OLFACTORY COMMUNICATION IN THE FERRET (*MUSTELA FURO* L.) AND ITS APPLICATION IN WILDLIFE MANAGEMENT

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ABSTRACT

Olfactory communication in the ferret (Mustela furo L.) and the use of ferret anal gland odours in wildlife management were investigated. Four hypothesised functions of ferret odours and predictions from these hypotheses were outlined and tested.

Predictions of spatial and temporal patterns of scent marking were tested by two years of observations on ferrets in an outside enclosure. A repertoire of scent marking actions was described. Both males and females performed anal drags after defaecation at conspicuous latrines throughout the year. Wiping, belly crawl and/or body rubbing, and chin rubbing, were performed more often by males, and peaked in spring. Chin rubbing was associated with food sites, and body rubbing with agonistic encounters. An experiment testing the use of anal gland odours in the maintenance of spatiotemporal separation of males was inconclusive.

An histological study of the skin revealed abdominal glands in both sexes around the urogenital opening, larger in males than in females. The odour-producing characteristics of these glands are discussed. Tubular and sebaceous glands were present over the whole body, and both atrichial and epitrichial tubular glands occurred in the feet and digits.

Gas chromatography on ten individual ferrets' anal sac extracts revealed sexually and individually distinct profiles of volatile compounds, but no consistent seasonal trends. Females had higher concentrations of 2,3-dimethylthietane and/or 3,4-dimethyl-1,2-dithiolane, while indole was usually the largest peak in male GC profiles. 2-propylthietane was an important constituent in most individuals of each sex.

Y- and T-maze preference tests showed that ferrets were attracted to ferret anal gland odour; could discriminate ferret odour from that of weasel, male from female, familiar from strange, familiar from their own, and fresh from one-day old ferret anal gland odours. Males preferred to investigate female odours, but could not discriminate

between oestrous and anoestrous odours.

Male ferrets' behaviour in the presence of various anal gland odours and an opponent showed them to be more confident in the presence of their own rather than their opponent's odour, and less confident with their opponent's than with a known dominant animal's odour.

With mustelids' predatory role in New Zealand and current predator control techniques in mind, the feasibility of using ferret anal gland odours as scent lures was investigated. A bioassay of synthetic anal gland compounds showed that the most attractive combination of compounds was trans- and cis-2,3-dimethylthietane and 2-propylthietane, which was used as the basis of an artificial scent lure in trapping experiments. Paired-trap design choice experiments showed that ferrets preferred to enter baited traps rather than those scented with the artificial lure; showed no preference between bait and a natural product anal gland odour lure; preferred the natural over the artificial lure; and the artificial lure over no odour. The removal of 2,3-dimethylthietane did not reduce the attractiveness of the artificial lure, and a lure containing only indole was also as attractive as the artificial lure. Comparisons between trap sites with bait/lure pairs and those with lure only indicated that scent lures should be as effective as bait in attracting ferrets, and this was confirmed in a field programme. Differences in the catches of males and females, through the year, and on fresh and stale lure were analysed, along with data on captures of non-target species.

Evidence for the hypothesised functions of odours is synthesised. The role of anal gland odour in providing an olfactory association between a resident and the defended area is supported, along with a scent matching mechanism, while a neighbour-neighbour avoidance mechanism cannot be rejected. Anal gland odour's role in sex attraction finds support, as does the antipredator defence hypothesis. Body odours are thought to play a more active role than anal gland odour in agonistic encounters, and chin rubbing could provide a bookkeeping system for efficient food searching. Ferret and other mustelid olfactory communication systems play similar roles in mediating spacing systems. Differences occur in the roles of odours as sex attractants where there are differences between species in social organisation or reproductive

physiology.

Results of the bioassay and trapping experiments are discussed in the context of the pheromone concept which is rejected for ferrets. Scent lures are seen as valuable additions to the current techniques used in mustelid control operations. The major priorities for future research are the confirmation of the presence of odorous secretions at scent marking sites; the study of latrine usage by wild ferrets; the development of the artificial lure in a long-lasting form; and the testing of the attractiveness of artificial and natural product lures to other mustelid species.

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INTRODUCTION

> "It has become apparent that for the complete understanding of the life of a species, information on its methods of communication is essential... Some investigators...also hope that through a better understanding of the animal's 'language' they may be able to design more efficient methods leading to the reduction (or even the complete elimination) of a pest species." -Mykytowycz 1970

1.1 RAISON D'ETRE

Although little is known about the impact of predators on the majority of contemporary New Zealand fauna, it is indisputable that in some places, at some times, mammalian predators such as mustelids are causing damage to particular species. Merton (1978) noted that on islands: "without exception, indigenous bird life has been depleted by introduced mustelids." Moors (1983, pers. comm.) found that native birds in Kowhai Bush, Kaikoura, lost 67% of their nests to predators, with stoats and weasels being responsible for 78% of this predation. Pierce (1982a) found that predation was the main reason for nesting failure of the endangered black stilt (Himantopus novaezelandiae). The main predators are ferrets (Mustela furo), cats (Felis catus), harriers (Circus approximans) and rats (Rattus norvegicus). Another localised mustelid-predation problem occurs at Tairoa Head, Otago, where Royal albatross (Diomedea epomophora) chicks fall prey to ferrets (King and Moors 1979). Predation by stoats cannot be excluded from consideration of factors limiting the population of takahe, Notornis mantelli, (Lavers and Mills 1978, King 1984) and North Island kokako, Callaeas cinerea wilsoni, (King 1984). Effective management programmes require knowledge of the biology of these predators. The keystone position communication holds in social behaviour of animals means that a knowledge of a species' communication system is essential for a full understanding of the life of that animal. This thesis reports on a 3-year study of the olfactory communication system of the ferret, that provides a test of possible functions of odours in communication. Building upon this knowledge of ferret olfactory communication, the use

of odours as wildlife management tools are investigated, with the aim of producing more effective mustelid control techniques.

1.2 THE FERRET IN NEW ZEALAND

The ferret (Mustela furo Linnaeus 1758) is probably a domesticated form of Mustela putorius, the European polecat (Carnivora:Mustelidae) (Rempe 1970, Corbet and Hill 1980, Zima and Král 1984). For convenience, and to distinguish between this domesticated form and its ancestral stock, the name M. furo is retained (Corbet and Southern 1977, Corbet and Hill 1980, Lavers and Clapperton in prep.). It was introduced into New Zealand in the late 1800's, along with stoats (M. erminea) and weasels (M. nivalis), in an attempt to control the alarming increase in the rabbit population (Oryctolagus cuniculus) (Thomson 1922, Gibb and Flux 1973). It was soon realised, however, that they were not controlling rabbit numbers, and that native birds were included in their diet (Thomson 1922). Ferrets have become widely distributed through New Zealand, living in pasture, rough grassland, and bush margins, their populations being concentrated in areas with large rabbit populations (Marshall 1963). They have not been reported from Stewart Island or any offshore islands (Fitzgerald et al. 1984).

There are published accounts of appearance, body size, weight, skull dimensions, reproduction and diet (Wodzicki 1950, McCann 1955, Fitzgerald 1964, Lavers 1973a, Roser and Lavers 1976, Robertson 1976, Gibb et al. 1978). This information is summarised by Lavers and Clapperton (in prep.). Male weight (average 1.0-1.3 kg) can be twice that of females (average 450-600 g), with weight and physical condition varying through the year (Fitzgerald et al. 1984). Testis weight increases rapidly in August, and is high until late summer. Females come into oestrus in September. After a 41-42 day gestation period, the first litter of 2-10 (usually 6-8) kittens is born in spring, and the young disperse from the natal area about three months later. The female can come back into oestrus and have a second litter before the end of the breeding season in March. Breeding coincides roughly with the peak supply of young rabbits. Rabbits, rodents and birds are the major prey, supplemented by frogs, carrion, fish and invertebrates. Ferrets spend little time above ground in the open, and although basically nocturnal, are sometimes active during daylight hours (Gibb

et al. 1978, pers. obs.).

Social organisation has been studied by Lavers (1973a) and Moors and Lavers (1981), who found that ferrets at Pukepuke Lagoon, coastal Manawatu, had an intrasexual territorial system typical of Mustela species (Powell 1979). The ranges of males and females overlapped extensively, but within the same sex individual ranges overlapped only near their borders. Males in particular maintained a well-defined spacing system. An individual's home range did not remain fixed throughout its life, but was affected by such factors as food sources and occupancy of neighbouring ranges. Moors and Lavers (1981) suggested that scent marking and dominance relationships were the principal mechanisms by which this spacing system was maintained. Individuals appeared to be solitary, except for reproductive purposes, and males engaged in fighting during the breeding season (Lavers 1973a, Moors and Lavers 1981). The term territory is thus used in the sense of a defended area, allowing priority of access to resources, leading to spatiotemporal separation of individuals of the same sex.

Knowledge of the ferret's communication system has been limited to overseas studies on vocalisations (Gossow 1970), polecat/ferret behaviour (Poole 1967, 1972a,b, 1973), including scent marking (Goethe 1940, 1964, Eibes-Eibesfeldt 1956), responses to odours (Wheeler 1978, Sokolov and Rozhnov 1983) and studies on anal gland structure (Stubbe 1972). Crump (1980b) identified some of the chemical components of ferret anal gland secretions. McCann (1955) suggested that smell was important in location of the opposite sex. Lavers (1973b) found that a significantly high proportion of ferrets was caught in traps that had recently held another ferret, and he suggested that this indicated that scent plays an important part in attracting ferrets to one another.

1.3 OLFACTORY COMMUNICATION

With this background information on the biology of the ferret, the research needed to understand ferret olfactory communication can be outlined. Eisenberg and Kleiman (1972) defined olfactory communication as: "the process whereby a chemical signal is generated by a presumptive sender and transmitted (generally through the air) to a presumptive receiver who by means of adequate receptors can identify, integrate and respond (either behaviourally or physiologically) to the signal". Mammalian odours can take the form of either body odours or scent

marks. Johnson (1973) defined scent marking as "behaviour by which glandular secretions are deposited on the ground or onto objects in an animal's environment", but it should be noted that faeces and urine can act as media for the deposition of such secretions.

The solitary and territorial way of life of the ferret suggests that odours could have a role in the maintenance of its spacing system. An early hypothesis of scent marking by mammals was that it was used to demarcate a spatially-fixed territory, and that conspecifics would be deterred from intruding into this marked area (Uexüll and Kriszat 1934). It has seldom been shown, however, that animals will be prevented from entering a scent marked area (Gosling 1982). Thus scent marks are not likely to act simply as intruder-deterrent boundary markers, especially in a species like the ferret, where male home ranges can be as large as 70 ha (R.J. Pierce pers. comm.). Such a system of boundary markers would provide just a single line of defence, which could not be renewed frequently enough by a solitary animal defending a large area. A more effective means of defence for such an animal is "hinterland marking" (Gorman and Mills 1984), the animal peppering the whole home range with scent marks. This allows some intrusion to occur, but ensures that sooner or later an intruder will encounter a scent mark.

Scent marks may intimidate intruders and/or enhance the confidence of residents (Mykytowycz 1975, Mykytowycz et al. 1976). (see Emendation 1) Gosling (1982) claimed that this was not directly testable, and rephrased the problem in terms of a cost/benefit asssessment of agonistic encounters. He suggested a mechanism by which intruders could recognise a resident. Scent marks were seen to provide an olfactory association between a resident and its defended area. Intruders encountering scent marks and then other animals would be able to recognise the resident by matching the odour of the scent marks with the body odour emanating from the animal it meets. Territorial disputes are thus settled on a "property tenure" basis (Gorman 1984a). Both animals would be able to assess the asymmetry of the encounter, and react appropriately. Both should avoid escalating the encounter to fighting if possible, but as the resident has more to lose, it should be prepared to defend its resources, while the intruder should be more likely to flee when the scent marks and body odours of the adversary match (Parker 1974, Maynard-Smith and

Parker 1976). Thus territorial disputes could be settled by odour communication and a minimum of fighting and associated injury.

Interactions between neighbours could also be mediated in this way, but a simpler model of neighbour-neighbour recognition and avoidance can also be proposed. As in auditory communication, neighbours could learn each others' signals by repeated exposure, and adjust their spatiotemporal arrangement without overt aggression, or even having to meet. As Leyhausen (1965) found in domestic cats, after only one agonistic interaction dominance relationships can be established, and animals will then avoid face-to-face encounters. Leyhausen and Wolff (1959) suggested that scent marks act as "railway signals", to minimise encounters between individuals by signalling how recently an animal has passed. If two animals resident in overlapping home ranges regularly encounter scent marks that contain information on individual identity and on the length of time since the mark was placed, they could learn to recognise each other's scent marks and movement patterns. In this way, subordinate individuals could avoid direct contact with dominant neighbours, and no further interactions or matching of scent would be necessary.

A territorial defence hypothesis can thus be put forward, with two possible mechanisms, each of which have particular predictions that can be tested (Table 1.1). If the scent marks are aimed at strangers intruding into the area, one can predict an increased rate of scent marking in the breeding season, when males are most actively defending their territories (Moors and Lavers 1981). If they are more important in neighbour-neighbour interactions, they may show no seasonalvariations i frequencies, as neighbours maintain spatiotemporal arrangements all year round. Both mechanisms require an ability to discriminate amongst odours of different individuals, and to show certain responses, depending upon the identity of the odours. Either mechanism could involve either a boundary or hinterland marking system. If scent marks are used as boundary-markers, they should be concentrated at the periphery of the territory. If a hinterland marking system is used, scent marks should be left in conspicuous places throughout the territory, concentrated at activity centres such as den sites and regularly-used pathways, where they are most likely to be encountered.

TABLE 1.1

Hypothesised functions of ferret odours and predictions to be tested. (see Emendation 2)

HYPOTHESIS 1

Scent marks provide an olfactory association between a resident and its defended area which allows intruders and neighbours to avoid escalating agonistic encounters with a resident.

MECHANISM 1

Intruders compare the scent of any animals they meet with the memorised scent of marks they have encountered in the vicinity. When these scents match the resident is identified and the intruders respond appropriately, usually by withdrawal.

Predictions:

(a) Scent marks will be left in places where they are most likely to be encountered.
(b) The frequency of scent marking will be highest in spring.
(c) Ferrets will be able to distinguish between their own and others' odours and amongst different individuals' odours.
(d) Residents will smell the same as their scent marks.
(e) Residents will be most confident when in the presence of their own odours.
(f) Intruders will be intimidated if the odour of nearby scent marks matches that of the animal it meets.

MECHANISM 2

Ferrets will remember and recognise the scent of neighbours they have previously encountered, and will avoid areas scent marked by fresh odour of dominant neighbours, thus avoiding agonistic encounters.

Predictions:

(a) Scent marks will be left in places where they are most likely to be encountered.
(b) Ferrets will scent mark all year round.
(c) Ferrets will be able to discriminate amongst different individuals' odours, and the freshness of odours.
(d) Ferrets will be least confident in the presence of the odour of known dominant neighbours.

(e) Ferrets will avoid areas freshly scent marked by dominant neighbours.

HYPOTHESIS 2

Scent marks and/or body odours act as sex attractants, one or both sexes being attracted to the odours of the opposite sex.

Predictions

(a) Scent marks will be left in places where they are most likely to be encountered by members of the opposite sex.

(b) Scent marking may vary seasonally in frequency or quality.

(c) Ferrets will be able to discriminate between male and female odours.

(d) Ferrets will approach the odour of the opposite sex in preference to that of its own sex, during the breeding season.

HYPOTHESIS 3

Scent marks act as a bookkeeping system to assist in efficient food relocation.

Prediction:

(a) Scent marks will be concentrated at food sites, either (i) at old food site where only odours and inedible remains are present, or (ii) at freshly deposited food stores.

HYPOTHESIS 4

Anal gland odours released in large amounts form an antipredator defence system.

Predictions:

(a) Wild ferrets will release large amounts of anal gland odour when captured by a predator (e.g. man).

(b) Predators will be deterred by this odour.

Odours can also be used in reproductive processes. An important signalling role for odours in reproduction is to indicate to conspecifics the sex and sexual state of the signaller (Stoddart 1980b). Odours could thus act as both a sex recognition system and as sex attractants, bringing the sexes together for mating, of particular importance in solitary-living species such as the ferret (Hypothesis 2, Table 1.1). For odours to act in sex attraction, ferrets must be able to discriminate between male and female odours and respond appropriately, at least during the breeding season.

Korytin and Solomin (1969) and Henry (1977) suggested that scent marks could assist in efficient foraging by scavenging species. Scent marks could be deposited when and where food is stored, or where no food remains at a cache, both systems acting to reduce the amount of time and energy spent in foraging by increasing the odour output from certain sites. These hypotheses can apply not only to scavenging species, but to any animal that stores food, no matter how it is obtained (Hypothesis 3, Table 1.1).

In addition to these intraspecific roles, odours could function in an interspecific context. Goethe (1964) noted that: "despite their mostly small size the mustelids have few enemies, unquestionably a result of their varied threatening and defensive behaviours, in which chemical defence in particular has a strong effect on all hostile macros matic mammals." Some species are well known for their readiness to release anal gland odour when frightened (Johnson 1921, Walker 1930, McCabe 1949, Alexander and Ewer 1959, Brinck et al. 1978). The odour of skunks (Mephitinae), which contains butyl mercaptan, was described by Ewer (1973) as "nauseous in the extreme". Adult ferrets in New Zealand lack the natural mammalian and raptorial predators with which they evolved in Europe (Goethe 1964), but an antipredator function for the use of anal gland secretion/odour in large quantities can be outlined (Hypothesis 4, Table 1.1).

The testing of the four hypotheses (Table 1.1) requires observations on how ferrets lay down scent marks, and how they respond to these and to body odours (Chapter 2). An examination of the possible sources of odours used in scent marking will allow a fuller understanding of the functions of odours from various glands (Chapter 3). For ferrets to be

able to discriminate amongst different odours, these odours must vary in some structural way (Chapter 4). The odour discrimination abilities of ferrets can be tested by preference experiments (Chapter 5), and further controlled experiments demonstrate ferrets' spontaneous responses to scent marks (Chapter 6). Information on odour release during handling of captured wild ferrets (Chapter 8) provides a test for the antipredator role of odours.

If anal gland odours are attractive to ferrets (i.e. if any of Hypotheses 1, 2, or 3, are operating), then the possible use of anal gland odours to bring mustelids to control devices can be investigated.

1.4 PREDATOR CONTROL IN NEW ZEALAND

Predator control procedures can be classed into two categories (King 1981). Large scale population control measures attempt to reduce overall population density permanently, while damage control measures attempt temporary reduction of numbers of a predator in an area and at the time when damage is occurring.

Ferret populations may be controllable by a "gamekeeper" population control approach. King and Moors (1979) describe the decline in numbers of polecats in England by intensive predator control on game estates. However, such procedures would be ineffective on mainland populations of stoats and weasels, because of their rapid reproductive potential (King and Moors 1979, King 1983). Control of damage done by all mustelid species in New Zealand, as in the examples above (section 1.1), remains viable, as does population control on small islands. The ability to control predators on small islands has been demonstrated, for example, by the extermination of cats from Little Barrier Island (Veitch 1982). Such eradication programmes are extremely difficult and exacting tasks, and Merton (1978) stressed that all ecologically-acceptable means of extermination should be used. Once an island is freed of a predator, continued predator control programmes on nearby, "stepping stone" islands may be necessary to prevent recolonisation. For either population control or damage prevention programmes to be effective they must be very intensive, and this requires techniques that are efficient in terms of money and manpower. There is a need thus for wildlife scientists to explore all possible

avenues to arrive at improved control measures.

The control of damage done by mustelids in New Zealand is achieved by preventing access to the prey species and by increasing mortality of the predator population. Ferret numbers may also be controlled by reducing the numbers of their staple food, the rabbit (Gibb and Flux 1973). Preventing access to the prey can be done only in small areas and in some habitats. Two predator exclosures form a mechanical barrier between ground predators and black stilt nests (Pierce 1982b), however, these two exclosures include only a small portion of the total breeding ground of the species. Augmenting mortality of mustelids is done by trapping, using Fenn traps for stoats and weasels and Gin traps or box traps for the larger ferrets (Plate 1.1). Catch rates are higher if there is some odour (bait or the smell of a previous capture) in the trap (King 1973, Lavers 1973b, King and Moody 1976, King and Edgar 1977), thus scent lures for mustelid traps could be valuable additions to the current techniques.

The attractive ingredients of ferrets' anal gland secretions is determined by a laboratory bioassay (Chapter 7). These are then used as the basis for synthetic trap lures, whose effectiveness compared to edible bait and natural product ferret lures are tested in field trials (Chapter 8).

Plate 1.1: Ferret caught in (a) Gin trap (b) Edgar live-trap.

(a)

(b)

Chapter 2
OBSERVATIONS ON SCENT MARKING BEHAVIOUR

> "The greatest need in scent marking studies is good descriptive information ... Most researchers interested in chemical communication ideally would like to understand the entire process as it functions in nature...However in general this is the most difficult approach, so many workers have turned to studies of captive animals to help provide insight into the way chemical communication functions in the wild." -Mech and Peters 1977

2.1 INTRODUCTION

The first step in a study of olfactory signalling is to observe the animals to see if they lay odours down as scent marks, and if so, in what situations. Scent marking actions have been described for a number of mustelid species. The European badger rubs its genital region on prominent objects in the environment (Frank 1940, Eibl-Eibesfeldt 1950), and has a "squat-marking" action, by which it marks the substrate with a mixture of secretions from its subcaudal and anal glands (Kruuk 1978, Kruuk *et al*. 1984). Wolverines (*Gulo gulo*) deposit "musk" from anal glands on trees and on the ground, and mark rocks and stumps with secretions from pregenital glands (Krott 1959, Pulliainen and Ovaskainen 1975, Koehler *et al*. 1980). Eibl-Eibesfeldt (1956) described tree martens (*Martes* sp.) climbing over objects in a conspicuous fashion and believed this to be a way of wiping off secretion from the anal glands. Herter and Ohm-Kettner (1954) observed similar marking actions, and Krott (1959) suggested that it was not secretion of the anal glands being laid down by martens, but rather that of the pregenital gland. A tame pine marten (*M. martes*) was observed by Goethe (1938) to rub the urogenital region, giving off glandular secretions, against a raised object. Hall (1926) described rubbing of the abdominal gland as a form of scent marking in *Martes caurina*.

Amongst Mustela species, the weasel marks with the whole body, with presumed glands of the genital region, and by cheek rubbing (Frank 1962), while the mink (M. vison) rubs the anal region against objects on the ground (Brinck et al. 1978). The European polecat slides its hindquarters over the ground after defaecation, leaving behind a trail of "scent" (Goethe 1940). It also climbs over objects with its tail raised, and was thought to wipe off anal gland secretion by this action (Eibl-Eibesfeldt 1956). The most comprehensive study of scent marking in a Mustela species to date is that of Erlinge et al. (1982) on the stoat. They described the anal drag, and assumed it to be a way of depositing anal gland secretions, and body rubbing, a means of marking with general body odours.

Many of these descriptions have been based on tame or captive animals, or casual observations in the wild. A full understanding of a species' olfactory communication system requires extensive, systematic observation, ideally in the wild. Even given modern technology, however, an attempt to study the behaviour of a wild population of small mustelids would result in many hours of unproductive effort. A more profitable approach is to confine several study animals into a large enclosure and allow them to live under semi-natural conditions and observe them directly. Such direct observational techniques allow the scent marking events to be described, along with not only the environmental but also the behavioural context in which they occur. Erlinge et al. (1982) based their descriptions of scent marking actions of stoats on observations of wild-caught animals in an enclosure, and Kruuk et al. (1984) observed squat-marking in badgers in a 1600m^2 enclosure. This approach appeared to be the most suitable for investigating the scent marking behaviour of the ferret.

Once it has been established that a species does lay down scent in the environment, additional questions can be posed. How often do individuals scent mark? At what times and in what seasons and locations? What is the sex of the marker? What effects do scent marks have on animals perceiving them? Three hypotheses were suggested in Chapter 1 to explain scent marking behaviour in ferrets, and a number of testable predictions outlined for each hypothesis. Those predictions involving the distribution and frequency of scent marking by various individuals, and responses to scent marks, can be tested by

direct observation work on scent marking behaviour.

2.2 METHODS

2.2.1 Enclosure

Observations on scent marking behaviour of ferrets were conducted in a 30 m by 35 m outside enclosure at Massey University (Fig. 2.1, Plate 2.1). It was divided into two equal areas by a 1 m high fence made of chicken netting in the first year and of corrugated iron in the second year. A 2 m length was left in chicken netting, to provide a window for visual, olfactory and auditory contact between the ferrets on either side. A gate in the dividing fence could be opened to allow the ferrets access to the opposite side and physical contact with each other. Two straw-filled plywood nest boxes set in earth mounds were provided on either side of the enclosure. Lengths of PVC piping or plywood formed entrance/exit burrows. Water was provided in containers on either side of the enclosure. Large dead tree limbs, small plants, lengths of PVC piping, wooden posts and other "landscaping" provided relief from the flat pasture on which the enclosure was built (Fig. 2.1, Plate 2.1). The grass was kept short by intermittent grazing by sheep. Food was provided ad libitum, usually in the form of petfood sausage.

2.2.2 Subjects

Four ferrets lived in the enclosure, one male/female pair on either side. Males Hans and Snark and females Jolie and Ulla were observed throughout the first year of the study (though Ulla was not present in spring). These ferrets were replaced by four new individuals, males Bilbo and Malli and females Pug and Satha for the next year. However, these four escaped after six months, and were replaced by males Chico and Ras and females Swuzzle and Titi for the final half year of the study. All were wild caught animals apart from Titi who was bred in captivity. Some were fitted with harnesses or collars made of reflective tape, or paint-marked to allow rapid identification during night observations.

2.2.3 Procedure

Observations were made at night, using a Noctron V night vision scope, with either a 135 mm or 80-200 mm zoom lens.

Figure 2.1: Diagram of the outside enclosure, and details of the perimeter fence.

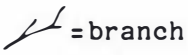
W =water container

○ =post

□ =nest box

✳ =plant

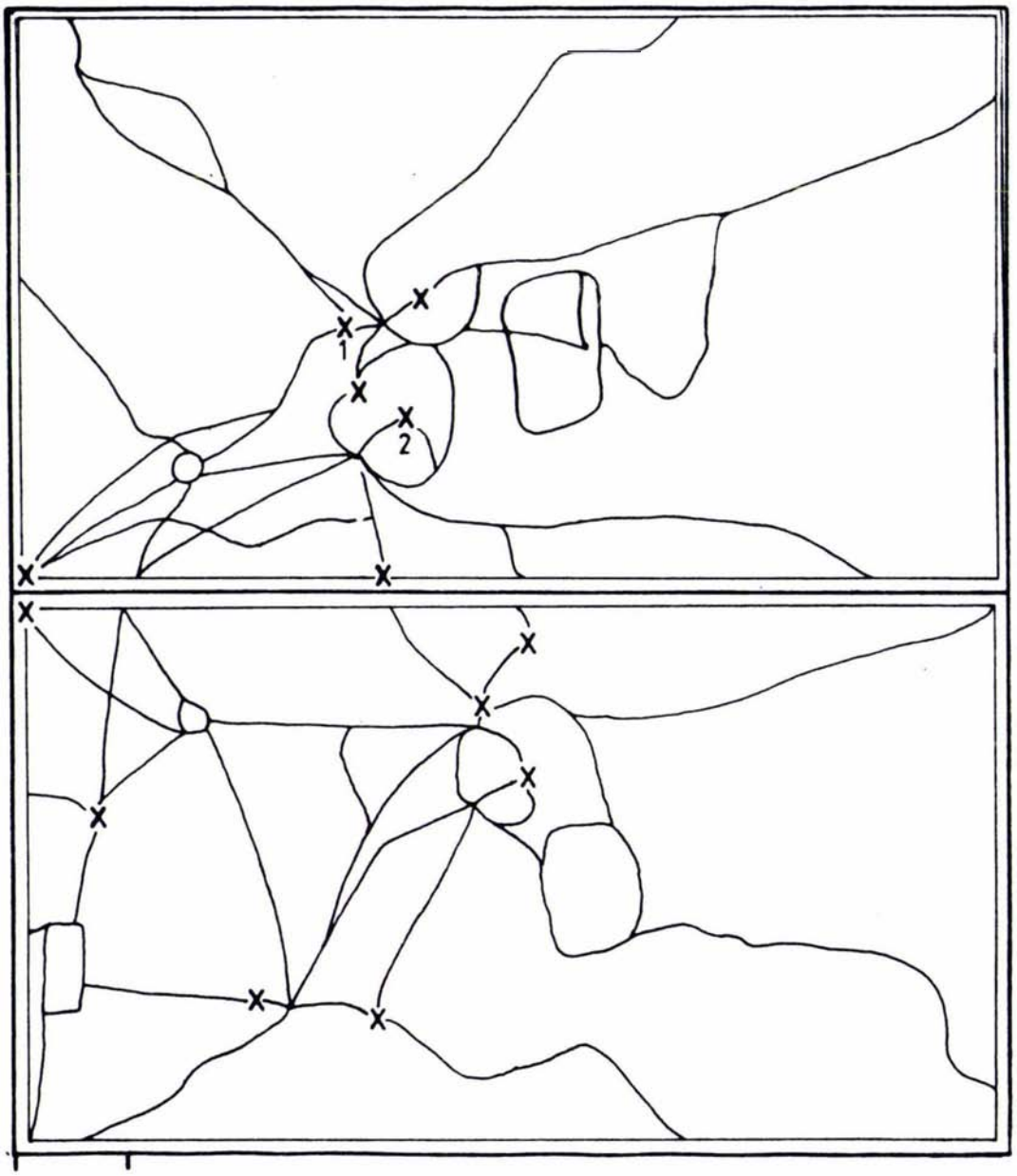
)::::(=burrow or piping

 =branch

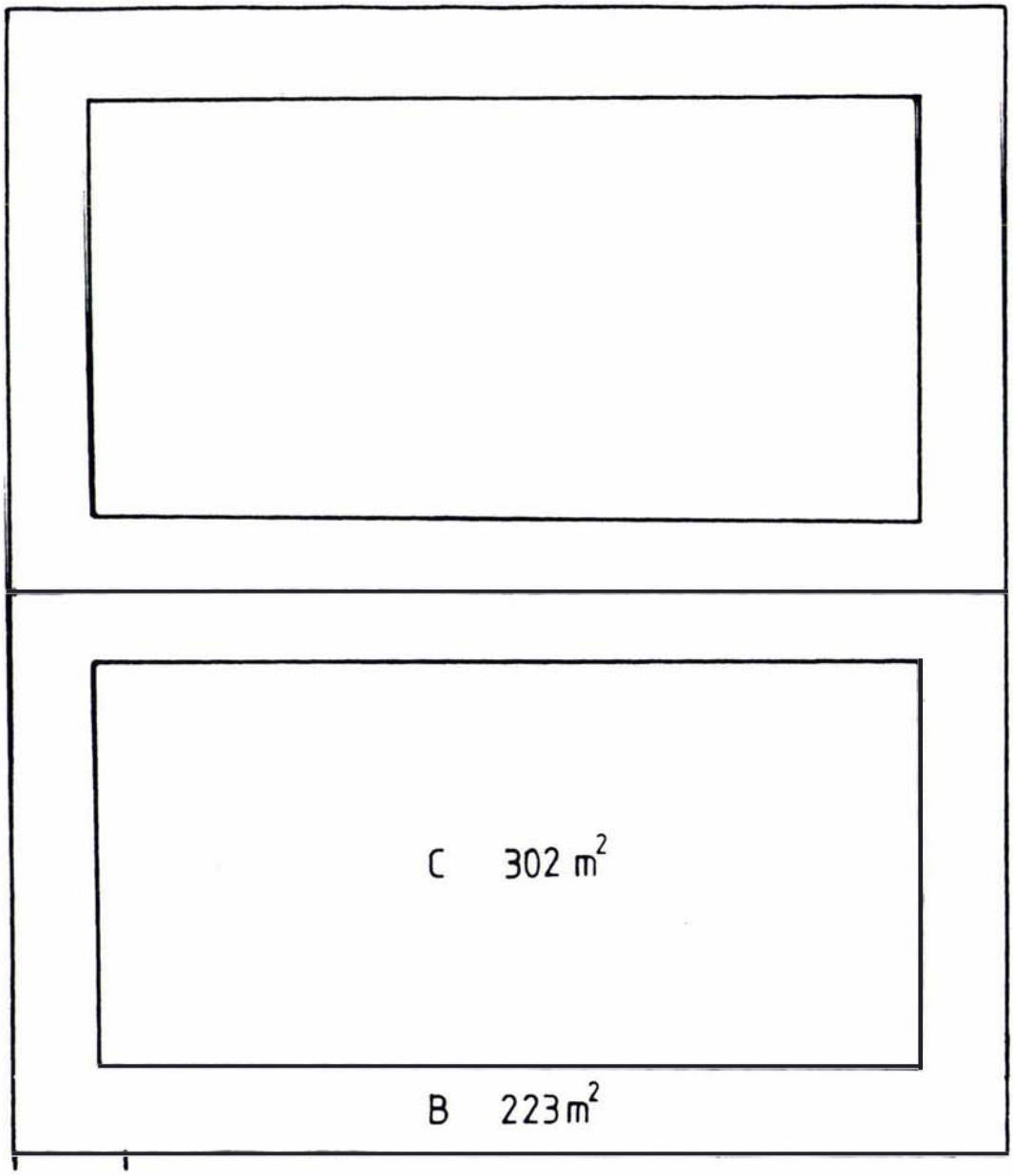
▱ =wood or plywood

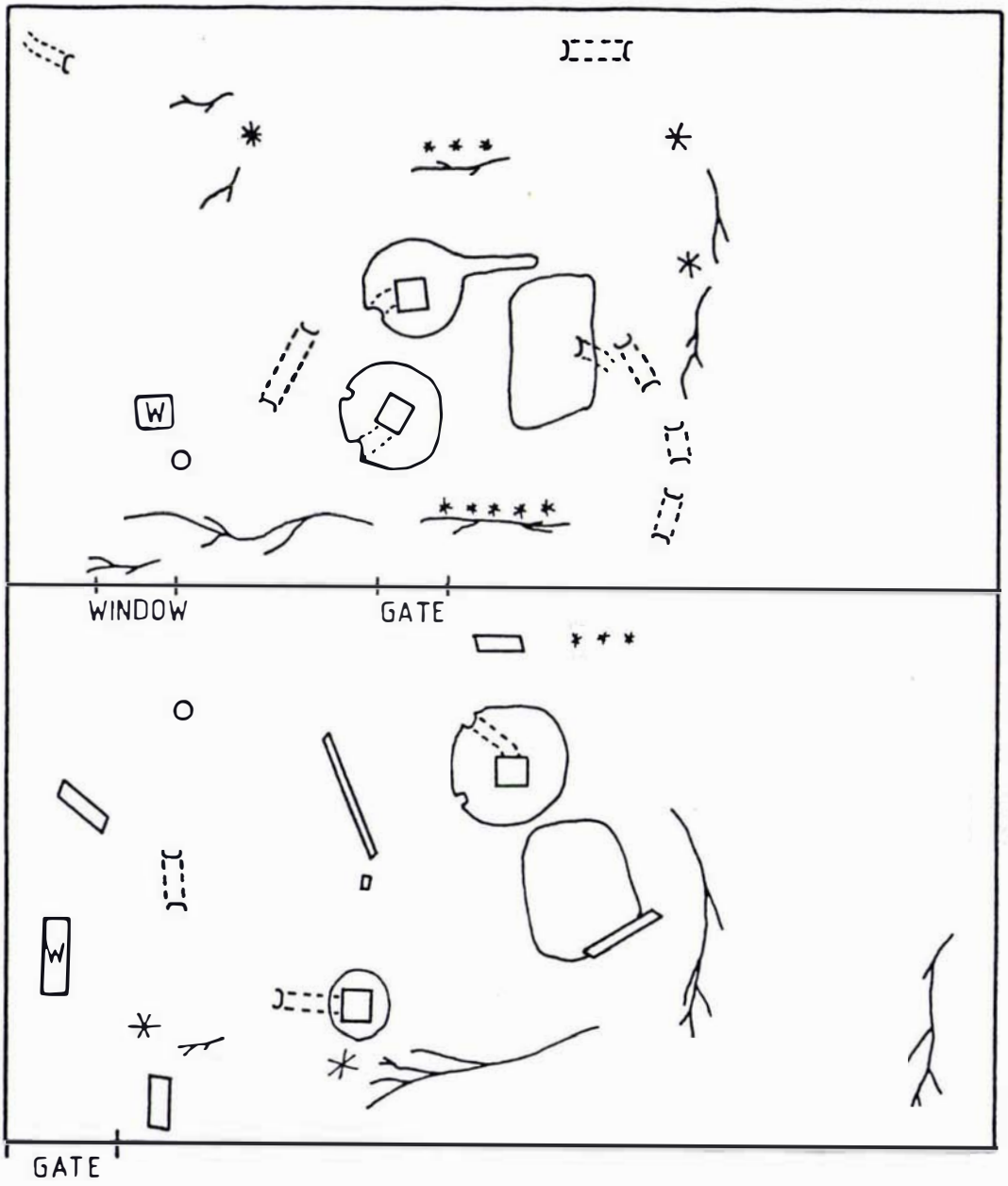
Overlays show (a) pathways and latrine sites (1 and 2 refer to the latrines used in the avoidance experiment, sections 2.2.3, 2.3.3) and (b) division of the enclosure into regions used in statistical analysis (C=central, B=boundary).

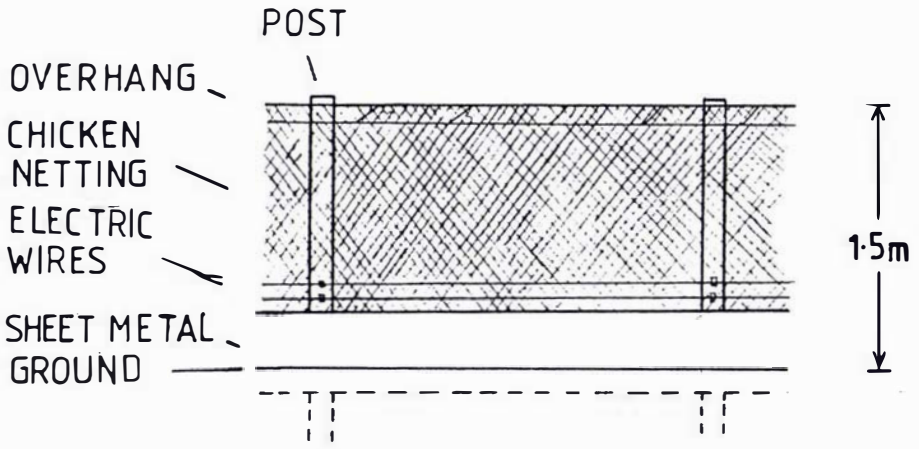
(a)



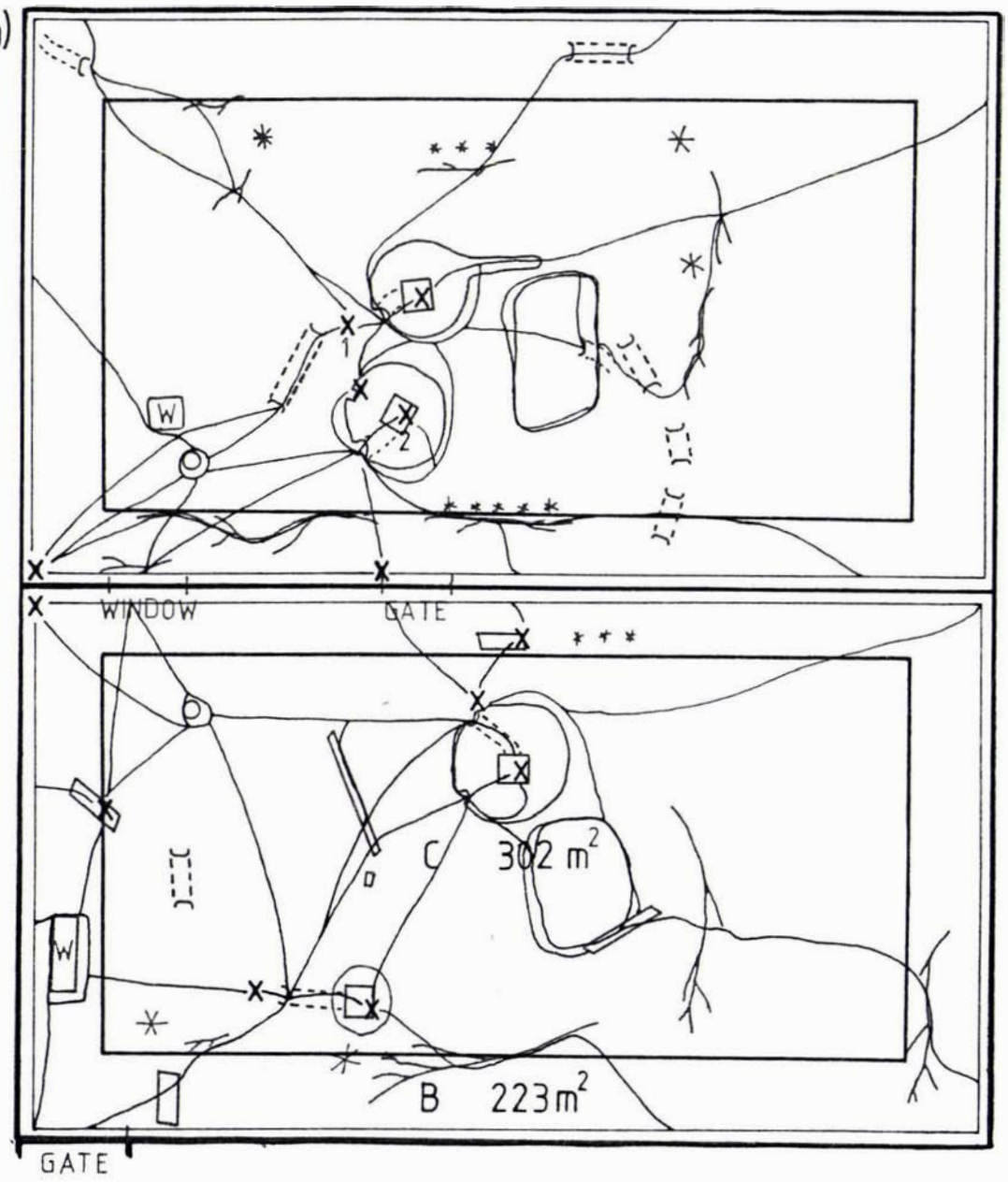
(b)

