daily activity. There is a tendency for both sexes to mark over scent marks left by a predecessor animal.

It is considered, on the basis of the data obtained in this and other investigations that the guinea pig is territorial. The pilo-erection and tooth chattering associated with s-nosing and vigorous scent marking in response to male conspecific odour suggest that the animals were motivated to aggression. Ralls (1971) points out that high rates of marking are commonly associated with aggression, and several workers have reported that pilo-erection and tooth chattering in the guinea pig occur during agonistic encounters (Pearson, 1970; Rood, 1972; Berryman, 1974; Coulon, 1975a).

The attraction to the odour of another male conspecific does not indicate that the guinea pig is not territorial. The response of attraction was accompanied by signs of aggression (vigorous scent marking, pilo-erection and tooth chattering) and suggests that a male guinea pig encountering an alien scent in his own territory is likely to respond with aggression. That the holder of the territory has the advantage in an agonistic encounter has been demonstrated in several species including the Norway rat (Barnett, 1963), the rabbit (Mykytowycz, 1968) and the black rat (Ewer, 1971). The increase in locomotion in response to male odour is also consistent with

motivation to aggression, and the chasing of an intruder from
a territory. The behaviour of groups of C. porcellus and C.
aperea towards an introduced animal (Rood, 1972) indicate that
in natural conditions an intruder into a territory would be
chased and attacked.

The response of an animal to an alien scent mark may vary
according to where the scent is encountered (Mykytowycz, 1968;
Mykytowycz and Hesterman, 1970). Thus rabbits show signs of
caution in another's territory, and while they mark over alien
scent marks in their own territory, they do not do so in alien
territory. It would seem possible that the response of the
guinea pig to alien scent marks may vary according to where
they are encountered.

It is also true that while scent marks would seem to have
a deterrent effect in the canids in certain conditions
(Macdonald, 1977; cited in Barrette and Messier, 1980; Rothman
and Mech, 1979; Barrette and Messier, 1980), several workers
have shown that an animal will enter alien territory, for ex-
ample, Norway rats (Barnett, 1963), black rats (Ewer, 1971)
and marmosets (Lacher, Bouchardet, da Fonseca and Alves, 1981).
Further data concerning territoriality and the response of
guinea pigs to scent marks are required, and it is suggested
that a naturalistic study might be suitable, similar in method-
ology to that of King (1956).

It is suggested that scent marking in the guinea pig is in-
volved in the establishment and maintenance of dominance hier-
archies. Beauchamp and Berüter (1973) found that frequency of
anogenital drag is dependent on rank; also that more sebum is

produced in the scent glands of dominant male guinea pigs. Rood (1972) also found that dominant males mark more than subordinates, and that a subordinate male will avoid the alpha male before he encounters it. Rood implies that this is mediated by the scent of the alpha male.

Scent marking would seem to be relevant to the maintenance of dominance in other species. Thus the size and secretory activity of the scent gland correlates with dominance in rabbits (Mykytowycz, 1968) and several species are able to use odour to convey dominance status, for example the rat (Krames, Carr and Bergman, 1977), the muntjac (Barrette, 1977), and the coyote (Barrette and Messier, 1980). Ewer (1971) reports data suggesting that the black rat can convey dominance status through olfactory stimuli, and the mongoose is able to determine whether a scent mark is that of an actively threatening animal (Rasa, 1973). Further research into the nature of marking and dominance is required. Thus it may act as a deterrent to subordinates, or it may act as a releaser pheromone, affecting the reproductive processes of the subordinated males (Ralls, 1971).

Conflicting reports concerning dominance in guinea pigs, particularly that of Fuchs (1980) and in other species (Rowell, 1967, 1974; Grant, 1973; Odell, 1977) suggest that a species which is essentially territorial develops dominance hierarchies in response to a decreased living area and increased population density (Ralls, 1971; Leroy, 1974).

Scent marking in guinea pigs may function to maintain group cohesion and to identify an area as familiar. As reported in this investigation guinea pigs scent mark in response to clean bedding. Berüter, Beauchamp and Muetterties (1974), who observed

the same behaviour, suggest that this may serve to mark the
home range and familiarise the environment. Johnson (1973)
makes a similar point. Marking in response to a change in
the environment has been reported in several species, in-
cluding the marsupial mouse (Ewer, 1968b), the tree shrew
(Martin 1968), and the gerbil (Baran and Glickman, 1970; Blum
and Lindzey, 1970). Other workers suggest that scent marking
aids group cohesion, thus Tyler (1973) in the horse, Rasa
(1973) in the mongoose, and Howe (1974) in the hutia.

The fact that guinea pigs tend to mark over scent marks of
preceding animals may mean that they use marking points, although
there is no independent evidence to suggest this. Johnson (1973)
suggests that marking over conspecific odour might indicate that
a species uses marking points, as do the wolf (Fiennes and Fiennes
1968), the mongoose (Rasa, 1973) and the tree shrew (Kawamichi
and Kawamichi, 1979). However, marking over conspecific odour
may have more than one function. As Ewer (1968a) suggests,
animals may mark both to reassure themselves and to threaten
others, the relative importance varying according to the
situation. Thus, while marking in response to an alien scent
could serve as a threat, marking in communal areas could serve
group cohesion and to identify an area as familiar. These poss-
bilities could be investigated in the guinea pig; it would be of
interest to ascertain whether guinea pigs in fact use marking
points and what function these might serve; also in what con-
ditions, if any, that scent marking in the guinea pig acts as
a threat.

Another factor which may aid group cohesion is the attraction

of male guinea pigs to female odour, as reported in the present investigation, and by Beauchamp (1973). Beauchamp suggests this may aid group cohesion as the females only come into oestrus every 66 to 70 days.

Scent marking is important in the sexual behaviour of the guinea pig where it may function to attract the animal of the opposite sex, and provides information on the reproductive status of the animal. Although Ruddy (1980) demonstrated that the male guinea pig is able to distinguish between oestrous and anoestrous olfactory stimuli, and the present study revealed that he is able to distinguish between oestrous and non-oestrous urine, possibly showing a preference for the latter, whether he is able to make this distinction in the natural environment is not known. Many species have been found to respond differentially to or to prefer oestrous to non-oestrous odours; these include rats (Le Magnen 1955; Carr and Caul, 1962), mice (Dixon and Mackintosh, 1975), the blacktailed deer (Müller-Schwarze, 1971), dogs (Beach and Gilmore, 1949), and the coyote (Barrette and Messier, 1980); possibly also the rhesus monkey (Curtis, Ballantine, Keveme, Bonsall and Michael, 1971), and Kleiman and Eisenberg (1973) report that in the Felidae the male locates the oestrous female on the basis of odour.

In view of the fact that neither Avery (1925), Louttit (1927), Beauchamp (1976) nor Beauchamp, Criss and Wellington (1979) found a difference in the response of male guinea pigs to oestrous and non-oestrous olfactory stimuli, it is possible that domestication has resulted in a diminished sensitivity to these odours, although it should be pointed out that the testing

conditions may have been responsible for the failure to dis-
criminate. While the data obtained in the present study also
suggest that the oestrous female may be attracted to the male,
the evidence is insufficient to warrant a conclusion with
regard to the guinea pig. However, an apparent attraction
has been reported in horses where an oestrous female will seek
out or follow the stallion (Tyler, 1972; Coldfoot and Gunther,
1979), and in the mountain gorilla where the female spends more
time with the male during oestrus (Harcourt, 1979).

The increase in the rate of marking in the female guinea
pig at oestrus, as indicated in the present study, and reported
by Birke (1981), resembles that found in other species; in the
rat (Calhoun, 1962; cited in Schultz and Tapp, 1973; Birke,
1978), in the hutia (Howe, 1974), and in several canids (Kleiman,
1966; van Lawick Goodall and van Lawick, 1970). It would seem
possible that olfactory stimuli distributed by the female guinea
pig serves to attract the male, and his response to the scent
marks of oestrous females in natural and semi-natural conditions
should be investigated further.

The male guinea pig also marks in response to female odour.
This is also reported in horses (Tyler, 1972) and in canids,
where "double marking" occurs during pair formation (van Lawick
Goodall and van Lawick, 1970; Rothman and Mech, 1979). The
possible function of marking in response to female odour is
not clear in the guinea pig, although marking in response to
conspecific odour of both sexes would aid group cohesion.

The present study reveals that both male and female guinea
pigs use perineal gland secretions and urine in scent marking,

and also suggests that defaecation is used in scent marking.
The use of more than one source of odour is widespread, and
is found in the mongoose (Rasa, 1973; Gorman, 1976), the
blacktailed deer (Müller Schwarze, 1971), the rabbit
(Mykytowycz, 1968), the muntjac (Barrette, 1980), the horse
(Tyler, 1972), and the Canidae (Fiennes and Fiennes, 1968;
van Lawick Goodall and van Lawick, 1970; Kleiman and Eisenberg,
1973; Peters and Mech, 1975). The majority of these use faeces
as one source of odour. Whether this is the case in the guinea
pig needs further investigation.

In summary, it is considered, on the basis of the data ob-
tained in this and other investigations, that the guinea pig is
territorial. Further data are required, and it is suggested
that a naturalistic study might be suitable, similar to that
of King (1956).

Scent marking in the guinea pig would seem to be involved
in the establishment and maintenance of dominance hierarchies.
Further research into the nature of marking and dominance is
required. Thus it may act as a deterrent to subordinates,
and it may act as a primer pheromone, affecting the reproductive
processes of the subordinate males. It is suggested that the
guinea pig forms dominance hierarchies in response to a res-
tricted environment.

Scent marking in the guinea pig functions to maintain group
cohesion, and to identify an area as familiar. This could be
investigated further. It would be of interest also to ascertain
whether guinea pigs do in fact use marking points and what
function these might serve.

Scent marking is of importance in the sexual behaviour of the guinea pig, where it may function to attract the animal of the opposite sex, and provides information as to the reproductive condition of the animals.

A great deal of further investigation is needed into the role of olfactory stimuli in the social behaviour of the guinea pig. It would seem that the social organization of this species is more complex and more variable than early investigators suggested. Different workers have obtained varying findings, and have reported variation between groups.

It should be borne in mind that the guinea pig has been domesticated for thousands of years, and it is likely that aspects of its social behaviour have been affected by this. It is suggested, therefore, that investigation into the behaviour of the guinea pig be paralleled by investigations using Cavia aperea. This would be of particular value where results obtained with C. porcellus are conflicting or ambiguous.

Scent marking may serve several functions in the guinea pig. That olfaction is of considerable importance to the social behaviour of this animal is emphasized by the fact that bulbectomized animals failed to form dominance hierarchies, showed virtually no inter-male aggression, markedly depressed sexual activity, and rarely scent-marked (Beauchamp, Magnus, Shmunes and Durham, 1977) Receptive behaviour in females with ablated olfactory lobes was disrupted (Donovan and Kopriva, 1965).

As has been pointed out, the guinea pig has more than one source of odour which can be distributed during scent marking.

It is not known whether these stimuli are used to convey different information, or the same information in different ways. Ralls (1971) asks why, if only one message is conveyed, should an animal use different signals? She suggests that this may increase the possibility of the information being received: each signal might be effective under a different set of environmental conditions. However, it is equally possible that the messages are different.

It is suggested that the following areas of research might prove valuable. The list is not exclusive; there are many areas where research is needed.

a. territoriality in the guinea pig

b. examine the hypothesis that the scent of the alpha male has aversive qualities

c. the relationship between dominance, territoriality, the number of males in a population, and population density

d. the hypothesis that low ranking males are those which tend to mount non-receptive females

e. the behaviour of the pro-oestrous female, and the pregnant female near term

f. the response of male guinea pigs to the scent marks of oestrous females

g. the distribution of scent marks in the guinea pigs' home range

h. the role of defaecation in scent marking in the guinea pig

i. that guinea pigs are able to distinguish between scent marks differing with respect to age

j. whether the different olfactory stimuli used in scent marking convey the same or different information

The comment of Schultz and Tapp (1973) with regard to the olfactory control of behaviour in rodents would seem to be a

fitting end to this investigation into the relationship between olfactory stimuli and social behaviour in the guinea pig.

> " ..... it appears that much of the world ..
> .... is viewed through their noses. That
> world appears to be rich and complex beyond
> our imagination."

APPENDICES

Each is numbered according to the Chapter
to which it is relevant.

———————

Appendix 2

Sexual responses in the guinea pig.

Agonistic responses in the guinea pig.

———————

III.

Sexual responses in the guinea pig.*

Avery (1925)

<u>Male</u>

Pursuit

Vocalisation: low guttural sound; chattering.

Circling: sometimes with hindquarters swaying.

Head Nosing: the male rubs the female's nose
head or neck with his own nose.

Licking excretions.

Atypical mounting: from the side or at the
neck.

<u>Female</u>

Signs of the receptive phase are :

1.   The vaginal closure membrane ruptures
near onset of oestrus.
2.   Posture lordosis when nosed by a male.

3.   Homosexual behaviour found to occur in
no less than from 10 - 15 per cent of
animals coming into oestrus.   Period
of receptivity lasts from 20 min. to
4 ars 25 min.

Louttit (1927)

<u>Male</u>

Vocalization: a purring noise made by the
male when he is sexually excited.   May
also be noticed when males are about
to fight.

Nosing: the male rubs or buts the female's
head, neck, sides, etc., with his nose.

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* Kunkel and Kunkel (1964) and Rood (1972) provide photographs
and line drawings which illustrate most of the sexual and
agonistic postures described.

Circling and Swaying: usually in a crouching
   position and swaying his hindquarters from
   side to side, walks slowly in circles.
   Rubs scrotal region on floor.

Jump over female.

Rumping female: he throws his hindquarters
   in her direction, and ejects a stream of
   urine at her.

Kissing: nibbles or licks mouth of the
   female.

Bites her hair.

Atypical mounting.

Licking and nibbling of the anal region.

Female

Nos:¬ng the male

Mounting

Following

Licking male's anal region.

Jumping over male.

Harper (1966)

Purring: a low growling or rumbling sound.

Swaying: shifting the weight from one hind
   foot to another, producing a lateral
   movement of the hips.

Circling: locomoting around another.

Chin thrust: rubbing the chin upward and
   forward on the rump of another.

Rumping: locomoting past, urinating upon,
   and striking another with the haunch.

Ano-genital dragging: dragging or rubbing
   the ano-genital region on the floor.

Headmount: mounting another's head or
   forequarters.

Crossmount: mounting another crosswise

Mount: mounting another (properly aligned)

Pelvic thrusts

Copulatory thrusts: longer, slower pelvic
   thrusts.

Rood (1972)

Naso-anal: the male sniffs, licks or nuzzles
   the ano-genital region of a female or
   juvenile.

Chin-rump follow: following females or
   juveniles with nose touching the rear of
   recipient.