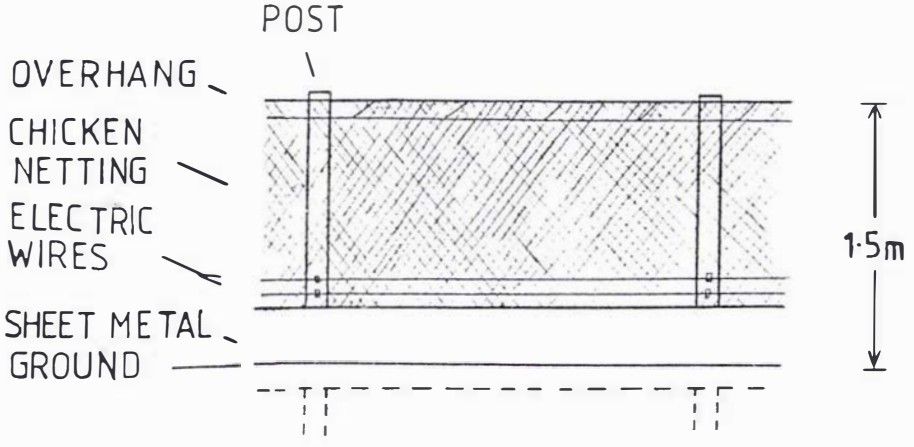


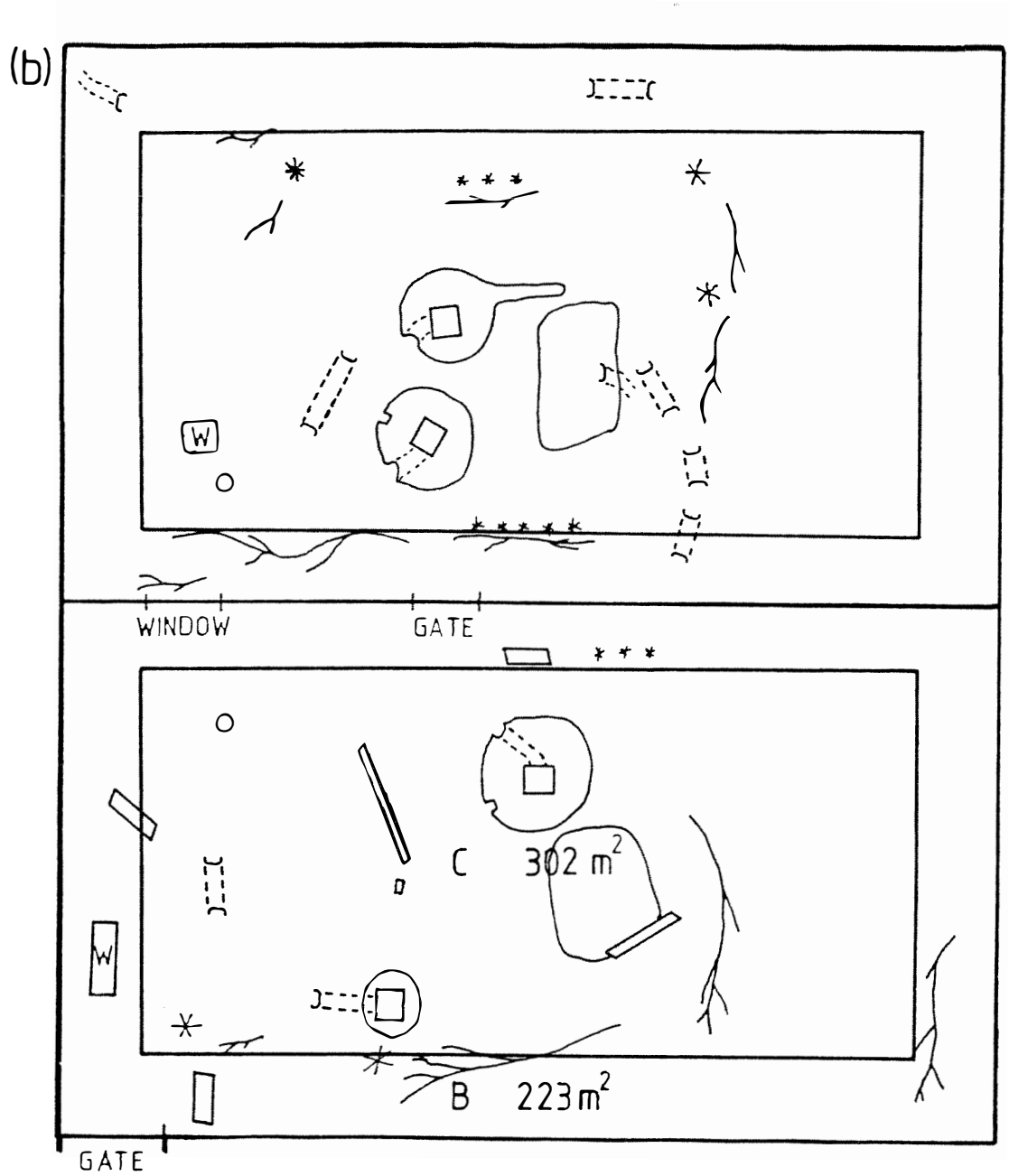

W
WINDOW
GATE
W
GATE


POST
OVERHANG
CHICKEN NETTING
ELECTRIC WIRES
SHEET METAL
GROUND
1·5m

(a)


W
WINDOW
GATE
C 302 m²
W
B 223m²
GATE


POST
OVERHANG
CHICKEN NETTING
ELECTRIC WIRES
SHEET METAL
GROUND
1·5m


(b)
W
WINDOW
GATE
C
302 m²
W
B
223m²
GATE

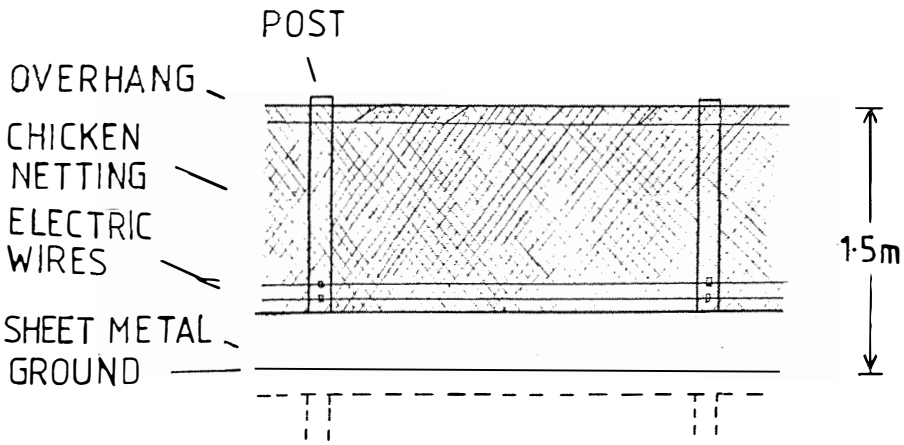
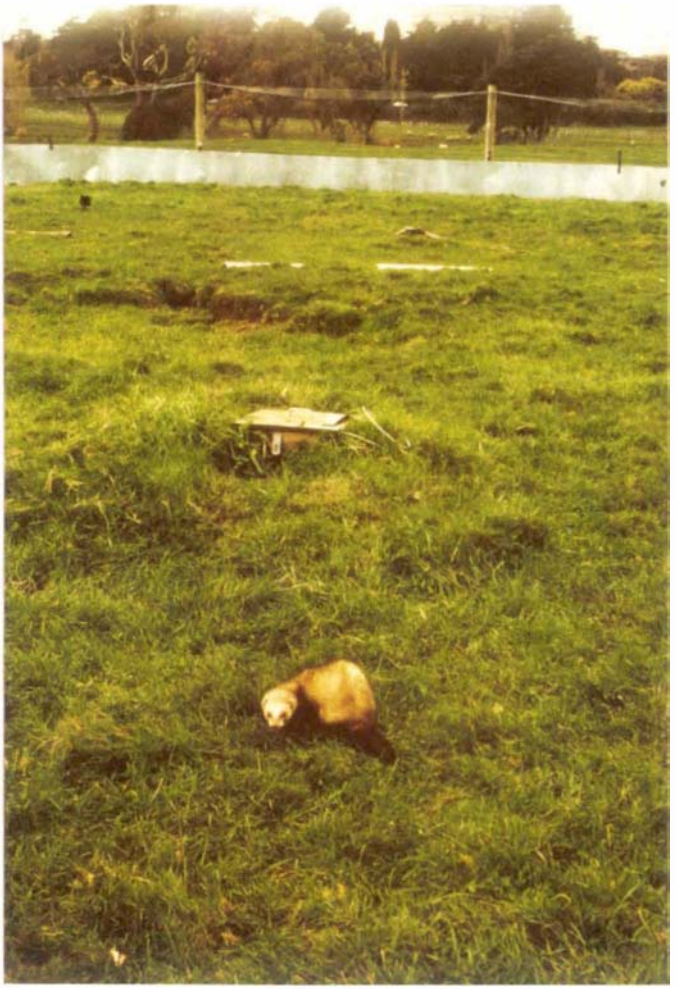

POST
OVERHANG
CHICKEN NETTING
ELECTRIC WIRES
SHEET METAL
GROUND
1·5m

Plate 2.1: View of the outside enclosure.



Torch light was used to improve visibility on dark nights, and to aid in identification of animals. The ferrets were observed at all times of the night from sunset to sunrise, in all seasons, from July 1983 to May 1985, for a total of 430 hours.

General behaviour was observed using an ad libitum sampling procedure (Altmann 1974). Postures and actions of ferrets engaged in scent marking were noted, along with the ferret's identity, sex, position in the enclosure, and orientation towards objects. Preceeding and subsequent behaviours of the scent marker, position and reaction of the other animals, time of night and weather conditions were also noted. This qualitative information allowed the formation of a repertoire of scent marking behaviour.

Quantitative data on scent marking were also collected. Each year was divided into four seasons - winter (June to August), spring (September to November), summer (December to February) and autumn (March to May). The night was divided into roughly equal early, middle and late observation periods or "watches", the length and start and finish hours varying with daylength. During a watch, a sampling session was defined as starting when an animal appeared from an entrance burrow, or if an animal was already out, from when it was first seen. Sampling finished when the animal disappeared from sight and remained out of sight for at least ten minutes. A focal subgroup sampling procedure was followed (see Altmann 1974), with a pair of animals being observed simultaneously during a watch, if they were both visible. The two pairs were watched usually on alternate nights, or on the same night if they were active at different times. More early watches were done than either middle or late watches, but the ratio of observations in the three periods was kept roughly equal through the year. Each half of the enclosure was divided into two regions - central (C) of 302 m^2, and boundary (B) of 223 m^2 (Fig. 2.1). The number and type of scent marking events occurring in each region were noted. Every minute the positions of the focal animals were recorded on a map of the enclosure, thus the number of scent marking events in a region, per time spent in that region, could be calculated. This gave a rate of scent marking for each animal for each region and each season. The time spent feeding in a region (animals were usually fed in C) was subtracted from the time in that region. Data on both the rate of scent marking per

total time observed in that season and the rate of scent marking per time in each region per season were analysed. The behavioural observations on each animal's first night in the enclosure were excluded from the data[1], which were converted into normalised ranks[2] and analysed using analysis of variance. Null hypotheses were rejected at the $\alpha=0.05$ significance level. Full analyses are given in Appendix 1.

The gate in the dividing fence was opened a few nights every season to allow observations on male-male and female-female interactions and responses of ferrets to their neighbours' scent marks. Scent marking actions on these nights were not included in the quantitative analysis.

In May 1985, at the end of the two-year sampling programme, the gate between the two sides of the enclosure was left open, giving all four ferrets access to the whole enclosure and all four nest boxes. The occupancy of nest boxes was noted on 22 days, to establish whether or not the males would avoid each other. Subsequently, the dominant male was removed on two nights and his anal gland secretion wiped across the grass in front of a latrine near one of the nest boxes (latrine 1 in Fig. 2.1 in the first trial and latrine 2 in the second trial). The behaviour of the other male was noted, in particular his entry into nest boxes.

2.3 RESULTS

2.3.1 General Behaviour

The ferrets were active intermittently throughout the night. Periods of activity generally lasted for about half an hour, and were separated by one and a half to three hours of rest. The exact times of activity were affected by when the animals were fed. They were seldom active during the day, with the exception of Titi, the captive-bred female. They regularly used specific pathways throughout the enclosure (Fig. 2.1), and would repeatedly stop and sniff at particular sites such as nest box lids, logs, and old food sites. They made use of the artificial nest boxes provided, but also spent time digging their own burrows. When food was placed in the enclosure, both males and females would take pieces of food and store them in the nest boxes and burrows.

1. The ferrets' behaviour was noticeably different from normal only on the first night.

2. The frquency distribution of the data was clearly non-normal.

Male and female pairs sometimes shared the same nest box, and sometimes were in separate nest boxes. When a male and female met out in the open, their first action was usually to sniff at each other's anal region, and often then the back of the neck. This anus and neck sniffing was also seen between members of the same sex. Some ritualised and play fighting (Poole 1972a) was observed between males and females, but no high intensity aggression. The females occasionally used deterrent, aversive, or even fearful defensive behaviour (Poole 1972a) to avoid the males. When unreceptive to a male's sexual advances they sometimes released anal gland odour while trying to escape.

When allowed physical contact, the males would chase each other, and fight aggressively, especially in spring, and, to a lesser extent, in summer. Males developed stable dominance relationships that did not depend on location in the enclosure. In the first year, Snark dominated Hans, and in the second half of the second year Ras dominated Chico. Bilbo and Malli were both very aggressive, and although Malli lost both his top canine teeth, he was not always intimidated. Amongst the females, few agonistic interactions were observed. A resident female would dominate an intruding neighbour in her own side of the enclosure. No fighting was seen between females, only chases.

2.3.2 Scent Marking Behaviour

2.3.2.1 Defaecation and Urination

Defaecation was an obvious action that usually started with the animal sniffing at the chosen site. The animal would then turn around and back into position, and stand still for five seconds or longer, with the body slightly stretched out and with the tail curled right over the body, or sometimes out to one side (Fig. 2.2a). Defaecation was often accompanied by urination, but urination also occurred throughout the enclosure. It did not always involve any obvious stance, and thus could not be accurately mapped or quantified. Faeces were deposited in conspicuous places, usually close to the nest boxes, including the nest box lids (Fig. 2.1). Individuals used the same sites for months at a time, and had two or three of these "latrines" in use at any one time. Male and female pairs had some communal and some separate latrines.

Figure 2.2: Repertoire of scent marking actions and associated behaviour; line drawings from photographs.

(a) Defaecation

(b) Sniffing at latrine

(c) Anal drag (side view)

(d) Anal drag (posterior view)

(e) Wiping (side view)

(f) Wiping (posterior view)

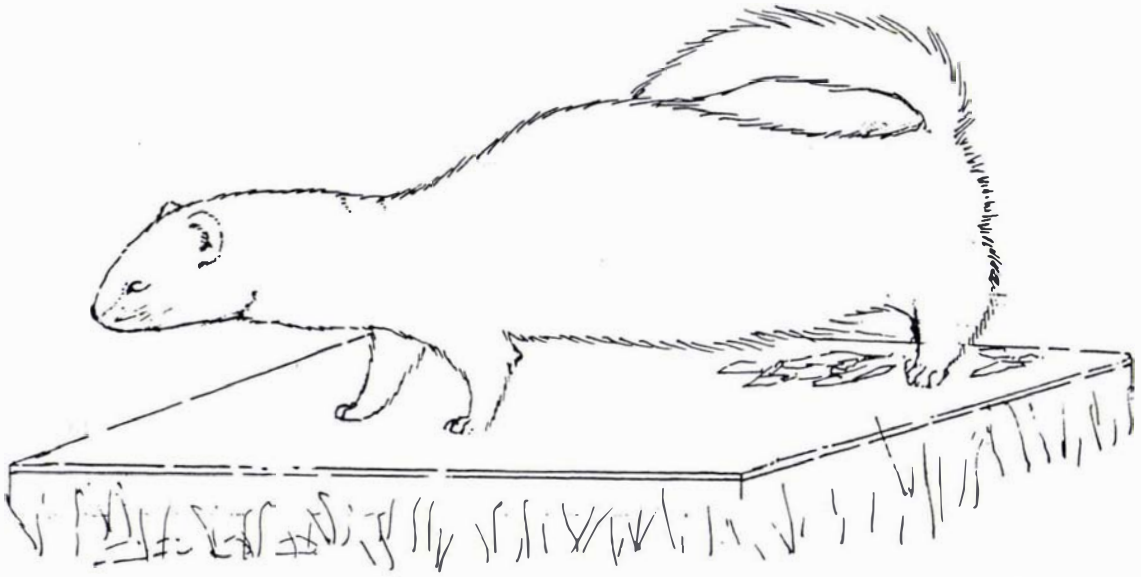
(g) Belly crawl

(h) Neck rubbing

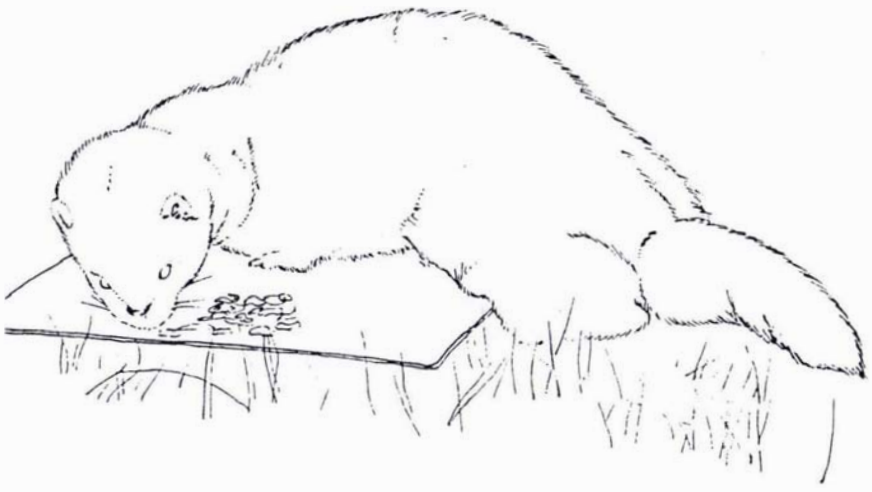
(i) Rolling

(j) Chin rubbing

(a) Defaecation

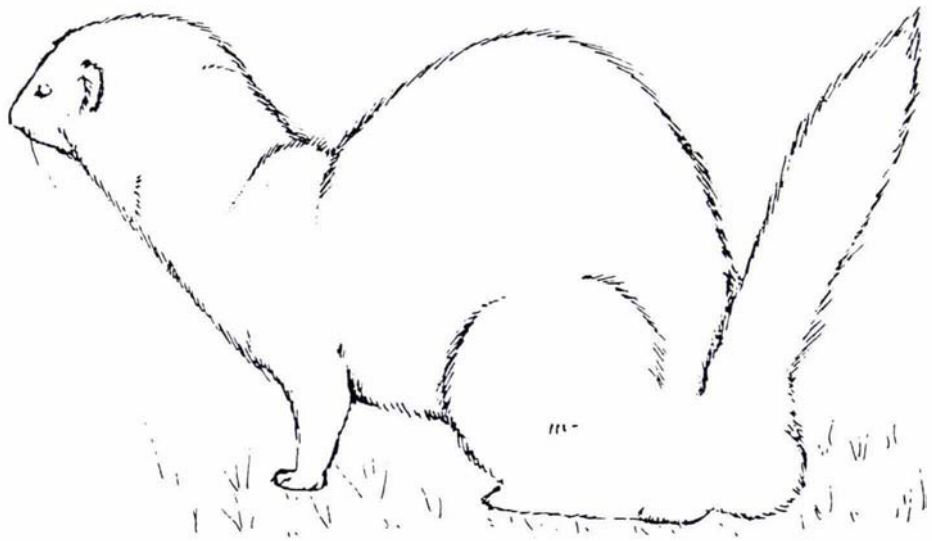


(b) Sniffing at Latrine

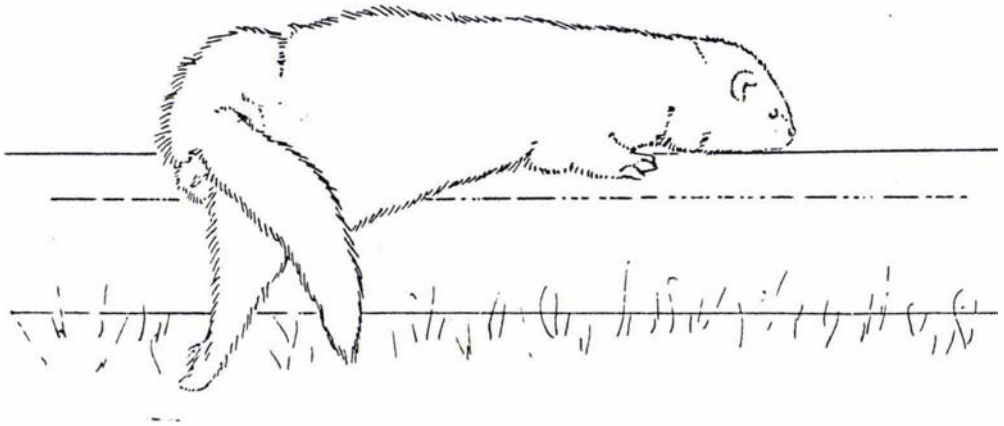


(c) Anal Drag (side view)

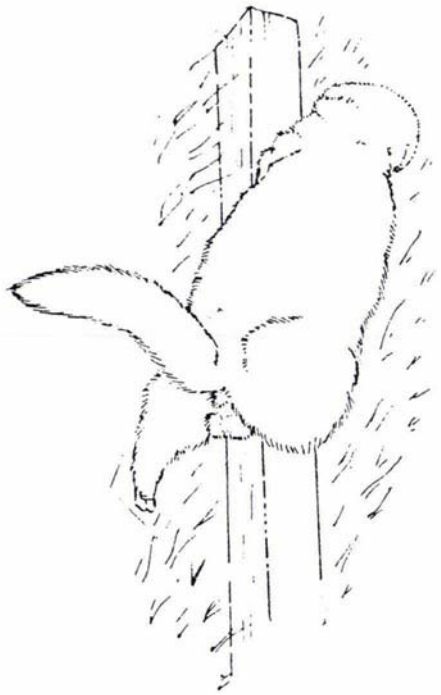
(d) Anal Drag (posterior view)



(e) Wiping (side view)

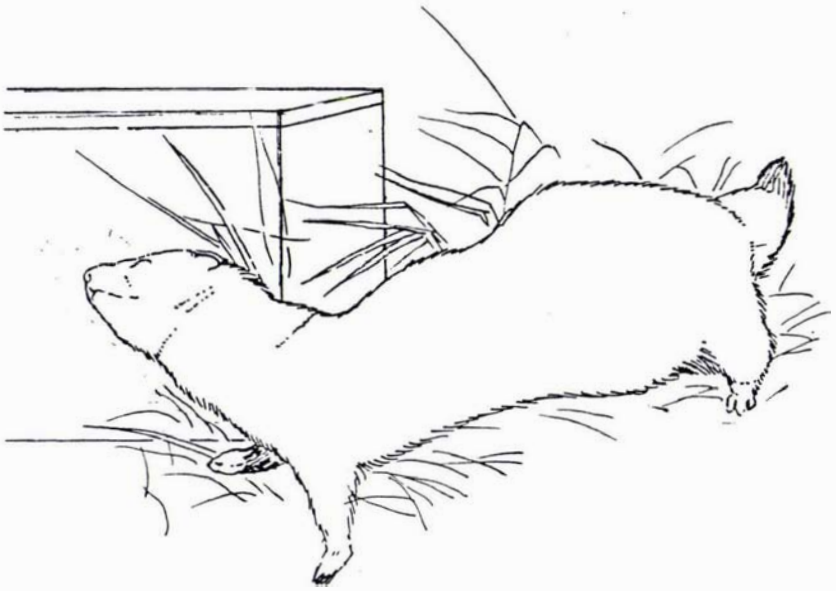


(f) Wiping (posterior view)

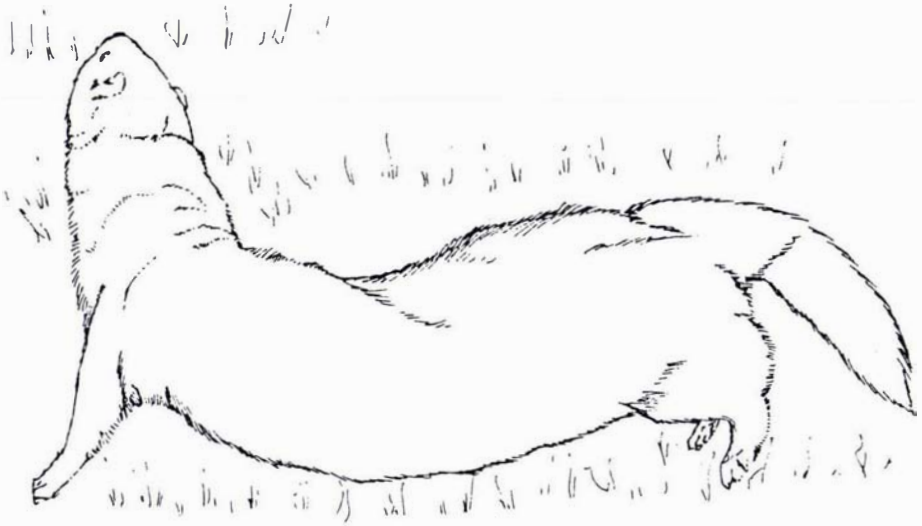


(g) Belly Crawl

(h) Neck Rubbing



(i) Rolling



(j) Chin Rubbing

The ferrets regularly visited the nest box lid latrines at the beginning and/or end of an activity period. A visit sometimes involved just sniffing at the latrine (Fig. 2.2b), with faeces not being deposited at every visit. Hans almost always sniffed at one of his latrines after interactions with Snark at the dividing fence during spring. When the animals were allowed into their neighbours' side of the enclosure, they would frequently sniff at the latrines there, but seldom defaecated there themselves.

2.3.2.2 Anal Drag

This action involved the pelvis being depressed so that the anus touched the substrate as the animal walked forward, making side to side wriggling movements of its hindquarters (Fig. 2.2c,d). The tail was raised and curled over the back. Anal drags occurred while the animal was moving away from a latrine, and seldom occurred separate from the act of defaecation. They usually lasted for less than half a metre, but occasionally the animal continued the anal drag for up to two metres. Males and females performed anal drags at similar frequencies, and the overall frequency of anal dragging did not vary with season, nor was there a significant sex and season interaction (Fig. 2.3a). This remains true if anal drags are expressed as proportions of observed defaecations.

Overall numbers of anal drags observed were significantly greater in the central than in the boundary region of the enclosure ($P \leqslant 0.001$, Fig. 2.3b), but anal drags occurred in C and B at equal numbers per time spent in those regions (Fig. 2.3c). There was no difference in the distributions of anal drags of males and females. There was a significant difference between males' and females' changes in distribution of anal drags with season ($P \leqslant 0.005$), but neither sex showed a regular pattern of change.

Insufficient numbers of defaecations and anal drags were observed for Snark and Chico to provide information on any relationship between rates of performing anal drags and dominance status. These two males used latrines out of sight, in nest box entrances.

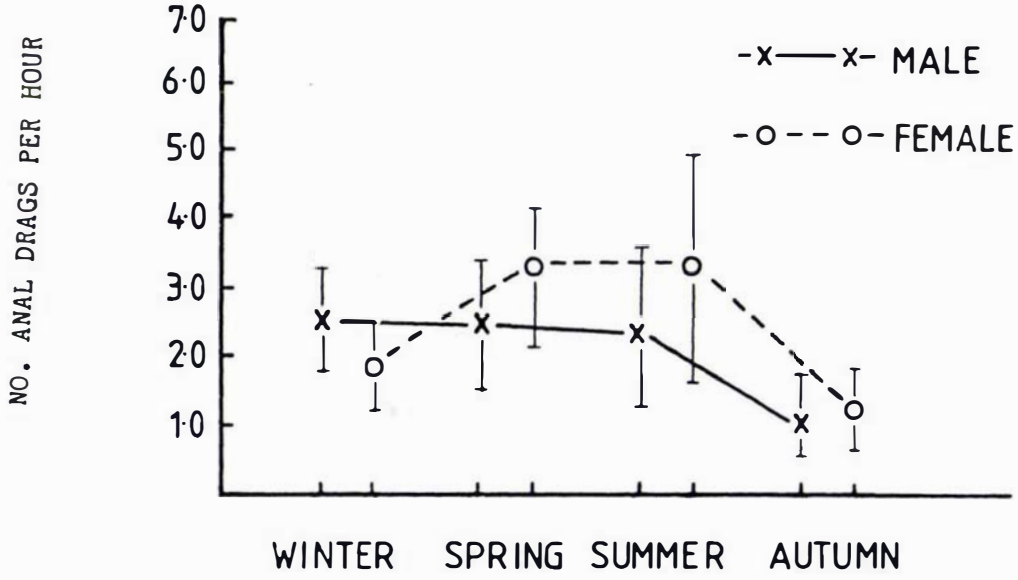
Figure 2.3: Frequencies of observed anal drags. Data are untransformed means ±SE.

(a) Seasonal changes in number per total hours of observation on each animal (n=4 for each sex, except for spring where n=3 for females).

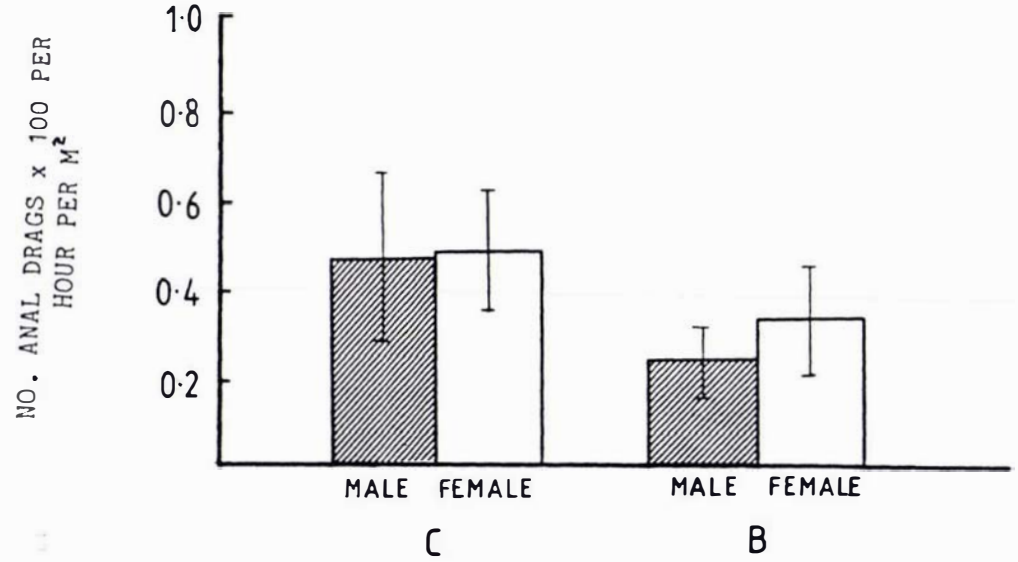
(b) Number of anal drags observed in the two regions per total hours of observation on each animal per area of each region (n=6 for each sex).

(c) Number of anal drags observed in the two regions per hours in that region per area (n=6 for each sex).

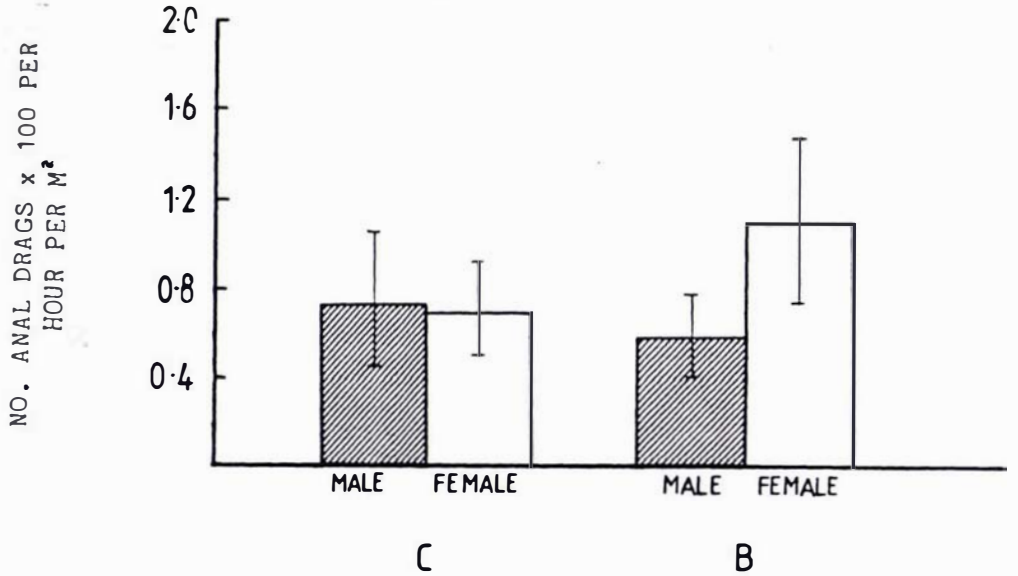
(a)


NO. ANAL DRAGS PER HOUR
7·0
6·0
5·0
4·0
3·0
2·0
1·0
-x—x- MALE
-o--o- FEMALE
WINTER SPRING SUMMER AUTUMN

(b)


NO. ANAL DRAGS x 100 PER HOUR PER M²
1·0
0·8
0·6
0·4
0·2
MALE FEMALE
MALE FEMALE
C
B

(c)


NO. ANAL DRAGS x 100 PER HOUR PER M²
2·0
1·6
1·2
0·8
0·4
MALE FEMALE
MALE FEMALE
C
B

2.3.2.3 Wiping

This category includes two actions that place the ventral body surface on the substrate: wiping and belly crawl. Males often wiped the urogenital region against objects in an obvious manner as they walked over them, sometimes raising one leg, and with the tail raised (Fig. 2.2e,f). Logs, nest box lids and lengths of piping were favourite objects for wiping. It was often accompanied by urination, and also occasionally occurred not on any particular object, but by the animal slipping down onto one haunch while walking, pressing the urogenital region on the ground. The anal region did not touch the ground during wiping by males (Fig. 2.2e,f). Females showed a similar wiping action in which the vulva was pressed on objects. It was never clear during female wiping whether or not the anus was touching the substrate. Wiping sites would often be sniffed at by the scent marker and by other ferrets. When males were allowed into their neighbours' side of the enclosure the dominant males would sniff and then wipe over the wiping sites of their neighbour. Subordinate males would usually just sniff at the dominant's wiping sites.

Belly crawl was performed by lowering the chest region onto the ground, and pushing forward with the back legs until all the ventral body surface, including the urogenital region, was flattened on the ground, and the back legs were splayed out either side (Fig. 2.2g). The animal would then slide further forwards by using wriggling movements, and paddling with the front legs. Because this action pressed the urogenital region onto the ground, and occurred in similar situations to abdomen wiping, data on belly crawl was combined with that of wiping for quantitative analysis.

Males engaged in significantly more wiping and crawling than females ($P \leq 0.01$). Males wiped/crawled more in spring than in any other season, while wiping/crawling behaviour of females remained at a low rate in all seasons ($P \leq 0.004$, Fig.2.4a). There was no significant difference in the frequency of these actions in the two regions of the enclosure, by males, females or all animals combined, neither per total hours observed (Fig. 2.4b), nor per time spent in each region (Fig. 2.4c). Dominant males Snark and Ras did more wiping and crawling than subordinate Hans and Chico, while Bilbo did more than Malli (Table 2.1).

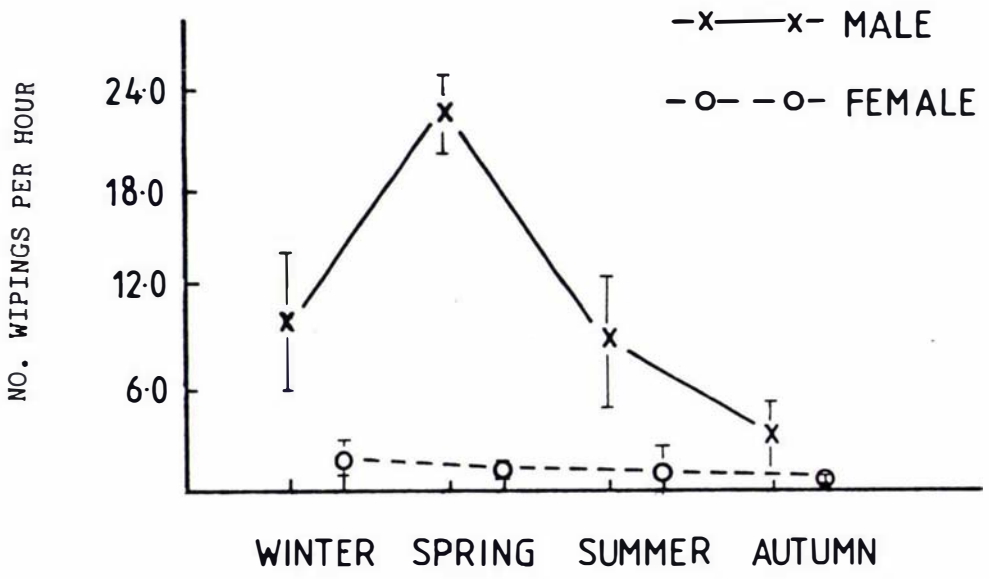
Figure 2.4: Frequencies of observed wipings. Data are untransformed means ±SE.

(a) Seasonal changes in number per total hours of observation on each animal (n=4 for each sex, except for spring where n=3 for females).

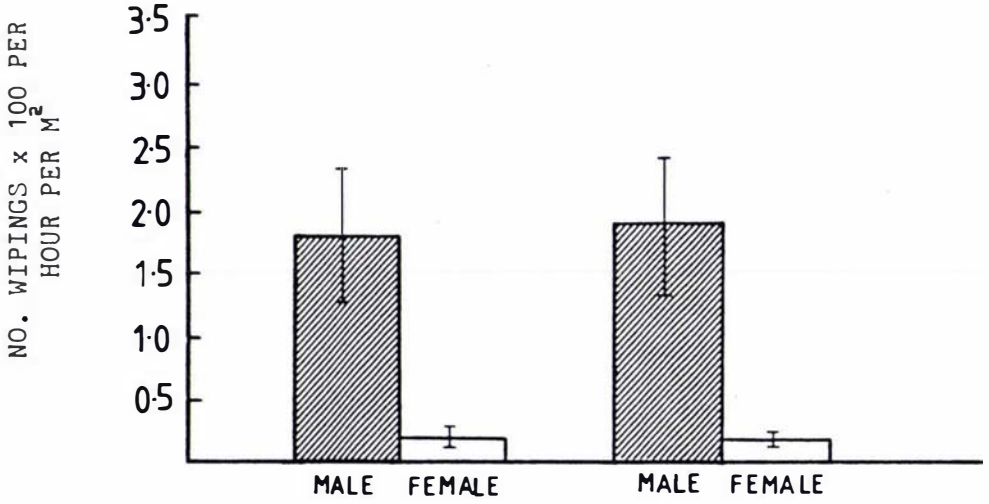
(b) Number of wipings observed in the two regions per total hours of observation on each animal per area of each region (n=6 for each sex).

(c) Number of wipings observed in the two regions per hours in that region per area (n=6 for each sex).

(a)


—x——x— MALE
—o— —o— FEMALE
NO. WIPINGS PER HOUR
24·0
18·0
12·0
6·0
WINTER SPRING SUMMER AUTUMN

(b)


NO. WIPINGS x 100 PER HOUR PER M²
3·5
3·0
2·5
2·0
1·5
1·0
0·5
MALE FEMALE
MALE FEMALE
C
B

(c)

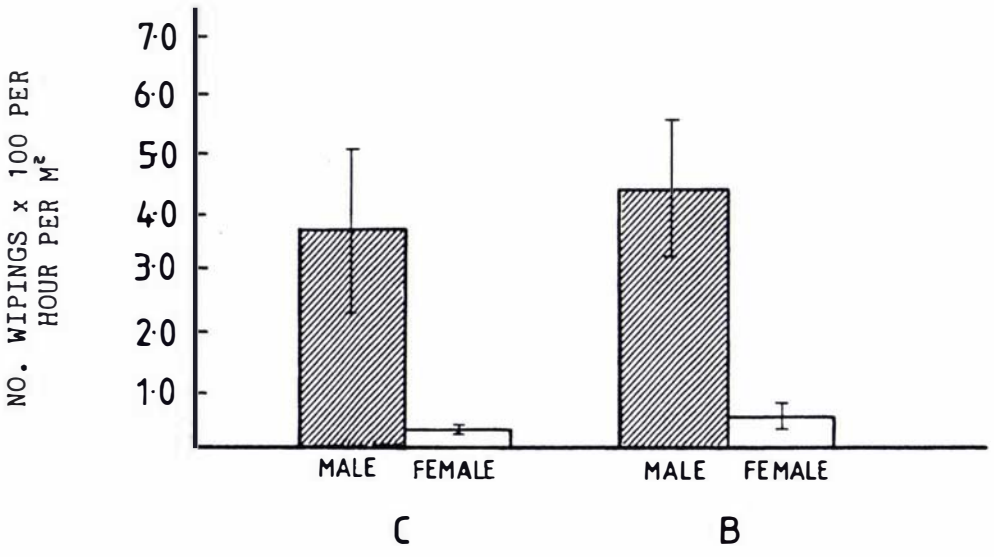

NO. WIPINGS x 100 PER HOUR PER M²
7·0
6·0
5·0
4·0
3·0
2·0
1·0
MALE FEMALE
MALE FEMALE
C
B

TABLE 2.1

Rates of scent marking per total hours of observation on each animal for each pair of neighbouring males.

	WIPING	BODY RUBBING	CHIN RUBBING
SNARK (dominant)	16.90	14.11	3.70
HANS (subordinate)	8.50	6.60	4.58
BILBO (dominant)	15.07	1.71	0.57
MALLI (subordinate*)	12.44	8.93	6.40
RAS (dominant)	4.25	0.00	1.03
CHICO (subordinate)	1.42	0.00	0.83

* Malli was equally dominant to Bilbo early in the observation hours, but lost encounters after he lost both his upper canine teeth.

2.3.2.4 Body Rubbing

This category includes neck rubbing, side rubbing and rolling. Neck rubbing involved the dorsal surface of the neck being rubbed backwards and forwards usually on upright objects (Fig. 2.2h). During side rubbing the cheek, and then the flank was rubbed on the ground. This often developed into rolling, in which the animal rubbed first one side and then the other on the ground, rolling from one to the other with the dorsal surface touching the substrate (Fig. 2.2i). There was no significant difference in mean rates of body rubbing between the two sexes. Some males frequently body rubbed, while others did none, and females seldom did any body rubbing at all. The males that did little or no body rubbing wiped in situations where the other males body rubbed, whereas females did neither. When body rubbing and wiping data are combined, males marked significantly more than females ($P \leq 0.017$). As in wiping, there was a significant sex/season interaction in rates of body rubbing, with males doing much more in spring than in other seasons, while females showed no peak in body rubbing ($P \leq 0.001$, Fig. 2.5a). There was also a very significant difference in the frequency of body rubbing between the two regions, with body rubbing occurring more frequently in B than in C, both in rate per total hours

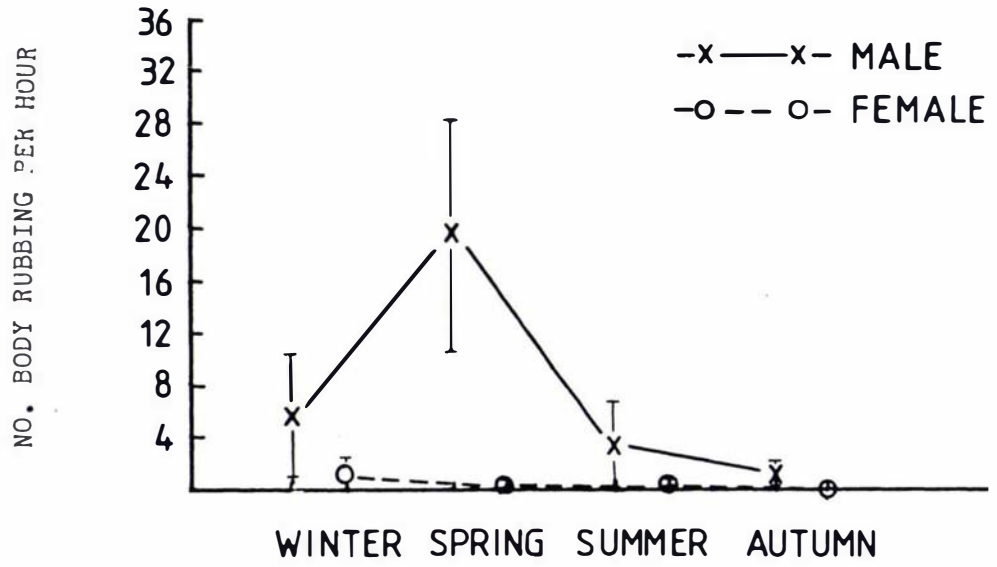
Figure 2.5: Frequencies of observed body rubbings. Data are untransformed means ±SE.

(a) Seasonal changes in number per total hours of observation on each animal (n=4 for each sex, except for spring where n=3 for females).

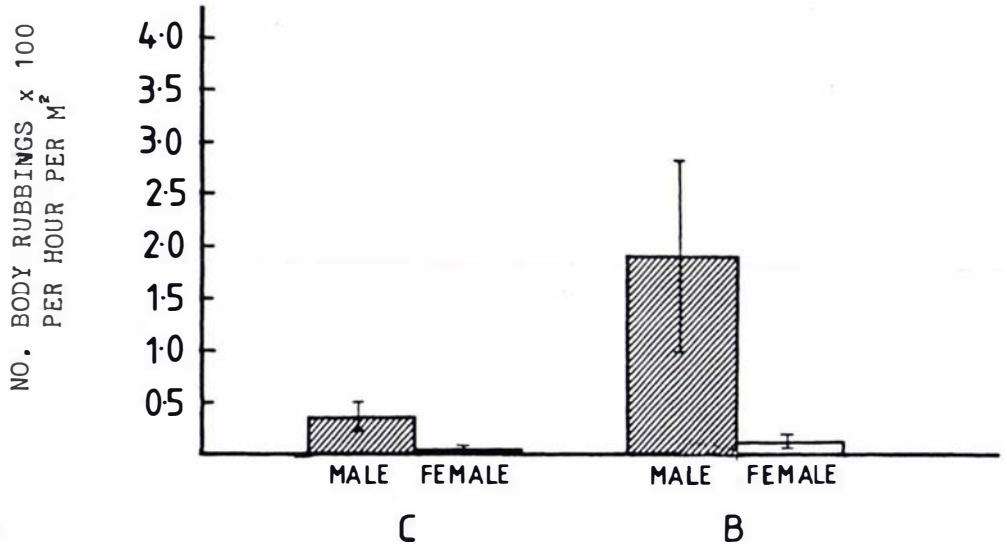
(b) Number of body rubbings observed in the two regions per total hours of observation on each animal per area of each region (n=6 for each sex).