Rumba: in a typical rumba the male slowly
   approached the female rhythmically
   oscillating the hindquarters from side to
   side and emitting a characteristic
   burbling vocalisation (the rumble). The
   head stretched forward held parallel to
   the ground. As he hesitantly nears the
   female his body may assume a curve re-
   sembling the threat posture. The rumba
   has three versions. In the prowl the
   male walks slowly forward and maycircle,
   follow, or move in a figure eight pattern.
   This often terminates in treading as the
   male stops his forward motion but continues
   to step in place shifting his weight from
   one hind leg to another. In the sway
   the amplitude of the sideways oscillations
   increase.

Rumping: the male throws one or both hind-
   legs over the back or rump of the female,
   often urinating on her. He may be
   several centimetres away and no bodily
   contact occur.

Copulation: male mounts with rapid pelvic
   thrusts which become long low strokes.
   Ejaculation occurs during a prolonged
   thrust and is typically accompanied by
   a drawing in of the flanks.

Agonistic responses in the guinea pig.

Rood (1972)

Primarily offensive

Head thrust: the animal jabs its head towards its opponent.
Usually directed forward but may be directed sideways.
(Also occurs as a defensive response as in a female towards
a male.)

Attack-lunge: A short run or jump at the opponent.

Stand-threat: involves two or more animals, one adopting the
curved body posture.   One or both moves the hindquarters
towards the opponent.   Dorsal hair frequently raised making
the animals appear larger.   They may tooth chatter.   The
mouth may be opened, and the anal glands may be periodically
everted.   They are likely to be broadside to one another.

Primarily defensive

Tail-up: the female turns her back towards the male, displaces
her hindlegs posteriorly and laterally and lifts her perineal
region.   The tail-up was sometimes accompanied by urine-
spraying, where the female ejects several jets of urine at
the male in rapid succession.

Facing: a female would whirl round and face a male at her rear.

Kick-back: The female may kick back with both hind feet at a
male which noses her rear.

Head up: head is thrown back so that the nose points straight
up.   This is a defensive act often given prior to a retreat.

Coulon (1975a) describes the offensive and defensive postures in
great detail.

VII.

Appendix 4.

Diagrams 1 and 2.

Diagram 1

Subject.   Exp.   Date

1   S   2

3   4

          comments:

5

Copy of cyclostyled sheet used for recording behaviour in the open field

Diagram 2
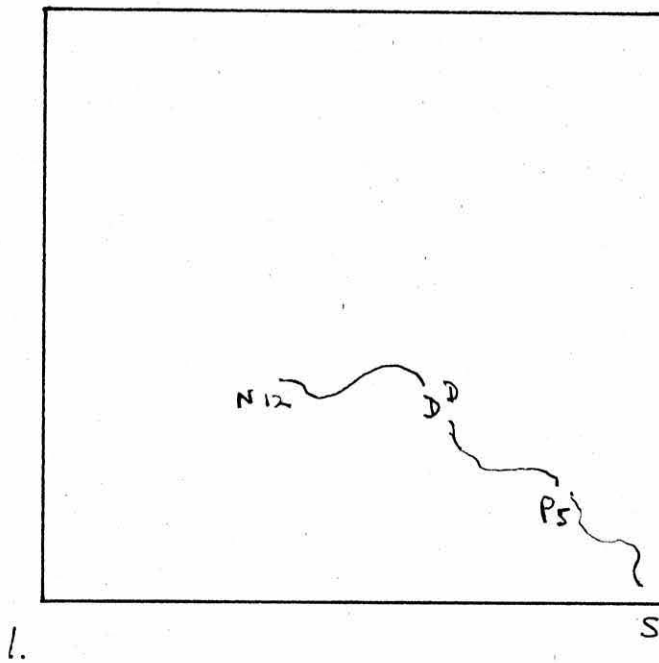
Example of the method of recording behaviour
in the open field.

Appendix 5

Data for Experiment I

S-nosing
Marking
∫ marking
Defaecation
Locomotion
Sniffing
Grooming
Immobility
Urination

KEYS

Key to counterbalancing in Experiment I

	Trial 1	Trial 2
A.	Experimental Condition	Control Condition
B.	Control Condition	Experimental Condition

Subjects in A. Fl, L, Sp, Cl, Sm.

Subjects in B. Sb, Col, Mp, P, A.

Key to Groups 1 and 2

Group 1. Sb, Col, Mp, P, Fl, Sp, Cl.
Group 2. A , L, Sm.
(The data for Group 1 precedes data for Group 2).

XI.

Experimental Condition.   (Score in seconds)

- M I N U T E S -

Subject	1	2	3	4	5	6	7	8	9	10	TOTAL
Sb	14	4	5	8	-	17	-	-	2	11	61
Col	44	28	34	5	16	-	6	7	6	-	146
Mp	55	16	6	14	32	22	15	17	5	3	185
P	31	34	11	18	3	16	8	7	10	4	142
Fl	15	8	19	14	3	-	2	7	23	11	102
Sp	-	2	-	-	-	30	10	5	6	12	65
Cl	5	-	8	5	4	24	2	-	-	2	50
Al	3	3	-	8	11	-	5	4	2	-	36
L	6	6	9	2	3	7	2	5	-	-	40
SM	17	22	24	10	15	8	13	6	10	8	133
TOTAL	190	123	116	84	87	124	63	58	64	51	960

Control Condition

- M I N U T E S -

Subject	1	2	3	4	5	6	7	8	9	10	TOTAL
Sb	-	-	-	4	-	-	-	-	-	-	4
Col	2	-	2	2	-	-	-	2	2	-	10
MP	-	3	-	3	-	-	-	-	-	-	6
P	-	4	-	-	12	2	6	-	-	-	24
Fl	-	-	-	2	-	-	-	-	-	-	2
Sp	-	-	-	-	2	-	-	-	-	-	2
Cl	2	-	-	-	-	-	6	-	-	-	8
A	-	-	-	-	-	-	-	-	-	-	-
L	-	-	2	-	-	-	-	-	-	-	2
Sm	2	-	-	2	-	2	2	2	-	2	12
TOTAL	6	7	4	13	14	4	14	4	2	2	70

XII.

Experiment I MARKING

Experimental Condition (No. of instances)

- M I N U T E S -

Subject	1	2	3	4	5	6	7	8	9	10	TOTAL
Sb	2	3	-	1	-	-	-	-	-	-	6
Col	4	2	4	1	1	-	-	-	2	-	14
Mp	-	-	4	5	2	7	-	2	1	2	23
P	1	2	1	2	-	2	2	2	1	-	1313
Fl	1	-	-	1	1	-	1	-	-	2	6
Sp	-	-	-	-	-	3	7	-	4	2	16
Cl	5	3	2	4	1	3	3	-	1	2	24
A	1	-	-	1	1	1	1	-	-	1	6
L	2	-	2	1	1	2	2	-	-	-	10
SM	3	2	4	2	1	1	1	1	2	1	18
TOTAL	19	12	17	18	8	19	17	5	11	10	136

Control Condition

- M I N U T E S -

Subject	1	2	3	4	5	6	7	8	9	10	TOTAL
Sb	-	-	-	-	-	-	-	-	-	-	-
Col	-	-	-	-	-	-	-	-	1	-	1
Mp	-	-	-	-	-	-	-	-	-	-	-
P	-	-	-	-	-	-	-	-	-	-	-
Fl	-	-	-	-	-	-	-	-	-	-	-
Sp	3	-	1	-	-	-	-	-	-	-	4
Cl	1	1	-	1	-	1	2	-	-	-	6
A	-	-	-	-	-	-	-	-	-	-	-
L	-	-	1	-	-	1	-	-	-	-	2
SM	1	1	-	-	-	-	-	-	-	-	2
TOTAL	5	2	2	1	-	2	2	-	1	-	15

XIII.

U-MARKING

Experimental Condition

(No. of instances)

- M I N U T E S -

Subject	1	2	3	4	5	6	7	8	9	10	TOTAL
Seb	▾	1	--	--	--	--	--	--	--	--	1
Col	--	--	1	--	--	--	--	--	--	--	1
MP	--	--	--	1	--	--	--	1	--	2	4
P	--	--	1	1	--	--	--	--	--	--	2
Fl	--	--	--	--	--	--	--	--	--	--	--
Sp	--	--	--	--	--	--	--	--	--	--	--
Cl	1	--	--	2	--	--	--	--	--	--	3
A	1	--	--	--	--	1	--	--	--	--	2
L	1	--	--	--	--	--	--	--	--	--	1
SM	--	--	1	--	--	--	1	--	--	--	2
TOTAL	3	1	3	4	--	1	1	1	--	2	16

Control Condition

- M I N U T E S -

Subject	1	2	3	4	5	6	7	8	9	10	TOTAL
Seb	--	--	--	--	--	--	--	--	--	--	--
Col	--	--	--	--	--	--	--	--	--	--	--
MP	--	--	--	--	--	--	--	--	--	--	--
P	--	--	--	--	--	--	--	--	--	--	--
Fl	--	--	--	--	--	--	--	--	--	--	--
Sp	--	--	--	--	--	--	--	--	--	--	--
Cl	--	--	--	--	--	--	--	--	--	--	--
A	--	--	--	--	--	--	--	--	--	--	--
L	--	--	--	--	--	--	--	--	--	--	--
Sam	--	--	--	--	--	--	--	--	--	--	--
TOTAL	--	--	--	--	--	--	--	--	--	--	--

Experiment I DEFAECATION (No. of pellets)

Experimental Condition

- M I N U T E S -

Subject	1	2	3	4	5	6	7	8	9	10	TOTAL
Sb	-	-	-	-	1	-	-	2	-	-	3
Col	-	1	2	3	-	-	1	-	5	-	12
Mp	-	-	1	-	-	2	-	5	1	-	9
P	-	-	2	-	1	-	-	-	-	-	3
Fl	-	1	-	-	1	2	-	-	-	2	6
Sp	-	-	-	-	-	-	2	-	1	2	5
Cl	2	-	-	-	-	-	-	-	-	-	2
A	-	2	-	2	-	-	-	1	-	-	5
Lw	1	1	3	-	-	1	-	-	-	1	7
Sm	1	-	2	1	-	-	1	-	2	-	7
TOTAL	4	5	10	6	3	5	4	8	9	5	59

Control Condition

- M I N U T E S -

Subject	1	2	3	4	5	6	7	8	9	10	TOTAL
Sb	-	-	-	-	-	-	-	-	-	-	-
Col	-	-	-	-	-	-	-	-	-	-	-
Mp	-	-	1	-	1	-	-	-	-	-	2
P	-	-	-	-	-	-	-	-	-	-	-
Fl	-	-	-	-	-	-	-	-	-	-	-
Sp	-	-	-	-	-	-	-	-	-	-	-
Cl	-	-	-	-	-	-	-	-	-	-	-
A	-	-	-	-	-	-	-	-	-	-	-
Lw	-	-	-	-	-	-	-	-	-	-	-
Sm	-	-	-	1	-	-	-	-	-	-	1
TOTAL	-	-	1	1	1	-	-	-	-	-	3

Experiment I LOCOMOTION

Experimental Condition (Score in feet)

- M I N U T E S -

Subject	1	2	3	4	5	6	7	8	9	10	TOTAL
Sb	6	9	6	3	1	1	-	6	2	3	37
Col	9½	8	7½	10	2½	-	3½	4½	6½	-	52
Mp	2½	3	6	8	4	6½	5	5½	1½	6½	48½
P	6	8	5	4	2	4½	5	4½	4	4	47
Fl	8	1	4½	10	3	2	5½	1½	3	7½	46
Sp	5½	-	-	-	-	6½	11	5	7	6½	41½
Cl	11½	8½	5	10	4	5	9	½	4½	8½	66½
A	7½	17	15	13½	8	16	9½	5½	11	15	118
L	9½	5	15	14	11	7	11	12½	8	9½	102½
Sm	7½	10	6	9	3	6	6	5	7	8	67½
TOTAL	73½	69½	70	81½	38½	54½	65½	50½	54½	68½	626½

Control Condition

- M I N U T E S -

Subject	1	2	3	4	5	6	7	8	9	10	TOTAL
Sb	2	-	-	4	6	5½	3	1	-	-	21½
Col	8	8	4	4	9	1	2½	10½	6	-	53
Mp	6½	4½	9½	12	-	-	-	-	-	-	32½
P	2	1½	2½	3	5½	5	4	3	½	2	29
Fl	7½	6	4½	7½	6½	9	2	-	2	5½	50½
Sp	8½	-	4½	-	-	1	3½	3½	1	1½	23½
Cl	10	3	-	3½	-	4½	9½	-	2½	1	34
A	16	17	12	11	12½	1½	9	12	6½	5½	103
L	1	3	4½	2½	4	7	2½	6	4	3	37½
Sm	5	5	4	5	7½	3½	4	5	4	4	47
TOTAL	66½	48	45½	52½	51	38	40	41	26½	22½	431½

XVI.

　　　　SNIFFING　　　　(Score in seconds)

Experimental Condition

- M I N U T E S -

Subject	1	2	3	4	5	6	7	8	9	10	TOTAL
Sb	2	3	-	9	16	4	-	6	-	2	42
Col	-	-	-	-	-	-	-	3	2	-	5
M	-	2	2	-	2	-	-	2	3	5	16
P	3	2	2	6	6	3	4	5	10	6	47
Fl	2	2	5	2	2	-	5	10	3	-	31
Sp	7	-	-	-	3	2	2	-	2	-	16
Cl	2	2	6	-	2	7	7	-	-	2	28
A	4	3	7	5	2	2	2	2	5	2	34
L	2	6	2	2	-	3	7	5	4	5	36
Sm	-	-	5	2	-	2	-	5	2	2	18
TOTAL	22	20	29	26	33	23	27	38	31	24	273

Control Condition

- M I N U T E S -

Subject	1	2	3	4	5	6	7	8	9	10	TOTAL
Sb	3	2	3	10	6	14	11	7	-	-	56
Col	3	-	2	-	-	-	-	2	1	-	8
M	2	-	5	2	2	-	-	-	-	-	11
P	2	2	5	6	13	9	11	3	-	2	53
Fl	-	2	5	-	2	3	-	-	-	2	14
Sp	2	-	2	-	-	1	3	3	1	1	13
Cl	4	2	-	2	2	6	-	-	3	2	21
A	-	2	4	2	-	2	3	3	7	2	25
L	5	2	17	7	5	8	2	6	1	5	58
Sm	1	1	-	2	2	-	2	2	6	3	19
TOTAL	22	13	43	31	32	43	32	26	19	17	278

Experiment I   GROOMING   (Score in seconds)