(c) Number of body rubbings observed in the two regions per hours in each region per area (n=6 for each sex).

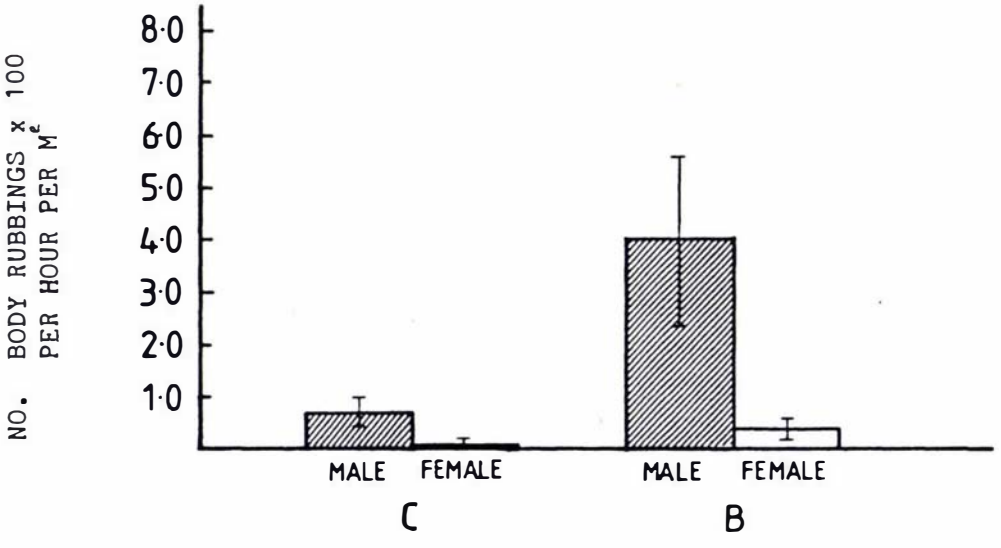
(a)


NO. BODY RUBBING PER HOUR
36
32
28
24
20
16
12
8
4
-x——x- MALE
-o-- o- FEMALE
WINTER SPRING SUMMER AUTUMN

(b)


NO. BODY RUBBINGS x 100
PER HOUR PER M²
4·0
3·5
3·0
2·5
2·0
1·5
1·0
0·5
MALE FEMALE
MALE FEMALE
C
B

(c)


NO. BODY RUBBINGS x 100
PER HOUR PER M²
8·0
7·0
6·0
5·0
4·0
3·0
2·0
1·0
MALE FEMALE
MALE FEMALE
C
B

observed ($P \leq 0.002$, Fig. 2.5b), and in rate per time spent in each region ($P \leq 0.001$, Fig. 2.5c). Dominant male Snark did more body rubbing than his subordinate neighbour Hans, while Malli did more body rubbing than Bilbo, and neither Ras nor Chico (observed only in summer and autumn) did any body rubbing (Table 2.1).

2.3.2.5 Chin Rubbing

During chin rubbing, the chin was moved backwards and forwards on the substrate (Fig. 2.2j). This sometimes developed into a belly crawl. Male and female frequencies of chin rubbing did not vary significantly, and there was a significant increase in frequency of chin rubbing in spring and summer ($P \leq 0.003$, Fig. 2.6a). Snark and Hans did similar amounts of chin rubbing, as did Ras and Chico, while Malli did more than Bilbo (Table 2.1). Chin rubbing occurred more frequently in the central region than in the boundary region, both per total hours observed and per hours in each region ($P \leq 0.001$, Fig. 2.6b,c). The ferrets were usually fed in C, and a large proportion of chin rubbing events occurred at feeding sites, or at nest box entrances after food had been stored inside (232 at food sites out of a total of 364 observed chin rubs). This can be compared to belly crawl, the next most common scent marking action at food sites, which occurred at food sites only 32 times out of a total observed of 328. There was a significant lack of independence between the type of scent marking (chin rubbing or belly crawl) and site (food site or non-food site, $\chi^2 = 213.1$, $P \leq 0.001$). Chin rubbing usually occurred when the scent marker was leaving a fresh feeding site, or had just deposited food in a nest box and was leaving it.

2.3.3 Avoidance Experiment

Over the 22 days that nest box occupancy was noted when all four animals had access to the whole enclosure, males Ras and Chico were found together only twice, both times near the end of the sampling period (Table 2.2). The animals were usually in male/female pairs but three times the females were together with one male. In both trials with Ras removed and his fresh anal gland odour at one of the latrines, Chico entered the nearby nest box, but on both occasions he did not first sniff the latrine. Both times he later sniffed at the latrine, then sniffed in the nest box entrance but did not enter it. The day after the first trial, however, Chico was in that nest box.

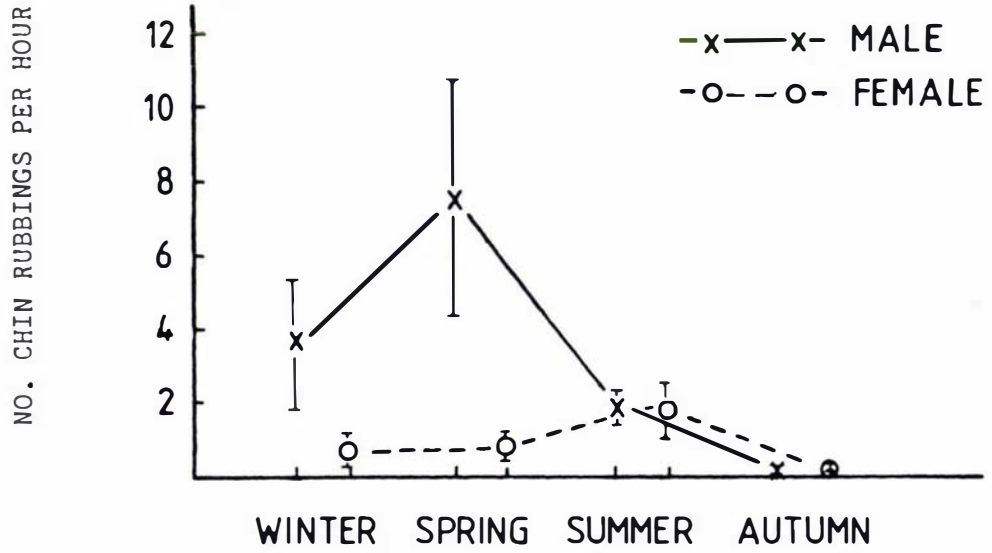
Figure 2.6: Frequencies of observed chin rubbings. Data are untransformed means ±SE.

(a) Seasonal changes in number per total hours of observation on each animal (n=4 for each sex, except for spring where n=3 for females).

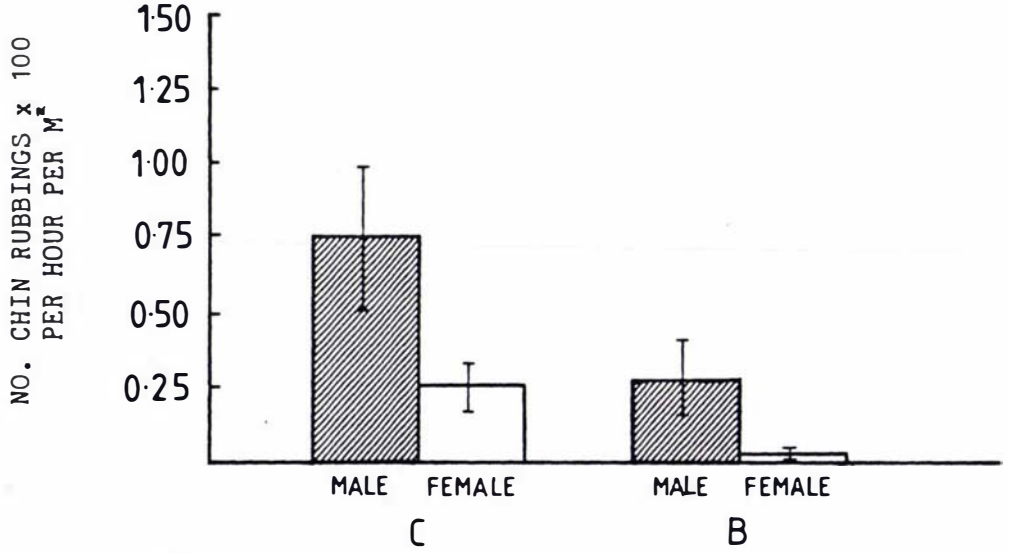
(b) Number of chin rubbings observed in the two regions per total hours of observation on each animal per area of each region (n=6 for each sex).

(c) Number of chin rubbings observedin the two regions per hours in that region per area (n=6 for each sex).

(a)


NO. CHIN RUBBINGS PER HOUR
12
10
8
6
4
2
-x—x- MALE
-o--o- FEMALE
WINTER SPRING SUMMER AUTUMN

(b)


NO. CHIN RUBBINGS x 100 PER HOUR PER M²
1·50
1·25
1·00
0·75
0·50
0·25
MALE FEMALE
MALE FEMALE
C
B

(c)

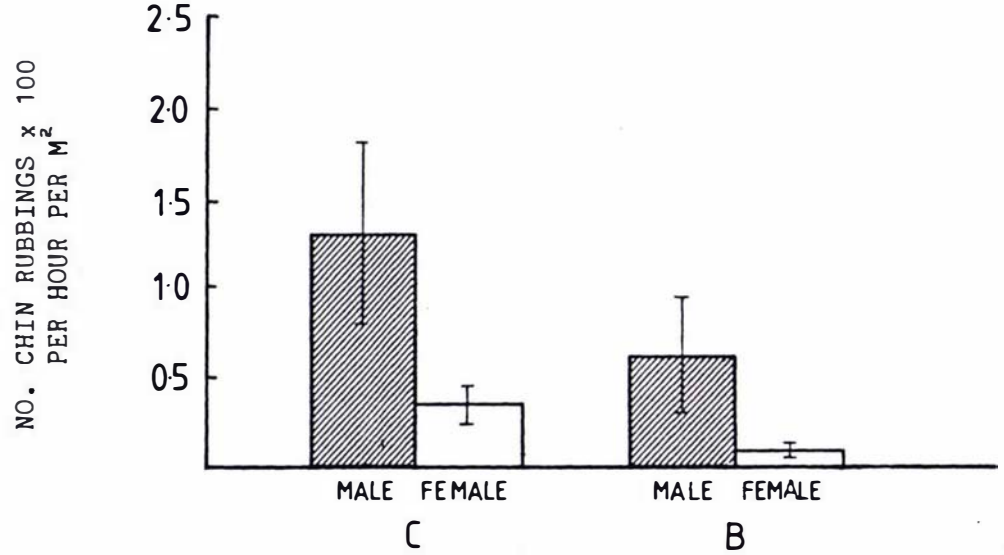

NO. CHIN RUBBINGS x 100 PER HOUR PER M²
2·5
2·0
1·5
1·0
0·5
MALE FEMALE
MALE FEMALE
C
B

TABLE 2.2

Nest box occupancy when all four ferrets had access to all four nest boxes during the avoidance experiment.

DAY	RAS	CHICO	SWUZZLE	TITI
1	2	1	1	3
2	2	1	2	3
3	4	2	2	4
4	1	2	2	3
5	2	4	2	2
6	2	4	2	1
7	2	1	4	2
8	4	2	2	1
9	4	2	2	4
10	4	1	2	?
11	4	1	1	4
12	3	1	1	3
13	1	2	1	1
14	4	1	1	4
15	1	2	2	1
16	1	2	1	2
17	2	2	2	1
18	1	2	2	1
19	1	2	1	4
20	1	2	2	1
21	2	1	2	2
22	1	1	2	1

2.4 DISCUSSION

This study of wild ferrets in semi-natural conditions, involving observations of fine details of scent marking behaviour over a long time span, has allowed the description of a repertoire of scent marking actions and associated behaviour. The anal sniffing behaviour on meeting may allow ferrets to identify each other, and may allow them to match the odour of the animal with those of nearby anal drag scent marks. This anal sniffing has also been observed in ferrets and polecats by Poole (1967), prior to fighting, especially in the non-breeding season when males engaged mainly in ritual aggression. He noted that it was the ferret resident in an experimental arena which initiated anal sniffing and also "neck nuzzling" of an intruder.

The placing of faeces, urine and anal gland secretion as latrines produces strong olfactory beacons. Ferret latrines have been found in the wild (Gibb et al. 1978, R.J. Pierce pers. comm.), often near den entrances. They do not, therefore, appear to be an artefact of this captive situation.

The anal drag action described here appears to be the action that Goethe (1940) referred to as wiping in the polecat. It is very similar to the anal drag of the stoat (Erlinge et al. 1982), but in the ferret it only occurred at latrines, not on other objects in the environment. Wemmer (1971) described the anal drag of mammals as an "ubiquitous cleaning movement" from which has developed ano-genital scent marking actions. It has never been demonstrated in any mustelid species that anal gland secretion is in fact left on faeces or on the substrate by the anal drag action. By marking the contents of anal sacs with coloured dyes and radio-active material that could be located when laid down in the environment, Asa et al. (1985) showed that wolves leave anal gland secretion at defaecation sites. In minute amounts mustelid anal gland secretion is invisible, but the fact that other ferrets sniff at anal drag sites suggests that some odorous substance is present.

The wiping action described by Eibl-Eibesfeldt (1956) was also seen in this study, but close observations have revealed that in males at least, the anal region does not touch the substrate during wiping,

while the urogenital region does. Anal gland odour may be placed on the skin by grooming actions and thus laid down by wiping and body rubbing, but ferrets appear to have a general body odour that is different from their anal gland odour (pers. obs.). The possibility of the ferret having other odour-producing glands in the urogenital region is investigated in Chapter 3. It is interesting that no similar wiping behaviour was described for the stoat (Erlinge et al. 1982), but the stoat was thought to anal drag in situations where the ferret wiped. No glands in the urogenital region of the stoat have been reported. Belly crawl has been previously described by Poole (1967), who observed it in dominant male polecats and ferrets after fighting in an experimental arena. He did not suggest a scent marking function for this action. Poole (1967) also observed body rubbing actions of ferrets, associated with aggressive interactions and performed by dominant males as was the case in this study. Chin rubbing at food sites has been noticed before (MacDonald 1985), and has been studied in more detail by Wildhaber (1984).

The use of neck and dorso-lateral regions in scent marking during agonistic encounters and in the boundary regions of the enclosure, compared to wiping and belly crawl throughout the enclosure, and chin rubbing's association with food sites, brings up the question of what odours are being laid down by these actions. Histological studies, (see Chapter 3) and chemical studies may provide some information to help determine whether different information is conveyed by the various body rubbing and wiping actions.

The quantitative analysis of scent marking behaviour has provided support for some of the communicative hypotheses outlined in Chapter 1. The fact that anal drags were not concentrated at the boundary of the enclosure suggests that anal gland secretion is not used simply as a keep-out signal to deter intruders. The fact that anal drags were performed by both males and females at similar frequency all year round not only in the breeding season suggests that they function not only in sex attraction. The location of anal drags at latrines that were sited at conspicuous places supports both the territorial defence and sex attraction hypotheses. The sniffing of the anus of conspecifics is also supportive of the sex attractant hypothesis and of the scent matching mechanism for territorial defence. The frequent visits to latrines, with or without

scent marking, suggests that these sites act as information centres, may enhance the territorial confidence of a resident, and inform a resident of the presence of the opposite sex and neighbours in that region of its territory (i.e. supports the sex attraction hypothesis and the neighbour-neighbour recognition system).

The fact that wiping (including belly crawl) and/or body rubbing was done more by males than by females suggests a different function for these types of scent marking from the anal drag. The occurrence of body rubbing, by males during close contact interactions suggests an active role in territorial defence for these scent marking actions. Both body rubbing and wiping peaked in spring, the season when males are most aggressive (pers. obs.), and when results for body rubbing and wiping are combined dominants did more marking than subordinates. Rubbing during agonistic encounters would reinforce their body odour, and may act as a threat signal to intimidate an opponent.

The association of chin rubbing with food sites suggests that odours from the chin could be used as a bookkeeping system as outlined in Hypothesis 3. The fact that chin rubbing occurred when food was present, and most often when leaving stored food, suggests that chin odour could increase the odour output from a food site, allowing its rapid location during later searching. Such an hypothesis requires, however, that odour laid down by chin rubbing is different from that used in all other types of scent marking. Histological and chemical studies are necessary to resolve this question. Marking of fresh food stores was seen in the stoat, which used body rubbing, the same action that was suggested to have a threat significance (Erlinge et al. 1982). Chin rubbing may be just a convenient way of leaving body odour at food sites, which are sites of particular importance in the environment.

The avoidance experiment did not support prediction (e) of the neighbour-neighbour avoidance mechanism of territorial defence (Table 1.1). It gave little support for anal gland odour, on its own, preventing a ferret from entering a nest box. This may have been due, however, to the fact that the experiment was run in the non-breeding season, when, in these confined conditions, the males became tolerant of each other's presence (as indicated by the males' sharing a nest box twice in the last week of the sampling period).

The limitations of this study in terms of numbers of ferrets observed and the area in which they lived makes it difficult to draw conclusions concerning the distribution and frequency of scent marking by free-ranging ferrets. The area of the enclosure was minute compared to the normal home range of a ferret (see section 1.2), but the fact that there were a number of different types of scent marking behaviours observed, with differing spatial and temporal patterns, suggests some reliability to the results. As captivity may affect the rates of scent marking (Ralls 1971), no weight should be placed on the absolute rates of scent marking observed in this study. The fact that males adapted better to captivity (became tamer and more docile) than did females means that the sexual differences in scent marking behaviour may be an artefact of the study conditions. Seasonal changes in rates of scent marking are not so likely to be affected by confinement, and are likely to be a reflection of ferret behaviour in the wild.

Chapter 3
STRUCTURE OF ODOUR-PRODUCING GLANDS

"All exudative processes have been implicated in odour production, and urine and faeces, laced with preputial and anal gland secretions, may be the most important odour vehicles for many species." - Stoddart 1980b

3.1 INTRODUCTION

Before ascribing any meaning to observed scent marking behaviour, it is essential to have a clear understanding of the apparatus an animal has for producing scent. In addition to urine and faeces, mammals possess scent-producing glands in various regions of the body. These are usually integumentary structures, classified into sebaceous (alveolar) glands and tubular (sudoriferous or sweat) glands. Sebaceous glands have a holocrine method of elaboration, with the entire glandular epithelial cells becoming the secretory product (Quay 1977, Banks 1981). Tubular glands can be atrichial (eccrine), their ducts opening directly onto the skin surface, or epitrichial, their ducts opening into hair follicles (Jenkinson et al. 1979). They have a merocrine secretory process, with only secretory products of the cells emptying into the gland lumen. Epitrichial glands are often termed apocrine, as it was once thought that apical cell buds added to the secretion, but this is an artefact due to histological processing (Jenkinson 1967).

Most carnivores possess paired anal sacs, described by Ewer (1973) as "vesicular cutaneous invaginations opening by a short canal or duct one on either side of the anus or just internal to it." These sacs act as reservoirs for secretions produced by aggregations of sebaceous and tubular glands. Anal sacs of the Mustelidae have been described in detail by Stubbe (1969, 1970, 1972). There are few published references to other odour-producing organs in mustelids. Most are listed by Macdonald (1985). The badger has a subcaudal scent pouch that has been studied by Gorman et al. (1984). Abdominal skin glands have been found in the American badger, Taxidea taxus, (Pocock 1920, 1925) and marten species (Hall 1926, Herman and Fuller 1974). Such a gland is also present in the wolverine, but was not recorded following examination of dried skins of Mustela vison, M. longicauda and M.

arizonensis (Hall 1926). Krott (1959) suggested that for Martes sp. it was not anal but pregenital gland odour which was used for scent marking. Frank (1962) assumed that the weasel had glands in the genital region, but none has been described.

During observations on scent marking behaviour in ferrets (see Chapter 2), it became evident that it was not the anal region but the ventral abdomen that was touching the substrate while performing wiping. It was not likely to be secretions from the anal sacs being laid down by this action as reported by Eibl-Eibesfeldt (1956) for polecats. Anatomical and histological studies were needed to find out if the ferret has any form of gland on the ventral abdomen that could be the source of odour laid down by wiping.

Stubbe (1969) thought that all mustelids probably had glands on the sole of the foot that were used as marking organs, but gave no description of these. Most carnivores have atrichial sweat glands in the footpads, but these have not been implicated in odour production (Banks 1981). Histological investigation of the ferret's foot may reveal whether or not this species has odour-producing foot glands.

Skin glands are well developed in nocturnal species for which odours are of particular importance in communication (Mykytowycz 1970, Müller-Schwarze 1983). Yamaji et al. (1981) have described the histochemical characteristics of dermal sebaceous and sweat glands of the Siberian weasel (Mustela sibirica). Erlinge et al. (1982) described body rubbing behaviour of the stoat and assumed this was a form of marking with scent. Ferrets show similar rubbing behaviour but use different parts of the body for rubbing in different contexts (see Chapter 2). The question therefore arises as to whether the ferret has specialised skin glands where odours may be produced. This could allow different information to be conveyed by different rubbing actions. To answer this question, the regions of the body used in rubbing should be examined.

In this chapter the structure of potential odour-producing organs of the ferret are identified and described. This information will help with the interpretation of the observed scent marking behaviour of this species.

3.2 METHODS

The external skin of numerous male and female ferrets was examined for any sign of glandular structures, particularly in the abdomen. Fifteen male and 13 female specimens were weighed, their anal sacs removed, cleared of fat material and weighed. General dissections were made of five male and four female ferrets. Some were frozen specimens, caught and killed by N.Z. Wildlife Service personnel at Pukepuke Lagoon or in the Mackenzie Basin, or fresh road-kill animals, and others were caught at Pukepuke Lagoon and killed just prior to examination. Samples of tissues from the anus and prepuce or vulva of five males and four females and skin tissues from the chin, dorsal neck, cheek, ventral and lateral thorax of three of each sex were examined histologically. They were dissected from the animals and long hairs shaved as close to the skin as possible. The tissues were fixed in Bouin's fluid for 24 hours, dehydrated in ethanol, cleared in xylene, and vacuum-embedded in paraffin wax. Sections were cut on a Leitz base sledge microtome at 6µm in thickness and stained in haemotoxylin and eosin. Sections from one male and one female were stained in Van Gieson and alcian blue. The front feet of one male and two females were decalcified in De Cal for 12 hours before vaccuum-embedding, sectioning and staining.

A random sample of thirty cells was taken from the tubular gland tissue of each of the anal and urogenital sections. Cell heights were measured using a micrometer eyepiece at 400x magnification, and mean male and female cell heights calculated.

3.3 RESULTS

3.3.1 Anal Glands and Sacs

In both males and females, there were large paired subcutaneous sacs, one on either side of the anus. The relative weights of the paired anal sacs of males and females were similar, with those of females accounting for the same or a slightly larger proportion of body weight than those of males (Fig. 3.1). These ovoid sacs consisted of a large lumen bordered by a stratified squamous, keratinising epithelium, and were filled with secretions from the anal gland complexes. These gland complexes consisted of both tubular and sebaceous glands (Plate 3.1).

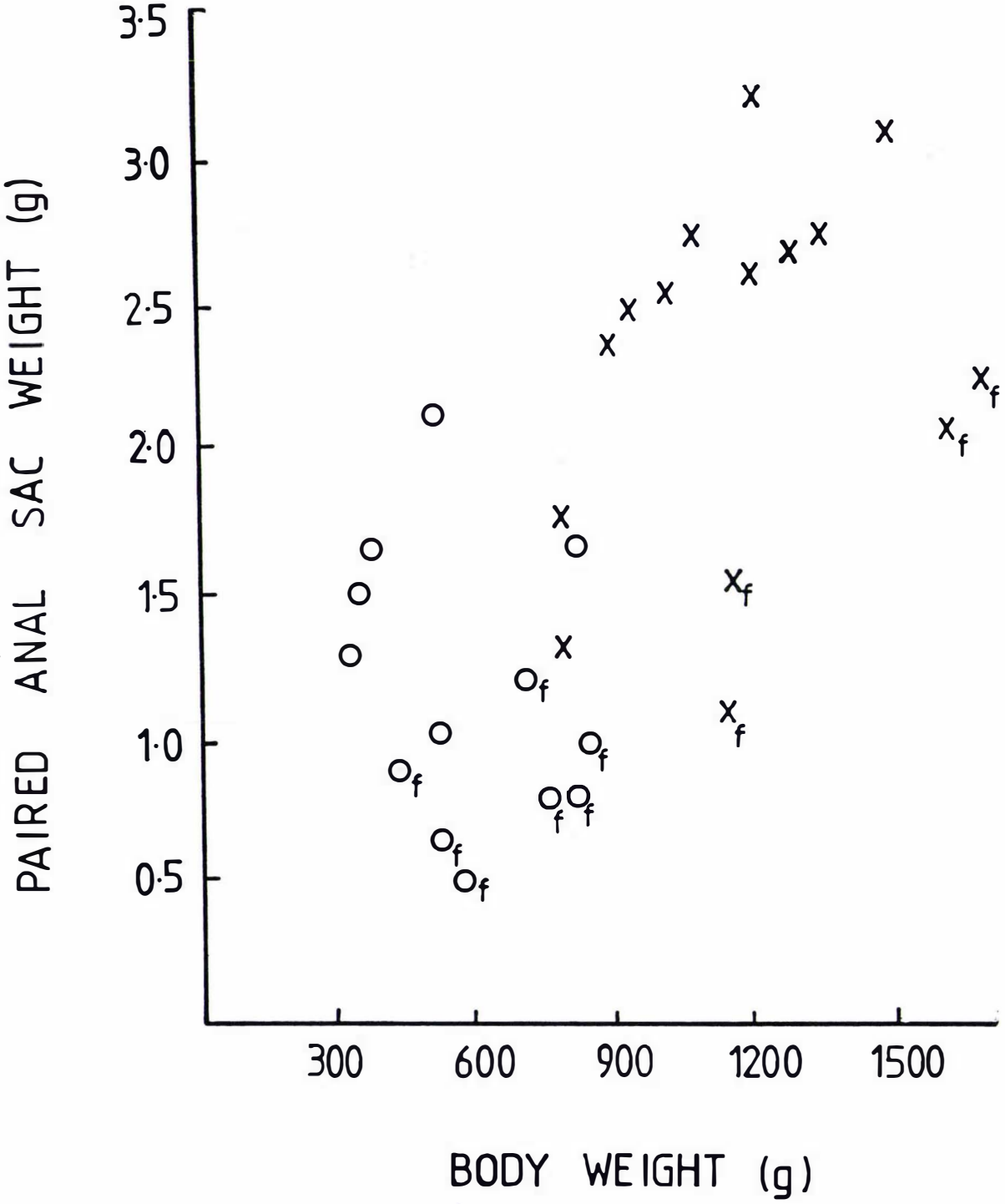
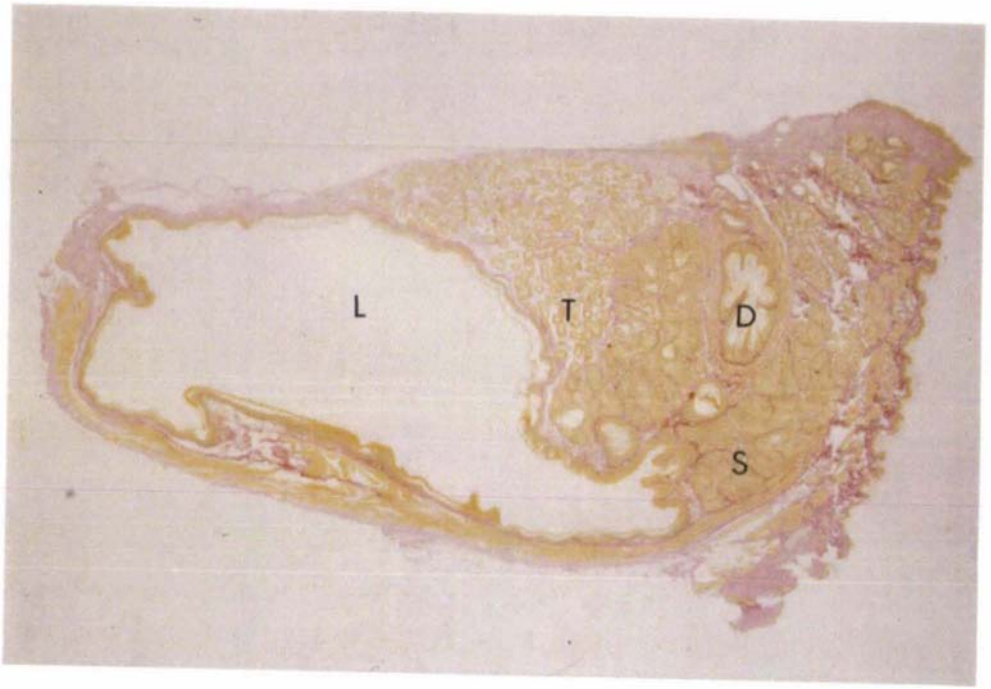


Figure 3.1: Paired anal sac weight as a function of body weight of males (X) and females (O). Some frozen (f) and some fresh samples.

Plate 3.1: Anal sac and glands. D=duct of anal sac, L=lumen of anal sac, S=sebaceous glands, T=tubular glands.


L
T
D
S
3mm

The tubular glands were very extensive and highly coiled, with high epithelial cells (mean cell height: male=17.4 μm, SE=1.18, n=5; female=19.2 μm, SE=4.66, n=2). The glands were clumped around the neck of each sac. The duct of the sac, with a sphincter of skeletal muscle, opened into the anal orifice.

3.3.2 Abdominal Glands

No glandular regions were obvious from examination of the external abdomen. The preputial skin was covered in dark guard hairs, continuous with the dark mid-ventral line of hair. The male prepuce was slightly raised and was a darker purplish-pink colour compared to the surrounding skin. Gentle palpation of the prepuce in live males caused droplets of a clear, sweet-smelling, oily secretion to form on the skin surface. Dissection of the males revealed in each two closely associated areas of pinkish-brown glandular tissue, on average 13.0 mm long (SE=0.147, n=5) by 8.5 mm wide (SE=0.87). They were subcutaneous, lying either side of the urogenital opening (Plate 3.2a,b). Females had two similar glandular regions around the vulva, but they were smaller (mean length=7.4 mm, SE=0.63; width=4.4 mm, SE=0.35, n=4) than in males (Plate 3.2c).

Male tissues contained enlarged compound tubular glands, consisting of low columnar epithelial cells (mean cell height=18.0 μm, SE=1.02, n=5) (Plate 3.3a). The glands appeared to be epitrichial, opening into the upper part of hair follicles of the preputial skin. The lumen contents stained pale pink with eosin, and contained cell debris. Some cells were alcian blue-positive. Much of the female glandular tissue consisted of cuboidal rather than low columnar epithelium (Plate 3.3b), with a mean cell height of 11.9 μm (SE=1.30, n=4). In the two females that were in oestrus, the glandular tissue did not extend into the swollen vulva.

3.3.3 Skin Glands

No complex glands were found in any of the other tissues examined, but all of them contained numerous dermal sebaceous glands and a few tubular glands (Plate 3.4a,b). The sebaceous glands varied qualitatively between the sexes and between the various parts of the body. The secretory cells of male sebaceous glands were more highly vacuolated than in the female glands. Within each sex, the sebaceous

Plate 3.2: Abdominal glands. S=sebaceous glands, T=tubular glands, U=urogenital opening.
(a) Male, longitudinal section.
(b) Male, cross section.
(c) Female, longitudinal section.

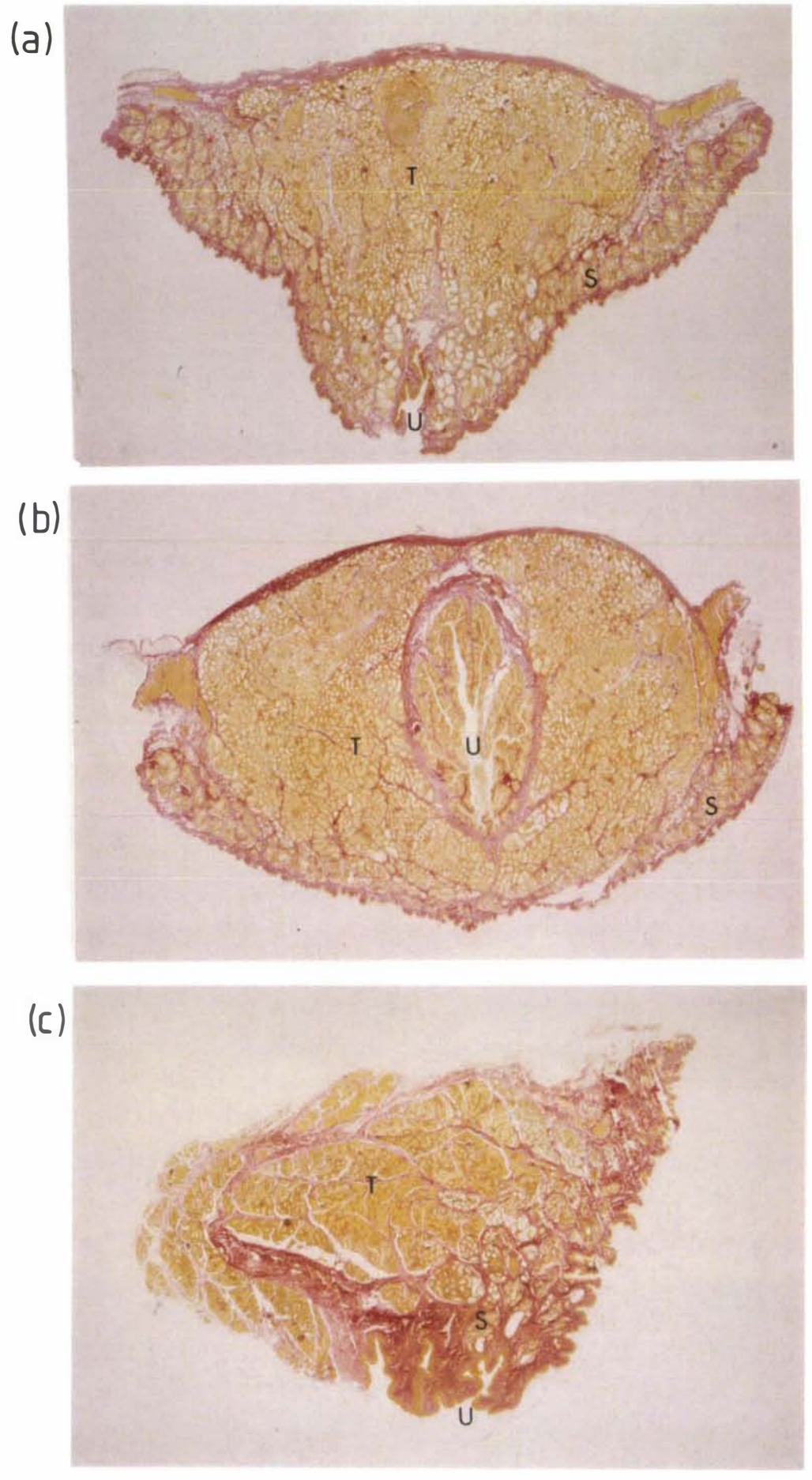
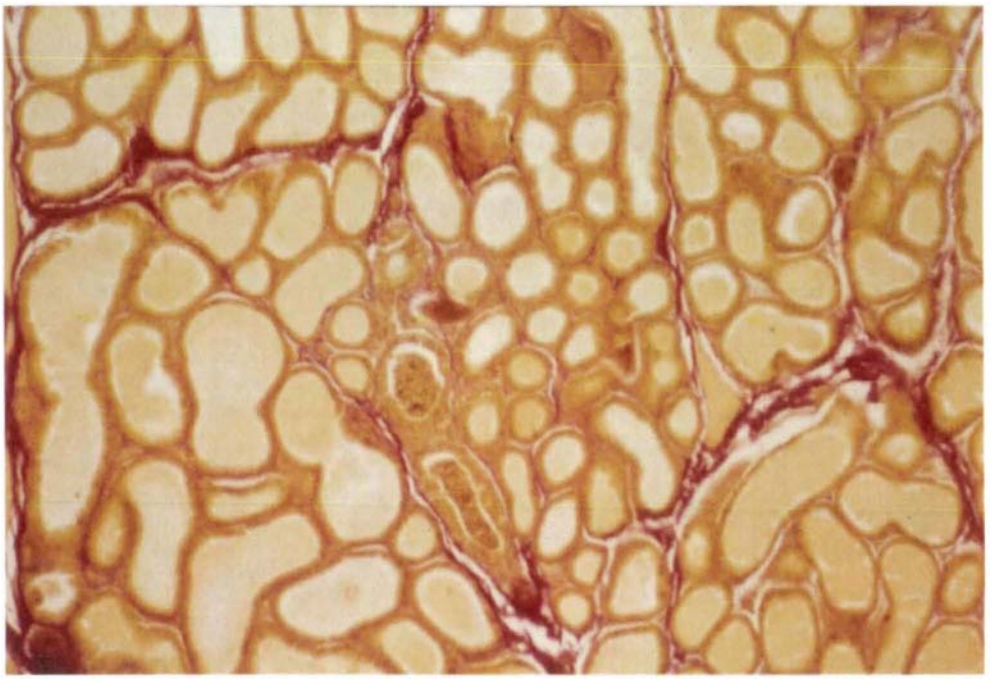

(a)
T
S
U
(b)
T
U
S
(c)
T
S
U
3 mm

Plate 3.3: Epitrichial tubular gland tissue of abdominal glands(x200).
(a) male. (b) female.

(a)



(b)

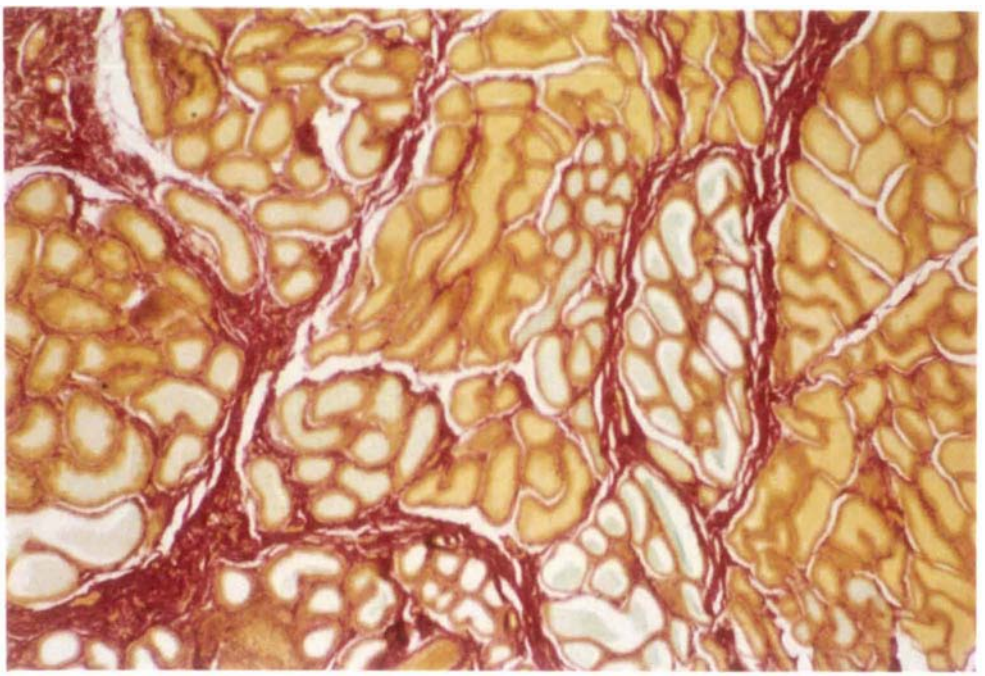
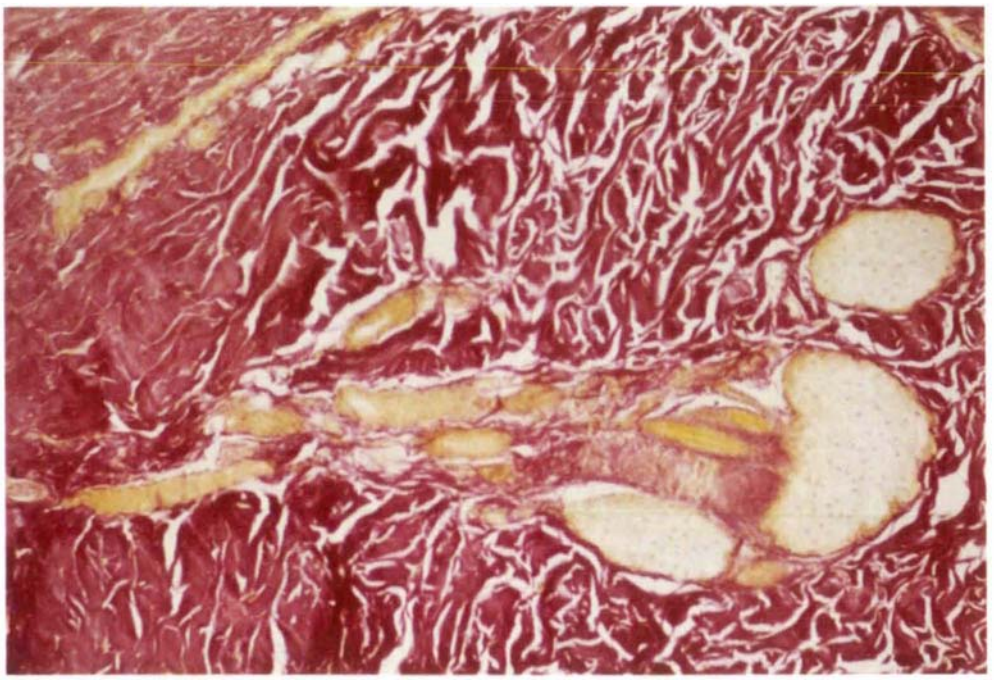


Plate 3.4: Skin glands.

(a) Sebaceous gland (x300).

(b) Epitrichial tubular gland (x700).