Experimental Condition

- M I N U T E S -

Subject	1	2	3	4	5	6	7	8	9	10	TOTAL
Sb	-	-	-	-	-	-	-	-	-	-	-
Col	-	-	-	-	2	-	-	-	4	14	20
Mp	-	-	-	-	-	-	2	-	20	-	22
P	-	-	-	-	6	-	-	-	-	-	6
Fl	-	-	-	-	-	-	-	2	2	-	4
Sp	-	-	-	-	-	-	2	-	2	-	4
Cl	-	-	2	-	-	-	-	-	2	-	4
A	-	-	-	6	-	-	2	-	-	-	8
L	-	-	2	-	-	-	-	-	-	2	4
Sm	-	-	-	-	-	-	-	-	-	-	-
TOTAL	-	-	4	6	8	-	6	2	3p	16	72

Control Condition

- M I N U T E S -

Subject	1	2	3	4	5	6	7	8	9	10	TOTAL
Sb	-	-	-	-	-	-	-	-	-	-	-
Col	-	-	2	-	-	-	-	-	-	-	2
Mp	-	-	-	-	-	-	-	-	-	-	-
P	-	-	-	-	-	-	-	-	-	-	-
Fl	-	-	-	-	-	-	-	-	-	-	-
Sp	-	-	-	-	-	-	-	-	-	3	3
Cl	-	-	-	-	-	-	-	-	-	-	-
A	-	-	-	-	-	-	-	-	-	-	-
L	-	-	-	-	2	-	-	-	-	-	2
Sm	-	-	-	-	-	-	-	-	-	-	-
TOTAL	-	-	2	-	2	-	-	-	-	3	7

Experiment I   IMMOBILITY   (Score in seconds)

Experimental Condition

— M I N U T E S —

Subject	1	2	3	4	5	6	7	8	9	10	TOTAL
Sb	10	5	14	12	5	10	60	9	27	32	184
Col	--	2	5	--	--	--	15	--	--	45	73
Mp	--	20	35	2	--	5	25	10	10	22	129
P	--	2	4	6	12	2	15	15	4	8	68
Fl	20	17	2	2	24	50	10	7	--	2	134
Sp	35	30	10	--	--	--	--	2	--	2	79
Cl	5	12	--	10	25	20	4	58	7	2	143
A	14	--	6	2	--	--	12	20	8	--	62
L	10	--	--	4	--	--	4	6	20	11	55
Sm	--	2	4	--	4	6	--	2	2	7	27
TOTAL	94	90	80	38	70	93	145	131	82	131	954

Control Condition

— M I N U T E S

Subject	1	2	3	4	5	6	7	8	9	10	TOTAL
Sb	50	55	50	27	5	6	14	40	60	60	367
Col	34	2	37	15	20	52	53	7	15	60	295
Mp	40	7	2	--	57	60	60	60	60	60	406
P	45	48	41	35	9	10	13	32	55	53	341
Fl	30	36	10	4	25	8	49	57	53	40	312
Sp	40	58	25	--	--	--	--	--	40	30	193
Cl	17	37	60	48	53	27	12	60	45	52	411
A	25	10	23	37	37	45	29	18	20	29	273
L	45	52	10	15	15	--	31	8	16	30	222
Sm	26	17	25	12	12	37	34	11	9	38	221
TOTAL	352	322	283	193	233	245	295	293	373	452	3041

Experiment I   URINATION   (No. of instances)

Experimental Condition

- M I N U T E S -

Subject	1	2	3	4	5	6	7	8	9	10	TOTAL
Sb	-	-	-	-	-	-	-	-	-	-	-
Col	-	1	-	-	-	-	-	-	-	-	1
Mp	-	-	-	-	-	-	-	-	-	-	-
P	-	-	-	-	-	-	-	-	-	-	-
Fl	-	1	-	-	-	-	-	-	-	-	1
Sp	-	-	-	-	-	-	-	-	-	-	-
Cl	1	-	-	-	-	-	-	-	-	-	1
Al	-	-	-	-	-	-	-	-	-	-	-
Lw	-	-	-	-	-	-	-	-	-	-	-
Sm	-	-	-	-	-	-	-	-	-	-	-
TOTAL	1	2	-	-	-	-	-	-	-	-	3

Control Condition

- M I N U T E S -

Subject	1	2	3	4	5	6	7	8	9	10	TOTAL
Sb	-	-	-	-	-	-	-	-	-	-	-
Col	-	-	-	1	-	-	-	-	-	-	1
Mp	-	-	-	-	-	-	-	-	-	-	-
P	-	-	-	-	-	-	-	-	-	-	-
Fl	-	-	-	-	-	-	1	-	-	-	1
Sp	-	-	-	-	-	-	-	-	-	-	-
Cl	-	-	-	-	-	-	-	-	1	-	1
Al	-	-	-	-	-	-	-	-	-	-	-
Lw	-	-	-	-	-	-	-	-	-	-	-
Sm	-	-	-	-	-	-	-	-	-	-	-
TOTAL	-	-	-	1	-	-	1	-	1	-	3

Appendix 6

Data for Experiment II

S-nosing
Marking
Defaecation
Locomotion
Immobility
Sniffing

Data for Experiment III

S-nosing
Marking
   -marking
Defaecation
Locomotion
Sniffing
Immobility

Experiment II   S-NOSING

No Scent   (Score in seconds)

-MINUTES-

Subject	1	2	3	4	5	6	7	8	9	10	TOTAL
Mp	-	3	-	3	-	-	-	-	-	-	6
Cl	2	-	-	-	-	-	6	-	-	-	8
Sb	-	-	-	4	-	-	-	-	-	-	4
Sm	2	-	-	2	-	2	2	2	-	2	12
Col	2	-	2	2	-	-	-	2	2	-	10
Sp	-	-	-	-	2	-	-	-	-	-	2
TOTAL	6	3	2	11	2	2	8	4	2	2	42

Hamster Scent

Subject	1	2	3	4	5	6	7	8	9	10	TOTAL
Mp	-	-	-	-	-	-	-	6	-	-	6
Cl	3	-	-	-	-	-	-	2	-	-	5
Sb	-	-	-	-	-	-	-	-	-	-	-
Sm	-	-	-	-	-	-	-	-	-	-	-
Col	-	4	2	-	2	-	4	-	-	-	12
Sp	-	-	-	-	2	2	-	-	5	-	9
TOTAL	3	4	2	-	4	2	4	8	5	-	32

Experiment II   MARKING

No Scent.   (No. of instances)

- M I N U T E S -

Subject	1	2	3	4	5	6	7	8	9	10	TOTAL
Mp	-	-	-	-	-	-	-	-	-	-	-
Cl	-	-	-	-	-	-	-	-	1	-	1
Sb	-	-	-	-	-	-	-	-	-	-	-
Sm	-	-	-	-	-	-	-	-	-	-	-
Col	-	-	-	-	-	-	-	-	1	-	1
Sp	3	-	1	-	-	-	-	-	-	-	4
TOTAL	3	-	1	-	-	-	-	-	2	-	6

Hamster Scent

- M I N U T E S -

Subject	1	2	3	4	5	6	7	8	9	10	TOTAL
Mp	-										
Cl	-										
Sb	-			MINUTES 2 - 10							
Sm	-			NO MARKING.							
Col	2										2
Sp	-										
TOTAL	2										2

Experiment II   DEFAECATION

No Scent

- M I N U T E S -

Subject	1	2	3	4	5	6	7	8	9	10	TOTAL
Mp	-	-	1	-	1	-	-	-	-	-	2
Cl	-	-	-	-	-	-	-	-	-	-	-
Sb	-	-	-	-	-	-	-	-	-	-	-
Sm	-	-	-	-	-	-	-	-	-	-	-
Col	-	-	-	-	-	-	-	-	-	-	-
Sp	-	-	-	-	-	-	-	-	-	-	-
TOTAL	-	-	1	-	1	-	-	-	-	-	2

Hamster Scent

- M I N U T E S -

Subject	1	2	3	4	5	6	7	8	9	10	TOTAL
Mp	-										
Cl	-										
Sb	-			MINUTES 2 - 10							
Sm	-			NO DEFAECATION							
Col	2										2
Sp	-										
TOTAL	2										2

Experiment II   LOCOMOTION   (Score in feet)

No Scent.