(a)



(b)

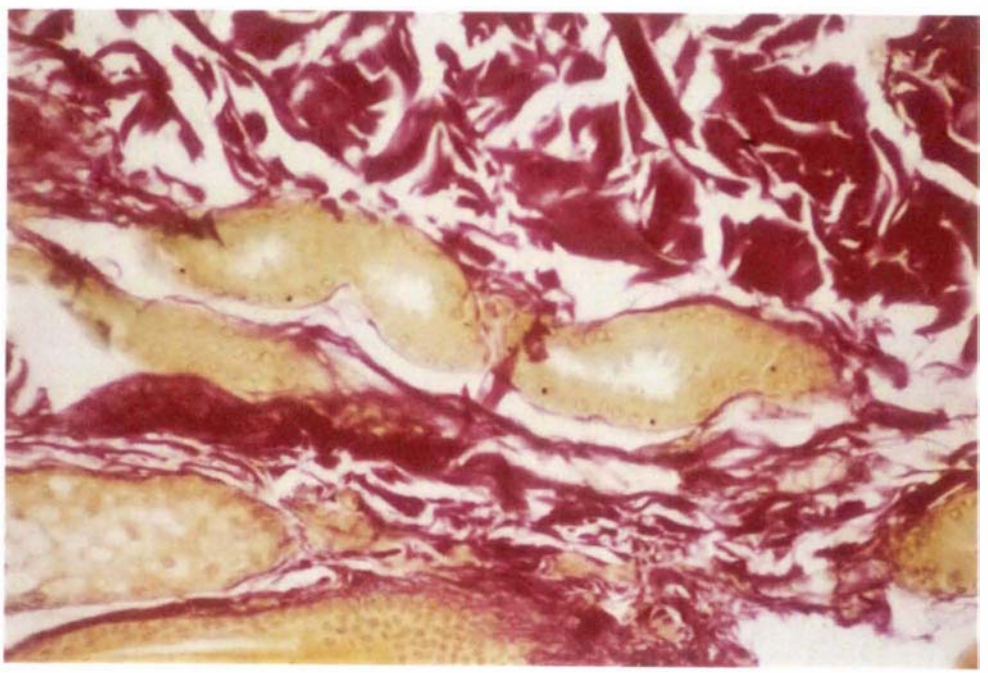
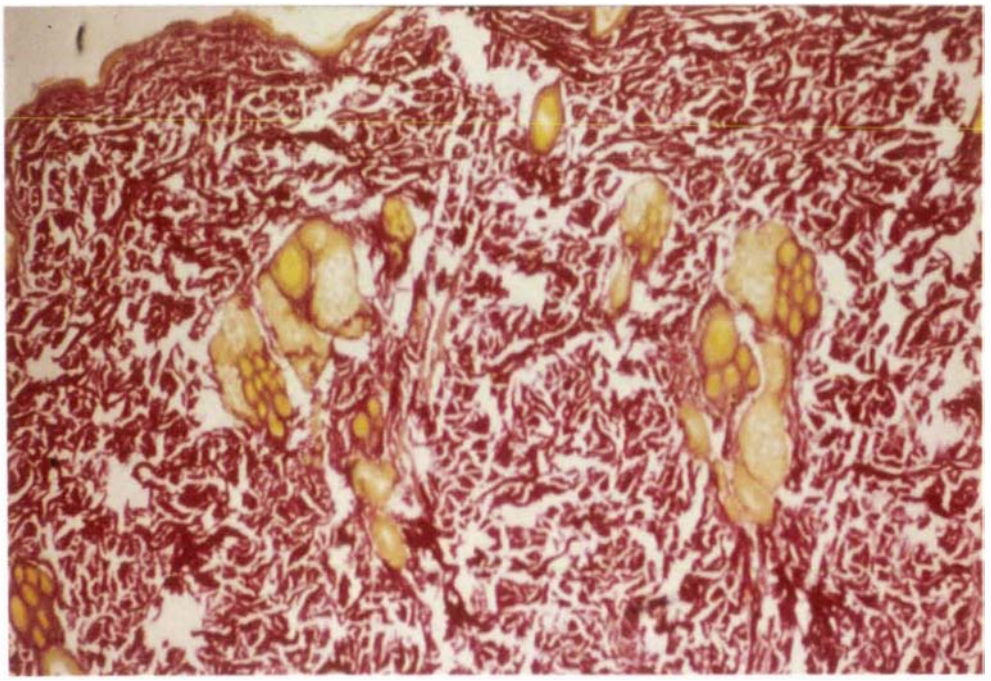


Plate 3.4 (cont'd): Skin glands (x200).

(c) Male dorsal neck.

(d) Female dorsal neck.

(c)



(d)

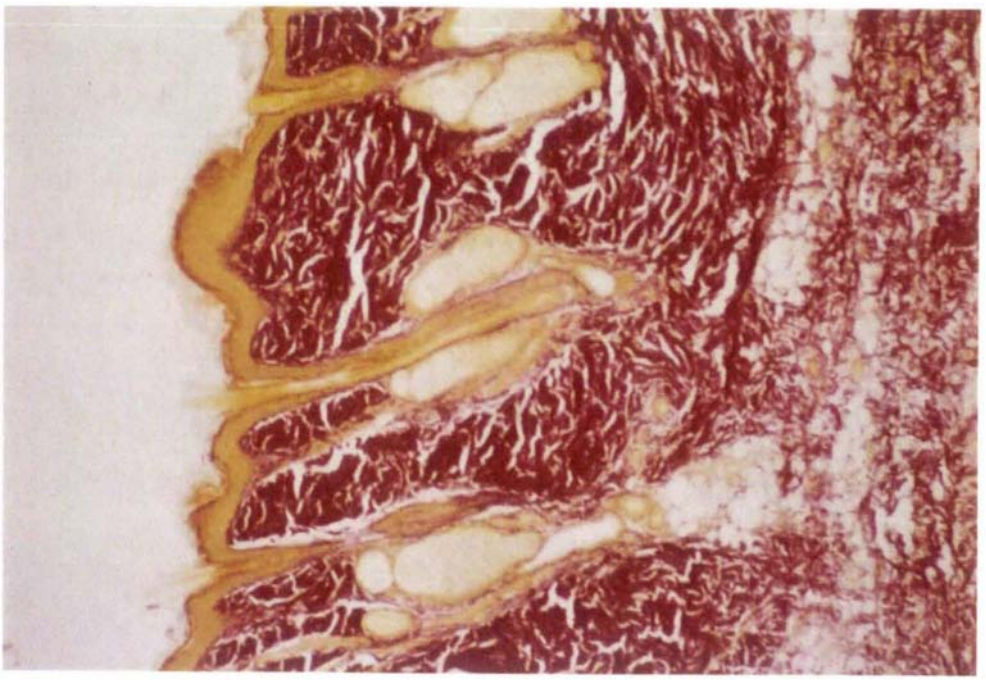
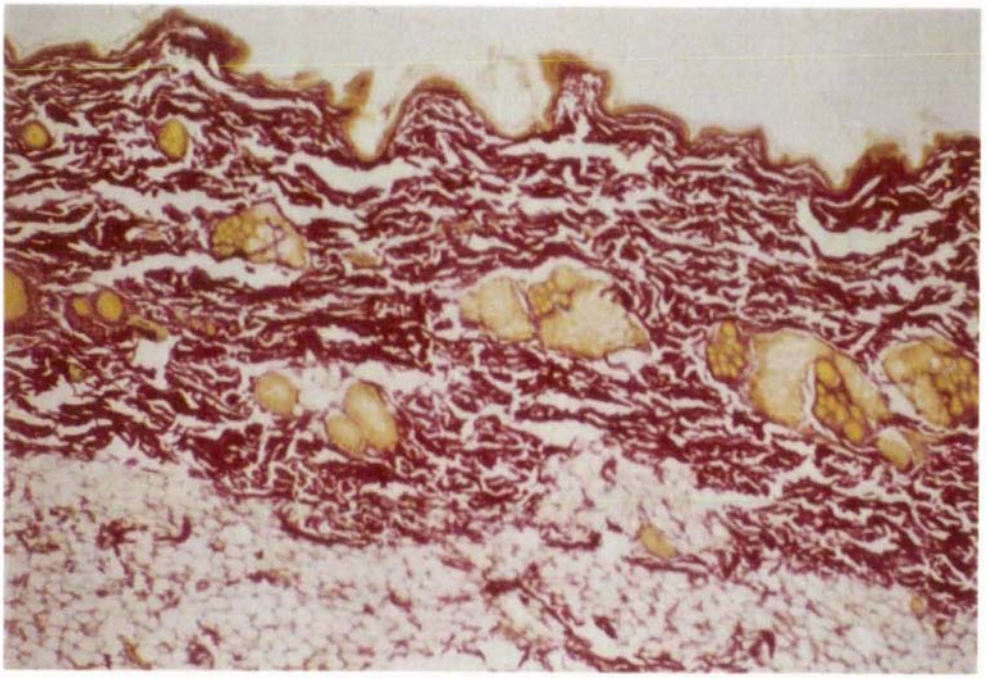


Plate 3.4 (cont'd): Skin glands (x200).

(e) Male lateral rib cage.

(f) Female lateral rib cage.

(e)



(f)

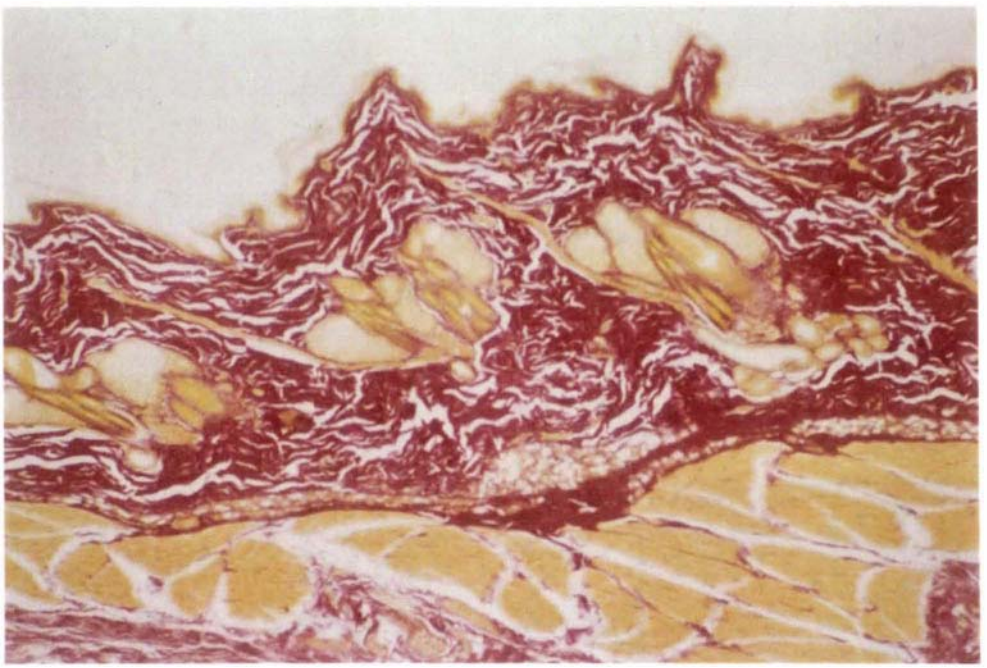
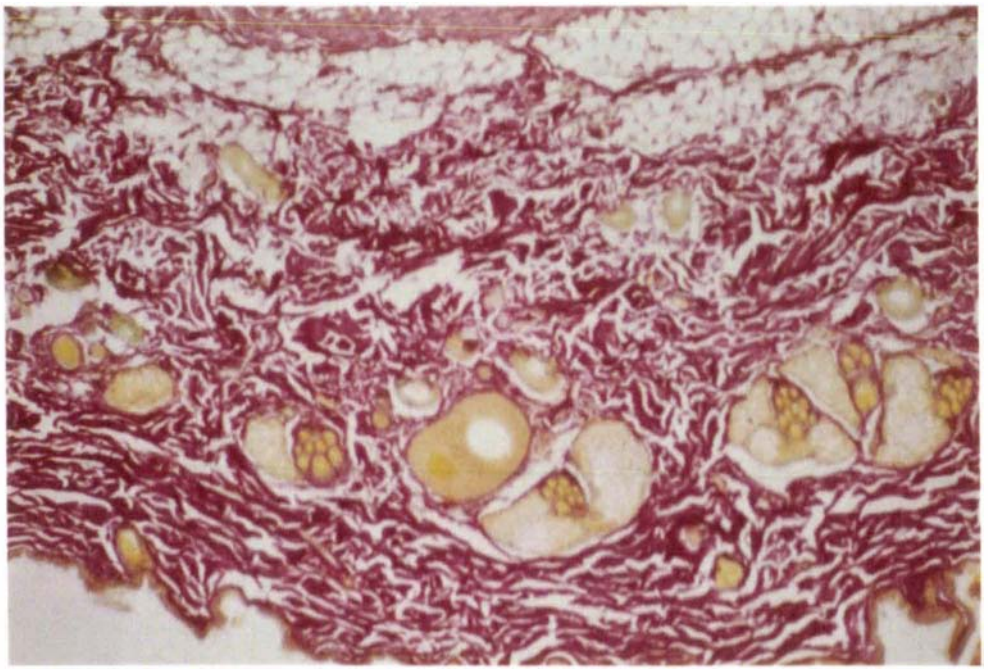


Plate 3.4 (cont'd): Skin glands (x200).

(g) Male ventral rib cage.

(h) Female ventral rib cage.

(g)



(h)

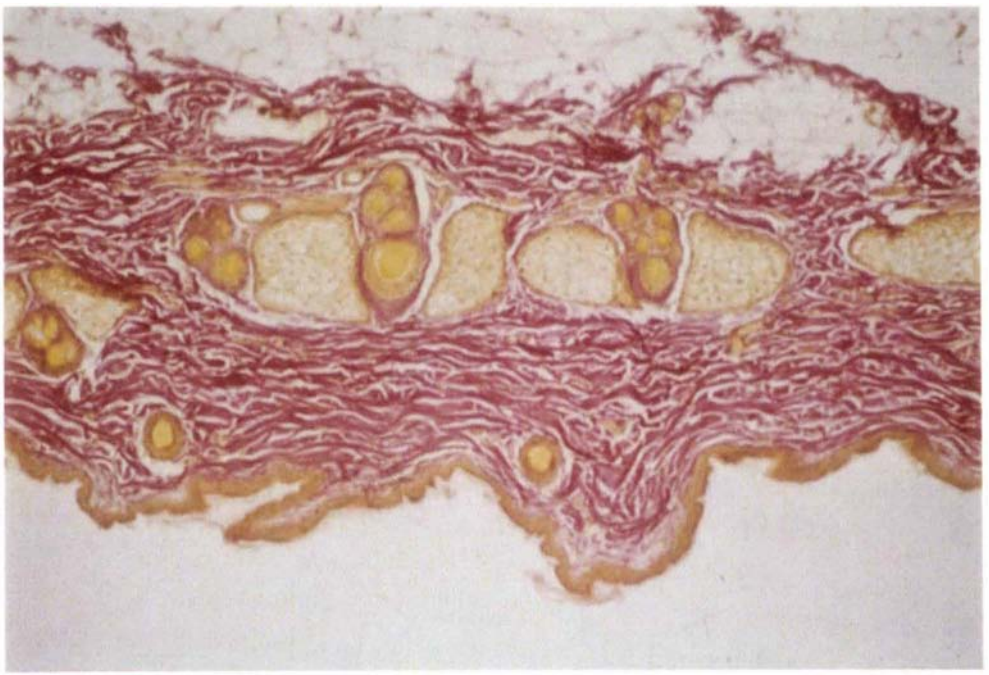
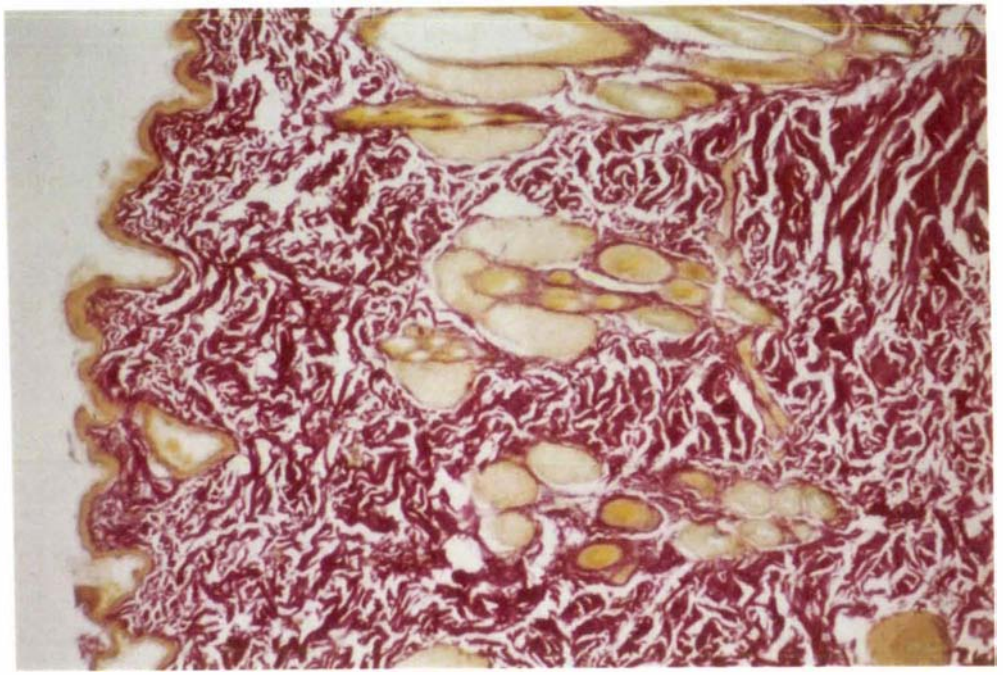


Plate 3.4 (cont'd): Skin glands (x200).

(i) Male cheek.

(j) Female cheek.

(i)



(j)

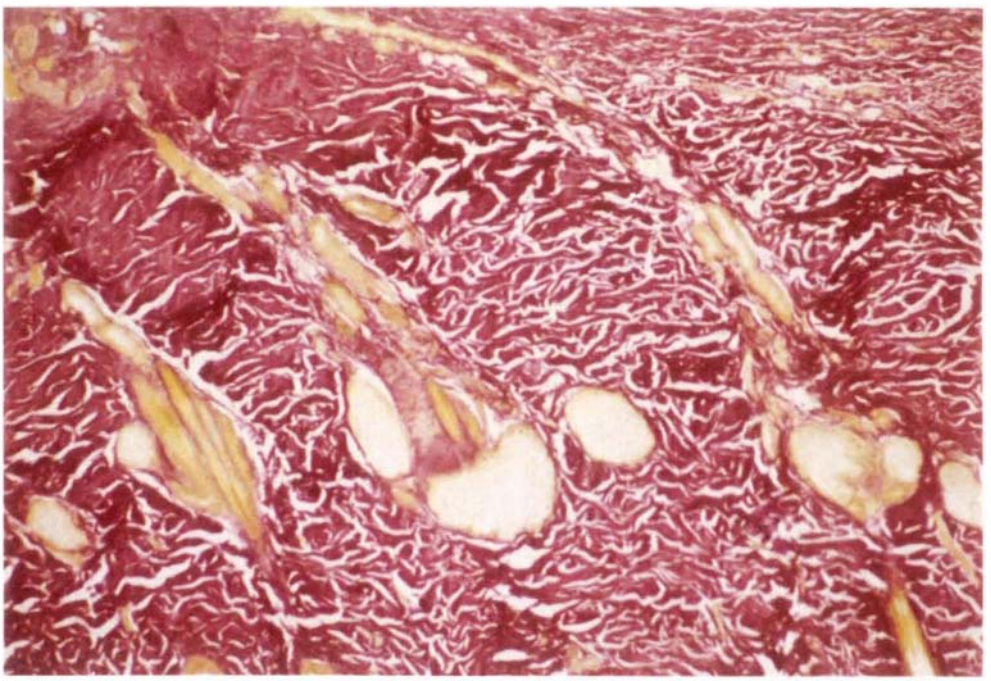
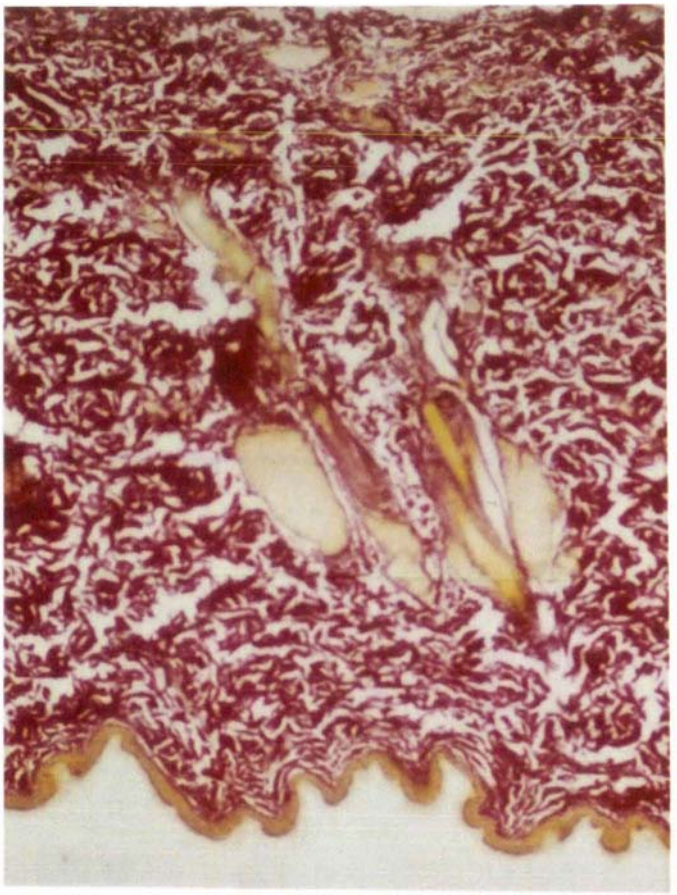
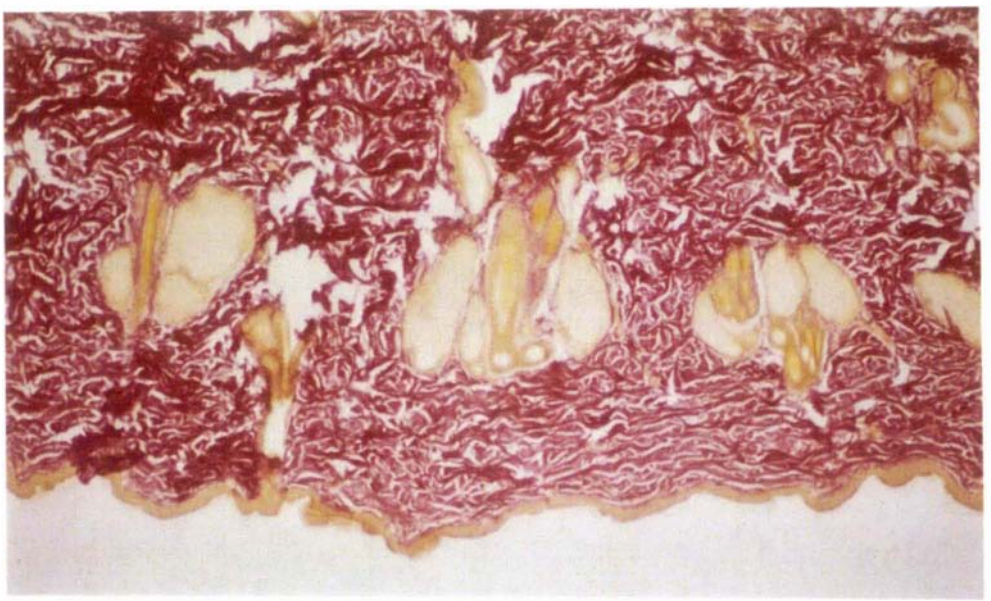


Figure 3.4 (cont'd): Skin glands (x200).
(k) Male chin.
(l) Female chin.

(k)



(l)



glands in the dorsal neck and lateral rib cage sections were most highly vacuolated and those of the cheek and chin showed the least vacuolation (Plate 3.4). Tubular glands were simple coils and were sparsely-distributed, often deep in the dermis. Some were alcian blue-positive.

3.3.4 Foot Glands

Sections through the digits, front foot and antebrachial region revealed both sebaceous and tubular glands in each region. In the hairless digital pads and plantar regions there were simple coils of atrichial glands, their ducts opening directly through the thick, cornified ventral epithelium (Plate 3.5a). The lumen contents were not active with alcian blue. In the areas covered in hair there were highly coiled epitrichial tubular glands that were alcian blue-positive. They opened into hair follicles at the same level as the sebaceous glands (Plate 3.5b). The latter were similar to those in other skin regions, with medium to high levels of vacuolation. Tubular glands were most highly developed in the interdigital regions, while on the dorsal surface they were similar to those found in other skin regions (Plates 3.5c). They became less developed proximally on the foot and antebrachial region.

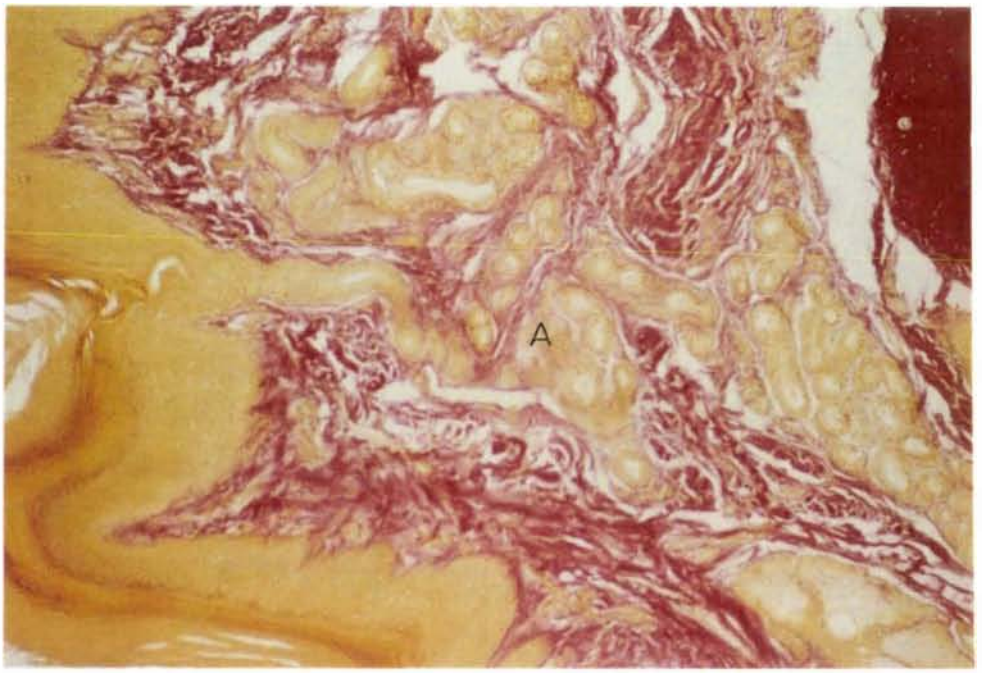
3.4 DISCUSSION

The structure of the anal sacs and glands of the ferret conform to the typical Mustela form (Stubbe 1969) and in particular to that described for the polecat (Stubbe 1972). Creed and Kainer (1981) also gave a brief histological description of ferret anal sacs and glands, and the present study confirms their findings.

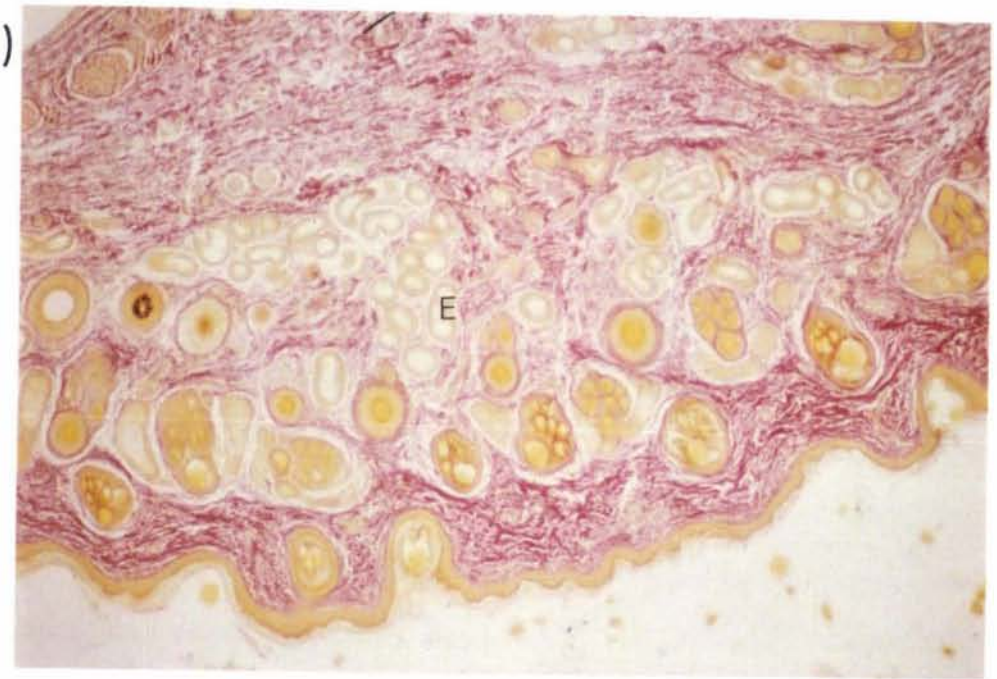
The gross structure of abdominal glands of male and female ferrets has been described above. Their great enlargement and modification compared to tubular glands found elsewhere in the skin may indicate an odour-production function. This is in line with the suggestion of Stoddart (1980b)that most scent-producing glands are hypertrophied normal skin glands. Eosinophilic reactions and positive alcian blue staining indicate the presence of odour-producing basic glycoproteins, as has been found in other species, for example the rabbit's submandibular gland (Mykytowycz 1965). The larger size of glands in

Plate 3.5: Foot glands. A=atrichial glands, E=epitrichial glands.
(a) Digital pad (x300).
(b) Interdigital region (x200).
(c) Dorsal foot region (x300).

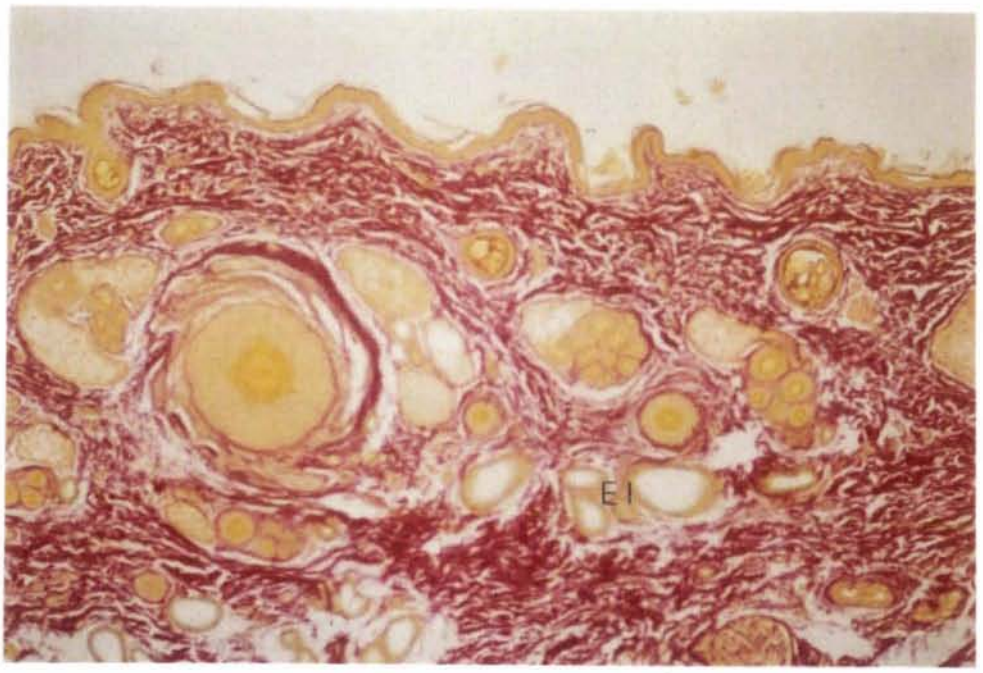
(a)



(b)



(c)



the male together with the fact that male abdominal glands consist of low columnar epithelial cells compared to the females' cuboidal cells suggests a capacity for larger output of odorous secretions from males than from females. This is in contrast to the anal sacs, which were as large in the females as in the males (with respect to body weight).

The ducts of abdominal glands appeared to open into hair follicles, not into the urogenital tract. Consequently the secretory pathway may not necessarily directly combine abdominal gland secretion with urine. Urine may still be tainted with the odour, but the secretion could also be deposited onto the substrate separately from the act of urination.

The male abdominal glands are similar in general form to the abdominal gland of the marten, as described by Hall (1926), which is also positioned around and anterior to the urogenital tract. In the same way that ferret abdominal glands appear to have the typical ferret smell, Hall noted for the marten's abdominal gland: "when crushed the substance of the gland produces an oily fluid possessing the characteristic marten odour". The abdominal glands of the American badger are in a similar position (Pocock 1925), but unlike the ferret each gland has a duct opening into the abdominal skin.

The discovery of abdominal glands in the ferret provides a potential source of odour that could be laid down as scent marks. The position and odour-producing characteristics of these glands make them good candidates for scent marking organs used in wiping, and the fact that they are more developed in males, the sex that does most wiping, also supports this idea (see Chapter 2).

Histological examination of the regions of the skin used in body rubbing revealed no other major gland complexes, but all skin samples contained numerous sebaceous and some tubular glands. It is not clear as to whether or not any of these glands are the source of odour laid down by body rubbing. Epitrichial glands may produce small amounts of secretion which give the skin a distinctive odour (Ham 1974), similar to abdominal gland odour. It remains unclear, however, whether these odours are identical, and whether or not wiping and body rubbing lay down the same odour. Quay (1977) and Adams (1980) noted that it is questionable whether the generally-distributed sebaceous glands of

mammals are significant in olfactory communication. The dermal sebaceous glands may produce waxy secretions (Stoddart 1976) that act to bind odorous secretions from other sources to the body fur, and thus abdominal odour could be set down by body rubbing. No matter what is the source of the secretion, bacterial action could be involved in making the secretion odorous (Quay 1977), as in the fox (Albone et al. 1977). Such microbial fermentation activities could thus create distinct odours from various parts of the body. It is possible that, as in the Siberian weasel (Yamaji et al. 1981), the histochemical characteristics of the skin glands vary with location on the body, thus allowing subtle differences in odours to occur.

Before we know what functions sebaceous glands have, the varying degree of vacuolation in these glands cannot be explained. It should be noted, however, that high vacuolation of secretory cells is associated with high lipid production (M.J. Birtles pers. comm.), and the most highly vacuolated glands occurred in the skin of the neck, where ferrets often sniff at each other. Male sebaceous glands were more highly vacuolated than those of the females. Males do much more body rubbing than do females (see Chapter 2), and male ferrets have a stronger odour than females (pers. obs.).

Glands found in the footpads of the ferret were of the typical carnivore atrichial form. There was no indication that these were odour-producing glands. In addition, there were epitrichial interdigital glands, producing glycoproteins, suggesting an odorous nature. As only one male and two female samples were used, sexual differences in foot glands were not examined.

The results and their interpretation presented in this chapter have attempted to elucidate the odour production capability of the ferret, and in particular has suggested a source of odour laid down by wiping behaviour. It has, however, left unanswered many questions on the roles of skin glands in communication that could be answered by more extensive histochemical studies.

Chapter 4
CHEMICAL ANALYSIS OF ANAL SAC EXTRACTS

"It seems that the only method to determine accurately the chemical messages involved in social behaviour... would be to determine the exact chemical nature of these olfactory substances." -Ropartz 1977

4.1 INTRODUCTION

Studies of the chemistry of odorous secretions have been undertaken in a variety of mammalian species over the last fifteen years. The composition of anal gland secretions of various members of the Mustelidae have been the subject of close chemical scrutiny. Sokolov et al. (1975, 1980) and Brinck et al. (1978) studied mink anal gland odours, and Schildknecht et al. (1976) identified mustelan as the major component of mink anal gland odour. Many sulphur-containing compounds have been identified from the anal sacs of the stoat, (Crump 1980a, Brinck et al. 1983), from those of weasel, polecat, pine marten and beech marten (Martes foina) (Schildknecht and Birkner 1983). Eleven components of the anal gland secretions of New Zealand ferrets were identified by Crump (1980b), and in addition 2-isopropylthietane (D.R. Crump pers. comm.).

These studies have provided the baseline data about anal gland odour composition on which further studies can build. Studies on the variation in composition between individuals and through time will provide vital information for determining the messages carried by these odours. In Chapter 1 four communicative functions for odours were hypothesised. Any hypothesis that requires ferrets to be able to discriminate between their own and other odours (e.g. for territorial defence by either scent matching or neighbour-neighbour recognition) makes the assumption that there is variation in the odour composition of different individuals. Another hypothesis was that anal gland odours act as sex attractants. For this to be true, the odours of males and females must be chemically distinct, at least during the breeding season, while variation throughout the year could provide information on the breeding state of the animals. An investigation of the sexual, individual and seasonal variation in ferret anal gland

secretions is the subject of this chapter.

4.2 METHODS

Samples of anal sac extracts were collected at five to six week intervals from five male and five female adult ferrets between October 1982 and April 1984, with the exceptions that one female, Furo, died in September 1983, and male Hob died in December 1983; sampling of female Satha began in July 1983, and of male Coonie in January 1984. Secretions were collected from the unanaesthetised animal by pressing the anal sacs using thumb and forefinger pressure around the anus. The secretion was collected in a pasteur pipette and transferred to a 1 ml capacity glass vial, sluicing it out of the pipette with an approximately equal quantity of diethyl ether. These ether/anal gland secretion mixtures were stored at -10°C until analysed (usually within one or two days of collection). Colour and viscosity of the extracts were observed by eye. After 30 seconds stirring on a "Vortex Genie" mixer, four microlitre aliquots were run through a Pye 104 or Varian aerograph series 2700 gas chromatogram, using a 1/4 inch by 6 foot glass column filled with 3% SE30 on 100/120 Gas Chrom Q. The oven temperature was kept at 40°C for eight minutes then increased at 10°/min to 180°C. Results were recorded on a chart recorder running at 1 cm per minute. Peaks were identified by comparison with recordings of synthetic thietanes and dithiolanes provided by D.R. Crump (see Crump 1980a for preparation details),and standard quinoline and indole. Identification of trans- and cis-2,3-dimethylthietane was confirmed by mass spectroscopy.

Samples with peaks large enough to measure were quantified. The area under the peaks formed by each compound was calculated using a compensating planimeter. Only peaks that were reliably identified were used in further analysis. These peaks were: trans- and cis--2,3-dimethylthietane (compounds 2 and 3 of Crump 1980b); 2-propylthietane (compound 4); trans- and cis-3,4-dimethyl-1,2dithiolane (compounds 6 and 7); 2-pentylthietane (compound 8); and indole (compound 11). The peak areas of the isomers 2 and 3, and 6 and 7 were combined in the statistical analyses. The proportion that the area under each peak represented of the total area of the peaks analysed were used as a measure of relative concentration of these compounds.

These data were arcsine transformed and analysed using multivariate and univariate analysis of variance (MANOVA and ANOVA) and discriminant function analysis (DFA). Data and details of the analyses are given in Appendix 2.

4.3 RESULTS

4.3.1 Sexual Differences

Female extracts generally had higher concentrations of the more volatile (shorter retention period) compounds, especially compounds 2+3 and 6+7, than those of males. In the males indole (compound 11) was usually (in 33 out of 43 samples) the highest peak on the GC traces. In the females, either compound 2, 4, or 6 was the highest peak, with the exception of Swuzzle for whom compound 11 was the highest in five samples. Examples of GC traces of three males and three females are given in Figs. 4.1, 4.2. There were significant differences in the relative concentrations of the various compounds between the male and female extracts ($P \leqslant 0.016$, Table 4.1). These differences are displayed graphically in Fig. 4.3, with males and females being well separated on the first discriminant function. Variables 2+3 and 6+7 were strongly positively correlated with the females, while 4 and 11 were correlated with the males. Compounds 2+3 and 6+7 varied significantly between the sexes ($P \leqslant 0.005$, $P < 0.016$ respectively, Table 4.1).

4.3.2 Individual Differences

The ten subject ferrets had individually distinct anal sac extract profiles (Figs. 4.1, 4.2). Separately, both males and females showed significant inter-individual variation in combinations of the various compounds ($P \leqslant 0.001$ for both males and females, Table 4.1). When the compounds were analysed separately, females showed significant variation in all five compounds, especially compounds 4, 8, and 11 (Table 4.1). All the compounds also varied significantly amongst the individual males, with compounds 4 and 8 showing the most consistent differences (Table 4.1). Compound 8 appears not to be an important discriminator amongst individuals in the DFA (Fig. 4.3), but this analysis did not differentiate between sexual and individual differences.

Figure 4.1: GC profiles of two samples of each of three males' anal sac extracts. The peaks used in quantitative analysis are numbered as in the text.
(a) Bandit (b) Hob (c) Malli

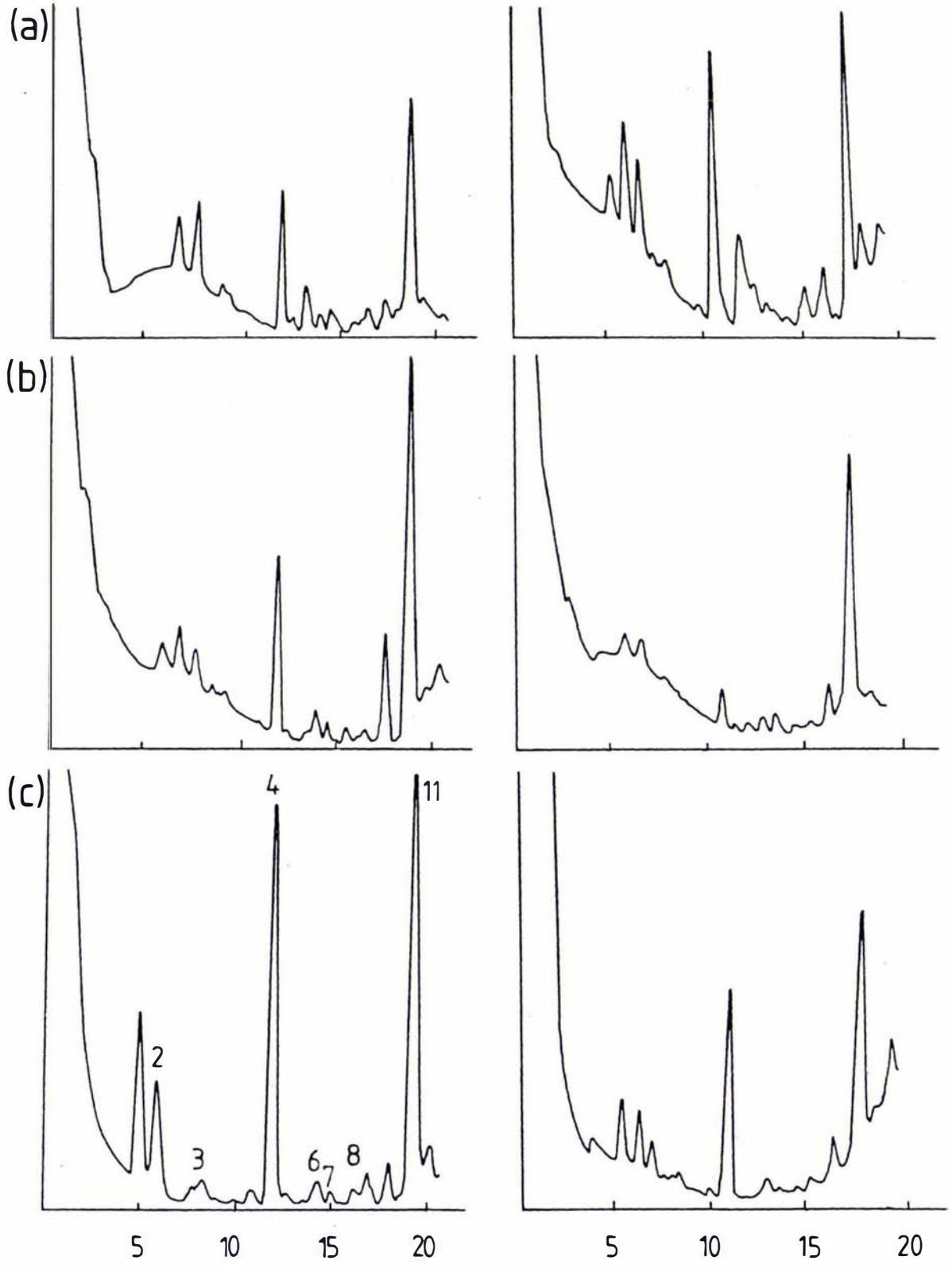

(a)
(b)
(c)
4
11
2
3
6
7
8
5
10
15
20
5
10
15
20
TIME (min)

Figure 4.2: GC profiles of two samples of each of three females' anal sac extracts. The peaks used in quantitative analysis are numbered as in the text.
(a) Jill (b) Pug (c) Swuzzle

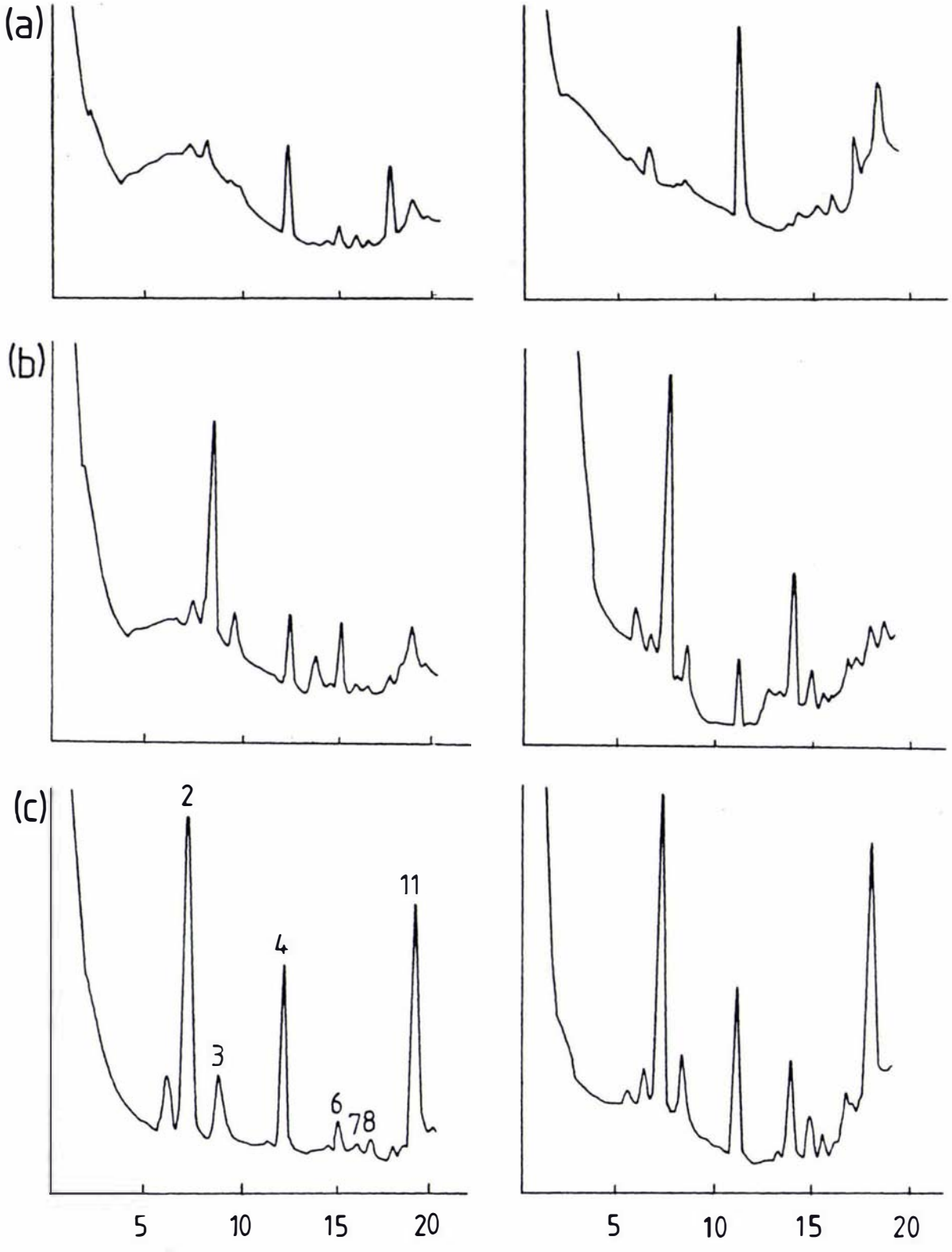

(a)
(b)
(c)
2
3
4
6
78
11
5
10
15
20
5
10
15
20
TIME (min)

TABLE 4.1

Untransformed mean (SD) peak proportions for males and females, and for each individual separately. Statistical comparisons are univariate and multivariate analyses of variance done on arcsine transformed data.

	2+3	4	6+7	8	11
SEX (n)					
MALE (42)	0.15(0.07)	0.24(0.15)	0.11(0.10)	0.03(0.04)	0.48(0.15)
FEMALE (53)	0.35(0.12)	0.17(0.11)	0.28(0.16)	0.03(0.03)	0.17(0.12)
F value	15.08	0.02	9.22	0.21	2.22
Significance	$P \leq 0.005$	N.S.	$P \leq 0.016$	N.S.	N.S.
MANOVA	$P \leq 0.016$				
INDIVIDUAL MALES					
BANDIT (7)	0.14(0.08)	0.27(0.07)	0.08(0.07)	0.02(0.02)	0.49(0.11)
COONIE (4)	0.25(0.02)	0.28(0.08)	0.14(0.12)	0.04(0.03)	0.29(0.11)
HOB (8)	0.14(0.10)	0.15(0.07)	0.07(0.04)	0.01(0.02)	0.61(0.10)
MALLI (13)	0.15(5.1)	0.39(0.10)	0.05(0.03)	0.02(0.01)	0.39(0.10)
SNARK (10)	0.11(0.06)	0.05(0.02)	0.22(0.11)	0.08(0.04)	0.55(0.12)
F value	2.66	12.43	4.19	5.76	4.38
Significance	$P \leq 0.041$	$P \leq 0.001$	$P \leq 0.005$	$P \leq 0.001$	$P \leq 0.004$
MANOVA	$P \leq 0.001$				
INDIVIDUAL FEMALES					
FURO (7)	0.40(0.18)	0.21(0.13)	0.26(0.14)	0.00(0.00)	0.17(0.07)
JILL (13)	0.25(0.08)	0.25(0.15)	0.32(0.18)	0.05(0.04)	0.12(0.12)
PUG (11)	0.38(0.14)	0.12(0.06)	0.34(0.10)	0.02(0.02)	0.14(0.12)
SATHA (9)	0.33(0.10)	0.08(0.02)	0.40(0.09)	0.02(0.04)	0.16(0.12)
SWUZZLE(13)	0.40(0.08)	0.16(0.07)	0.11(0.05)	0.03(0.03)	0.28(0.13)
F value	3.06	6.17	4.13	8.09	5.38
Significance	$P \leq 0.023$	$P \leq 0.001$	$P \leq 0.005$	$P \leq 0.001$	$P \leq 0.001$
MANOVA	$P \leq 0.001$				

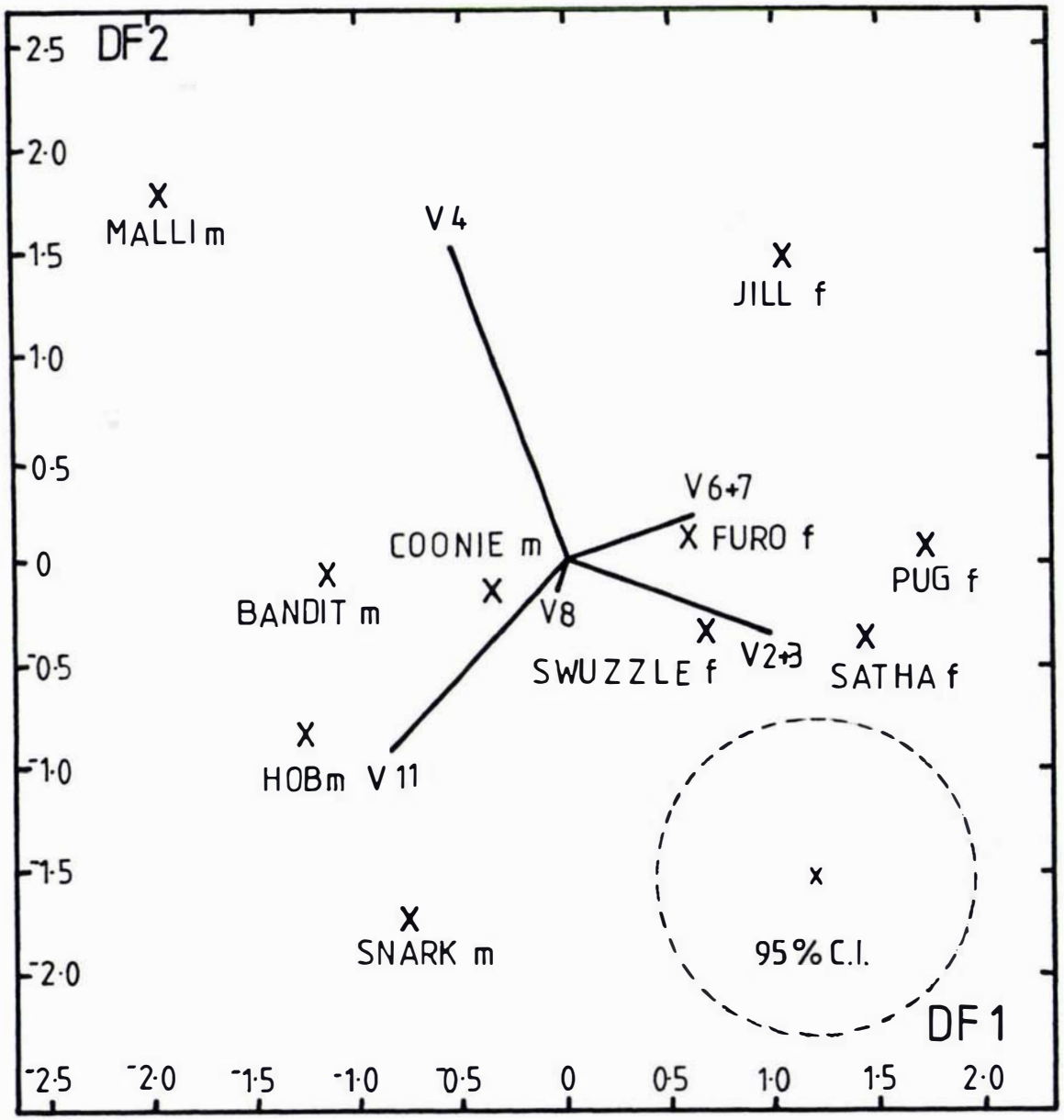


Figure 4.3: Discriminant function analysis; the position of the centroid values of each individual, and each variable (vectors) on the first two discriminant function axes.
95% confidence interval: radius=$\sqrt{\chi^2_{.05[2]}/N}$.

Individuals showed not only quantitative but also consistent qualitative differences in their anal sac extracts. Male Snark always produced a dark brown, viscous secretion which yielded low levels of volatile compounds, and had a weak odour to the human nose. In contrast, male Malli and female Swuzzle had pale yellow secretions, with little insoluble material. These two individuals always gave the "best quality" GC traces. The other ferrets were intermediate between these extremes.

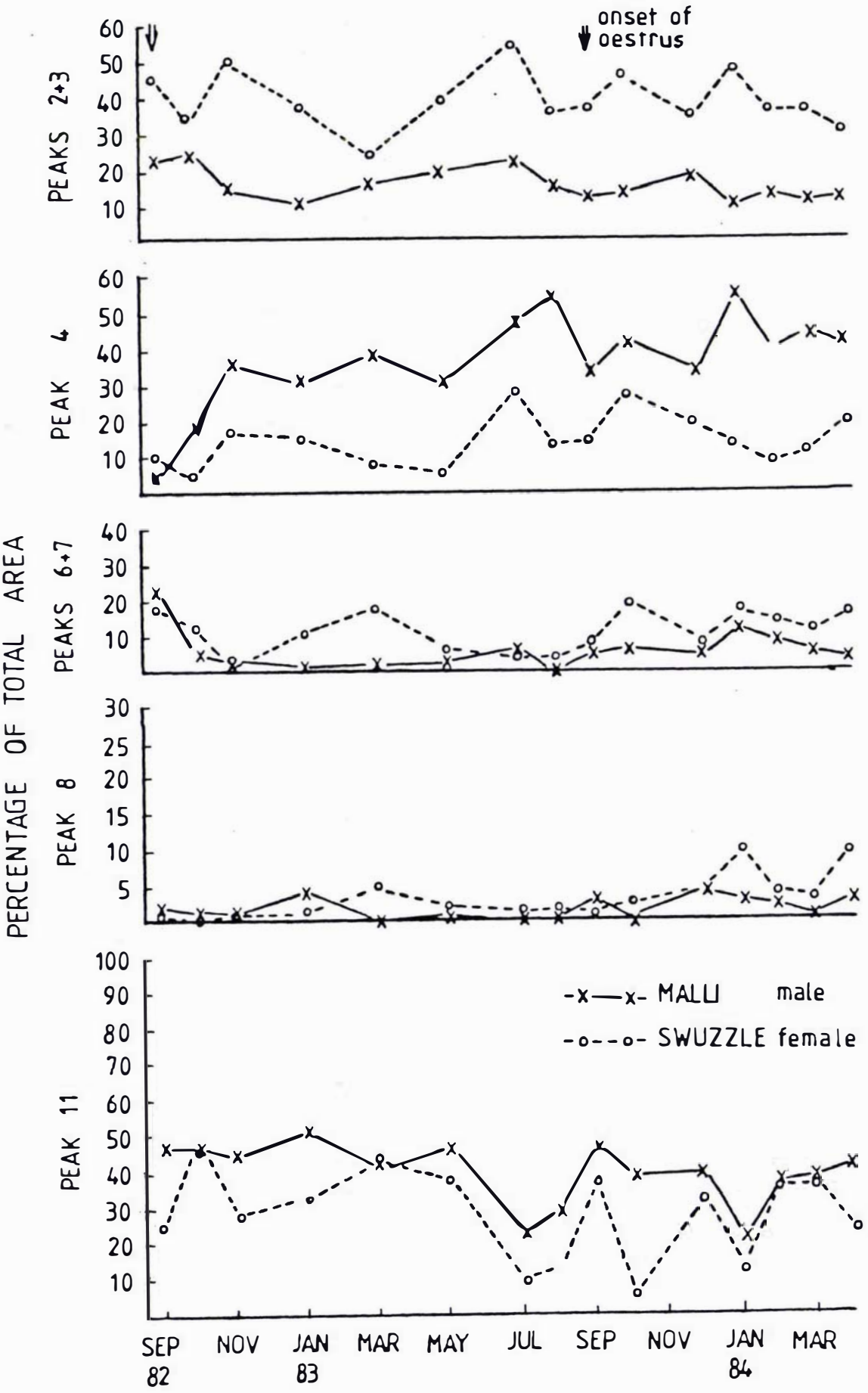
4.3.3 Seasonal Differences

Concentrations of volatiles showed no consistent seasonal trends in either males or females. In Fig. 4.4 the concentrations of the compounds as percentage of total concentration of the five compounds are plotted against time for male Malli and female Swuzzle. Although these two individuals showed similar trends in changes in concentration of compound 4 over the first year of sampling, other individuals did not show the same trend. Other measures were also calculated - concentration of each compound as a percentage of the largest peak, ratio of various pairs of compound peak areas. None of these measures elucidated any form of seasonality. When comparing the changes in concentrations of compounds with the oestrous cycle of the individual females, no consistent patterns emerged. Some variation in odour and viscosity of the extracts were noted, but again these did not conform to any seasonal pattern.

4.4 DISCUSSION

The analysis of variation in composition of anal sac extracts has provided support for some communicative functions of anal gland odours. The fact that ferrets have individually distinct anal sac extract profiles means it would be possible for a ferret to recognise its own odour as different from others, and thus allow it to enhance territorial confidence. It would allow an intruder to match the odour left by scent marking with those on animals it meets, so that it will recognise the resident. A recognition system between neighbours could also operate. The consistent differences in relative amounts of volatiles in male and female ferrets provides the basis for anal gland odours to act as sex attractants, and interestingly, female secretions had higher relative concentrations of the more volatile components than

Figure 4.4: Seasonal variation in relative concentrations of anal gland secretion compounds (peaks). Peak areas are expressed as percentage of the total peak area.


onset of oestrus
PERCENTAGE OF TOTAL AREA
PEAKS 2+3
PEAK 4
PEAKS 6+7
PEAK 8
PEAK 11
-x—x- MALLI male
-o--o- SWUZZLE female
SEP 82
NOV
JAN 83
MAR
MAY
JUL
SEP
NOV
JAN 84
MAR

did the male secretions. Indole was usually a very important component of male secretions. It is a commonly encountered microbial product, found in the anal gland secretion of the red fox, and in vaginal secretions and saliva of humans (Albone 1984). Thus it may not have much communicative value itself, but is important in this study as indicating the relative concentrations of the sulphur-containing compounds in males and females.

Another prediction from the sex attractant hypothesis is that odours may show variation through the year, depending upon the breeding state of the animal. Crump (1980b) found that at least one female ferret had low levels of volatiles in an anal sac extract taken at the onset of oestrus. This secretion was muddy brown and lacked odour. Lack of ability to identify animals being sampled in that study made it impossible to be sure if the secretion from that particular female had changed from other times of the year (D.R. Crump pers. comm.). In the present study no such changes in secretions were associated with the onset of oestrus (and individuals did have different coloured secretions). No seasonal trends were found in the changes of relative concentrations of the major components of the anal gland secretions of either male or female ferrets. Some variation did occur, but not in any regular pattern. This does not mean that the relative concentrations of these compounds cannot act as sex attractants, only that they cannot indicate when the animals are sexually active. Any seasonal changes in these compounds would conflict with the individuality of the odours. It seems likely then, that seasonality would, if present, be indicated by factors other than the relative concentration of the major volatiles. One possibility is that minor volatile components, not measured in this study, vary with season. Another possibility is that the total amount of volatiles in the secretion changes over time. There was some indication that this may have been happening over the sampling period, with low GC profiles occurring in the non-breeding season. A detailed quantitative study of the relative amount of volatile to non-volatile components would be necessary to confirm this.

The compounds used in the analysis to test for these differences may not be the only cues the ferrets themselves could use to discriminate sex and individual identity. As Preti et al. (1977) pointed out,

minor components of odorous secretions may be of critical importance to animals' perception of odours. The cis and trans isomers of two of the compounds were combined in the analysis. Although there appeared to be no consistent pattern to the relative concentrations of these isomers, it should be noted that some animals can discriminate between geometric isomers of the same compound (Müller-Schwarze et al. 1976).

There have been no detailed, long-term studies on the anal gland secretions from known individual males and females of any other Mustela species. Erlinge et al. (1982) mentioned that in the stoat they found quantitative and qualitative differences amongst GC traces of different individuals, and that these patterns were stable through time. However they analysed two extracts from each of only two males, and gave no quantitative data. Crump (1980a) found that one component of male stoat secretions (a non-sulphur compound) was missing from the female secretions, while 2-ethylthietane and 3-ethyl-1,2-dithiolane occurred in the female samples only. Brinck et al. (1978), using ten individual mink, (five of each sex) found individual patterns in anal sac extracts that were stable through time, and found no specific sex differences, but they gave no quantitative analysis of these patterns. More in depth studies have been done on other mustelids. Gorman et al. (1978) failed to demonstrate any sexual differences in the anal secretions of otter, and found that individual differences were too labile with time to be of use in recognising individuals. The most comprehensive published account of odorous secretions from any mustelid species to date is that of Gorman et al. (1984) on the sub-caudal pouch secretions of the badger, where they found individual but no sexual differencs in the secretions.

In a few other mammal species, sexual and/or individual differences have been demonstrated. For example, Goodrich and Mykytowycz (1972) showed that for each of three types of glands - anal, chin and inguinal, in the European rabbit, secretions varied in composition depending upon both sex and individual identity. Gorman (1976) showed that there was sufficient inter-individual variation in the anal secretions of the Indian mongoose (Herpestes auropunctatus) to allow them to be used as an individual recognition system.

Although only ten ferrets were used in the present study, sufficient sampling allowed very significant male/female and individual differences to be demonstrated. It must now be determined whether or not ferrets can make use of these chemical cues for sexual and individual recognition.

Chapter 5
ODOUR PREFERENCE TESTS

"The recognition of an individual...and species is possible in many vertebrates by virtue of odour alone." -Stoddart 1980b

5.1 INTRODUCTION

For scent marks and body odours to play any role in communication, not only must some information be encoded within them, but the animals must also be able to decode this information. A basic piece of information that could be derived from odour is species recognition. Animals must first be able to identify conspecifics for any of the complexities of social behaviour to operate. Comparisons within and amongst the studies of Crump (1980a,b) and Brinck et al. (1983) show that there are species-specific components to the anal gland secretions of ferrets and other Mustela species. Mustelid anal gland odours do therefore possess the chemical basis for a species recognition system. It must now be shown that ferrets can discriminate between anal gland odour of their own species and that of a sympatric species.

Odours may convey not only information on species identity, but also sex and individual identity. The hypotheses put forward in Chapter 1 to explain roles of odour in communication require that ferrets be able to discriminate amongst different categories of odours. A prediction of the scent matching mechanism by which scent marks give an association between a resident and its territory requires that ferrets intruding into occupied space be able to recognize the odour of a scent mark as being the same as that on an animal it meets, and that the resident be able to recognise his own odour. If anal gland odours act as a neighbour-neighbour recognition system, ferrets must be able to discriminate their own odour from that of their neighbours, and their neighbours' odours from those of strangers. They could do this by either recognising each neighbour as a separate individual, or just by being able to discriminate between familiar and strange odours. It has already been shown (Chapter 4) that there are individual differences in ferret anal gland odours, and there are also sexual differences. For anal gland odours to act as sex attractants, males and/or females must

be able to discern these differences, and must be more attracted by the odour of the opposite sex, at least during the breeding season.

As Johnston and Schmidt (1979) pointed out: "the quality of the odour of most mammalian scent marks changes in a predictable manner with time, as the concentration of highly volatile components decreases relative to the concentration of less volatile components." If ferrets' anal drag scent marks play some role in territorial defence or in bringing the sexes together, then the ability to determine the age of scent marks would be advantageous as it would allow a ferret to determine the likelihood of meeting a conspecific, and thus modify its behaviour appropriately.

The procedures used in determining the ability of animals to discriminate between odours fall into two categories (Brown 1979). The preference test method measures the spontaneous responses of the animal to different odours. The responses used as measures of attractiveness are usually the time spent investigating the odours, time taken to approach the odours, the choice of odour first investigated and the amount of scent marking at the odour sources. The second procedure is the reinforcement-training method in which the subject is taught using reinforcement or punishment conditioning to respond to one or other of the odours. In both methods the odours can be presented simultaneously or successively.

Both procedures have advantages and disadvantages. A criticism of the preference test method is that a lack of difference in response to two odours does not necessarily indicate an inability to discriminate the two, but simply a lack of motivation to choose between them. That is to say, the odours may be perceived as different but evoke the same response in the subject animal. A problem with the reinforcement-training method is that it does not reveal the animal's natural responses to and preferences for the odours.

The same type of test apparatus can be used for either of these procedures. The simplest are Y- and T-mazes which consist of a starting arm and two goal arms with odours at their ends, between which the animal must choose. Such a maze was used by Bowers and Alexander (1967) in their classic study of individual odour recognition in mice

(Mus musculus), and by Hughes (1964, 1965) in his studies on spontaneous alternation in the ferret. Discrimination boxes and arenas of varying complexity have also been used (Stevens 1975).

No matter what the design, an olfactometer must incorporate the following general features (and see Salmon and Marsh 1977):

1. The apparatus must provide enough space to allow the animal to move about normally.
2. If odours are presented simultaneously, they must not be allowed to mix as this could produce a confusing signal.
3. Measures of response must be specific enough to assure accurate interpretation.
4. The animals should not be aware of the sensing method.

The exact design of the apparatus and the experiment will depend upon the animal used and the aim of the study. The aim of this study was to find out if ferrets have the sensory ability to discriminate amongst anal gland odours of different ferrets, and to see if they showed any preferences for investigating odours from different categories of animals, as required for the hypothesised functions of odour in communication.

5.2 METHODS

5.2.1 Subjects

Six male and nine female ferrets were used in various combinations as subjects for odour discrimination tests. Four of each sex were wild-caught animals that had lived in captivity for at least seven months prior to testing. The remainder were captive-bred, and were used only in experiment 7, when they were thirteen months old. The ferrets were housed in two areas (more than one km apart), allowing each to habituate to the odours of some individuals but not others.

5.2.2 Odour Materials and Collection

For T-maze experiments 1 and 2 the extracts of anal sacs of dead specimens of male ferrets and male weasels, all caught at the same time of year (September/October 1980), were used. These animals were stored whole at -10° C until used. The anal sacs were dissected out and their

secretion smeared onto a 2 cm diameter circle on a piece of filterpaper. These filterpaper/odour samples were kept in airtight plastic containers. Any one odour sample was used the same night as collection, and on the next two nights. In experiment 2 the ferrets were tested against either fresh ferret and fresh weasel, or one-day old samples of both, or two-day old samples of both.

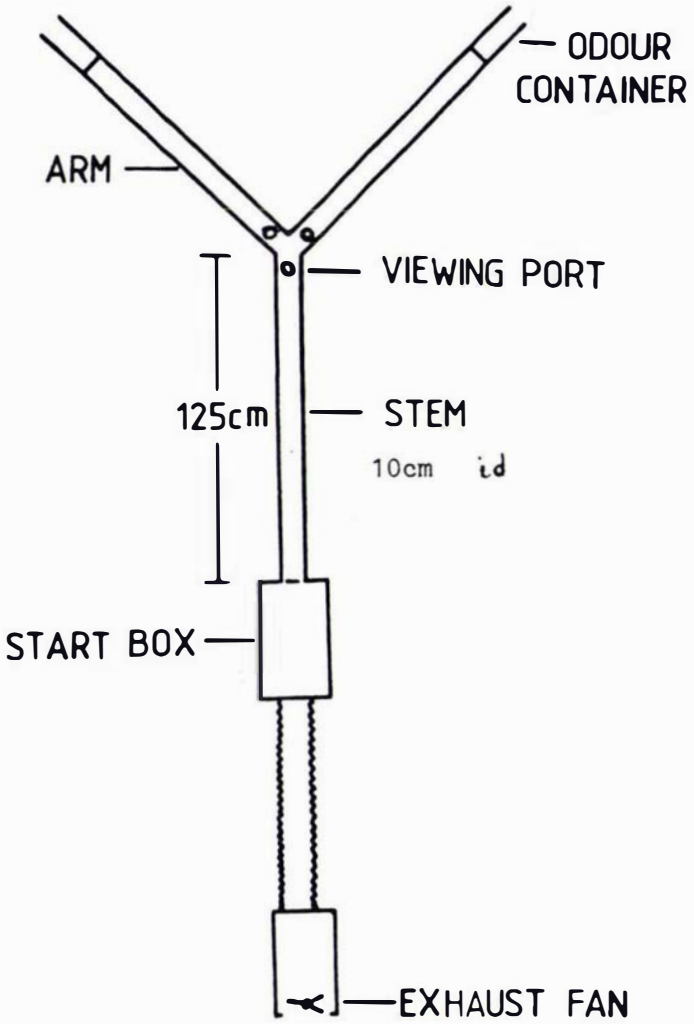
In preliminary Y-maze tests and T-maze experiments 3 to 7, anal gland secretions from live ferrets were used. Samples were collected by holding the donor animal around the back of the neck with one hand, supporting the pelvic region with the palm of the other hand and using thumb and forefinger to express the secretion from the anal sacs. Filterpaper was blotted onto the secretion, which usually formed a blob over the anus. The sacs were squeezed until the 2 cm area was covered thinly with secretion. Care was taken to avoid rubbing the filterpaper across the urogenital region and against the fur except around the anus. Samples were used within 24 hours of collection.

5.2.3 Y-Maze Test

Preliminary odour discrimination trials were carried out in a grey PVC Y-maze (Fig. 5.1a) with perspex viewing ports set into the top. A plywood start-box was attached onto the stem, with a guillotine door at the joint. An exhaust fan drew air through the maze and start-box, and helped to mask extraneous noises. The odour samples were placed in PVC containers that fitted onto the end of each arm of the maze. A nylon mesh prevented sight and access to the odour samples.

At the beginning of each trial the fan was started and an odour placed in the container at one or other end of the maze. A blank piece of filterpaper was placed in the other container. The subject was placed in the start-box with the door shut for two minutes, allowing time for the odour to be drawn through the apparatus. The door was then raised and timing began, using a digital stopwatch. Time the animal took to reach the Y junction was measured (Time 1), along with the time spent at the junction (Time 2) before entering an arm. The arm chosen was also noted. The animal was then removed and the apparatus thoroughly cleaned with water and chlorine bleach (Janola) before the next trial. All animals were run on the same or subsequent morning. The animals were not tested again until four days had elapsed. Each animal was

(a) Y-MAZE



(b) T-MAZE

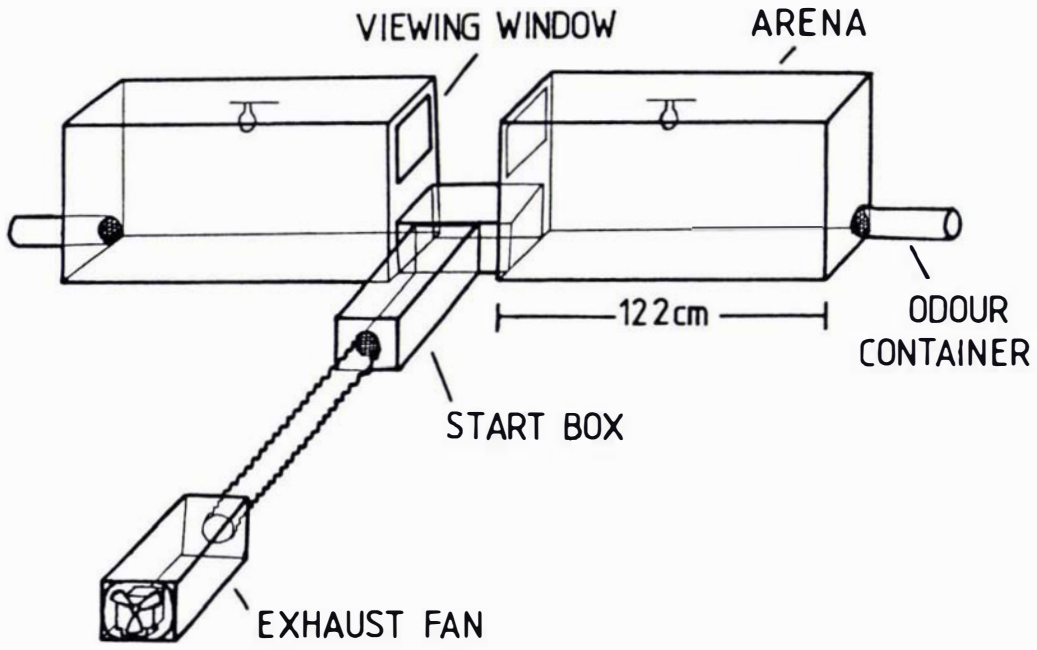


Figure 51: Apparatus used in preference tests.

tested against strange and familiar odours of both males and females, in a design balanced to avoid confounding effects due to order of presentation of odours. The data (Time 1 plus Time 2) were converted into normalised ranks and analysed using a 3-way analysis of variance. Missing values were estimated to minimise the residual sums of squares. Data and analysis are given in Appendix 3.

5.2.4 T-Maze Tests

Preference tests were run in a T-maze apparatus (Fig. 5.1b) made of two particleboard arenas and a connecting tunnel, varnished inside to facilitate cleaning. A guillotine door made of a plywood frame and wire mesh fitted the opening from the start-box to the maze. The exhaust fan drew air from both arenas back through the start-box, preventing mixing of odours at their sources. The odour containers used in the Y-maze attached onto the end of each arena with wire mesh providing a visual and mechanical barrier between the odour samples and the subject animals. Above the entrance to each arena from the connecting tunnel, the wall consisted of a sheet of tinted glass, allowing visibility into the arenas for the observer, who sat above and just behind the start-box, without the ferret being able to see out. Each arena was lit by a 25-watt red light, attached to the centre of the roof of the arena, to provide dim lighting.

All the preference tests were run during the breeding season (September to March). For experiments 1 to 3 all trials were run in the evening (9pm-11pm), while those for experiments 4 onwards were run during the day (8am-11am, and 3pm-5pm). Prior to experiment 1, each subject spent all of one day in the T-maze, with free access to both arenas. This allowed them time for familiarisation with the apparatus.

At the beginning of each trial newspaper was laid on the floor of the maze, and straw from the home cage of the subject was placed in the start-box. The lights and fan were turned on and the guillotine door shut. The subject was then placed in the start-box and left for five minutes before the odour samples were placed in their containers. One minute then elapsed, giving time for the odours to be drawn through the apparatus before the door was raised and timing began. When the animal's head appeared in either arena the time was noted and its initial choice response left or right was recorded. Measurements were

then made of the total time spent sniffing at the odour ports (nose less than 10 cm from the port).

Trials lasted five minutes for experiment 1, 30 minutes for experiment 2, while 15 minute trials were used for all subsequent experiments. At the end of the trial the animal was removed along with the straw and newspaper. The whole maze was cleaned and left to dry for nearly 24 hours before the next trial. No subject was used more than once every four days. Information of the general behaviour of the subjects in the T-maze is given in Appendix 4.

Pairs of odours were tested simultaneously. The right/left position of the two odours tested in any trial was randomised to avoid biases of possible subjects' preferences for turning right or left. Time data were analysed using the Wilcoxon matched-pairs signed-rank test (assuming independence between trials when the subjects were tested more than once), and ANOVA in experiment 5. The binomial test was used for the analysis of choice data. Data and analysis of subjects' responses are given in Appendices 5 and 6.

5.3 RESULTS

5.3.1 Y-Maze Test

Preliminary trials in the Y-maze apparatus were designed to test for discrimination between strange and familiar, and male and female ferret anal gland odours. The speed with which the subjects responded to the odour (time taken from start-box to choosing right or left arm) varied depending upon the combination of sex of the subject and sex of the odour. Neither of these factors explained a significant part of the variation by itself, but the interaction term was a significant factor ($P \leq 0.01$, Table 5.1). Males responded quicker to female odours, while the reverse was true for the female subjects. There was a non-significant trend to respond quicker to strange odours than to familiar ones (see Table 5.1). Four times (twice by male Malli and once each by females Furo and Pug) the subjects gave no response (i.e. remainded in the start-box or did not reach the Y junction). Each of these were during a test of responses to a familiar odour. Out of the 28 trials in which the subjects did respond, 21 times the subjects chose the arm with the odour ($P \leq 0.006$ Binomial). Five out of the seven

times when the blank arm was chosen the odour in the other arm was that of a stranger (N.S. Binomial).

TABLE 5.1

Mean values and significance levels (ANOVA) of subjects' speed of response (Time 1 + Time 2) to odours in the preliminary Y-maze experiment. Data are normalised ranks; n=8 (4 males, 4 females).

FACTOR		MEAN VALUES		F	SIGNIFICANCE
		MALE	FEMALE		
SEX OF SUBJECT		-0.04	0.31	0.379	N.S.
SEX OF ODOUR		0.24	0.03	0.896	N.S.
INTERACTION		SUBJECT			
		MALE	FEMALE		
ODOUR	MALE	0.43	0.06	10.169	P<0.01
	FEMALE	-0.50	0.57		
		FAMILIAR	STRANGE		
FAMILIARITY		0.30	-0.02	2.010	N.S.

5.3.2 T-Maze Preference Tests

5.3.2.1 Experiment 1. Male Ferret Odour vs Blank

All the subjects that responded (seven out of eight) spent more time sniffing the ferret odour port than the blank ($P \leqslant 0.01$, Table 5.2). Six out of the seven went initially to the odour ($P \leqslant 0.062$, Table 5.2).

5.3.2.2 Experiment 2. Male Ferret vs Male Weasel

The differences in time spent at the two odour ports was not significant - all four male subjects spent more time investigating the ferret odour, but three of the females spent more time at the weasel odour port. Seven out of eight of the subjects, however, chose to investigate the ferret odour first ($P \leqslant 0.031$, Table 5.2). The exception was female Swuzzle who went initially to the weasel odour.

TABLE 5.2

Mean time spent sniffing at the two odour ports (statistical comparisons are Wilcoxon matched-pairs signed-rank tests), and initial choice of odour port (statistical comparisons are binomial tests) as a function of odour treatment.

EXPT	SUBJECTS x TRIALS	TIME SPENT AT ODOUR PORT(s)	NO. CHOOSING EACH ODOUR PORT
1	8x1	FERRET BLANK 59.3 12.0 P≤0.01	FERRET BLANK 6 1 P≤0.062
2	8x1	FERRET WEASEL 55.9 40.7 N.S.	FERRET WEASEL 7 1 P≤0.031
3	8x3	SAME SEX OPPOSITE SEX 20.2 22.4 N.S.	SAME SEX OPPOSITE SEX 6 15 P≤0.039
4	4x3	OESTROUS ANOESTROUS 43.0 49.2 N.S.	OESTROUS ANOESTROUS 8 4 N.S.
5	10x2	STRANGE FAMILIAR 38.7 27.8 P≤0.05	STRANGE FAMILIAR 14 4 P≤0.015
6	10x1	FAMILIAR OWN 41.7 41.1 N.S.	FAMILIAR OWN 5 5 N.S.
7(a)	8x1	FRESH 2 HOUR 47.9 50.1 N.S.	FRESH 2 HOUR 3 5 N.S.
7(b)	8x1	FRESH 1 DAY 72.0 51.0 P≤0.039	FRESH 1 DAY 4 4 N.S.

5.3.2.3 Experiment 3. Male vs Female Ferret Odour

There were no significant differences between the time spent at male and female odour ports nor at ports with odours of the same and opposite sex to the subjects. But again there was a significant trend to first investigate one odour port over the other - in this case that of the opposite sex from the subject was the chosen odour ($P \leqslant 0.039$, Table 5.2), a result that was due mainly to the responses of the male subjects. On the first run all four males approached the female odour first, and over three runs the males showed a significant preference for the female odours ($P \leqslant 0.019$). In contrast, five times the females chose the male odour port, and four times the female odour, while in the other three runs there was no response.

5.3.2.4 Experiment 4. Oestrous vs Anoestrous Female Odour

The four male ferrets showed no discrimination between the odours of oestrous and anoestrous females, either in time spent in investigation or in initial choice (Table 5.2).

5.3.2.5 Experiment 5. Strange vs Familiar Odour

Subjects were tested twice - once with strange and familiar odours of the same sex as themselves, and once with those of the opposite sex. The subjects showed significant preferences for both spending longer investigating the strange odour ($P \leqslant 0.05$, Table 5.2; $P \leqslant 0.01$, ANOVA) and for initially approaching the strange odour ($P \leqslant 0.015$, Table 5.2). The four (out of eighteen) times that the familiar odour was chosen (twice by males and twice by females) were all responses to odours of the same sex as the subjects.

5.3.2.6 Experiment 6. Familiar vs Own Odour

The subjects did not spend significantly different lengths of time investigating their own and familiar (same sex) odours (Table 5.2), nor did they show a preference for initially approaching one or other of the odours (Table 5.2). But for the first time throughout these experiments, the subjects responded to an odour by performing an anal drag (see Chapter 2). Six out of ten of the subjects anal dragged, always in the arena containing their own odour.

5.3.2.7 Experiment 7. Fresh vs Stale Odour

Eight ferrets were tested first to see if they would discriminate between fresh (collected within 10 minutes of the start of the trial) and two-hour old anal gland odour. Both samples came from the same female donor animal. They showed no discrimination between these two odours, neither in length of investigation nor initial choice, nor in scent marking. By contrast, when they were tested on fresh vs one-day old odour, all eight subjects spent longer sniffing at the fresh odour ($P \leqslant 0.004$ Table 5.2). Four out of eight chose each side to first investigate. For seven out of eight of the subjects, however this last experiment (fresh vs one-day old) was carried out in a different building from all the previous tests and six out of seven went to the right-hand arena first, giving a right side preference not seen in any previous experiments.

5.4 DISCUSSION

The odour discrimination abilities of ferrets, and their preferences for some odours over others demonstrated here support the terriorial defence and sex attraction functions of anal gland odours, and are in accord with the results of the chemical analysis of anal sac extracts (Chapter 4).

The fact that ferrets chose to investigate ferret odour first in preference to that of a closely related sympatric species indicates an ability to distinguish the odour of conspecifics from other mustelids. Sokolov and Rozhnov (1983) found that polecats discriminated between the urine of conspecifics and that of Mustela lutreola, but not between urine of polecats and ferrets. They also investigated the ability of polecats to discriminate between conspecific and other species "excrement". They reported that there was no significant difference in time spent sniffing the two odours and concluded that it was impossible to demonstrate any species information value in anal gland secretions and faeces. The present study similarly produced no difference in time spent sniffing odours of this species and another species (M. nivalis), but the additional response variable of initial choice of odour to approach gave a significant response criterion. Anal gland odour may thus form part of the polecat/ferret species recognition system.

The discrimination between male and female anal gland odours, in both the Y- and T-maze experiments, and the fact that males preferred female odour supports the sex attractant hypothesis. The important variables for discrimination were the speed of approach (in Y-maze tests) and choice of odour (in T-maze tests). Again there was no difference in length of time spent sniffing the different odours as was also found to be the case for polecats' responses to male and female excrement by Sokolov and Rozhnov (1983). They did find a difference in sniffing time of male polecats at male and female urine, there being a preference for female odour (c.f. Wheeler 1978). It seems likely then that both anal gland secretions and urine (or abdominal gland secretions?) convey information on the sex of the animal.

There were no significant differences in the responses of male subjects to the anal gland odour of oestrous and anoestrous females. This is not surprising, considering that no consistent differences were found in the major volatile components of oestrous and anoestrous anal gland secretions (Chapter 4). Sokolov and Rozhnov (1983) similarly found no difference in the time males spent sniffing urine or faeces from oestrous and anoestrous females. In the outside enclosure (see Chapter 2) the males, who come into breeding condition before females (Fitzgerald 1964, pers. obs.) attempted to mate with females before they were fully in oestrous. Thus males may not use any signal from the females to determine their receptivity. (see Emendation 3)

The results of experiments 5 and 6 support the territorial defence hypothesis. The fact that the ferrets discriminated not only on initial choice of odour but also on length of time spent sniffing the strange and familiar odours indicates that the discrimination between neighbours and intruders may be an important function of anal gland odour. In the familiar versus own odour tests, neither of these responses proved useful discriminating criteria. This may be due to a lack of motivation to investigate either of these familiar odours more than the other. The fact that the subjects anal dragged only in response to their own odour does, however, suggest some ability to recognise one's own odour. It could be confirmed by reinforcement-training tests. Sokolov and Rozhnov (1983) found that male polecats discriminate between familiar and strange urine, spending more time sniffing the strange urine. They did not test polecats'

abilities to discriminate between familiar and strange excrement.

Stoddart (1980) expressed the opinion that discrimination of individuals through scent probably occurs in all macrosmatic vertebrate species. Many species, however, produce more than one type of scent, and not all of them may carry information on individual identity. For example the African Dwarf Mongoose, Helogale undulata, can distinguish between anal gland odour from different individuals but not between different cheek odours (Rasa 1973). In the ferret, anal gland odour appears to carry this information, but odour derived from the chin region may not (Wildhaber 1984).

The familiar/strange preference tests carried out on ferrets are equivalent to the habituation-preference tests used by other workers (Halpin 1974, Harrington 1976). In these tests Mongolian gerbils (Meriones unguiculatus), and lemurs (Lemur fulvus) were habituated to one strange odour for a certain time period and then presented with that odour and/or a second strange odour. A preference to sniff at the second odour indicated an ability to discriminate between the two. In the ferret tests the subjects had been habituated to the 'familiar' odour by living in adjacent cages (or the same cage) for a number of months, and they had never been exposed to the 'strange' odour. None of these tests can tell us if animals can recognise others as individuals by odour, only that they can classify familiar (neighbouring) animals as different from strange (intruding) animals. Reinforcement tests, using animals trained to discriminate between a number of odours of equal familiarity would be necessary to resolve this question. Such experiments have shown abilities to discriminate amongst familiar odours in the Dwarf Mongoose (Rasa 1973), the Indian Mongoose (Gorman 1976), the badger (Gorman et al. 1984) and the European otter (Trowbridge 1983).

Ferrets possess the ability to discriminate between fresh and one-day old anal gland odour (experiment 7). The fact that they showed no difference in time spent sniffing the fresh and two-hour old odours, nor in initial choice of these odours does not negate the possibility that they can discriminate between them, it only shows that they do not show different reactions to them. Determination of their limits of discrimination between odours of closer ages would require

reinforcement-training tests. This procedure was used by Rasa (1973) to show that a Dwarf Mongoose could discriminate between 'fresh', one-hour old and two-hour old anal gland odours.

In the ferret preference tests, the initial choice of odour proved to be the more useful measure of preference. Ferrets may be able to assimilate rapidly the information content of scent marks, thus as Halpin (1974) suggested, their responses to odours may happen rapidly, and further responses would be superfluous. This possibility is supported by observations of the ferrets in the outside enclosure (see Chapter 2), where they would approach and briefly sniff at defaecation and anal drag sites (and other scent marks), and then immediately either move away or scent mark over the existing mark.

The preference test method using Y- or T-mazes has its limitations. As already discussed, it does not allow the demonstration of discrimination between odours to which animals naturally show no preference. The Y-maze used in the preliminary trials proved unsatisfactory in that it was too cramped for the animals (especially the males) to move around normally. It was also limited in the response variables that could be measured. The T-maze allowed free movements by the subjects, and both length of time spent sniffing at the odours and scent marking behaviour could be observed and quantified. The main problem with the T-maze was that although a stream of air was being sucked through the apparatus, this air originated from opposite sides of the experiment room, and impurities may have been introduced with one or other of the odours. This seems to have been a real possibility in experiment 7, where the last seven trials were carried out in a different experiment room and six out of seven of the subjects chose the right hand arena to investigate first. It should also be noted that the experiments were run with the observer aware of which odour was on each side. Although this may have biased how the observer recorded the data it could not have biased how the animals responded - they could not have been using any cues from the observer as to right and wrong responses because they were not being reinforced for their responses. The use of an automatic recorder such as photoelectric cells or mechanical trip devices (Doty 1975, Salmon and Marsh 1977) would have removed any potential biases in data collection, however if an observer had not been present the scent

marking behaviour in experiment 6 would have gone unnoticed.