- M I N U T E S -

Subject	1	2	3	4	5	6	7	8	9	10	TOTAL
Mp	6½	4½	9½	12	-	-	-	-	-	-	32½
Cl	10	3	-	3½	-	4½	9½	-	2½	1	34
Sb	2	-	-	4	6	5½	3	1	-	-	21½
Sm	5	5	4	5	7½	3½	4	5	4	4	47
Col	8	8	4	4	9	1	2½	10½	6	-	53
Sp	8½	-	4½	-	-	1	3½	3½	1	1½	23½
TOTAL	40	20½	22	28½	22½	15½	22½	20	13½	6½	211½

Hamster Scent

- M I N U T E S -

Subject	1	2	3	4	5	6	7	8	9	10	TOTAL
Mp	-	-	-	-	-	-	-	2	-	-	2
Cl	-	½	-	-	-	-	-	2½	3½	3	9½
Sb	-	-	-	-	-	-	-	-	-	-	-
Sm	-	-	-	-	-	-	-	-	-	-	-
Col	6½	6	-	-	-	2½	-	-	-	-	15
Sp	3½	½	-	-	-	1	7½	-	4	2	18½
TOTAL	10	7	-	-	-	3½	7½	4½	7½	5	45

Experiment II

IMMOBILITY   (Score in seconds)

No scent

- M I N U T E S -

Subject	1	2	3	4	5	6	7	8	9	10	TOTAL
Mp	40	7	2	-	57	60	60	60	60	60	406
Cl	17	37	60	48	53	27	12	60	45	52	411
Sb	50	55	50	27	5	6	14	40	60	60	367
Sm	26	17	25	12	12	37	34	11	9	38	221
Col	34	2	37	15	20	52	53	7	15	60	295
Sp	40	58	25	-	-	-	-	-	40	30	193
TOTAL	207	176	199	102	147	182	173	178	229	300	1893

Hamster Scent

- M I N U T E S -

Subject	1	2	3	4	5	6	7	8	9	10	TOTAL
Mp	60	60	60	60	60	60	60	40	60	60	580
Cl	50	45	60	60	60	60	60	12	15	51	473
Sb	45	60	60	60	60	60	60	60	60	60	585
Sm	30	35	50	60	60	60	60	60	60	60	535
Col	35	30	60	60	60	55	60	60	60	60	540
Sp	39	60	60	60	50	15	50	60	19	30	443
TOTAL	259	290	350	360	350	310	350	292	274	321	3156

Experiment II   SNIFFING   (score in seconds)

No scent

- M I N U T E S -

Subject	1	2	3	4	5	6	7	8	9	10	TOTAL
Mp	2	–	5	2	2	–	–	–	–	–	11
Cl	4	2	–	2	2	6	–	–	3	2	21
Sb	3	2	3	10	6	14	11	7	–	–	56
Sm	1	1	–	2	2	–	2	2	6	3	19
Col	3	–	2	–	–	–	–	2	1	–	8
Sp	2	–	2	–	–	1	3	3	1	1	13
TOTAL	15	5	12	16	12	21	16	14	11	6	128

Hamster scent

- M I N U T E S -

Subject	1	2	3	4	5	6	7	8	9	10	TOTAL
Mp	–	–	–	–	–	–	–	4	–	–	4
Cl	13	–	–	–	–	–	–	3	2	–	18
Sb	16	–	–	–	–	–	–	–	–	–	16
Sm	7	18	2	–	–	–	–	–	–	–	27
Col	–	–	–	–	–	–	–	–	–	–	–
Sp	4	3	2	2	3	1	3	–	2	2	22
TOTAL	40	21	4	2	3	1	3	7	4	2	87

Experiment III

S-NOSING   (Score in seconds)

Experimental Condition.

Subject	Day 1	Day 2	Day 3	Day 4	Day 5	TOTAL
P	64	59	57	54	66	300
Sb	64	88	69	76	104	401
Mp	71	23	46	21	26	187
Lw	6	47	21	17	24	115
TOTAL	205	217	193	168	220	1003

Control Condition.

Subject	Day 1	Day 2	Day 3	Day 4	Day 5	TOTAL
Cl	-	2	-	1	-	3
Al	-	1	2	2	-	5
Sm	10	13	6	15	10	54
Sp	13	7	23	18	-	61
TOTAL	23	23	31	36	10	123

Experiment III   MARKING   (No. of instances)

Experimental Condition

Subject	Day 1	Day 2	Day 3	Day 4	Day 5	TOTAL
P	3	6	12	9	10	40
Sb	-	3	1	4	7	15
Mp	5	13	21	15	15	69
Lw	5	5	-	1	11	22
TOTAL	13	27	34	29	43	146

Control Condition

Subject	Day 1	Day 2	Day 3	Day 4	Day 5	TOTAL
Cl	2	1	-	1	-	4
Al	4	-	2	1	2	9
Sm	-	-	1	2	-	3
Sp	-	-	-	-	-	-
TOTAL	6	1	3	4	2	16

Experiment III

U-MARKING   (No. of instances)

Experimental Condition

Subject	Day 1	Day 2	Day 3	Day 4	Day 5	TOTAL
P	-	-	2	2	1	5
Sb	-	-	1	1	1	3
Mp	-	-	1	2	2	5
Lw	-	1	-	1	3	5
TOTAL	-	1	4	6	7	18

Control Condition

Subject	Day 1	Day 2	Day 3	Day 4	Day 5	TOTAL
Cl	-	-	-	-	-	-
Al	1	-	1	1	1	4
Sm	-	-	-	-	-	-
Sp	-	-	-	-	-	-
TOTAL	1	-	1	1	1	4

Experiment III   DEFAECATION   (No. of pellets)

Experimental Condition

Subject	Day 1	Day 2	Day 3	Day 4	Day 5	TOTAL
P	1	5	6	5	5	22
Sb	-	2	3	1	4	10
Mp	6	5	10	9	8	38
Iw	4	5	1	6	5	21
TOTAL	11	17	20	21	22	91

Control Condition

Subject	Day 1	Day 2	Day 3	Day 4	Day 5	TOTAL
Cl	-	1	-	-	-	1
Al	2	1	-	2	4	9
Sm	-	-	1	1	⊖	2
Sp	-	-	-	-	-	-
TOTAL	2	2	1	3	4	12

Experiment III

LOCOMOTION   (Score in feet)

Experimental Condition

Subject	Day 1	Day 2	Day 3	Day 4	Day 5	TOTAL
P	$15\frac{1}{2}$	27	37	37	$46\frac{1}{2}$	163
Sb	$4\frac{1}{2}$	22	22	29	$34\frac{1}{2}$	112
Mp	27	$33\frac{1}{2}$	53	$44\frac{1}{2}$	$57\frac{1}{2}$	$215\frac{1}{2}$
Lw	$58\frac{1}{2}$	47	86	$66\frac{1}{2}$	78	336
TOTAL	$105\frac{1}{2}$	$129\frac{1}{2}$	198	177	$216\frac{1}{2}$	$826\frac{1}{2}$