A problem common to both experimental set-ups was in the concentration of odours used. These were not accurately quantified; a smear of a certain size on a piece of filterpaper was the standard odour sample. This produced an odour just perceptible to the human nose, but may have been stronger than that normally set down by anal dragging. This problem of accurate repeatable presentation of an appropriate odour concentration is a fault common to many published preference test studies.

A criticism of any highly controlled laboratory experiment on odour discrimination was given by Johnston (1977), who pointed out that such experiments can tell us only what effects a signal can have in these prescribed situations, not what effects it does have within the context of the species' total behavioural repertoire. The testing of what effects odours do have on ferrets in more complex situations is the subject of the next chapter.

Chapter 6
CONFIDENCE ASSESSMENT TESTS

> "It is often not appreciated that for each chemical secretion suspected of having communication functions a great deal of behavioural work needs to be done in order to understand these functions." -Johnston 1977

6.1 INTRODUCTION

The results of observational, histological, chemical and experimental studies presented in the previous chapters support the territory defence hypothesis put forward in Chapter 1. Anal gland scent marks and body odours may enhance the confidence of territory-holders, intimidate intruders and mediate spacing systems by neighbour-neighbour recognition. The results so far are also consistent with the scent matching mechanism. These roles for scent marks can now be tested further by manipulation experiments in controlled conditions.

One of the predictions from Hypothesis 1 (scent marks provide an olfactory association between a resident and its defended area) is that an animal should be more "confident" when in the presence of its own scent marks than when in the presence of those of other animals. This concept of territorial confidence could be quantified as the likelihood of an animal escalating an encounter to actual combat, but could also take the form of more subtle behavioural traits. The predisposition of an animal on its home ground to win an agonistic encounter is well known. Poole (1973) found that when ferrets or ferret/polecat hybrids were introduced into a neutral area, those first introduced where more likely to win subsequent fights. Erlinge (1977) similarly found that "established" stoats dominated "introduced" ones. Eibl-Eibesfeldt (1950) showed experimentally that badgers were calmed in unfamiliar terrain by their own fresh scent marks. To test the effect scent marks have on this territorial confidence, Mykytowycz *et al*. (1976) placed pairs of European wild rabbits in a neutral area in the presence of various odours. They found that the rabbits were most confident in the presence of their own chin odour, and to a lesser extent anal odour, than in the presence of odours from other rabbits.

If scent matching is the mechanism by which territorial confidence/intimidation is determined, one would expect not only that an animal would be most confident in the presence of its own scent marks, but also that an animal would show least confidence (or least likelihood to fight) when the scent marks encountered match the body odour of his opponent. If, on the other hand, scent marks are used to recognise neighbours, then an animal's confidence will depend on the relative dominance status of the various individual odour donors. If the opponent is a subordinate animal and the odour donor a dominant animal then the predictions from the two mechanisms will be quite different. If scent matching occurs, the subject will be least confident in the presence of scent marks of the opponent, but if the subject recognises scent marks as belonging to particular, known individuals, it will be least confident in the presence of the third animal's scent marks.

Experiments such as those conducted by Mykytowycz et al.(1976) can be used to investigate these various hypothesised functions of ferret anal gland scent marks and body odours. Quantifying animals' responses to odours requires the use of some measurable forms of behaviour, and familiarity with details of behaviour of the species (Mykytowycz et al. 1976). Such detailed information on ferret behaviour is given by Poole (1972a, 1973, 1974). When allowed to interact during the breeding season, male ferrets will fight and develop a hierarchical ranking. Poole (1973, 1974) used ciné film recordings of fighting behaviour to observe and describe all the actions and postures used by ferrets of various status while interacting with each other. In addition to these active behaviours, the general deportment of ferrets can be easily observed in controlled laboratory conditions. The aim of this chapter is, using the available knowledge of ferret behaviour, to investigate the spontaneous responses of ferrets to scent marks, in order to test predictions from the hypothesised territorial defence function of ferret anal gland odours.

6.2 METHODS

6.2.1 Subjects and Apparatus

Five adult male ferrets were the subjects of these confidence assessment tests. With the exception of Snark and Hans, they had never

indoors

before come into physical contact. The experiments were carried out in an open arena made of particleboard (Fig. 6.1) and lit from above by fluorescent lights. Two start-boxes were attached to one side of the arena, and were closed by either wire mesh or solid doors (see below). A fan blew air from the far side of the arena towards the start-boxes. The observer sat on a chair between the two start-boxes.

6.2.2 Dominance Assessment Tests

Subjects were tested in pairs, with all ten pair combinations being used to determine dominance ranks without any odour being present. Two trials were conducted per day, and three or four days elapsed between experimental days. A subject was placed in each start-box with the wire mesh door in place, and left for one minute. The doors were then opened simultaneously, allowing the ferrets free access to the arena and to each other. The ferrets were observed for the next ten minutes, and records were made of the number of times one ferret approached another, the number of chases, attacks (either lunge or oblique attacks, see Poole 1974) and the number of defensive actions, that included ward off, back away, and extricate, as defined by Poole (1974), and running away. Length of time spent fighting, intensity of fighting, the instigator and winner of fights were also noted. Records were made on a cassette tape recorder, a noise that the ferrets ignored. At the end of the ten minute trial, (unless the ferrets had to be separated prematurely to prevent severe injury to one or the other), the subjects were removed and the floor and walls of the arena cleaned with water and chlorine bleach. The tape was transcribed and the ferrets assigned an aggression score as devised by Poole (1972). This consisted of scoring either two for a high intensity attack, one for a low intensity attack, or zero for not being the instigator, two for high intensity fighting, one for low intensity fighting, or zero for no fighting, and one for not being intimidated at the end of the trial, or zero for being intimidated. Thus the scores could range from zero to five. General levels of aggression during the trial were also noted - animals could be classified as showing high or low intensity aggression, no aggression, aversive defensive or fearful defensive behaviour. Dominance relationships between the pairs were thus determined. In any one trial a ferret could be dominant, equal, intimidated submissive or fearful submissive, and a rank order for the five ferrets was formed.

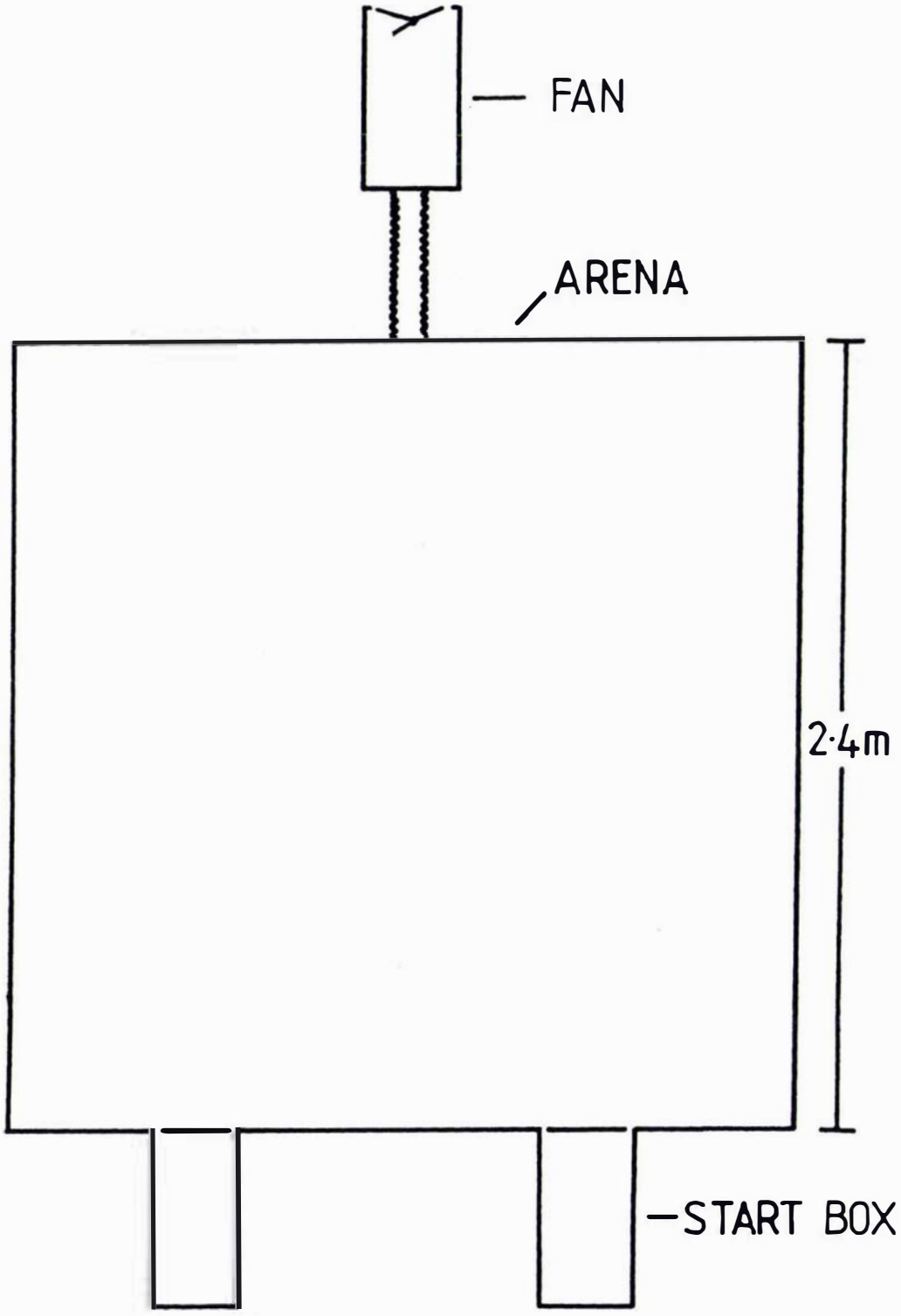


Figure 6.1: Arena used in dominance and confidence assessment tests.

6.2.3 Odour Tests

Odour samples were collected by expressing anal gland secretion as described in Chapter 5, and smearing a just visible amount onto two pieces of filterpaper. These odour samples were placed into the arena, one about 25 cm in front of each start-box. The fan was started and the two subjects placed in the start-boxes, with the wire mesh doors in place. After one minute the solid doors were put in place to seal off the start-boxes and the two ferrets placed manually in the arena simultaneously. This avoided the problem of one ferret not emerging from the start-box. The same observations were made as in the dominance assessment trials. In addition, the general deportment, including postures and level of activity, was noted. Later these observations were used to calculate a confidence score for each animal, using a scale from one to ten, as shown in Table 6.1.

TABLE 6.1

Scale of "confidence" used in the odour trials. The behavioural terms are those defined by Poole (1972).

1.	Fearful defensive and releasing anal gland odour.
2.	Fearful defensive, no odour release.
3.	Aversive defensive and trying to escape from arena.
4.	Aversive defensive and evading opponent.
5.	Deterrent defensive, evasive, watchful, uneasy.
6.	Evasive but moving confidently.
7.	Moving confidently or lying relaxed, not evasive.
8.	Moving confidently, brief, low intensity aggression.
9.	Moving confidently, delayed, high intensity aggression.
10.	Confident, immediate high intensity aggression.

Each ferret was tested three times with each of the other subjects, once in the presence of his own anal gland odour, once with his opponent's odour, and once with odour from the most dominant of the subjects not involved in the test. For half the replicates the odour of the more dominant of the pair was used in the first trial, and for the other half the odour of the subordinate was the first odour tested.

Six pairs were then tested in the presence of the odour of the other member of the pair and four with the dominant "other" odour, and vice versa in trial 3. Data were analysed using the Wilcoxon's matched-pairs signed-rank test, assuming independence amongst pairs.

6.3 RESULTS

6.3.1 Dominance Assessment Tests

In the preliminary trials without odour, high levels of aggression often occurred.

Individual Hans was clearly the most dominant, always showing aggressive behaviour, and individual Kupe never won an encounter. Bandit was never an aggressor, but was never intimidated. Although there was no dominant/submissive relationship between Bandit and Snark or between Snark and Ayya, the rank order amongst these three was determined because Bandit dominated Ayya (Table 6.2).

6.3.2 Odour Tests

The ferrets were significantly less confident in the presence of their opponent's odour than in the presence of their own odour ($P \leq 0.005$, Table 6.3), but there was no significant difference between their levels of confidence in the presence of their own and the other (dominant individual's) odour (Table 6.3). When comparing their levels of confidence in the presence of the opponent's odour and the other odour, the subjects were less confident in the presence of the opponent's odour ($P \leq 0.021$, Table 6.3). When only the responses of subjects to subordinate opponent odour and dominant other odour are compared, the trend remains but the sample size becomes too small to show any significant result (Table 6.3). Overall then, it was the presence of the opponent's odour that made the subjects less confident, rather than the presence of their own odour making them more confident.

The levels of aggression were lower in all the odour trials than in the preliminary trials. There was a similar trend as in the confidence scores, with the subjects showing more aggression in the presence of their own odour than in the presence of their opponent's odour ($P \leq 0.05$, Table 6.4)[1]. There was no significant difference between their aggression scores in the other comparisons (opponent vs other, own vs other, Table 6.4).

1. This result was due mainly to the responses of Hans and Bandit.

TABLE 6.2

Results of dominant assessment tests, with no odour.

HIA=high intensity aggression
LIA=low intensity aggression
NA=non-aggressive
AD=aversive defensive
FD=fearful defensive
D=dominant
E=equal
IS=intimidated submissive
FS=fearful submissive

SUBJECT	OPPONENT	AGONISTIC BEHAVIOUR	AGGRESSION SCORE	DOMINANCE RANK	ANAL ODOUR RELEASE
HANS	BANDIT	HIA	5	D	X
	SNARK	HIA	5	D	X
	AYYA	LIA	2	D	X
	KUPE	HIA	5	D	X
BANDIT	HANS	FD	1	FS	✓
	SNARK	NA	1	E	X
	AYYA	LIA	1	D	X
	KUPE	NA	1	E	X
SNARK	HANS	FD	1	FS	X
	BANDIT	NA	1	E	X
	AYYA	NA	1	E	X
	KUPE	HIA	5	D	X
AYYA	HANS	AD	2	IS	X
	BANDIT	FD	0	FS	✓
	SNARK	NA	1	E	X
	KUPE	HIA	5	D	X
KUPE	HANS	HIA/AD	2	IS	X
	BANDIT	NA	1	E	X
	SNARK	AD	1	IS	X
	AYYA	FD	1	FS	✓

TABLE 6.3

Confidence scores of subjects in the three odour trials.

SUBJECT	OPPONENT	OWN ODOUR	OPPONENT ODOUR	OTHER ODOUR
HANS	BANDIT	8	7	7
	SNARK	10	9	9
	AYYA	7	7	7
	KUPE	8	8	7
BANDIT	HANS	7	3	5
	SNARK	6	6	7
	AYYA	6	5	6
	KUPE	7	6	7
SNARK	HANS	3	2	2
	BANDIT	7	5	5
	AYYA	7	7	7
	KUPE	8	8	9
AYYA	HANS	4	5	6
	BANDIT	7	6	6
	SNARK	7	5	5
	KUPE	7	5	6
KUPE	HANS	5	4	5
	BANDIT	5	5	5
	SNARK	4	2	1
	AYYA	5	5	7

COMPARISON	n	Ts	SIGNIFICANCE
OWN/OPPONENT	13	4.5	$P \leq 0.005$
OWN/OTHER	14	31.0	N.S.
OPPONENT/OTHER	11	10.0	$P \leq 0.021$
SUBORDINATE OPP/ DOMINANT OTHER	6	3.5	N.S.

TABLE 6.4

Aggression scores of subjects in the three odour trials.

SUBJECT	OPPONENT	OWN ODOUR	OPPONENT ODOUR	OTHER ODOUR
HANS	BANDIT	3	1	1
	SNARK	5	4	5
	AYYA	1	1	1
	KUPE	4	2	1
BANDIT	HANS	1	0	1
	SNARK	1	0	1
	AYYA	4	1	1
	KUPE	1	1	1
SNARK	HANS	0	0	0
	BANDIT	1	1	1
	AYYA	1	1	1
	KUPE	4	5	3
AYYA	HANS	0	1	1
	BANDIT	1	1	1
	SNARK	1	0	1
	KUPE	1	1	1
KUPE	HANS	0	0	0
	BANDIT	1	1	1
	SNARK	0	0	1
	AYYA	1	1	1

COMPARISON	n	Ts	SIGNIFICANCE
OWN/OPPONENT	9	8	$P \leq 0.05$
OWN/OTHER	6	4	N.S.
OPPONENT/OTHER	6	9	N.S.
SUBORDINATE OPP/ DOMINANT OTHER	4	4	N.S.

6.4 DISCUSSION

The preliminary trials without odour allowed the subjects to establish dominance relationships, and identified the odour donor for the dominant "other" odour in the odour trials. They also ensured that the subjects had had physical contact with each of their opponents before the first odour trial was run. Without these preliminary trials, much higher levels of aggression may have occurred in the first odour trial, confounding the effect of order of the trials with the effect of the odours.

The results of the odour trials reinforce the findings of Chapter 5 concerning the abilities of ferrets to discriminate between anal gland odours of different individuals, including the ability to recognise their own and another odour. The fact that they were more confident in the presence of their own odour than their opponent's odour supports the hypothesis that odours act as an olfactory association between a resident and its defended area, enhancing territorial confidence or intimidating intruders. The scent matching mechanism by which this system could operate is also supported by the results of the comparison of responses to opponent and other odours, with the prediction that animals would be intimidated when scent marks match the body odours of the animals they meet. The prediction from the neighbour-neighbour recognition system was the opposite, that ferrets would recognise the odour of the other, dominant animal, and be less confident when this was present than when the odour of a subordinate opponent was present, and this was not supported. The fact that the subjects were no less confident in the presence of the other odour than in the presence of their own odour suggests that they were not recognising the odours of known individuals. It indirectly supports the scent matching idea, which predicts that animals will not be intimidated when the scent marks do not match their opponent's body odour.

The scent matching and neighbour-neighbour recognition mechanisms are not mutually exclusive; both may be operating, with the scent matching system overriding the recognition system when an opponent is in close proximity, as in these trials. A further test of the neighbour-neighbour recognition system would be to present single subjects, without opponents, with their own, a subordinate and a

dominant odour from known individuals, and examine their differences in confidence levels. This alternative approach would also rule out one possible biasing factor in the paired tests, that of the subjects' responding to the changed behaviour of their opponents rather than to the odour directly. This possible bias does not negate the fact that odours are responsible for the changes in behaviour, but makes it impossible to say whether their effects are to increase the confidence of the odour donor, or to decrease the confidence of the opponent.

Another possible methodological problem is that the trials were not run blind, that is, the observer was aware of the identity of both the ferrets and the source of the odour. However the confidence scores and aggression scores of the subjects in earlier trials were not known, so it is unlikely that there were any biases in recording of the data.

The results of these experiments thus support the suggestion that anal gland odours are important in mediating social organisation. The olfactory association hypothesis and scent matching mechanism are supported, while the neighbour-neighbour recognition mechanism should not be dismissed without further testing.

Chapter 7
BIOASSAY OF COMPONENTS OF ANAL GLAND SECRETIONS

"The best possible outcome of a bioassay is the elicitation of a specific behavior pattern by a defined chemical stimulus."-Müller-Schwarze 1977

7.1 INTRODUCTION

One of the main aims of this research was to determine how ferret anal gland odours could be incorporated into mustelid control methods. The previous chapters have shown that ferrets do investigate anal gland odours and that these odours are important in intraspecific communication. This suggests that they could be used as attractants to bring ferrets to control devices. If some components of anal gland secretions are strong enough attractants on their own, then a synthetic trap lure could be a viable alternative to edible bait for trapping mustelids.

A bioassay procedure is required to show which components of anal gland odours act to attract ferrets. The bioassay was defined by O'Connell (1977) as "a test procedure which endeavours to use the occurrence of a unique behavioural or physiological response to evaluate the various steps involved in the chemical fractionation, isolation, and identification of the active compounds which occur in an animal's chemical communication system." Initially developed by entomologists, the procedure has been successfully used to isolate sex pheromones in insects, which have been used in biological control programmes against damage to crops (e.g. Beroza 1976). Recently, mammalogists have adopted the technique for investigating the concept of pheromones in mammals. They quickly found that mammals, unlike insects, do not respond in a stereotyped manner to specific chemical stimuli (see O'Connell 1977, Müller-Schwarze 1977, Shumake 1977). Factors such as the exact environment and behavioural situation in which the bioassay is performed, previous experience, hormonal levels, and social dominance of the animal can all affect its responses to the chemical stimulus.

Despite all these confusing factors, researchers have demonstrated the biological activity of particular chemicals in a variety of species, for example the attractiveness to males of dimethyl sulphide in the vaginal secretion of the golden hamster (Singer et al. 1976), acidic fractions of oestrous coyote (Canis latrans) urine, (Murphy et al. 1978), and isovaleric acid in the pronghorn, Antilocapra americana, (Müller-Schwarze et al. 1974). Preti et al. (1977) and Müller-Schwarze (1977) give further examples.

O'Connell (1977) stated: "it is axiomatic that there should first be some certitude about the fact that chemical signals are involved in modulating an animal's behaviour". The detailed background information on behavioural responses of ferrets to anal gland odours needed to give this certitude has been described in previous chapters. Also available (from Crump 1980b and Chapter 4) is the information on the chemical composition of anal gland odours necessary for a bioassay procedure to be developed.

O'Connell (1977) suggested three basic dicta to be followed when designing a bioassay:

1. Care must be taken to maintain the chemical stimuli in their pristine form.
2. The delivery of these signals should mimic as closely as possible the natural route of application.
3. The most specific biological response appropriate to the chemical signals should be used as a response criterion.

Ideally a bioassay would be carried out in the field, but this is seldom practical (see Müller-Schwarze 1977), especially for a nocturnal, wide-ranging animal of fossorial habit such as the ferret. In addition, it is impossible to control many variables such as changes in environmental conditions in such field experiments. Although results of laboratory experiments are limited in their application to wild animals, they can provide preliminary information collected under well-controlled conditions that can be used as a basis for further studies in the field. The aim of this chapter then, is to give information on the relative attractiveness to ferrets of various compounds in their anal gland secretions, using a well-controlled bioassay procedure.

7.2 METHODS

7.2.1 Subjects and Apparatus

Ten or twelve subject ferrets were used in each bioassay experiment. These experiments used the T-maze (see Chapter 5), set up in the same way as for the preference tests.

7.2.2 Odour Compounds

The sulphur-containing compounds were synthesised by D.R. Crump, according to the procedure described by him (1980a), and stored in sealed glass ampules. Quinoline and indole were obtained "off the shelf" from the Chemistry Stores of Massey University, and Applied Biochemistry Division, D.S.I.R. All these pure compounds were diluted with hexane[1] to a ratio of one part odour compound to five parts hexane. For the combinations of two odour compounds the ratio was 1:1:10. These made-up solutions were kept in 1 ml capacity teflon-sealed glass vials, and stored at -10° C.

7.2.3 Experimental Procedure

Bioassay experiments were all conducted between 8am and 5pm. Only three trials (two a.m., one p.m.) were done on any one day, and each animal was tested no more than once every four days. The general experimental procedure was the same as for the odour preference tests of Chapter 5. The subject was given five minutes in the start-box while five µl of the odour solution was mixed with two drops of diethylene glycol succinate (DEGS) to prevent too rapid evaporation, and spread on a piece of filterpaper. This odour sample was then placed in one of the odour containers, chosen at random, and a blank (filterpaper plus DEGS and hexane) in the other container. Thirty seconds elapsed before the door was raised and timing began. The time the subject took to approach and sniff at the odour, and the total time spent sniffing the odour and the blank during the 15-minute trial were recorded, along with the animal's initial choice of odour port. At the end of the trial the animal was removed and the apparatus cleaned using chlorine bleach and water. At least four hours separated one trial from the next, allowing time for the apparatus to dry out completely.

1. Hexane was a solvent of appropriate volatility.

7.2.4 Experimental Design

The odours were bioassayed in the order in which they became available (Table 7.1). Each animal was tested against all the odour combinations. Experiments 1 to 3 were Latin square designs, fully balanced to avoid residual effects of order of presentation of the odours and odour/blank positions were randomised to account for right/left preferences. In experiment 4 only three odour combinations were tested, not allowing a fully balanced design.

The time data were ranked, then normalised and subjected to a 3-way analysis of variance (see Appendix 7) to explain the effects on responses of the sex of the subjects, the odour that they were tested against and the order in which they were tested. A covariate was included in the subject stratum of the analysis to account for the differences in tameness/age of the various subjects. Tukey's multiple range tests were used to determine which odour responses differed significantly from each other.

7.3 RESULTS

7.3.1 Experiment 1

In experiment 1, which compared the attractiveness of compounds 2 and 3, compound 4 and compound 9, and combinations of these, there were significant differences amongst the time spent sniffing at the various odours ($P \leqslant 0.0005$, Fig. 7.1a). Males and females did not respond differently, nor was the interaction between odour and sex a significant factor, but the covariate for tameness explained a significant amount of the variation in the subjects' responses ($P < 0.01$). The combination of compounds 2+3 and 4 was the most attractive overall and to both males and females separately. It was significantly more attractive than all the other odours except for compound 4 on its own, while compound 4 was significantly different from compound 9 only ($P < 0.005$, Fig. 7.1a). There was no tendency to first investigate one side (right or left) over the other (Table 7.2). Comparing the time spent investigating the odour port and the blank port, with 2+3+4, 4 and 2+3 the subjects spent significantly longer at the odour port ($P \leqslant 0.01$, $P \leqslant 0.05$, $P < 0.014$ respectively, Wilcoxon), showed no preference for odour or blank with 2+3+9 and 4+9, and spent longer at the blank than with compound 9 ($P < 0.024$, Wilcoxon, Fig. 7.1a).

TABLE 7.1

Combinations of synthetic compounds used in the bioassay experiments.

EXPT	COMBINATIONS OF COMPOUNDS	CHEMICAL NAMES
1	2+3	trans- and cis-2,3-dimethylthietane
	4	2-propylthietane
	9	3-propyl-1,2-dithiolane
	2+3+4	
	2+3+9	
	4+9	
2	2+3+4	
	I	indole
	Q	quinoline
	B	blank
	2+3+4+I	
	2+3+4+Q	
3	2+3+4	
	1	2,2-dimethylthietane
	6+7	trans- and cis-3,4-dimethyl-1,2-dithiolane
	1+2+3+4	
	2+3+4+6+7	
	1+6+7	
4	2+3+4	
	8	2-pentylthietane
	2+3+4+8	

Figure 7.1: Subjects' responses to odours in bioassay experiment 1. Data are untransformed means (±SE).

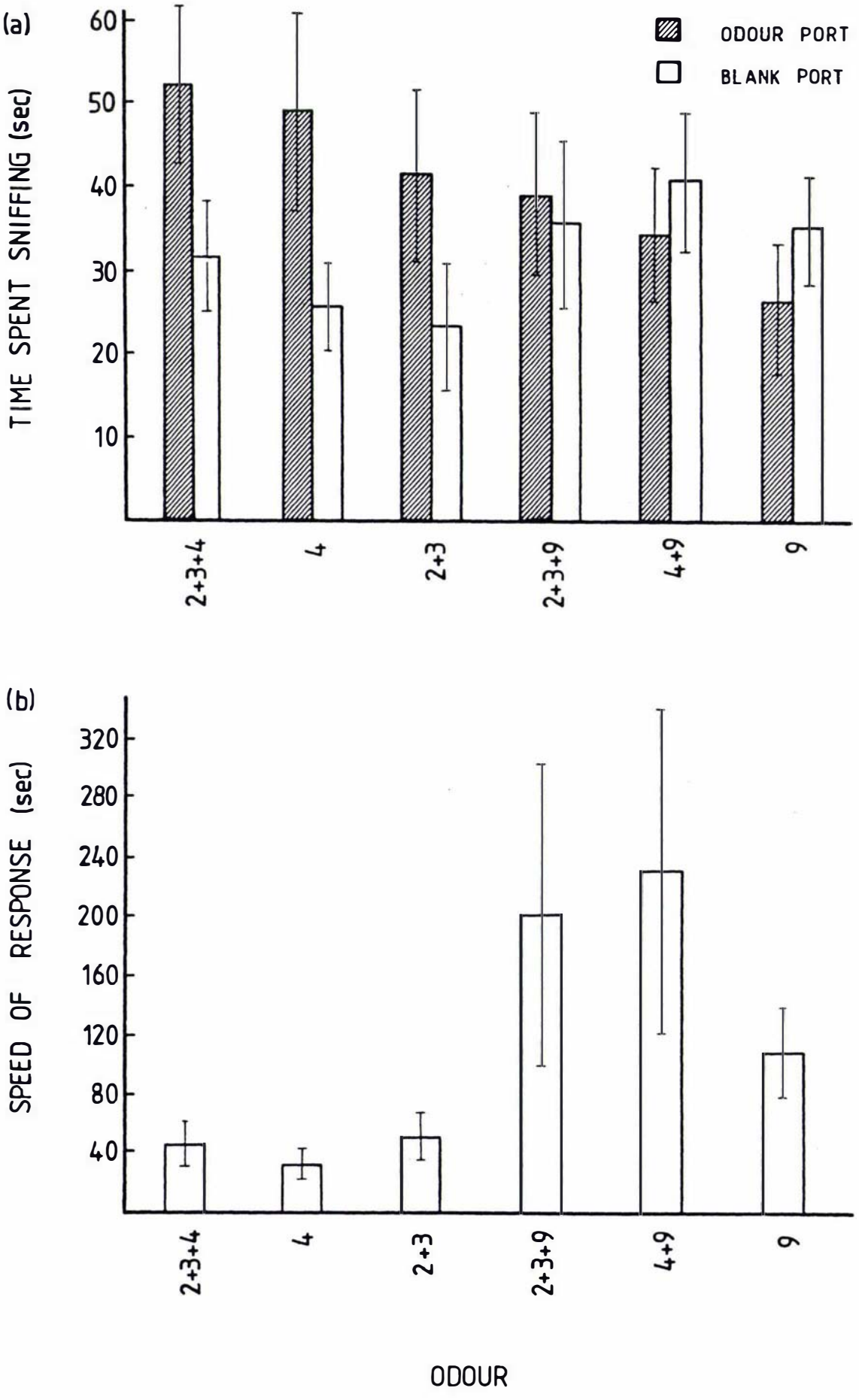

(a)
TIME SPENT SNIFFING (sec)
60
50
40
30
20
10
ODOUR PORT
BLANK PORT
2+3+4
4
2+3
2+3+9
4+9
9
(b)
SPEED OF RESPONSE (sec)
320
280
240
200
160
120
80
40
2+3+4
4
2+3
2+3+9
4+9
9
ODOUR

TABLE 7.2

Initial right/left preferences shown by the subjects in the bioassay experiments. Statistical comparisons are the χ^2 goodness-of-fit test.

EXPT	NO. CHOOSING LEFT ODOUR PORT	NO. CHOOSING RIGHT ODOUR PORT	SIGNIFICANCE
1	28	28	N.S.
2	11	36	$P<0.001$
3	19	38	$P<0.025$
4	11	16	N.S.

There were also significant differences amongst the subjects' speeds of approach to the various odours ($P<0.005$, Fig. 7.1b). Males and females did not, overall, show differences in speed of responses, even when the differences in tameness/age were accounted for, but responded differently to different odours ($P<0.0025$). Overall, it was again 2+3 and 4 combined that provided the most attractive odour, although the speed of response to this combination differed significantly only to that of compound 9 ($P<0.025$) and 4+9 ($P<0.05$). Responses were also significantly faster to 4 than to 9 ($P<0.05$). Males and females differed in that males responded relatively faster to compound 9 and slower to 2+3+9 than did the females. The order of presentation did not affect the relative attractiveness of the odours on either of the response criteria (Appendix 7).

7.3.2 Experiment 2

The second bioassay experiment tested the attractiveness of Q and I, the addition of these to the combination of 2+3+4, and the subjects' responses when there was no odour at either end (B). No simple pattern of reponses emerged. There was a significant difference in the time spent sniffing the different odours ($P<0.005$), with 2+3+4 and I being significantly more attractive than B ($P<0.01$) and 2+3+4+I ($P<0.025$, Fig. 7.2a). Males and females found different odours more attractive ($P<0.001$). For the females, the addition of Q to 2+3+4 reduced its attractiveness to less than that of the blank filterpaper (but not

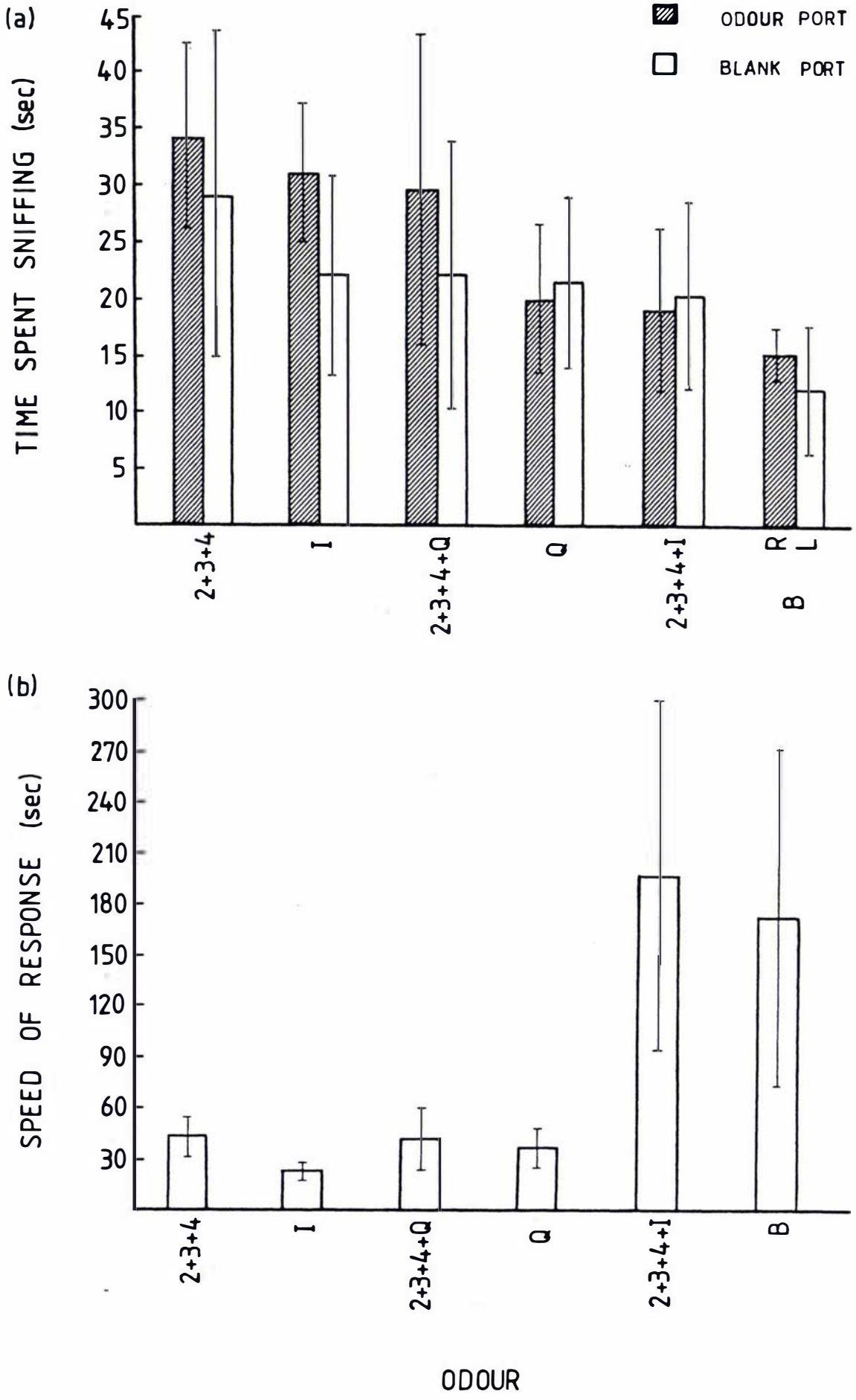
significantly so) and Q on its own was less attractive still, however the addition of I did not cause this drop in attractivenes. In the males, 2+3+4+I was no more attractive than the blank, and these two were significantly less attractive than I ($P<0.001$), 2+3+4 ($P\leq0.01$) and Q ($P<0.025$). There was no difference in the time spent at the odour and blank ports for any of the odours tested (Fig. 7.2a).

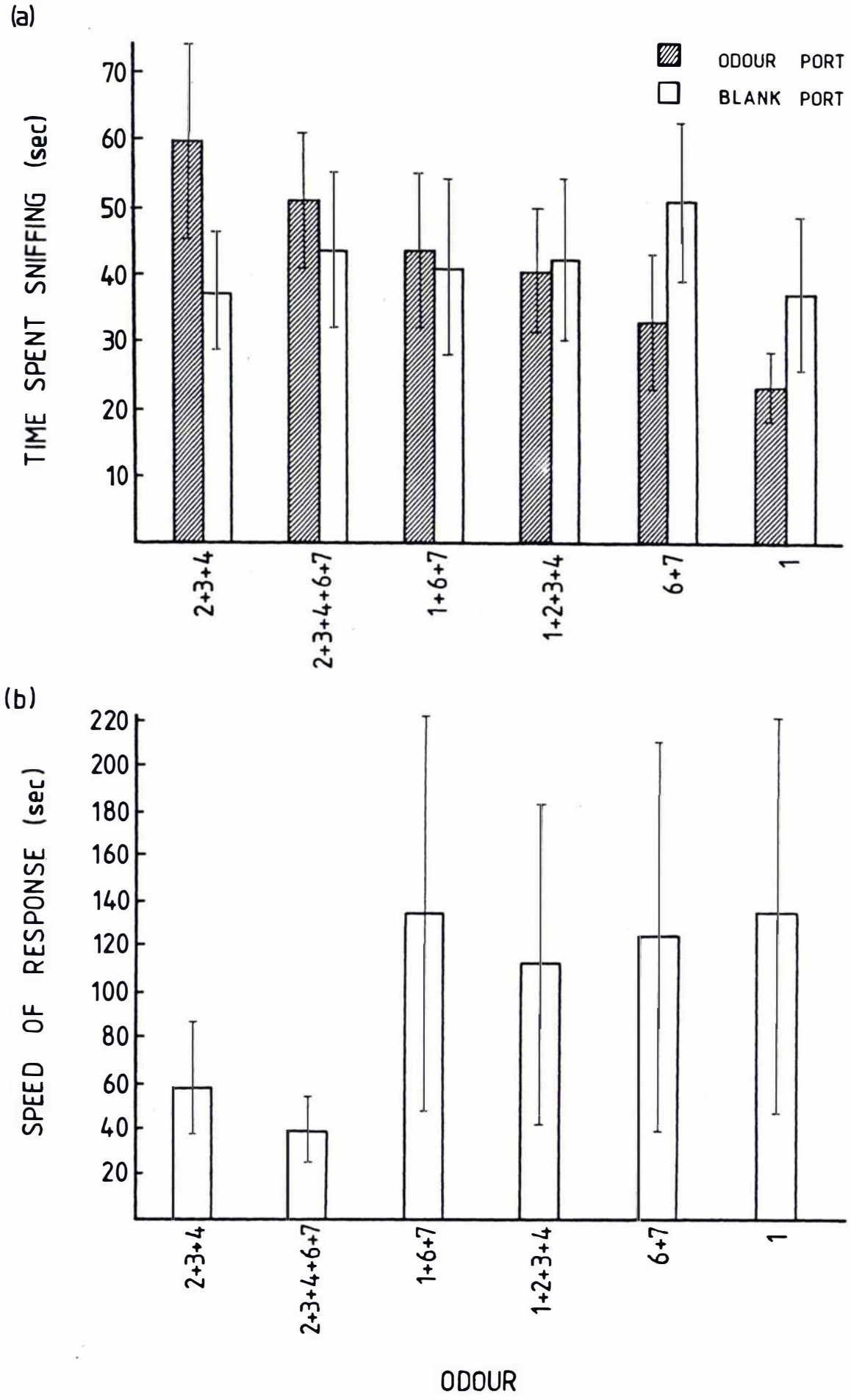
In terms of speed of response, females responded significantly faster than males ($P<0.025$) and there was no significant effect of tameness/age of the subjects. Overall, there were significant differences in the subjects' speeds of response to the various odours ($P<0.005$), due mainly to a rapid response to I compared to 2+3+4+I ($P\leq0.01$) and the blank ($P\leq0.025$, Fig. 7.2b). Males and females responded at different speeds depending upon the odour being tested ($P<0.05$), with the males responding relatively faster to Q than did the females. Order of odour presentation was not an important factor determining either the time spent sniffing the odours or speed of response, but the subjects showed a tendency to first investigate the right odour port ($P<0.001$, Table 7.2).

7.3.3 Experiment 3

Experiment 3 tested the attractiveness of compounds 1 and 6+7 (see Table 7.1) compared to 2+3+4 and the various combinations of these. The subjects spent significantly different lengths of time sniffing the different odours ($P<0.025$). The sexes did not differ significantly, nor was there a significant sex/odour interaction, but the young tame animals spent significantly longer at the odours than did the adults ($P<0.01$). The most attractive odour was again 2+3+4, but this was significantly greater than compound 1 only ($P<0.025$, Fig. 7.3a), and none of the other compounds varied significantly from each other. The subjects showed no preferences for sniffing longer at the odour or the blank ports (Fig. 7.3a). There were no significant differences in the subjects' speeds of response in experiment 3 (Fig. 7.3b). Order of presentation did not affect the subjects' responses to the odours, but as in experiment 2, the subjects preferred to first investigate the right odour port ($P\leq0.025$, Table 7.2).

Figure 7.3: Subjects' responses to odours in bioassay experiment 3. Data are untransformed means (±SE).


(a)
TIME SPENT SNIFFING (sec)
45
40
35
30
25
20
15
10
5
ODOUR PORT
BLANK PORT
2+3+4
I
2+3+4+Q
Q
2+3+4+I
R
L
B
(b)
SPEED OF RESPONSE (sec)
300
270
240
210
180
150
120
90
60
30
2+3+4
I
2+3+4+Q
Q
2+3+4+I
B
ODOUR


(a)
TIME SPENT SNIFFING (sec)
70
60
50
40
30
20
10
ODOUR PORT
BLANK PORT
2+3+4
2+3+4+6+7
1+6+7
1+2+3+4
6+7
1
(b)
SPEED OF RESPONSE (sec)
220
200
180
160
140
120
100
80
60
40
20
2+3+4
2+3+4+6+7
1+6+7
1+2+3+4
6+7
1
ODOUR

7.3.4 Experiment 4

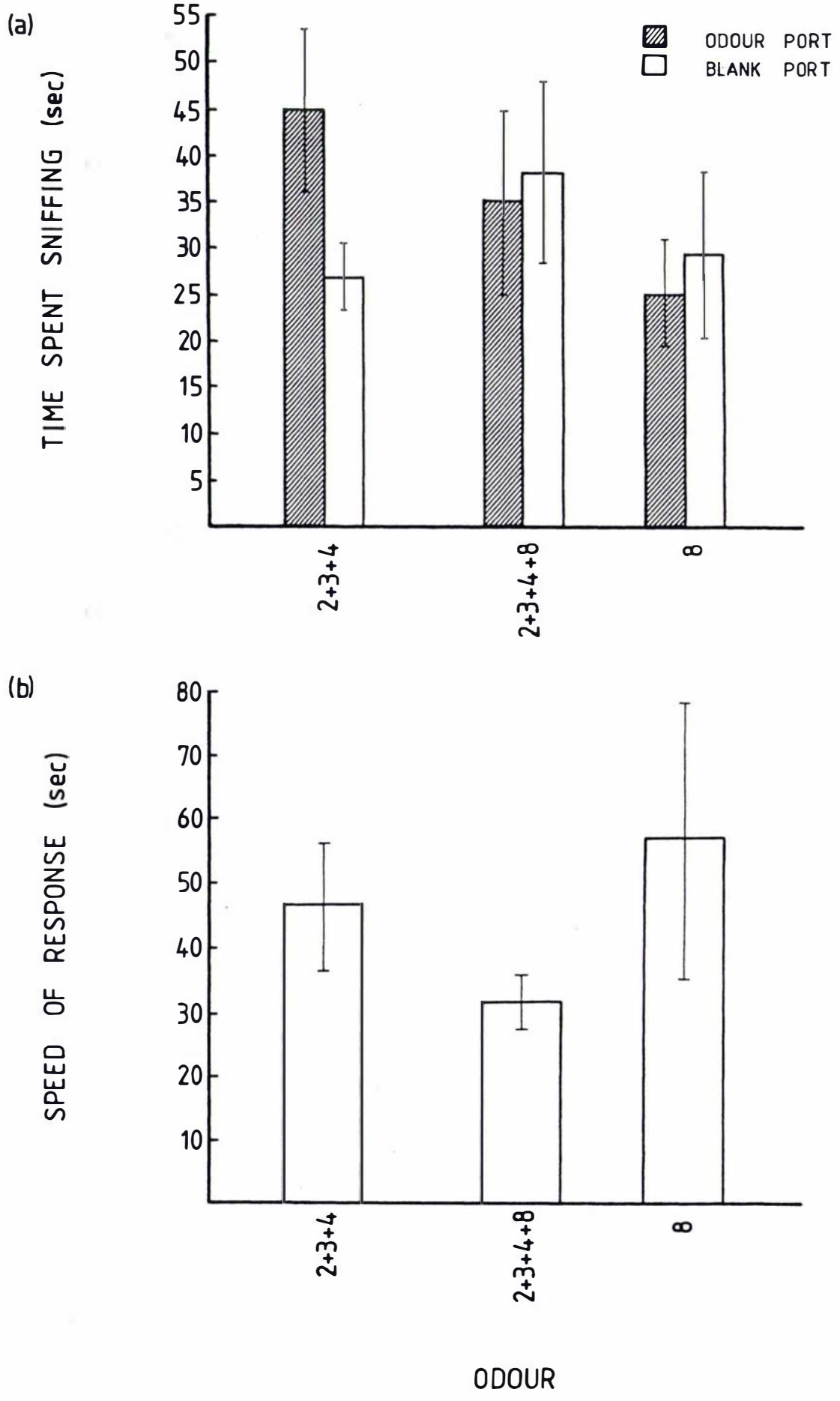
In experiment 4, only three odours were compared 2+3+4, 8 and 2+3+4+8, (Table 7.1). With the results of the males' and females' responses combined, no significant differences in attractiveness were found, either in the time spent sniffing the odours, or in speed of response (Fig. 7.4a,b). Looking at the male and female data separately, differences in responses to the odours were still not significant, but there was a tendency for the subjects to be less attracted to compound 8 than compound 2+3+4. There were no right/left preferences demonstrated (Table 7.2). The subjects spent longer sniffing at the odour port with 2+3+4 compared to the blank ($P \leqslant 0.01$, Wilcoxon) but showed no preferences for odour/blank ports when the test odour was 8 or 2+3+4+8 (Fig. 7.4a).