Control Condition

Subject	Day 1	Day 2	Day 3	Day 4	Day 5	TOTAL
Cl	$16\frac{1}{2}$	$17\frac{1}{2}$	12	8	–	54
Al	$89\frac{1}{2}$	91	$93\frac{1}{2}$	$66\frac{1}{2}$	$53\frac{1}{2}$	394
Sm	$18\frac{1}{2}$	16	11	$5\frac{1}{2}$	$1\frac{1}{2}$	$52\frac{1}{2}$
Sp	21	14	$7\frac{1}{2}$	$1\frac{1}{2}$	2	46
TOTAL	$145\frac{1}{2}$	$138\frac{1}{2}$	124	$81\frac{1}{2}$	57	$546\frac{1}{2}$

Experiment III

SNIFFING   (Score in seconds)

Experimental Condition

Subject	Day 1	Day 2	Day 3	Day 4	Day 4	TOTAL
P	12	13	8	8	8	49
Sb	16	13	9	11	13	62
Mp	7	14	4	3	2	30
Lw	8	5	5	16	11	45
TOTAL	43	45	26	38	34	186

Control Condition

Subject	Day 1	Day 2	Day 3	Day 4	Day 5	TOTAL
Cl	13	21	10	14	11	69
Al	22	5	26	14	12	79
Sm	10	13	6	15	10	54
Sp	8	4	3	17	6	38
TOTAL	53	43	45	60	39	240

Experiment III

IMMOBILITY   (Score in seconds)

Experimental Condition.

Subject	Day 1	Day 2	Day 3	Day 4	Day 5	TOTAL
Pog	128	42	69	37	28	304
Seb	148	69	80	16	15	328
MP	120	10	69	65	42	306
Lw	60	21	18	89	37	225
TOTAL	456	142	236	207	122	1163

Control Condition

Subject	Day 1	Day 2	Day 3	Day 4	Day 5	TOTAL
Clint	89	163	186	218	287	943
Alex	91	164	60	116	167	598
Sam	155	208	166	236	258	1023
Sp	213	273	259	255	275	1275
TOTAL	548	808	671	825	987	3839

Appendix 8

Data for Experiment VII

S-nosing
Marking
U-marking
Defaecation
Locomotion
Sniffing
Immobility
Grooming

Experiment VII

S-NOSING (Score in Seconds)

Male Scent.

- M I N U T E S -

Subject	1	2	3	4	5	6	7	8	9	10	TOTAL
Sb	14	4	5	8	-	17	-	-	2	11	61
Col	44	28	34	5	16	-	6	7	6	-	146
Mp	55	16	6	14	32	22	15	17	5	3	185
Al	3	3	-	8	11	-	5	4	2	-	36
Lw	6	6	9	2	3	7	2	5	-	-	40
Sp	-	2	-	-	-	30	10	5	6	12	65
Cl	5	-	8	5	4	24	2	-	-	2	50
Sm	17	22	24	10	15	8	13	6	10	8	133
TOTAL	144	81	86	52	81	108	53	44	31	36	716

Female Scent

- M I N U T E S -

Subject	1	2	3	4	5	6	7	8	9	10	TOTAL
Seb	5	28	18	13	8	7	30	6	4	10	129
Col	46	29	47	23	17	17	15	21	39	38	292
MP	23	28	54	28	15	21	8	29	10	2	218
Alex	31	23	10	24	18	19	8	18	26	17	194
Lw	29	24	16	31	8	20	2	42	12	7	191
Sp	22	2	6	-	1	-	12	7	12	8	70
Cl	3	9	6	16	13	3	2	3	1	2	58
Sam	18	22	48	22	14	17	6	20	7	7	181
TOTAL	177	165	205	157	94	104	83	146	111	91	1333

Experiment VII

Experiment VII   MARKING   (No. of instances)

Male Scent

- M I N U T E S -

Subject	1	2	3	4	5	6	7	8	9	10	TOTAL
Sb	2	3	-	1	-	-	-	-	-	-	6
Col	4	2	4	1	1	-	-	-	2	-	14
Mp	-	-	4	5	2	7	-	2	1	2	23
Al	1	-	-	1	1	1	1	-	-	1	6
Lw	2	-	2	1	1	2	2	-	-	-	10
Sp	-	-	-	-	-	3	7	-	4	2	16
Cl	5	3	2	4	1	3	3	-	1	2	24
Sm	3	2	4	2	1	1	1	1	2	1	18
TOTAL	17	10	16	15	7	17	14	3	10	8	117

Female Scent

- M I N U T E S -

Subject	1	2	3	4	5	6	7	8	9	10	TOTAL
Seb	1	1	4	1	2	1	-	2	-	-	12
Col	-	4	1	-	1	2	-	-	-	-	8
MP	-	2	1	4	1	-	2	2	2	-	14
Alex	4	2	1	-	1	1	1	-	-	-	10
Lw	-	-	-	-	-	1	-	-	-	-	1
Sp	-	-	-	-	-	-	-	-	3	1	4
Cl	2	1	-	5	4	2	-	-	-	-	14
Sam	-	1	1	2	1	1	1	1	1	-	9
TOTAL	7	11	8	12	10	8	4	5	6	1	72

Experiment VII   U-MARKING   (No. of instances)

Male Scent.

- M I N U T E S -

Subject	1	2	3	4	5	6	7	8	9	10	TOTAL
Sb	-	1	-	-	-	-	-	-	-	-	1
Col	-	-	1	-	-	-	-	-	-	-	1
Mp	-	-	-	1	-	-	-	1	-	2	4
Al	1	-	-	-	-	1	-	-	-	-	2
Lw	1	-	-	-	-	-	-	-	-	-	1
Sp	-	-	-	-	-	-	-	-	-	-	-
Cl	1	-	-	2	-	-	-	-	-	-	3
Sm	-	-	1	-	-	-	1	-	-	-	2
TOTAL	3	1	2	3	-	1	1	1	-	2	14

Female Scent

- M I N U T E S -

Subject	1	2	3	4	5	6	7	8	9	10	TOTAL
Sb	-	-	1	-	-	-	-	-	-	-	1
Col	-	-	-	-	-	-	-	-	-	-	-
Mp	-	2	-	-	1	-	1	-	1	-	5
Alex	-	2	-	-	-	-	-	-	-	-	2
Lw	-	-	1	-	-	1	-	-	-	-	2
Sp	-	-	-	-	-	-	-	-	-	1	1
Cl	-	-	-	-	-	-	-	-	-	-	-
Sm	-	-	-	-	-	-	-	1	-	-	1
TOTAL	-	4	2	-	1	1	1	1	1	1	12

Experiment VII

DEFAECATION   (No. of pellets)

Male Scent.

- M I N U T E S -

Subject	1	2	3	4	5	6	7	8	9	10	TOTAL
Sb	-	-	-	-	1	-	-	2	-	-	3
Col	-	1	2	3	-	-	1	-	5	-	12
Mp	-	-	1	-	-	2	-	5	1	-	9
Al	-	2	-	2	-	-	-	1	-	-	5
Lw	1	1	3	-	-	1	-	-	-	1	7
Sp	-	-	-	-	-	-	2	-	1	2	5
Cl	2	-	-	-	-	-	-	-	-	-	2
Sm	1	-	2	1	-	-	1	-	2	-	7
TOTAL	4	4	8	6	1	3	4	8	9	3	50

Female Scent

- M I N U T E S -

Subject	1	2	3	4	5	6	7	8	9	10	TOTAL
Sb	-	2	2	-	-	-	-	-	-	-	4
Col	-	1	-	-	2	2	-	-	-	-	5
Mp	-	-	-	-	-	-	-	-	-	-	-
Al	-	1	-	-	-	1	-	2	-	-	4
Lw	1	-	-	-	-	1	1	-	-	-	3
Sp	-	-	1	-	2	-	-	-	1	1	5
Cl	-	-	-	-	-	-	-	-	-	-	-
Sm	-	-	-	-	-	-	-	-	-	-	-
TOTAL	1	4	3	-	4	4	1	2	1	1	21

Experiment VII

LOCOMOTION (Score in feet)

Male Scent

- M I N U T E S -

Subject	1	2	3	4	5	6	7	8	9	10	TOTAL
SB	6	9	6	3	1	1	-	6	2	3	37
Col	9½	8	7½	10	2½	-	3½	4½	6½	-	52
Mp	2½	3	6	8	4	6½	5	5½	1½	6½	48½
Al	7½	17	15	13½	8	16	9½	5½	11	15	118
Lw	9½	5	15	14	11	7	11	12½	8	9½	102½
Sp	5½	-	-	-	-	6½	11	5	7	6½	41½
Cl	11½	8½	5	10	4	5	9	½	4½	8½	66½
Sm	7½	10	6	9	3	6	6	5	7	8	67½
TOTAL	59½	60½	60½	67½	33½	48	55	44½	47½	57	533½

Female Scent

- M I N U T E S -

Subject	1	2	3	4	5	6	7	8	9	10	TOTAL
Sb	6½	5½	6	8	6½	5½	3½	2	3½	3	50
Cl	7	9½	3½	6½	4½	2	7	5	2½	5½	53
Mp	17	12½	2½	12½	12½	10½	9½	9	15½	12½	114
Al	17½	12½	21	12	13½	18	17	13½	20	11	156
Lw	4	6	9	5½	9	9½	9	2½	10	6	70½
Sp	4	1½	5	2	3	-	-	4½	6½	4	30½
Cl	3	1½	2½	6	6½	11	7½	8	2½	4½	53
Sm	17	14	7½	11½	7	9	9	8	11	9	103
TOTAL	76	63	57	64	62½	65½	62½	52½	71½	55½	630

Experiment VII SNIFFING (Score in seconds)

Male Scent

- M I N U T E S -

Subject	1	2	3	4	5	6	7	8	9	10	TOTAL
Sb	2	3	-	9	16	4	-	6	-	2	42
Col	-	-	-	-	-	-	-	3	2	-	5
Mp	-	2	2	-	2	-	-	2	3	5	16
Al	4	3	7	5	2	2	2	2	5	2	34
Lw	2	6	2	2	-	3	7	5	4	5	36
Sp	7	-	-	-	3	2	2	-	2	-	16
Cl	2	2	6	-	2	7	7	-	-	2	28
Sm	-	-	5	2	-	2	-	5	2	2	18
TOTAL	17	16	22	18	25	20	18	23	18	18	195

Female Scent

- M I N U T E S -

Subject	1	2	3	4	5	6	7	8	9	10	TOTAL
Sb	4	-	1	-	-	2	-	1	-	-	8
Col	-	-	-	-	-	2	3	-	-	3	8
Mp	1	-	-	-	-	4	-	-	1	1	7
Al	-	-	2	2	-	6	3	2	-	1	16
Lw	-	-	2	-	-	-	2	1	-	-	5
Sp	-	2	3	2	-	-	-	2	1	2	12
Cl	3	1	3	3	1	4	2	1	-	3	21
Sm	-	-	-	-	-	-	-	-	2	-	2
TOTAL	8	3	11	7	1	18	10	7	4	10	79

Experiment VII IMMOBILITY (Score in seconds)

Male Scent

- M I N U T E S -

Subject	1	2	3	4	5	6	7	8	9	10	TOTAL
SB	10	5	14	12	5	10	60	99	27	32	184
Col	-	2	5	-	-	-	15	2	4	45	73
Mp	-	20	35	2	-	5	25	10	10	22	129
Al	14	-	6	2	-	-	12	20	8	-	62
Lw	10	-	-	4	-	-	4	6	20	11	55
Sp	35	30	10	-	-	-	-	2	-	2	79
Cl	5	12	-	10	25	20	4	58	7	2	143
Sm	-	2	4	-	4	6	-	2	2	7	27
TOTAL	74	71	74	30	34	41	120	109	78	121	752

Female Scent

- M I N U T E S -

Subject	1	2	3	4	5	6	7	8	9	10	TOTAL
Sb	20	-	-	-	5	21	4	28	25	25	128
Col	-	-	-	22	26	20	11	20	10	-	109
Mp	-	-	-	-	-	-	-	-	-	19	19
Al	-	-	-	-	-	3	-	-	-	-	3
Lw	25	-	-	-	-	-	-	4	-	12	41
Sp	9	31	36	44	16	60	37	30	39	6	308
Cl	19	30	19	5	10	10	17	24	53	46	233
Sm	-	-	-	-	-	-	-	-	10	17	27
TOTAL	73	61	55	71	57	114	69	106	137	125	868

Experiment VII   GROOMING   (Score in seconds)

Male Scent

- M I N U T E S -

Subject	1	2	3	4	5	6	7	8	9	10	TOTAL
Sb	-	-	-	-	-	-	-	-	-	-	-
Col	-	-	-	-	2	-	-	-	4	14	20
Mp	-	-	-	-	-	-	2	-	20	-	22
Al	-	-	-	6	-	-	2	-	-	-	8
Lw	-	-	2	-	-	-	-	-	-	2	4
Sp	-	-	-	-	-	-	2	-	2	-	4
Cl	-	-	2	-	-	-	-	-	2	-	4
Sm	-	-	-	-	-	-	-	-	-	-	-
TOTAL	-	-	4	6	2	-	6	-	28	16	62

Female Scent

- M I N U T E S -

Subject	1	2	3	4	5	6	7	8	9	10	TOTAL
Sb	-	-	-	-	-	-	-	-	-	-	-
Col	-	-	-	-	6	-	-	-	-	-	6
Mp	-	-	-	-	-	-	12	-	-	-	12
Al	-	-	-	-	-	-	-	...	...	-	-
Lw	-	-	-	-	-	-	-	-	-	-	-
Sp	-	-	-	-	-	-	-	-	-	-	-
Cl	-	-	-	-	-	-	-	-	-	-	-
Sm	-	-	-	-	-	-	-	-	-	-	-
TOTAL	-	-	-	-	6	-	12	-	-	-	18

APPENDIX 10

Scent marking in relation to the
oestrous cycle.

Scent marking in relation to the oestrous cycle

Subjects		Days				Days			
P.		-2	-1	1	2	7	8	9	10
cycle 1		1	7	2	2	1	1	1	5
cycle 2		2	7	2	2	4	1	2	2
cycle 3		2	5	4	2	1	1	4	2
	T	5	19	8	6	6	3	7	9
	$\overline{m}$	1.7	6.3	2.7	2.0	2.0	1.0	2.3	3.0

G.									
cycle 1		6	3	0	0	0	2	3	0
cycle 2		2	5	4	3	2	2	0	2
	T	8	8	4	3	2	4	3	2
	$\overline{m}$	4.0	4.0	2.0	1.5	1.0	2.0	1.5	1.0

B.									
cycle 1		12	6	12	4	1	4	1	2
cycle 2		6	4	6	1	3	2	1	3
	T	18	10	18	5	3	6	2	5
	$\overline{m}$	9.0	5.0	9.0	2.5	1.5	3.0	1.0	2.5

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