7.4 DISCUSSION

In all four bioassay experiments, it was the combination of compounds 2+3 (trans- and cis-2,3-dimethylthietane) and compound 4 (2-propyl-thietane) that was the most attractive, based on time spent investigating the odours. Although the results of the experiments based on speed of response are not so unequivocal, the odour of 2+3+4 was still at least as attractive as the most attractive compounds. Compounds 2+3 and 4 were the most volatile of the compounds tested, and were usually at high concentrations in female anal sac extracts (see Chapter 4). In experiment 2, indole proved to be very attractive. This is the least volatile of the compounds tested, and has been described as being long-lasting, with a "floral" odour (Anon 1980). The combination of 2+3+4 and indole was not as attractive as either 2+3+4 or I on their own. Perhaps the fact that 2+3 or 4 is strong in female odours and I is strong in male odours (see Chapter 4) means that their combination at equal concentrations produced a confusing signal to the subjects. Similarly, combining Q, compound 1 and compound 8, all of which are normally minor components of ferret anal gland odours, with 2+3+4 at equal concentrations may not have been the appropriate way of testing these combinations.

In running these bioassay experiments attempts were made to follow the advice of O'Connell (1977) as outlined earlier. The purity of the chemical stimuli was ensured by the storage methods.

Figure 7.4: Subjects' responses to odours in bioassay experiment 4. Data are untransformed means (±SE).


(a)
TIME SPENT SNIFFING (sec)
55
50
45
40
35
30
25
20
15
10
5
ODOUR PORT
BLANK PORT
2+3+4
2+3+4+8
8
(b)
SPEED OF RESPONSE (sec)
80
70
60
50
40
30
20
10
2+3+4
2+3+4+8
8
ODOUR

This is important, because as Bedoukien (1970) noted, slight impurities are often the cause of response to an odour, rather than the actual odour itself. There are advantages in using synthesised pure compounds as test stimuli, rather than fractions of the natural products, as contamination can easily be introduced into samples during collection of natural animal products (see Murphy et al. 1978). Contamination could have occurred, however, later in the bioassay procedure. One problem with the design of the T-maze apparatus was that the air sucked through the maze originated from either side of the experiment room, thus contamination may have entered one side of the maze but not the other. This was accounted for in the experimental design by randomising the right/left location of the odour for each trial. The fact that no consistent right/left preference was shown by the subjects in experiments 1 and 4 suggests that no such contamination was occurring, but it may have been a problem in experiments 2 and 3, when there was a significant trend to investigate the right arena first, and there was no difference in the time spent at the odour and blank ports. This may have increased the unexplained variation in the results, making it harder to demonstrate differences in responses to the odours.[1] Thorough cleaning of the T-maze between trials ensured that the subjects themselves did not leave behind odours that would affect the outcome of the next trial.

The delivery of stimuli in a natural manner poses problems in a laboratory experiment. The anal gland odours of ferrets are normally delivered in two different ways, actively by the anal drag scent marking action after defaecation, and passively by being present on the ferret's anus, where other ferrets sniff (see Chapter 2). Mykytowycz et al. (1976) presented rabbit anal gland odours on faeces to simulate the normal method of delivery, but this technique, or placing the odour on live or model ferrets, runs the risk of introducing other odours to which the ferrets may also respond. Also, such modes of delivery could not be efficiently incorporated into a trap lure, making such experiments of limited application to the development of mustelid control methods.

The use of the pure chemical compounds diluted by hexane provided an odour at a known, but arbitrarily determined concentration, and DEGS provided a matrix that would control the speed of release of the odour

1. The non-significant results in experiments 2 and 3 may thus be misleading.

compounds. Little or no odour is detectable to the human nose from anal drag scent marks, and only a slight anal gland odour is normally noticeable on a ferret's anal region. Five ul odour samples were used, as they appeared to simulate this unquantified ferret anal smell. Preliminary trials with 100 µl, 5 µl and 0.5 µl of the odour/hexane mixture indicated that ferrets would not closely approach the highest quantity, and they showed no preference for the lowest quantity over the blank port.

The speed of approach and time spent sniffing the odours were used as the response variables, as approach and sniffing are the natural responses to both anal drag scent marks and the presence of anal gland odour on another ferret. In addition, approach and investigation of odours are the responses required if an odour is to be used as a trap lure. The fact that both the response criteria are very generalised behaviour patterns means, however, that it is difficult to show differences in responses to different stimuli. They are prone to being affected by extraneous stimuli (e.g. odours or noises) and such effects will increase the random variation in the data. The subjects' responses will also be affected by factors intrinsic to the animals. The differences in responses of males and females were accounted for in the analysis, as were effects of the age/tameness of the subjects. This tameness factor proved to be very significant, as was also found by Müller-Schwarze (1977) for the responses of black-tailed deer, Odocoileus hemionus columbianus, to "alarm pheromones".

Each subject was tested at the same time of day throughout each experiment, and all trials of any one experiment were run in the same season to avoid variation in responses due to diurnal and seasonal factors. This meant there had to be a trade-off between running the trials as close together as possible to keep all the trials within a short period, and spacing them out to allow the apparatus to be cleaned and dried, and to avoid habituation to the odour stimuli. Repeated exposure meant the subjects possibly habituated to the odour of 2+3+4, making them show relatively high responses to the "novel" odours in the later experiments. Such a tendency in ferrets to investigate novel stimuli has been demonstrated (Hughes 1964). Even so, 2+3+4 was always as attractive as the other odours tested. This problem of habituation was noted by Müller-Schwarze (1977), who described habituation as the

most common change in responsiveness in "pheromone experiments".

The difficulties of showing significant differences in responses when using small sample sizes are also evident in these experiments, especially experiments 3 and 4, when only ten subjects were available. This is a common problem in bioassay experiments on mammalian species. Similar investigations on pronghorns (Müller-Schwarze et al. 1974), golden hamsters (Singer et al. 1976), coyotes (Murphy et al. 1978), beagles, Canis familiaris, (Kruse and Howard 1983), black-tailed deer (Crump et al. 1984), and river otters, Lutra canadiensis, (Robson and Humphrey unpublished data) used only 2-12 subjects.

Even considering all the possible sources of error and reduction in power of the analysis, the fact remains that some components of ferret anal gland odours elicited more responsiveness than others. Results of these experiments have suggested which of the compounds found in ferret anal gland secretions should be tested for effectiveness in attracting ferrets to control devices. The real test of their attractiveness must come from field experiments using trappability of ferrets as a response measure. This is the subject of the next chapter.

Chapter 8
FIELD TRIALS OF SCENT LURES

"Although attractants have been employed for many years to draw predators to control devices such as traps...few of these lures have been evaluated statistically for efficacy or species specificity. Thus, there is a need for standardised methods for evaluating the attractiveness of lures..."

-Turkowski *et al.* 1979

8.1 INTRODUCTION

If an odorous substance is to act as a trap lure it must have sufficient attractiveness to draw the target species to the trap from some distance in the face of competing stimuli. Final testing of odour attractants must therefore be done in the field under normal trapping conditions. Although commercial trappers of fur-bearing and other economically important animals have used various lure and bait formulae as attractants, little work has been done to evaluate the effectiveness of these substances. An exception to this is the major research effort devoted to coyote control in the United States, where extensive trials of artificial trap lures have been undertaken (Shumake 1977, Turkowski *et al.* 1979, 1983). The effects odours have on trapping success have also been studied by ecologists concerned with the problem of their effects on determining rodent population estimates (Boonstra and Krebs 1976, Mazder *et al.* 1976, Daly *et al.* 1978, 1980, Stoddart 1982a,b, Stoddart and Smith 1984).

The laboratory bioassay described in the previous chapter indicated which components of ferret anal gland secretions are most likely to be of use as trap lures. The attractiveness of these synthetic compounds must now be tested in the field, and compared with that of natural ferret anal sac extracts, and baiting procedures currently used in trapping ferrets. Appropriate experimental design and analysis are essential to allow the full interpretation of such field experiments. For mustelids that use regular runways for moving around the home range (King 1973, and see Chapter 2) the siting of a trap can be one of the most important factors determining its catch rate, and a trapping programme must account for such spatial variation in trap efficacy.

Any study that involves trapping mustelids must be long term, because of low population densities and the low trappability of these small carnivores (e.g. King 1980). In addition, the study of odour attractants should continue for at least one full year, to account for possible seasonal variation in the efficacy of the lures.

Handling of live ferrets also gives the opportunity to collect information on whether or not ferrets use anal gland odour as an antipredator defence system (Hypothesis 4, Table 1.1).

8.2 METHODS

8.2.1 Live-trapping Experiments

Trapping experiments were carried out at Pukepuke Lagoon between February 1984 and June 1985 to test ferrets' preferences for various trap lures and bait in a field situation.

8.2.1.1 Study Area

Pukepuke Lagoon Wildlife Management Reserve (Plate 8.1a) is set in the dune country of Manawatu (40°20'S, 175°16'E). It is managed by the N.Z. Wildlife Service, primarily for waterfowl. Ferrets and feral cats are the main ground predators, while stoats and weasels are also present. The reserve consists of one large lagoon and a number of smaller ponds surrounded by 89 ha of swamp. The vegetation consists of raupo (Typha orientalis), niggerheads (Carex secta), flax (Phormium tenax), cabbage trees (Cordyline australis) and associated plants (Ogden and Caithness 1982). Grassy paths run through the firmer parts of the swamp, with wooden walkways constructed through the damper regions. Farmland surrounds the reserve, consisting of established pasture to the east, but elsewhere the ground is very sandy, and there are large areas of lupins (Lupinus arboreus). There are stands of cut-over pine forest (Pinus sp.), especially to the west of the reserve.

8.2.1.2 Materials

Forty-two Edgar live-traps (650 mm long by 150 mm wide by 160 mm high) were used. They were given one coat of polyurethane varnish inside for ease of cleaning to remove odours. Synthetic lures consisted of one part odour compound to five parts hexane or pentane by volume. The

Plate 8.1: Trapping experiment study areas.
(a) Pukepuke Lagoon, Manawatu
(b) Cass River, South Canterbury

(a)

(b)

diluted odour compounds were combined with white petroleum jelly which made up 93% of the lure by weight. The odour compounds used in the various lures were as follows. Lure 1 was half trans- and cis-2,3-dimethylthietane (compounds 2+3 in Chapters 4 and 7) and half 2-propylthietane (compound 4); lure 2 contained only 2-propylthietane; and lure 3 only indole. Lure 4 was a natural product ferret lure: female anal sac extracts (from either dead specimens provided by R.J. Pierce, or live ferrets), were mixed with white petroleum jelly to produce a lure of approximately the same strength as the synthetic lures. The blank control lure consisted of 93% white petroleum jelly and 7% hexane. The made-up lures were stored at -10°C in airtight containers. A smelly bait was made from dead, cut open laboratory mice.

8.2.1.3 Experimental Procedure

In the late afternoon, bait was placed directly into the traps and the lures were smeared onto 40x40 mm galvanised iron plates that were then put in the traps. Care was taken to avoid contaminating the next trap with the previous treatment. The traps were checked the next morning, cleaned with water and chlorine bleach and closed. Captured ferrets were ear-tagged, sexed and weighed. Their age (adult or juvenile, see Moors and Lavers 1981) and breeding condition were noted, along with the trap position and treatment. The release of anal gland secretion/odour during handling was also noted. Non-target species were released and recorded on the data sheets.

8.2.1.4 Experimental Design

In a preliminary trial in February 1984, forty traps were set out singly throughout the reserve (Appendix 8). The traps were sited on animal runways, to maximise the likelihood of catching ferrets at every site. The traps were operated for eight consecutive nights. On each of the first four nights one quarter of the traps had each of the following treatments - bait plus lure 1, bait only, lure only, and clean. The traps were divided into groups of four, and treatments assigned according to a Latin square design. At the end of four nights all the traps were moved to new sites and the experiment repeated.

In all subsequent trials twenty-one trap sites were used, with two traps set side by side at each site. Trap sites were not changed within a trial. A trial consisted of six consecutive nights of trapping. The trap sites were divided into groups of three and the treatment pairs rotated amongst them. Each pair of treatments had equal exposure at each site, and the experimental design was balanced for order of presentation. From March to May 1984 treatments were renewed every day, while in subsequent trials treatments were renewed every second day, with the treatments being swapped between the traps at each site for the second night. The treatment pairs used in each trial and number of trap nights for each treatment pair are given in Table 8.1. After March 1984, a trap site was closed for one night if it had caught a ferret the night before. The data were analysed using chi-square goodness-of-fit and independence tests to determine the effect on capture success of treatment, sex of the captured ferrets, time of year and freshness of treatment, and interactions of these factors.

8.2.2 Kill-trapping Experiment

The synthetic lure 1 was incorporated into the regular trapping programme of the N.Z. Wildlife Service in the Mackenzie Basin, South Canterbury, from 4 September to 10 October 1984.

8.2.2.1 Study Area

Scented traps were operated in a 6.5 km stretch of the Cass River bank (Plate 8.1b), and the outside perimeter of the "Mailbox Predator Exclosure" (Pierce 1982b) and adjacent tussock grassland on the edge of Lake Tekapo. The glacial river is surrounded by steep mountains. The shingle river banks are stabilised by *Raouli* sp. and *Muehlenbeckia axillaris*, and adjoin tussock grasslands that cover the edges of the valley floor and the lower hillsides. Cover is provided by matagouri (*Discaria toumatou*), *Olearia* sp., willows (*Salix* sp.) and occasional stands of *Pinus* sp. (Pierce 1982a).

8.2.2.2 Experimental Procedure

Ninety-one leghold Gin traps were set singly in an irregular pattern. The sets were typically enclosed spaces amongst matagouri bushes, between rocks or near rabbit burrows, or surrounded by a palisade of sticks. The trap was camouflaged, and a narrow entranceway constructed

TABLE 8.1

Treatment pairs, the trials in which they were tested and the number of trap nights for which they were operated in the live-trapping experiments.

TREATMENT PAIRS	NON-BREEDING SEASON TRIALS	NIGHTS	BREEDING SEASON TRIALS	NIGHTS	TOTAL NIGHTS
BAIT VS LURE 1	MAR 84, APR 84, MAY 84, JUN 84, JUL 84	174	OCT 84, NOV 84, DEC 84, JAN 85a	151	325
BAIT VS LURE 4	MAR 85, APR 85, JUN 85	103	JAN 85b, FEB 85	79	182
LURE 1 VS LURE 4	MAR 85	37	JAN 85a,b, FEB 85	116	153
LURE 1 VS BLANK	MAR 85	37	JAN 85a,b, FEB 85	117	154
LURE 1 VS LURE 2	MAY 84, JUN 84, JUL 84, APR 85, JUN 85	165	OCT 84, NOV 84, DEC 84	121	286
LURE1 VS LURE 3	MAY 84, JUN 84, JUL 84, APR 85, JUN 85	167	OCT 84, NOV 84, DEC 84	118	285
BAIT VS BAIT/LURE	MAR 84, APR 84	81	---	---	81
LURE 1 VS BAIT/LURE	MAR 84, APR 84	78	---	---	78

to ensure that the animals stepped on the trigger plate. Bait (fresh rabbit or occasionally hare or fish) was hung on a hook and lure put on a metal plate beyond the trap in blind sets, and the plate camouflaged to prevent removal by magpies (Gymnorhina tibicen) and to avoid direct sun. In walk-through sets the bait or lure plate was hidden underneath the trigger plate. Traps were checked each morning or early in the afternoon. Ferrets, stoats, cats and harriers) were shot with a .22 rifle, and other species (hedgehogs, Erinaceus europaeus, and various bird species) removed and the traps reset. If the bait had been taken it was replaced either by fresh bait or a piece from another trap to maintain the appropriate "freshness" of treatments (see experimental design). Ferrets were sexed and weighed.

8.2.2.3 Experimental Design

Half the traps (every alternate one the trapper checked) were treated with lure and the others with bait. Treatments were renewed every third day, and swapped between traps every third or sixth day to counterbalance location bias. The variation in numbers of animals caught relating to treatment, freshness of treatment, species and sex of captured animals were analysed using chi-square goodness-of-fit and independence tests.

8.3 RESULTS

8.3.1 Live-trapping Experiments

In the preliminary live-trapping experiment at Pukepuke Lagoon in February 1984, 25 ferrets were caught over the eight nights, six on bait/lure traps, 9 on bait only traps, seven on lure only and three on clean traps. These differences in success rates are not significant.

The paired-trap design experiments yielded capture rates of four to 20 ferrets per six nights of trapping, and the same individuals were regularly caught. On average, two to three male and five female ferrets were resident in the trapping region at any time, with residents being defined as individuals caught in more than one trial (Appendix 8). A slightly higher catch rate was achieved in late summer/early autumn than at other times of the year, with a flush of juveniles being caught in late summer, and also an increased catch rate of adults. Full trapping data are given in Appendix 9.

Over the 325 trap nights in which bait vs lure 1 trap pairs were operated, significantly more ferrets were caught on bait than on lure 1 ($P<0.005$), while there was no significant difference between the choice of treatment in the breeding and non-breeding seasons or between the sexes. The first night treatments were not significantly more successful than second night treatments (for bait $\chi^2=0.17$, for lure $\chi^2=2.15$), and choice of treatment was independent of freshness of treatment (Table 8.2).

The difference in the numbers of captures on bait and lure 4 were not significant (Table 8.2). However, when comparing these results with bait vs lure 1, the trend to catching more ferrets on bait than on lure was independent of the type of lure ($\chi^2=1.60$). Only females were caught on lure 4, giving a significant difference between the male and female choices ($P\leqslant 0.05$). Captures on these two treatments did not vary with season nor with freshness of treatment (Table 8.2).

Lure 4 was preferred over lure 1 ($P\leqslant 0.05$), and choice was independent of season, sex and freshness (Table 8.2). Significantly more ferrets were caught on lure 1 than on the blank treatment ($P<0.025$), and again males and females had similar likelihoods of being caught on the two treatments. All four ferret captures on the blank occurred on the second night of treatment, giving a significant lack of independence between choice and freshness of treatment ($P\leqslant 0.025$). Lure 1 was preferred over the blank in both the non-breeding and breeding seasons. Both lure 2 and lure 3 were as attractive as lure 1, and in neither case was the success of the different lures dependent upon season, sex or freshness of treatment (Table 8.2). With the results of all four scent lures combined, the number of ferrets caught on the first night was not significantly higher than on the second night ($\chi^2=2.22$). The small samples obtained for the lure 1+bait vs bait and lure 1+bait vs lure 1 pairs (6 vs 4 and 1 vs 4 respectively) indicate that the combination of lure 1 and bait would be no more attractive than either of the treatments on their own.

Comparisons of the captures amongst treatment pairs reveals that the trap sites having two lure traps were just as successful as those with one bait and one lure trap, and trap site success was independent of sex (Table 8.3).

TABLE 8.2

Number of ferrets caught on the various treatments in the live-trapping experiments. Statistical comparisons are χ^2 goodness-of-fit and independence tests with correction factor for small (n<10) expected values (Pirie and Hamden 1972). ?=sex unknown

TREATMENT PAIRS	TOTAL	NONBREEDING SEASON	BREEDING SEASON	MALE	FEMALE	1st NIGHT	2nd NIGHT
BAIT VS	17	6	11	5	12	12	5
LURE 1	4	2	2	1	3	4	0
χ^2	8.05	0.22		0.02		1.62	
	P<0.005	N.S.		N.S.		N.S.	
BAIT VS	16	9	7	6	10	8	8
LURE 4	9	6	3	0	9	6	3
χ^2	1.96	0.28		4.36		0.68	
	N.S.	N.S.		P<0.05		N.S.	
LURE 1 VS	4	0	4	1	3	1	3
LURE 4	13	4	9	5	7+1?	9	4
χ^2	4.76	0.35		0.40		2.58	
	P<0.05	N.S.		N.S.		N.S.	
LURE 1 VS	14	5	9	5	7+2?	11	3
BLANK	4	1	3	3	1	0	4
χ^2	5.55	0.14		1.42		7.90	
	P<0.025	N.S.		N.S.		P<0.025	
LURE 1 VS	13	11	2	6	7	8	5
LURE 2	9	6	3	3	5+1?	5	4
χ^2	0.73	0.93		0.12		0.07	
	N.S.	N.S.		N.S.		N.S.	
LURE 1 VS	14	7	7	6	7+1?	5	9
LURE 3	10	4	6	2	8	5	5
χ^2	0.67	0.22		1.65		0.51	
	N.S.	N.S.		N.S.		N.S.	

TABLE 8.3

Number of captures on bait vs lure 1 and bait vs lure 4 combined (501 trap nights), compared to those on all the lure vs lure and lure 1 vs blank pairs (878 trap nights). Statistical comparisons as in Table 8.2.

TREATMENTS	TOTAL	MALE	FEMALE
BAIT VS LURE	46	12	34
LURE VS LURE	76	31	45
χ^2	0.06	1.40	1.41
	N.S.	N.S.	N.S.
χ^2 2x2		2.71	
		N.S.	

TREATMENTS	MALE		FEMALE	
	NONBREEDING	BREEDING	NONBREEDING	BREEDING
BAIT VS LURE	8	4	16	18
LURE VS LURE	12	19	22	23
χ^2 2x2	4.76		0.03	
	P≤0.05		N.S.	
χ^2 2x2x2		5.17		
		N.S.		

Overall, trap site success was also independent of season (χ^2=0.64), but males were caught more often at lure vs lure sites in the breeding season than expected (P≤0.05, Table 8.3).

Seven non-target species were caught (Table 8.4). The most common was the hedgehog, which was caught in traps independent of treatment type. Seven weasels were caught, all but one on scent lures, and the two stoats caught were both on scent lures. Five rats (Rattus norvegicus)

were caught on the artificial lures, none on the natural product lure (lure 4).

TABLE 8.4

Number of captures of non-target species on the various treatments in the live-trapping experiments.

TREATMENTS	WEASEL	STOAT	RAT	HEDGEHOG	POSSUM	CAT	MOUSE
BAIT VS	1			4			
LURE 1	3			8	1		
BAIT VS			1	2		1	
LURE 4	1			7			
LURE 1 VS			1	5			
LURE 4				7			
LURE 1 VS			3	9			1
BLANK			1	5	4		
LURE 1 VS	1	1		4			
LURE 2	1			4	2		
LURE 1 VS				6			
LURE 3		1	1	9	1		

Of the 169 times ferrets were handled during live-trapping, 114 (67.5%) released anal gland secretion/odour. There was no significant difference in the release rates of males and females (71.2% and 65.4% respectively), nor between adults and juveniles (70.5% and 57.5% respectively). Ferrets were just as likely to release odour on subsequent captures (66.4%) as on their initial capture (75.6%, Table 8.5, Appendix 9).

TABLE 8.5

Number of times ferrets released anal gland secretion/odour during handling after capture in the live-trapping experiments.

	TOTAL	MALE	FEMALE	ADULT	JUVENILE	INITIAL CAPTURE	SUBSEQUENT CAPTURE
CAPTURES	169	59	110	129	40	44	125
ODOUR RELEASES	114	42	72	91	23	31	83
χ^2		0.19		0.74		0.08	
		N.S.		N.S.		N.S.	

8.3.2 Kill-trapping Experiment

Gin traps in the Cass River study area treated with artificial scent lure (lure 1) were as successful in trapping ferrets as those baited with meat (Table 8.6). The catch rate per 100 trap nights on lure was 2.11, compared to 1.79 on bait.

More males than females were caught on lure, due to an overall higher catch of males (41 males to 24 females), but treatment success was independent of sex (Table 8.6). The number of ferrets caught on lure varied with freshness of treatment, with most ferrets being caught when the lure was fresh, and only five being caught on three-day old treatment ($P \leq 0.025$). The catch rate on bait did not drop significantly over the nights, but the rate of drop in catch rate was independent of treatment (Table 8.6).

The captures of important non-target species are summarised in Table 8.7. Sixteen cats were caught, only three of them on lure ($P \leq 0.025$), while none of the 29 harriers caught were on lure ($P \leq 0.001$). Hedgehogs were caught equally often on bait and lure (1.27 and 0.87 per 100 trap nights respectively). Only two other mustelids were caught, both stoats, and both on lure.

TABLE 8.6

Comparison of the number of ferret captures on the two treatments, bait (1727 trap nights) and artificial scent lure (1605 trap nights) in the kill-trapping experiment.

	BAIT		LURE
TOTAL	31		34
χ^2		0.44	
		N.S.	
MALE	18		23
FEMALE	13		11
χ^2 2x2		0.64	
		N.S.	
1st NIGHT	11		19
2nd NIGHT	12		10
3rd NIGHT	8		5
χ^2	0.84		6.67
	N.S.		$P<0.025$
χ^2 2x2		2.64	
		N.S.	

8.4 DISCUSSION

Results of both the long term live-trapping and the intensive kill-trapping experiments demonstrate the viability of scent lures for attracting both male and female ferrets to control devices. Although ferrets preferred to enter bait traps when given a choice, trap sites with lure only were just as successful as those with bait in both experiments. Neither treatment was tested against no treatment in a single trap design experiment. However, previous workers' findings

TABLE 8.7

Comparisons of number of captures of non-target species on the two treatments, bait and artificial scent lure, in the kill-trapping experiment.

SPECIES	BAIT	LURE
CAT	13	3
χ^2	5.55	
	$P<0.025$	
HARRIER	29	0
χ^2	26.95	
	$P<0.001$	
HEDGEHOG	22	14
χ^2	1.24	
	N.S.	
STOAT	0	2

that mustelid traps were more successful when baited than not baited (King 1973, Lavers 1973b, King and Edgar 1977) suggest that it was the treatments not some other feature of the traps that accounted for their success. This is also indicated by the significant drop in catch rate on scent lure in the kill-trapping experiment (and a similar trend on bait) as the treatments became stale. The natural product lure was preferred over the artificial lure, but as in the bait versus lure situation, comparisons of their effectiveness in isolation would be necessary before concluding that one would be more effective in a real trapping programme.

These trapping experiments have also provided general information on the trappability of ferrets, responses of ferrets and non-target species to scent lures, and ferrets' use of anal gland odour in defence against predators. The higher catch rates of females than males at Pukepuke Lagoon and vice versa in the Cass River may have been a product of the spacing of traps. At Pukepuke Lagoon only a small area was trapped relative to male ferret home ranges (see section 1.2), but this encompassed a number of female home ranges (Appendix 8). King (1975, 1980) found similar effects of spacing of traps on the capture of weasels and stoats. The larger catch rate in summer and early

autumn was probably due to both the presence of juveniles dispersing from their natal territories, and the increased movements of adult at that time of year (Moors and Lavers 1981). King (1980) reported a similar peak in the catch rate of stoats in summer.

It is surprising that more females than males were caught on the natural product lure. The reverse would be predicted on the basis of the preference tests (Chapter 5), which indicated that anal gland odours of females attract males. However, the small sample sizes, the prevalence of females, and the fact that no trapping was done at Pukepuke early in the breeding season when the females were in oestrus (September) should all be noted. Examining the between-trap site analysis, it is evident that males in the breeding season were more likely to be caught at sites where there were two lures rather than bait and lure. The synthetic lure was also successful in attracting males in the breeding season in the Cass River trials.

The capture of the other mustelids on the artificial ferret scent lures is not surprising, considering that one of the components, 2-propylthietane is an important component of stoat anal gland secretions (Crump 1980a), and that weasel anal gland secretions contain 2,3-dimethylthietane (Brinck et al. 1983). Cats were not attracted by the lures, and harriers were not expected to be caught on the lure as they are visual rather than olfactory hunters (Brown 1976).

It is not clear why the choice experiments yielded different results from the between-trap site analysis and no-choice experiments. These results do, however, have implications for the design of experiments for testing the effects of odours on trappability. If only choice experiments had been used, this may have led to the incorrect conclusion that the scent lures would not be as effective as bait in attracting ferrets. Recent investigations on rodents have used choice experiments, with two or three traps with different treatments at each site, to look at the effects of different odours on trappability and, ultimately, their effects on population estimates (Daly et al. 1980, Stoddart 1980a, Wuensch 1982, Stoddart and Smith 1984). However, the demonstration of a choice does not imply that, given only one trap to enter, odours will be sufficient to attract animals or deter them from entry. Given sufficient replication and an experimental design that

does not allow biases from siting of traps to be a confounding factor, such information is obtainable from no-choice experiments (e.g. Gorman 1984b, Van der Berk and Müller-Schwarze 1984). Choice experiments can, however give information on the complex social interactions found in communities of small mammals (Stoddart and Smith 1984). An experimental design that includes analysis of both within and between trap site differences in trap success rate provides more information than either approach on its own (e.g. Stoddart 1982a, this study).

Suitable experimental procedure is also essential. The traps used in the live-trapping experiments were designed especially for the capture of ferrets. They were modified Edgar mustelid live-traps (King and Edgar 1977), increased in size on the advice of Mr. R. Edgar (pers. comm.), and following the report of Jensen (1978) that slightly larger than normal traps yielded better catches of mustelids.

Repeated live-trapping of the same individuals opens up the possibility of the animals habituating to the smell of the lures, causing a drop in their effectiveness over time. There was no indication that this was happening, and there was no sudden increased catch rate when lure treatments were changed between months (see Appendix 9). It is also possible that some individuals became "trap-happy", and were not making any choice based on treatment in the traps. The fact that significant differences occurred between captures on some pairs of treatments suggests that this was not an important problem.

The effects of the odour of previously-captured animals on the catch rate (see Lavers 1973b) are a possible source of bias in this type of experiment. It became evident in the first few trials that cleaning the traps with water and a cleansing agent was not sufficient to remove the ferret smell from traps. The removal and thorough soaking and cleansing possible with small, light rodent traps (Daly *et al.* 1980, Wuensch 1982) was not practicable with the ferret traps. In subsequent trials the closure of a successful trap site for one night avoided the problem of ferrets being caught in traps that had held a ferret the night before. The rotation of treatments amongst the traps prevented any effects of capture odours being added to any one treatment.

It was difficult to standardise the amount of lure placed in each trap, and this may have added extra variance to the results. A smear of the lure was placed on a standard-sized metal plate, but this smear was not a quantified amount. This is a common problem in studies of the effects of odours on trap capture rates. Many workers give no indication at all that any attempt was made to standardise odour concentrations (e.g. Daly et al. 1978, 1980, Wuensch 1982, Gorman 1984b, Stoddart and Smith 1984). Sample sizes obtained were small, as is "inevitable in field experiments with carnivores" (King 1980), but sufficient to show that some treatments were preferred over others.

The release of anal gland secretion/odour by 67.5% of the captured ferrets supports the view that anal gland odours in large quantities are a form of defence against predators. The fact that the percentage was not higher may relate to the history of domestication of the ferret (Corbet and Southern 1977). Feral ferrets behave differently from wild polecats (Eibl-Eibesfeldt 1956, Poole 1972b). Many would sit quietly in the trap when the lid was removed (Plate. 1.1b), requiring no effort to restrain them, and were thus unlikely to release anal gland odour.

Chapter 9
SYNTHESIS AND DISCUSSION

"With the little knowledge that we already
have it is possible to begin to appreciate
our ignorance." - Johnston 1977

9.1 FERRET OLFACTORY COMMUNICATION

Four hypotheses to explain the use of odours in communication were suggested in Chapter 1, that were compatible with our knowledge of the ferret's biology and social organisation. The testing of predictions from these hypotheses and detailing of relevant background information on ferret behaviour, gland structure and chemistry were carried out. The results can now be brought together to determine the support for the hypotheses and to explain the roles odours play in the life of the ferret. Comparisons can be drawn between the use of odours by the ferret and other mustelid species.

9.1.1 Territorial Defence Hypothesis

The results of this study support the suggestion of Moors and Lavers (1981) that scent marking is one of the principal mechanisms by which ferrets maintain their spacing system. It was hypothesised that scent marks provide an olfactory association between the resident and its defended area, which allows intruders, including neighbours, to avoid escalating encounters with residents to actual combat. There is support for both mechanisms that were outlined; residents memorising and recognising the odour of their neighbours, and intruders matching the odour of scent marks with those of animals it meets. Anal drag scent marks (Chapter 2) could inform other animals of the sex and individual identity of the marker. This is indicated by the sexual and individual differences in anal sac extracts (Chapter 4), and the ability of ferrets to discern these differences (Chapter 5). Anal gland scent marks could thus act as olfactory signatures for neighbour-neighbour recognition. The freshness of the scent marks in an area will allow a subordinate animal to assess the likelihood of meeting a dominant neighbour. Scent marks could thus act as railway

signals, allowing neighbours who live in overlapping home ranges, to maintain their spatiotemporal separation by mutual avoidance.

When an intruder enters a territory, the presence of fresh anal drag scent marks at latrines near dens and other conspicuous places will soon inform it that the area is already occupied (Chapter 2). If, as is suggested by this study, they leave anal gland scent marks not only at territory boundaries but throughout the home range all year round, then ferrets are using a hinterland marking system. In a species with a large home range perimeter this is an effective way of marking (Gorman and Mills 1984, see section 1.3). If an intruder meets another ferret, it could match the odour of nearby anal drags with the odour of the animal by anus sniffing (Chapter 2), allowing it to recognise the territory-holder and take the appropriate action (usually escape). The scent marker itself will also smell the anal drags, making it aware that it is on home ground and thus more confident and prepared to fight, as indicated by the results of confidence assessment tests (Chapter 6).

Latrines thus act as information centres, conveying chemical messages that modify the behaviour of animals encountering them. It has been assumed that anal gland odour is laid down at latrines. Even if this is not true, latrines are strong olfactory beacons, containing the odour of faeces and urine that have their own information content (Wheeler 1978, Sokolov and Rohznov 1983), possibly including secretions from proctodael glands (Stubbe 1970) and abdominal glands (Chapter 3). They probably also assist a resident to orientate itself in its environment, but such an idea is not directly testable (Gosling 1982).

Further support for the territorial defence role of anal gland odours comes from the live-trapping experiments (Chapter 8), where not just males but also females were attracted to the natural product lure, that was made from the secretions of female ferrets. In both the live-trapping and the kill-trapping experiments (Chapter 8), females were also attracted to the artificial lure, with active ingredients that were synthetic analogues of two compounds usually at high concentrations in female anal sac extracts (Chapter 4).

The use of abdominal gland and/or general body odours in scent marking appears to be of importance in encounters with intruders, especially encounters between males in the breeding season (Chapter 2). Neck sniffing may be a way of determining an individual's body odour. Neck rubbing and rolling by dominant males could act to intimidate the opponent by providing a fresh source of odour matching that of nearby wiping or body rubbing scent marks. This is in line with our knowledge of ferrets' increased aggressive behaviour in the breeding season (Moors and Lavers 1981, pers. obs.). However, it is not known if body odours are individually distinct. Anal gland and abdominal gland odours could act together in these situations, the former providing the information on individual identity, and the latter acting as a threat signal. Chin rubbing could be a convenient way of laying down these threat signals at food stores (Chapter 2).

9.1.2 Sex Attraction Hypothesis

Olfactory recognition of sex is widespread, not only within mammalian taxa, but throughout the vertebrates (Stoddart 1980b). It is generally assumed that scents play an important role in sex attraction in solitary-dwelling carnivores, and Stoddart (1980b) comments on the adaptive significance of the use of strong scents in such species. However, supportive evidence from field studies is scarce. In the ferret, the location of anal drag scent marks in conspicuous places and particularly at latrines near den sites is consistent with the sex attraction hypothesis, allowing a male to easily locate a female in her home range. Neither the frequency of scent marking with anal gland odour nor the chemical composition of anal sac extracts varied during the year, and males did not discriminate between oestrous and anoestrous female anal gland odours. It has already, however, been suggested that anal gland odours play roles in intrasexual communication throughout the year (Hypothesis 1), not just intersexual communication. Seasonality in anal gland odour use is not essential for a sex attraction hypothesis. Male ferrets are sexually active only for part of the year and are thus likely to use scent marks as a means of finding females for reproductive purposes only during this period. Also, because all females come into oestrus at the same time of year, there is little need for an olfactory mechanism for distinguishing between oestrous and anoestrous females. The important findings in regards to the sex attraction hypothesis were that the relative

concentrations of components of the anal sac extracts of males and females differed (Chapter 4), and that not only could ferrets discriminate these differences but also that males were more attracted to the female anal gland odours, in tests that were run during the breeding season (Chapter 5). The attraction of males to the scent lures, especially in the breeding season (Chapter 8) also supports a sex attraction role.

9.1.3 Bookkeeping Hypothesis

Hypothesis 3 was that scent marks act as a bookkeeping system to assist in efficient food searching. The lack of association between the anal drag action and the presence of food (Chapter 2) allowed this hypothesis to be rejected for anal gland odours. The fact that ferrets regularly showed chin rubbing behaviour while storing food (Chapter 2) suggested that odours from the chin may well increase the odour output from food stores, leading to more efficient food recovery. The peak in frequency of male chin rubbing in spring however, suggests, another role of defence of food stores from other ferrets. Wildhaber (1984) found that her subject ferrets spent less time feeding at a food site where an unfamiliar ferret's chin odour was present than when no odour was present. She could not, however, show that ferrets could discriminate between their own and other ferrets' chin odours. A further unknown factor is whether chin odour differs from the odour deposited by other body rubbing and wiping actions. The histological investigation of Chapter 3 showed that there was no discrete glandular region in the chin, but the possibility of histochemical or bacterial differences affecting odours cannot be ruled out. The exact role of chin rubbing behaviour in food searching or food defence remains unclear.

9.1.4 Antipredator Defence Hypothesis

Results from Chapter 8 support the suggestion that ferret anal gland odours are important in defence against predators. In the live-trapping experiments, a large proportion of the ferrets released anal gland odour while being handled. Another occasion in which anal gland odour was released in large concentrations was during the preliminary dominance assessment tests of Chapter 6. It was always the subordinate individual which released the odour, in tests when its opponent showed high intensity aggression. This intraspecific use of

odour does not detract from the antipredator defence hypothesis; the
ıse to a dominant, aggressive opponent is the same as to a predator in this situation. Females occasionally released anal gland odour in large amounts when trying to escape from a male's sexual advances, when they were not receptive (e.g. early in the breeding season when they were not fully in oestrus).

The ferret anal gland odour is not, however, as well developed for antipredator defence as in some other mustelids. Species with a very well developed anal gland odour display aposematic colouring that acts to warn away potential predators (Halonen and Denny 1979). These take the form of contrasting black and white stripes or spots, displayed by special threat postures, such as the "handstand" posture of the spotted skunk, Spilogale sp., (Howell 1920, Johnson 1921). No such striking colouring or postures are found in the ferret.

There is little known about the effects mustelid anal gland odours have on potential predators. Regarding the odour of skunks, Matthews (1971) commented that "their scent is so powerful and unpleasant that other animals quickly learn not to molest them...the stink is so overpowering that it almost chokes the victim, for it temporarily inhibits breathing." Goethe (unpublished, cited in Goethe 1964) found that dogs retreated with a gesture of disgust from the caudal end of freshly-killed polecats. When a young ferret first met a dog it let off anal gland odour, at which point the dog backed off (pers. obs.). Casual observations on people's responses to ferret anal gland odours indicate that they find them distasteful, and even nauseous. Thus the production of an obnoxious odour by the ferret could act as an important part of an antipredator defence system.

9.1.5 Comparisons with Other Mustelids

The same anal drag has been seen in the stoat, whose anal sac extracts also differed between individuals (Erlinge et al. 1982). Unlike the ferret, the stoat anal dragged not only at latrines but also in situations where ferrets wiped. Dominant stoats showed a higher frequency of anal drags than subordinates, and males showed an increased rate of performing anal drags in spring. These were not the case for anal drag in the ferret, but were true for wiping. Without knowing whether or not stoats possess abdominal glands, nor being sure

whether or not anal gland odour is present at ferret wiping sites, it is not possible to explain the differences in scent marking between these two species. The same conclusions about the use of anal drags to place the individual's odour in the environment for territorial defence are drawn in both studies, while Erlinge et al. (1982) emphasise the role of stoat anal gland odour in allowing the assessment of the asymmetry of a conflict, and do not suggest a role in neighbour-neighbour avoidance. Crump (1980a) found differences in the chemical composition of male and female stoat anal sac extracts, but neither he nor Erlinge et al. (1982) commented on possible signalling roles for these odours in reproduction.

Body rubbing occurred in similar situations in both species, and the conclusions of Erlinge et al. (1982) that it is associated with agonistic encounters, and seems to have a threat significance could equally be applied to the ferret. Their suggestion that body rubbing increases self-confidence was not tested in the ferret. Erlinge et al. (1982) noted that body rubbing was done by both sexes throughout the year, but gave no quantitative support for these comments. If there was no difference in rates of body rubbing between the sexes and in different seasons then these differences in body rubbing between the stoat and the ferret are not easily explained, without a fuller understanding of both species' social behaviour.

Erlinge et al. (1982) also observed body rubbing immediately after food had been stored, but did not comment on the significance of this. A comparison of rubbing behaviour at food sites by stoats and ferrets would be merely speculative without further information from both species.

European badgers, with their communal lifestyle (Kruuk 1978) and subcaudal as well as anal glands (Gorman et al. 1984), have a more complex olfactory communication system. They use odours for territorial defence, but rather than the simple individual identity message conveyed by ferret and stoat anal drags, badger squat marks act as a group signature (Kruuk et al. 1984). These scent marks have an additional role in communication amongst clan members not found in the solitary ferret.

Gorman et al. (1984) did not find any consistent differences in the chemical composition of male and female subcaudal gland secretions. This information may be carried in the anal gland secretion, but the fact that males and females live in close-knit family groups suggests that the role of odour in location of the opposite sex would not be necessary.

The European otter does not show any scent marking actions, but leaves droppings in conspicuous spraint piles (Trowbridge 1983). Although the otter is probably not territorial, spraint piles play the same role as information centres as do ferret latrines. They are distributed such that they are most likely to be encountered by otters, and spraints contain the necesssary information on individual identity (possibly from anal gland secretion) for them to affect the movements of individuals of different dominance status, thus maintaining the species spacing system (Trowbridge 1983). Unlike the ferret or polecat (Sokolov and Rohznov 1983), spraint piles also convey information on female otter sexual receptivity, carried in urine (Trowbridge 1983). Female otters are periodically in oestrus throughout the year, while ferrets have a definite breeding season and thus little need to advertise sexual receptivity.

The scent marking behaviour of the ferret is thus similar to that of other mustelids, and similar roles for odours in mediating spacing systems have been suggested for the various species. Differences occur in the roles of odours as sex attractants where there are differences in social organisation (ferret vs badger) or reproductive physiology (ferret vs otter).

9.1.6 Priorities for Future Research

Before any firm conclusions can be made on the communicative roles of anal drag scent marks, it must be confirmed that anal gland secretion is indeed deposited by this action and not elsewhere. This could be done by testing for minute amounts of odorous secretions at latrines, or by marking the anal sac contents with a dye or radioactive material, so they could be detected in the environment. A study of the location of anal drag sites (latrines) in the wild relative to individuals' home ranges and to den sites would be valuable in relating the results of this captive study to free-living ferrets. A further test of a

neighbour-neighbour avoidance system could involve testing a subordinate animal's avoidance of an area (e.g. a den site) scent marked by a dominant neighbour, as attempted in Chapter 2. Such an experiment would best be done in the breeding season, when males are very aggressive, and if possible, in the wild to avoid problems associated with confinement affecting the animals' behaviour. Reinforcement-training experiments to test ferrets' abilities to discriminate between anal gland odours of different freshness and their abilities to memorise odours could provide information on the details of how ferrets use odours to avoid each other.

In the study of the roles of abdominal gland and body odours in communication, the greatest priority must be given to the determination of whether or not the same odour is involved in wiping, body rubbing and chin rubbing. This would require a chemical study of the odours from different parts of the body, and may also require an investigation of bacterial activity in the various regions of the body skin, as discussed in Chapter 3.

9.2 PRACTICAL APPLICATION IN WILDLIFE MANAGEMENT

9.2.1 Development of Scent Lures

The first step in the development of a trap lure for ferrets was to find out how ferrets responded to anal gland odours. The results of Chapters 2 and 5 indicated that these odours were attractive to ferrets. The findings that anal gland odours are important in both inter- and intra-sexual communication and that males were particularly attracted to female odours (Chapter 5) suggested that a lure based on the major components of female anal gland odours would be an effective lure for both males and females. The bioassay experiments of Chapter 7 showed that the odours of some combinations of compounds were significantly more attractive than others. The combination of trans- and cis-2,3-dimethylthietane (compounds 2+3) and 2-propylthietane (4) was always very attractive. The next step was to look at the efficacy of a synthetic lure containing these components, in comparison to no odour, and to a standardised bait. For these field experiments, using trappability of wild ferrets as a response criterion was essential. As Stoddart (1980a) pointed out: "field studies are potentially able to yield different sorts of results from laboratory studies because the

test subjects, living their lives under natural conditions, are free from the unquantifiable influences created by captivity." But of course field experiments have their own problems, as discussed in Chapter 8. Thus the combination of laboratory and field studies represents the most comprehensive way of assessing the responses of animals to odours. These studies showed that scent lures could be viable alternatives to edible bait as attractants for ferrets.

9.2.2 Ferret Odours and the Pheromone Concept

Early studies on mammalian olfaction used theories and techniques derived from insect sex pheromone studies. They attempted to isolate releaser and primer "pheromones", chemicals that are "secreted to the outside by an individual and received by a second individual of the same species, in which they release a specific reaction, for example a definite behaviour or developmental process" (Karlson and Lüscher 1959).

Few releaser pheromones have, to my knowledge, been identified in mammals. An often quoted example of a mammalian pheromone is the salivary steroid in the domestic boar (*Sus scrofa*), isolated by Claus (1975), that releases the mating stance in oestrous sows. Other authors have used the term pheromone to describe compounds that do not appear to fit the usual criteria implied when designating a semiochemical as a releaser pheromone (Beauchamp *et al*. 1976, see also Katz and Shorey 1979, Beauchamp *et al*. 1979). Müller-Schwarze (1969) found that not just one but all four substances of the male black-tailed deer's tarsal scent released responses quantitatively identical to the total tarsal scent. Although Singer *et al*. (1976) describe dimethyl sulphide as an attractant pheromone in oestrous hamster vaginal secretions, they noted that there may be other compounds that contribute to the activity of the secretion.

The results of the bioassay experiments (Chapter 7) indicated that no simple releaser pheromone would be identified for the behavioural responses of ferrets to anal gland odours. The term pheromone for describing ferret attractants is unjustifiable on at least two grounds. First, the responses to anal gland odours are generalised responses that are not unique to these chemicals. Second, it was not just one or a few of the components of anal gland odours that proved attractive.

It is the complexity of chemical composition of anal gland odours that is of particular significance in communication (e.g. differences in relative concentrations of compounds as indicators of identity) rather than the separate elements. Ferret anal gland odours would fit the definition of "informer" pheromone (Müller-Schwarze 1977), but so would any other odour that plays some role in communication. Thus the term seems synonymous with "social odour" (Stoddart 1976). As discussed by Beauchamp et al. (1979), the broadening of the term pheromone to include all intraspecific odours would imply a misleading similarity between social odours as found in the ferret and odours that produce very specific responses.

9.2.3 The Value of Mustelid Scent Lures

So long as there is a need for predator control in New Zealand (see section 1.1) there is a benefit in using the most effective and efficient means of control. Fitzgerald et al. (1984) listed the study of scent marking behaviour and the development of scent lures as two of their major priorities for research in mustelids and cats in New Zealand. Crawley (1982) suggested that we could adopt a "game warden" approach to conservation, which could well prove to be an effective way of controlling ferret populations (King and Moors 1979). The use of scent lures could lead to savings in time and money in such control programmes, and in damage control programmes on all the mustelids, with edible bait not having to be acquired. This could lead not only to more efficiency in trapping, but also more effective trapping. For example, the time saved by not having to acquire fresh meat baits could be used in checking an extended trap line, allowing a larger proportion of a ferret population to be trapped at any one time. Using odour lures in conjunction with other baits may be another way of increasing the efficacy of trapping. Changing from one type of attractant to another may increase the catch rate by allowing the capture of trap-shy individuals, who have habituated to one type of attractant (N.Z. Wildlife Service personnel pers. comm.).

The synthetic lure may have the additional advantage of being producable in a long-lasting form. This could increase trapping efficiency by reducing the amount of time spent in dealing with every trap, with lures being renewed every few weeks instead of every few days. In trapping programmes where traps are checked infrequently it

would increase the number of nights traps are attractant to the target species. Synthetic mustelid anal gland compounds have been used in their pure form in capillary tubes as repellants to prevent browsing by herbivores, and Sullivan and Crump (1984) found them to be effective for at least five weeks without renewal.

There is also a possible advantage to the natural product ferret lure. With the development of ferret (fitch) farming in New Zealand, there should be a ready supply of ferret anal sacs which could provide a cheap means of producing an effective ferret lure.

The artificial scent lures developed here have potential value in control programmes for other mustelids as well as ferrets. The successful synthetic ferret lure contained compounds which are found in stoat and weasel anal sac extracts and both species were caught on the lures (Chapter 8).

Both the natural and artificial lures were to some extent species specific, a feature which could improve trapping efficiency by reducing the number of traps made unproductive by the capture of non-target species. In Chapter 8 it was shown that cats and harriers were not attracted to the synthetic ferret lure, however it did not deter hedgehogs, nor did the natural product lure. Species specificity is also a valuable feature if the lure is to be used in ecological research, such as estimating population densities by monitoring numbers of visits to scent stations. The use of synthetic lures is also valuable in such work because of their consistent chemical properties. Another advantage of inedible lures is in studies where the stomach contents or faeces of the captured animals are to be examined, and edible baits can be confused with prey items.

9.2.4 Priorities for Future Research

The highest priorities for future research into mustelid trap lures are to test the synthetic lures in a long-lasting form in the field, and to try them and natural product lures out on a stoat population.

Costing out the production of a natural ferret lure could begin by discussion with fitch farmers, and consideration should be given to the best way of dispensing such a lure.

Further field studies could include the comparison of synthetic lures containing different concentrations of the active components, and the relative attractiveness of the natural product lure made from male and female donor animals. However these are just some of the lines the work could take, as "research is a Gordian knot whose loose ends trail off in so many directions that no one project can hope to untie it" (Schaller 1973).

SUMMARY

1. The ferret is a mustelid that has a predatory role in the New Zealand ecosystem. This means that we need effective means of controlling the damage it does to native fauna at certain times and in certain localities (1.1). To develop effective control techniques we must have sound knowledge of the species behaviour. The ferret's solitary and territorial way of life suggests that odours are important means of communication. One aim of this study was to determine what roles odours play in ferret olfactory communication (1.2, 1.3).

2. Four hypothesised communicative functions of odours were proposed, each with testable predictions (1.3). The first hypothesis was that scent marks and body odours aid in territorial defence, by providing an olfactory association between a resident and its defended area. There are two possible mechanisms: scent matching and neighbour-neighbour recognition. Hypothesis 2 was that anal gland odours are involved in sex attraction. Hypothesis 3 was that scent marks act as a bookkeeping system for efficient food searching. Hypothesis 4 was that anal gland odours in large quantities serve as an antipredator defence system.

3. The use of scent lures to attract ferrets (and other mustelids) to control devices was seen as a means by which damage done by mustelid predation could potentially be reduced. The second aim of this study was to develop a scent lure for ferrets based on the contents of their anal gland secretions (1.4). A procedure for determining the effectiveness of odours as trap lures was outlined. This included a laboratory bioassay of the components of anal gland secretions and field trials of scent lures containing attractant components.

4. Testing some of the predictions of the four odour communication hypotheses required direct observations of ferret behaviour. Twelve ferrets observed over two years in an outside enclosure used regular pathways and latrine sites. On meeting, ferrets often sniffed at each other's anal region, and at the back of the neck (2.3.1). Their repertoire of scent marking actions comprised of the anal drag, thought to be a way of laying down anal gland odour; wiping and belly crawl, where the the urogenital region touched the substrate and the anal region did not; rolling and body rubbing; and chin rubbing (2.3.2).

5. The frequency of performing anal drags did not vary seasonally nor between the sexes. Anal drags usually followed defaecations at latrines, which were concentrated on conspicuous objects and in the central regions of the enclosure, where the ferrets spent most of their time. Wiping was done throughout the enclosure, mostly by males in spring. Body rubbing showed the same seasonal pattern, but only some males body rubbed, and there was no sexual difference in frequency. Some males wiped in situations where others did body rubbing, e.g. during close contact male-male encounters, which usually occurred in the boundary regions of the enclosure. Chin rubbing also showed a peak frequency in spring and was done by both sexes. It occurred frequently at food storage sites (2.3.2).

6. The presence of fresh anal gland secretion of a known dominant male at a latrine did not prevent a subordinate male from entering a nearby nest box. However, the observations were made during the non-breeding season, when captive males were tolerant of each other (2.3.3).

7. An anatomical and histological examination of various regions of the skin confirmed the structure of anal glands and sacs as the same as in the published literature (3.3.1). It revealed the presence of abdominal glands in both sexes around the urogenital opening. These glands consisted of large complexes of epitrichial tubular glands producing glycoproteins, suggesting that they function in the production of odorous secretions. They were larger in males than in females (3.3.2). Regions of the skin used in body and chin rubbing contained numerous sebaceous glands and a few alcian blue-positive tubular glands (3.3.3). The foot contained both atrichial glands in the pads and highly coiled, alcian blue-positive epitrichial glands in the interdigital regions (3.3.4).

8. Hypotheses 1 and 2 require that there are individual and sexual differences in anal gland secretions. Gas chromatography of anal sac extracts from ten ferrets revealed such differences in relative concentrations of volatile compounds. Consistent differences in the colour and viscosity of individuals' anal sac extracts were also noted (4.3.1, 4.3.2). The anal sac extracts had no regular seasonal changes in their GC profiles or visual appearance (4.3.3).

9. Further predictions from hypotheses 1 and 2 are that ferrets can discriminate between different odours. Simultaneous preference tests in Y- and T-mazes showed that ferrets preferred to investigate ferret anal gland odour rather than no odour, and ferret rather than weasel odour. Both sexes, but males especially, discriminated between male and female odours, preferring to investigate the odour of the opposite sex. Males did not show any ability to discriminate between the odours of oestrous and anoestrous females in tests run during the breeding season. Subjects discriminated between familiar and strange odours. Initially they preferred to approach the strange odour and to spent longer sniffing at it than at the familiar odour. They spent as much time investigating their own odour and that of a familiar ferret of the same sex, but, for the first time during the preference tests six of the subjects performed anal drags, always in front of the odour port containing their own anal gland odour. They could discriminate between fresh and one-day old odours from the same female donor, but not between fresh and two-hour old odours (5.3.1, 5.3.2).

10. The scent matching mechanism of hypothesis 1 predicts that ferrets will be confident in the presence of their own odour, and intimidated when the odour of scent marks matches that of a nearby animal. To determine how anal gland odours affect the confidence of ferrets, levels of male confidence and aggression were measured during paired tests in the presence of odours from various donors. Males were significantly less confident in the presence of their opponent's odour than in the presence of either their own odour or that of a known dominant individual. They were no less confident in the presence of this third dominant odour than with their own odour. This is also supportive of the scent matching mechanism. Aggression scores showed similar trends (6.3).

11. A bioassay of synthetic anal gland compounds was run using successive trials in the T-maze apparatus. Some combinations of compounds were more attractive than others. In the first bioaassay experiment the combination of cis- and trans-2,3-dimethylthietane and 2-propylthietane was more attractive (as judged by time spent sniffing at the odour port and speed of approaching the odour) than the other combinations tested (7.3.1). This successful combination was then used as the basis of comparison for further combinations of compounds

(7.3.2, 7.3.3, 7.3.4). It remained at least as attractive as all other combinations of compounds tested. Compounds cis- and trans-3,4-dimethyl-1,2-dithiolane and indole were also highly attractive.

12. Cis- and trans-2,3-dimethylthietane and 2-propylthietane were used as the active ingredients of a scent lure tested in field trials. The attractiveness of this scent lure was tested against various other treatments in live-trapping, paired-trap choice experiments at Pukepuke Lagoon, Manawatu (8.3.1). Ferrets preferred edible bait to the artificial lure and chose the lure over no odour. There were no preferences amongst various artificial lures. Lure containing natural female anal gland secretion was as attractive as bait and was preferred to artificial lure. The combination of bait and artificial lure was not more attractive than either treatment on its own. In bait versus natural product lure pairs, success was dependent upon sex of the captured ferrets, with all the ferrets caught on the lure being female. The success of treatments in all the pairs was independent of season (breeding/non-breeding), and one-day old treatments were as successful as fresh treatments.

13. Trap sites containing two lure traps were as successful as those with one lure trap and one bait trap (8.3.1). Treatment pair success was independent of sex.

14. Ferrets often released anal gland secretion/odour while being handled during live-trapping. Males and females, and juveniles and adults were equally likely to release odour. Ferrets were no more likely to release odour on their initial capture than on subsequent captures (8.3.1).

15. The artificial scent lure was as successful as edible bait at attracting ferrets during a kill-trapping experiment in the Mackenzie Basin, South Canterbury (8.3.2). Catch rates were independent of sex, but the success of the scent lure varied with freshness, with most ferrets being caught when the lure was freshest.

16. In both live- and kill-trapping experiments various non-target species were caught. Hedgehogs showed no preference between bait and scent lure, while cats and harriers preferred bait. Both stoats and

weasels were caught on the scent lure, as were rodents and possums (8.3.1, 8.3.2).

17. The hypothesised territorial defence role for anal gland odours is supported. Anal drag scent marks were distributed in a way that they were most likely to be encountered by both the scent marker and other ferrets. Anal gland odours were found to carry the necessary information on individual identity for them to mediate neighbour-neighbour spacing systems, and ferrets could discern this information. The presence of anal gland odour in the environment in the form of anal drag scent marks, and on the animals themselves, and the fact that ferrets sniffed at each other's anal region during encounters support the scent matching mechanism. The fact that ferrets were intimidated in the presence of an odour that matched that of an opponent in a conflict situation also supports this mechanism (9.1.1).

18. Latrines appear to act as information centres. Whether or not anal gland odour is present, latrines will still be strong olfactory beacons containing the odours of faeces and urine (9.1.1).

19. The sex attraction hypothesis is supported by the fact that there were differences in anal gland secretions between the sexes, that ferrets were able to discriminate these differences and that they were attracted to the odour of the opposite sex (9.1.2).

20. Anal gland odours released in large quantities could act as an antipredator defence system. This is suggested by the readiness of captured ferrets to release odour while being handled, and by the release of anal gland odour by intimidated ferrets being attacked by aggressive, dominant opponents (9.1.4).

21. Neck sniffing behaviour and the use of abdominal and/or body odours in scent marking the territory and in close contact encounters could provide an olfactory association between a resident and its defended area. It is not known, however if these odours convey information identifying the scent marker. It is possible that they are just used as a threat signal (9.1.1).

22. Chin rubbing behaviour may set down an odour at food stores which aids in their relocation, or may be a way of laying down body odour to defend food stores against conspecifics (9.1.3).

23. Compared to other mustelids, scent marking behaviour of the ferret shows some similarities and some differences, which are related to similarities and differences in their social organisation and reproductive physiology (9.1.5).

24. The presence of anal gland odour at latrines should be confirmed and the results of this captive study compared to the wild situation before any strong conclusions are drawn on the roles these odours play in the social organisation of the ferret. Detailed chemical and histological studies of other skin glands and their secretions are necessary before details of the ferret's olfactory communication system can be fully understood (9.1.6).

25. The combination of bioassay experiments in controlled conditions and field trials in natural conditions was seen as the most comprehensive way of assessing the responses of ferrets to odours. It allowed the development of artificial and natural product scent lures that were effective in attracting ferrets (and other mustelids) to traps (9.2.1).

26. The responses of ferrets to anal gland odours were not compatible with the definition of a releaser pheromone. Anal gland odours could be defined as informer pheromones, but it is argued that this name is misleading in implying a similarity in action between these social odours and specific pheromones (9.2.2).

27. The artificial and natural product scent lures could prove valuable in improving the efficacy of current predator control operations, due to their attractiveness to both male and female ferrets throughout the year, and to other mustelids. Efficiency of trapping could be improved by producing lures in a long-lasting form. The species-specific and non-edible characteristics of scent lures make them useful also in ecological research (9.2.3).

28. Further studies are needed to maximise the efficacy and efficiency of the scent lures. In particular, the artificial lure should be tested in a long-lasting form, and its efficacy in attracting stoats could also be tested more rigorously (9.2.4).

APPENDIX 1

Untransformed data and analyses of variance for the scent marking results of Chapter 2. Data from the early, mid and late watches are given consecutively for each season. N.S.= P>0.05.

SUBJECT	SEASON	REGION	TIME (mins)	DATA ANAL DRAG	WIPING	BODY RUBBING	CHIN RUBBING
MALES							
SNARK	WINTER	C	184	6	106	25	29
		B	329	8	51	123	18
		C	9	0	5	1	2
		B	30	1	1	11	0
		C	34	2	13	4	6
		B	47	2	11	21	1
	SPRING	C	78	2	61	18	16
		B	191	7	39	111	19
		C	39	0	33	6	5
		B	40	3	11	38	11
		C	19	3	15	0	4
		B	29	0	5	24	1
	SUMMER*	C	125	1	66	9	9
		B	173	3	36	48	1
		C	47	1	31	4	2
		B	37	3	10	9	1
		C	39	0	17	4	0
		B	61	4	12	11	0
	AUTUMN*	C	122	2	39	1	2
		B	268	0	17	19	1
		C	21	1	5	1	0
		B	93	2	7	12	2
		C	30	1	5	0	0
		B	114	1	14	8	3
HANS	WINTER*	C	221	20	23	3	25
		B	90	2	21	11	6
		C	15	4	3	1	2
		B	17	0	4	4	2
		C	42	4	5	1	1

		B	17	0	1	2	2
	SPRING*	C	60	6	27	10	17
		B	55	0	11	33	8
		C	66	10	15	2	5
		B	45	0	8	26	6
		C	50	7	10	7	3
		B	21	1	6	13	2
	SUMMER	C	107	12	9	9	7
		B	39	3	4	4	2
		C	34	5	1	0	2
		B	14	0	0	0	0
		C	42	2	3	0	0
		B	19	1	1	1	0
	AUTUMN	C	73	3	4	2	0
		B	46	0	9	2	1
		C	26	5	2	0	0
		B	18	0	2	0	0
		C	45	3	0	0	0
		B	31	0	0	0	0
BILBO	WINTER	C	77	1	11	0	0
		B	28	1	8	0	0
		C	43	1	2	0	1
		B	9	1	1	0	0
		C	35	1	5	0	0
		B	19	0	3	0	0
	SPRING	C	53	0	22	1	3
		B	64	0	30	9	0
		C	30	1	3	0	0
		B	10	0	7	1	0
		C	11	1	1	0	0
		B	43	0	13	1	0
MALLI	WINTER	C	119	1	13	1	16
		B	64	6	4	2	0
		C	65	4	9	0	4
		B	27	0	1	0	0
		C	74	5	9	1	2
		B	30	0	0	1	1
	SPRING	C	45	3	22	14	25
		B	34	0	21	25	4

		C	19	2	13	4	5
		B	17	0	5	10	0
		C	25	1	9	3	1
		B	25	0	7	20	0
RAS	SUMMER	C	87	2	2	0	7
		B	64	4	15	0	0
		C	51	2	2	0	2
		B	11	2	2	0	0
		C	29	1	3	0	0
		B	27	1	10	0	0
	AUTUMN	C	72	1	1	0	0
		B	36	1	0	0	0
		C	53	2	0	0	0
		B	16	0	0	0	0
		C	50	1	1	0	0
		B	26	0	1	0	0
CHICO	SUMMER	C	126	0	6	0	6
		B	16	0	0	0	0
		C	48	0	0	0	1
		B	9	0	0	0	0
		C	56	0	5	0	0
		B	5	0	0	0	0
	AUTUMN	C	104	0	1	0	1
		B	25	0	0	0	0
		C	67	0	1	0	0
		B	11	0	0	0	0
		C	55	0	0	0	0
		B	28	0	0	0	0
FEMALES							
JOLIE	WINTER	C	221	9	20	11	12
		B	136	3	11	21	2
		C	33	4	1	0	0
		B	12	0	0	0	0
		C	13	1	0	0	0
		B	11	0	2	0	0
	SPRING	C	75	8	1	0	1
		B	27	0	1	0	1
		C	33	4	1	0	0
		B	6	0	0	0	0

		C	51	2	0	0	0
		B	9	1	1	0	0
	SUMMER*	C	96	10	0	1	5
		B	24	2	1	1	0
		C	38	6	0	0	2
		B	12	3	1	0	0
		C	22	4	1	0	1
		B	7	0	0	0	0
	AUTUMN*	C	98	2	1	0	2
		B	62	2	2	0	0
		C	44	3	0	0	0
		B	48	2	1	0	0
		C	52	4	0	0	1
		B	28	1	1	0	0
ULLA	WINTER*	C	83	1	2	0	0
		B	8	0	1	0	0
		C	29	0	0	0	0
		B	10	0	0	0	0
		C	29	0	0	0	0
		B	5	0	0	0	0
	SPRING*	C	-	-	-	-	-
		B	-	-	-	-	-
		C	-	-	-	-	-
		B	-	-	-	-	-
		C	-	-	-	-	-
		B	-	-	-	-	-
	SUMMER	C	89	2	3	0	2
		B	55	2	0	0	0
		C	23	0	0	0	1
		B	3	0	0	0	0
		C	15	2	0	0	0
		B	10	0	0	0	0
	AUTUMN	C	116	2	1	0	0
		B	44	0	1	0	0
		C	43	0	0	0	0
		B	7	0	0	0	0
		C	24	0	0	0	0
		B	3	0	0	0	0
PUG	WINTER	C	74	4	2	0	1

		B	24	0	1	0	0
		C	50	2	0	0	0
		B	6	0	0	0	0
		C	56	2	1	0	1
		B	14	0	0	0	0
	SPRING	C	95	1	1	0	5
		B	25	0	0	1	0
		C	33	3	1	0	0
		B	7	0	0	0	0
		C	40	2	0	0	0
		B	12	0	0	0	0
SATHA	WINTER	C	113	1	1	0	1
		B	22	4	0	0	0
		C	75	1	0	0	0
		B	12	4	1	0	0
		C	35	2	0	0	0
		B	15	0	0	0	0
	SPRING	C	59	3	1	0	1
		B	37	1	2	0	0
		C	29	2	0	0	0
		B	11	1	0	0	0
		C	23	4	2	0	0
		B	26	1	0	0	0
TITI	SUMMER	C	57	1	1	0	6
		B	34	2	2	1	2
		C	28	1	0	0	1
		B	17	2	0	0	0
		C	22	3	2	0	0
		B	13	0	0	0	0
	AUTUMN	C	55	0	0	0	1
		B	57	4	0	0	0
		C	40	2	1	0	0
		B	32	2	1	0	0
		C	37	0	0	0	0
		B	48	2	0	0	0
SWUZZLE	SUMMER	C	134	0	0	0	1
		B	10	1	0	0	0
		C	72	2	0	0	3
		B	18	1	0	0	0

	C	69	0	0	0	0
	B	1	0	0	0	0
AUTUMN	C	107	0	0	0	0
	B	11	0	0	0	0
	C	68	1	0	0	0
	B	13	0	0	0	0
	C	62	0	0	0	0
	B	19	2	0	0	0

*= Data not used in the statistical analyses.

ANALYSIS OF VARIANCE - GENSTAT COMMANDS

```
'REFE'    ENCL
'UNIT'    $144
'NAME'    TI=EARLY,MID,LATE
  :       SX=MALE,FEMALE
  :       ID=SNARK,HANS,BILBO,MALLI,RAS,CHICO,JOLIE,
             ULLA,PUG,SATHA,TITI,SWUZZLE
  :       SE=WINTER,SPRING,SUMMER,AUTUMN
  :       RE=C,B
'FACT'    SEX $SX=72(1,2)
  :       INDIV $ID=12(1...12)
  :       PERIOD $TI=2(1,2,3)24
  :       SEASON $SE=(6(1...4),6(1,2)2,6(3,4)2)2
  :       REGION $RE=(1,2)72
'SET'     S1=AD,WIP,BR,CR
  :       S2=AD%,WIP%,BR%,CR%
  :       S3=NAD,NWIP,NBR,NCR
'READ/P'  TIME,S1
'CALC'    S2=S1/TIME/(0.000302*(REGION .EQ 1)+
             0.000223*(REGION .EQ 2)
'FOR'     A=S2;B=S3;D=FLEV(1...4);E=F(1...4)
'GROU'    E=RANK(A;D)
'CALC'    B=NED((VARFAC(E)-0.5)/144)
'REPE'
'BLOC'    SEX/INDIV
```

```
'TREA'    SEX*SEASON*REGION
'ANOV/PROB=Y'
PRIN/P'   SEX,INDIV,SEASON,REGION,TIME,S1,S2,S3
          $5(7.0),5(5.0),4(7.1),4(7.3)
'RUN'
```

NOTE: PARTIAL CONFOUNDING OF SEASON, SEX.SEASON IN SEX.INDIV STRATUM

ANOVA - ANAL DRAG PER TOTAL HOURS

FACTOR	DF	SS	MS	F	SIGNIFICANCE
SEX.INDIV STRATUM					
SEX	1	0.318	0.3179	0.063	N.S.
SEASON	3	2.612	0.8708	0.173	N.S.
SEX.SEASON	3	1.159	0.3864	0.077	N.S.
RESIDUAL	4	20.145	5.0363		
SEX.INDIV.*UNITS* STRATUM					
SEASON	3	2.347	0.782	1.489	N.S.
REGION	1	11.002	11.002	20.944	P<.001
SEX.SEASON	3	0.814	0.271	0.517	N.S.
SEX.REGION	1	0.016	0.016	0.031	N.S.
SEASON.REGION	3	3.313	1.104	2.102	N.S.
SEX.SEASON.REGION	3	7.029	2.343	4.460	P<0.005
RESIDUAL	118	61.987	0.525		

ANOVA - ANAL DRAG PER HOURS IN EACH REGION

FACTOR	DF	SS	MS	F	SIGNIFICANCE
SEX.INDIV. STRATUM					
SEX	1	0.483	0.483	0.093	N.S.
SEASON	3	2.010	0.670	0.129	N.S.
SEX.SEASON	3	0.457	0.152	0.029	N.S.
RESIDUAL	4	20.717	5.179		
SEX.INDIV.*UNITS* STRATUM					
SEASON	3	3.523	1.174	1.927	N.S.
REGION	1	2.093	2.093	0.434	N.S.
SEX.SEASON	3	0.653	0.218	0.357	N.S.
SEX.REGION	1	0.374	0.374	0.613	N.S.
SEASON.REGION	3	4.636	1.545	2.535	N.S.
SEX.SEASON.REGION	3	3.762	1.254	2.058	N.S.
RESIDUAL	118	71.912	0.609		

ANOVA - WIPING PER TOTAL HOURS

FACTOR	DF	SS	MS	F	SIGNIFICANCE
SEX.INDIV STRATUM					
SEX	1	34.574	34.574	21.612	$P<0.010$
SEASON	3	18.717	6.239	3.900	N.S.
SEX.SEASON	3	6.229	2.076	1.298	N.S.
RESIDUAL	4	6.399	1.600		
SEX.INDIV.*UNITS* STRATUM					
SEASON	3	3.834	1.278	4.392	$P<0.006$
REGION	1	0.933	0.933	3.205	N.S.
SEX.SEASON	3	4.173	1.391	4.780	$P<0.004$
SEX.REGION	1	0.040	0.040	0.138	N.S.
SEASON.REGION	3	0.205	0.068	0.235	N.S.
SEX.SEASON.REGION	3	0.723	0.241	0.828	N.S.
RESIDUAL	118	34.339	0.291		

ANOVA - WIPING PER HOURS IN EACH REGION

FACTOR	DF	SS	MS	F	SIGNIFICANCE
SEX.INDIV. STRATUM					
SEX	1	32.894	32.894	18.675	P<0.012
SEASON	3	19.627	6.542	3.714	N.S.
SEX.SEASON	3	6.173	2.058	1.168	N.S.
RESIDUAL	4	7.045	1.761		
SEX.INDIV.*UNITS* STRATUM					
SEASON	3	3.060	1.020	3.269	P<0.024
REGION	1	0.156	0.156	0.500	N.S.
SEX.SEASON	3	3.574	1.191	3.818	P<0.012
SEX.REGION	1	0.031	0.031	0.098	N.S.
SEASON.REGION	3	0.058	0.019	0.062	N.S.
SEX.SEASON.REGION	3	0.724	0.241	0.773	N.S.
RESIDUAL	118	36.819	0.312		

ANOVA - BODY RUBBING PER TOTAL HOURS

FACTOR	DF	SS	MS	F	SIGNIFICANCE
SEX.INDIV STRATUM					
SEX	1	13.400	13.400	3.895	N.S.
SEASON	3	10.500	3.500	1.017	N.S.
SEX.SEASON	3	7.577	2.526	0.734	N.S.
RESIDUAL	4	13.760	3.440		
SEX.INDIV.*UNITS* STRATUM					
SEASON	3	2.040	0.680	4.397	P<0.006
REGION	1	1.573	1.573	10.173	P<0.002
SEX.SEASON	3	3.372	1.124	7.267	P<0.001
SEX.REGION	1	0.67	0.675	4.364	P<0.039
SEASON.REGION	3	1.816	0.605	3.913	P<0.011
SEX.SEASON.REGION	3	1.346	0.449	2.900	P<0.038
RESIDUAL	118	18.250	0.155		

ANOVA - BODY RUBBING PER HOURS IN EACH REGION

FACTOR	DF	SS	MS	F	SIGNIFICANCE
SEX.INDIV. STRATUM					
SEX	1	13.381	13.381	3.898	N.S.
SEASON	3	10.582	3.527	1.028	N.S.
SEX.SEASON	3	7.586	2.529	0.737	N.S.
RESIDUAL	4	13.731	3.433		
SEX.INDIV.*UNITS* STRATUM					
SEASON	3	2.104	0.701	4.516	P<0.005
REGION	1	1.715	1.715	11.040	P<0.001
SEX.SEASON	3	3.222	1.074	6.914	P<0.001
SEX.REGION	1	0.700	0.700	4.505	P<0.036
SEASON.REGION	3	1.766	0.589	3.789	P<0.012
SEX.SEASON.REGION	3	1.193	0.398	2.560	P<0.058
RESIDUAL	118	18.329	0.155		

ANOVA - WIPING + BODY RUBBING PER TOTAL HOURS

FACTOR	DF	SS	MS	F	SIGNIFICANCE
SEX.INDIV STRATUM					
SEX	1	34.484	34.484	15.380	P<0.017
SEASON	3	21.797	7.266	3.241	N.S.
SEX.SEASON	3	6.459	2.153	0.960	N.S.
RESIDUAL	4	8.968	2.242		
SEX.INDIV.*UNITS* STRATUM					
SEASON	3	3.447	1.149	4.720	P<0.004
REGION	1	0.000	0.000	0.000	N.S.
SEX.SEASON	3	3.086	1.029	4.225	P<0.007
SEX.REGION	1	0.181	0.181	0.744	N.S.
SEASON.REGION	3	1.199	0.400	1.642	N.S.
SEX.SEASON.REGION	3	1.815	0.605	2.485	P<0.064
RESIDUAL	118	28.728	0.244		

ANOVA - WIPING + BODY RUBBING PER HOURS IN EACH REGION

FACTOR	DF	SS	MS	F	SIGNIFICANCE
SEX.INDIV STRATUM					
SEX	1	34.442	34.442	18.665	P<0.012
SEASON	3	22.781	7.594	4.115	N.S.
SEX.SEASON	3	6.187	2.062	1.118	N.S.
RESIDUAL	4	7.381	1.845		
SEX.INDIV.*UNITS* STRATUM					
SEASON	3	3.653	1.218	5.116	P<0.002
REGION	1	0.435	0.435	1.827	N.S.
SEX.SEASON	3	3.184	1.061	4.460	P<0.005
SEX.REGION	1	0.223	0.223	0.937	N.S.
SEASON.REGION	3	1.172	0.391	1.641	N.S.
SEX.SEASON.REGION	3	0.868	0.289	1.216	N.S.
RESIDUAL	118	28.084	0.238		

ANOVA - CHIN RUBBING PER TOTAL HOURS

FACTOR	DF	SS	MS	F	SIGNIFICANCE
SEX.INDIV STRATUM					
SEX	1	6.459	6.459	1.617	N.S.
SEASON	3	4.695	1.564	0.392	N.S.
SEX.SEASON	3	5.055	1.685	0.422	N.S.
RESIDUAL	4	15.983	3.995		
SEX.INDIV.*UNITS* STRATUM					
SEASON	3	4.472	1.491	4.893	P<0.003
REGION	1	8.757	8.757	28.740	P<0.001
SEX.SEASON	3	0.790	0.263	0.864	N.S.
SEX.REGION	1	0.435	0.435	1.427	N.S.
SEASON.REGION	3	2.979	0.993	3.259	P<0.024
SEX.SEASON.REGION	3	0.518	0.173	0.567	N.S.
RESIDUAL	118	35.952	0.305		

ANOVA - CHIN RUBBING PER HOURS IN EACH REGION

FACTOR	DF	SS	MS	F	SIGNIFICANCE
SEX.INDIV STRATUM					
SEX	1	6.639	6.639	1.568	N.S.
SEASON	3	4.950	1.650	0.390	N.S.
SEX.SEASON	3	5.035	1.678	0.397	N.S.
RESIDUAL	4	16.932	4.233		
SEX.INDIV.*UNITS* STRATUM					
SEASON	3	4.132	1.378	4.477	P<0.005
REGION	1	7.727	7.727	25.115	P<0.001
SEX.SEASON	3	0.694	0.231	0.752	N.S.
SEX.REGION	1	0.593	0.593	1.926	N.S.
SEASON.REGION	3	2.367	0.789	2.564	P<0.058
SEX.SEASON.REGION	3	0.722	0.241	0.782	N.S.
RESIDUAL	118	36.305	0.308		

APPENDIX 2

Data, analyses of variance and discriminant function analysis for peak proportion analysis of anal sac extracts (Chapter 4). *=missing value. N.S.= P>0.05. Accuracy of the raw data was to the 1% level.

DATA (untransformed)

SUBJECT	SAMPLE DATE	PEAKS 2+3	4	6+7	8	11
MALES						
BANDIT	OCT 82	0.176	0.272	0.045	0.015	0.492
	NOV	0.158	0.299	0.033	0.025	0.483
	JAN 83	0.211	0.354	0.009	0.023	0.402
	MAY	*	*	*	*	*
	JUL	*	*	*	*	*
	AUG	0.215	0.215	0.000	0.000	0.568
	SEP	0.172	0.345	0.137	0.000	0.345
	OCT	*	*	*	*	*
	DEC	0.013	0.151	0.151	0.009	0.677
	JAN 84	0.067	0.238	0.183	0.057	0.452
	FEB	*	*	*	*	*
	MAR	*	*	*	*	*
	APR	*	*	*	*	*
COONIE	OCT 82	*	*	*	*	*
	NOV	*	*	*	*	*
	JAN 83	*	*	*	*	*
	MAY	*	*	*	*	*
	JUL	*	*	*	*	*
	AUG	*	*	*	*	*
	SEP	*	*	*	*	*
	OCT	*	*	*	*	*
	DEC	*	*	*	*	*
	JAN 84	0.244	0.369	0.098	0.049	0.244
	FEB	0.218	0.320	0.000	0.000	0.461
	MAR	0.276	0.195	0.263	0.048	0.218
	APR	0.250	0.237	0.214	0.064	0.232
HOB	OCT 82	0.049	0.070	0.091	0.021	0.768
	NOV	0.069	0.223	0.043	0.023	0.642
	JAN 83	0.046	0.231	0.037	0.003	0.683
	MAY	0.222	0.111	0.148	0.000	0.518
	JUL	0.323	0.161	0.000	0.000	0.484

	AUG	0.211	0.154	0.068	0.000	0.567
	SEP	0.072	0.060	0.096	0.048	0.722
	OCT	0.151	0.247	0.075	0.000	0.527
	DEC	*	*	*	*	*
	JAN 84	*	*	*	*	*
	FEB	*	*	*	*	*
	MAR	*	*	*	*	*
	APR	*	*	*	*	*
MALLI	OCT 82	0.253	0.188	0.068	0.013	0.478
	NOV	0.146	0.365	0.032	0.012	0.444
	JAN 83	0.104	0.305	0.012	0.041	0.518
	MAY	0.195	0.302	0.027	0.007	0.470
	JUL	0.227	0.477	0.068	0.000	0.227
	AUG	0.156	0.550	0.000	0.000	0.293
	SEP	0.115	0.339	0.045	0.027	0.474
	OCT	0.127	0.422	0.063	0.001	0.386
	DEC	0.185	0.339	0.040	0.040	0.396
	JAN 84	0.089	0.556	0.126	0.027	0.202
	FEB	0.125	0.392	0.089	0.019	0.364
	MAR	0.105	0.447	0.055	0.002	0.389
	APR	0.116	0.408	0.030	0.027	0.418
SNARK	OCT 82	0.105	0.027	0.156	0.062	0.650
	NOV	0.075	0.030	0.077	0.049	0.769
	JAN 83	0.177	0.032	0.026	0.080	0.685
	MAY	*	*	*	*	*
	JUL	*	*	*	*	*
	AUG	*	*	*	*	*
	SEP	0.104	0.080	0.224	0.112	0.480
	OCT	0.053	0.041	0.342	0.000	0.563
	DEC	0.105	0.064	0.166	0.060	0.605
	JAN 84	0.000	0.082	0.365	0.146	0.407
	FEB	0.125	0.067	0.290	0.067	0.446
	MAR	0.133	0.064	0.242	0.103	0.457
	APR	0.188	0.068	0.286	0.121	0.438
FEMALES						
FURO	OCT 82	0.140	0.346	0.403	0.007	0.104
	NOV	0.472	0.189	0.220	0.009	0.110
	JAN 83	0.269	0.078	0.461	0.000	0.192
	MAY	0.527	0.136	0.209	0.000	0.128
	JUL	0.332	0.204	0.178	0.005	0.281

	AUG	*	*	*	*	*
	SEP	0.683	0.083	0.100	0.000	0.133
	OCT	0.366	0.411	*	0.000	0.223
	DEC	*	*	*	*	*
	JAN 84	*	*	*	*	*
	FEB	*	*	*	*	*
	MAR	*	*	*	*	*
	APR	*	*	*	*	*
JILL	OCT 82	0.283	0.304	0.145	0.051	0.152
	NOV	0.309	0.567	0.010	0.010	0.103
	JAN 83	0.237	0.382	0.252	0.010	0.119
	MAY	0.417	0.206	0.222	0.005	0.155
	JUL	0.304	0.304	0.261	0.022	0.109
	AUG	0.297	0.281	0.157	0.000	0.266
	SEP	0.170	0.440	0.240	0.080	0.100
	OCT	0.178	0.118	0.526	0.039	0.138
	DEC	0.174	0.153	0.485	0.083	0.104
	JAN 84	0.213	0.224	0.419	0.109	0.034
	FEB	0.307	0.166	0.337	0.147	0.047
	MAR	0.104	0.065	0.597	0.057	0.178
	APR	0.283	0.026	0.576	0.052	0.062
PUG	OCT 82	0.538	0.139	0.172	0.010	0.139
	NOV	0.495	0.176	0.215	0.017	0.102
	JAN 83	0.546	0.103	0.283	0.015	0.055
	MAY	0.545	0.045	0.383	0.000	0.045
	JUL	0.294	0.216	0.392	0.039	0.059
	AUG	*	*	*	*	*
	SEP	*	*	*	*	*
	OCT	0.351	0.156	0.458	0.001	0.034
	DEC	0.416	0.124	0.385	0.062	0.012
	JAN 84	0.256	0.047	0.413	0.039	0.244
	FEB	0.298	0.063	0.461	0.022	0.157
	MAR	0.242	0.204	0.213	0.031	0.309
	APR	0.156	0.086	0.403	0.001	0.349
SATHA	OCT 82	*	*	*	*	*
	NOV	*	*	*	*	*
	JAN 83	*	*	*	*	*
	MAY	*	*	*	*	*
	JUL	0.303	0.114	0.542	0.004	0.038
	AUG	0.329	0.069	0.288	0.000	0.313

	SEP	0.380	0.086	0.239	0.014	0.288
	OCT	0.179	0.078	0.429	0.000	0.313
	DEC	0.211	0.095	0.453	0.031	0.209
	JAN 84	0.361	0.082	0.470	0.000	0.087
	FEB	0.344	0.070	0.409	0.117	0.058
	MAR	0.525	0.058	0.374	0.031	0.011
	APR	0.344	0.061	0.444	0.032	0.119
SWUZZLE	OCT 82	0.335	0.048	0.121	0.002	0.494
	NOV	0.508	0.171	0.018	0.009	0.293
	JAN 83	0.384	0.159	0.114	0.010	0.330
	MAY	0.398	0.072	0.072	0.024	0.385
	JUL	0.558	0.281	0.046	0.011	0.102
	AUG	0.354	0.139	0.045	0.014	0.139
	SEP	0.374	0.152	0.088	0.012	0.374
	OCT	0.458	0.272	0.191	0.025	0.054
	DEC	0.345	0.197	0.099	0.042	0.317
	JAN 84	0.478	0.135	0.165	0.091	0.132
	FEB	0.363	0.089	0.145	0.040	0.363
	MAR	0.361	0.118	0.114	0.033	0.369
	APR	0.309	0.193	0.166	0.097	0.235

ANALYSIS OF VARIANCE - SPSS COMMANDS

```
RUN NAME        ALL or MALE or FEMALE or DFA
VARIABLE LIST   SEX INDIV REPL V2 V4 V6 V8 V11
INPUT FORMAT    FREEFIELD
MISSING DATA    V2 TO V11  (-1)
COMPUTE         V2T=ATAN(SQR((V2/100)/(1-(V2/100))))*180/4ATAN(1)
COMPUTE         V4T=ATAN(SQR((V4/100)/(1-(V4/100))))*180/4ATAN(1)
COMPUTE         V6T=ATAN(SQR((V6/100)/(1-(V6/100))))*180/4ATAN(1)
COMPUTE         V8T=ATAN(SQR((V8/100)/(1-(V8/100))))*180/4ATAN(1)
COMPUTE         V11T=ATAN(SQR((V11/100)/(1-(V11/100))))*180/4ATAN(1)
MANOVA          V2T TO V11T BY SEX (1,2) INDIV (1,10)/
                DESIGN=SEX VS 1, INDIV VS WITHIN=1 VS WITHIN
                or V2T TO V11T BY INDIV (1, 5)/
                or V2T TO V11T BY INDIV (6, 10)/
DISCRIMINANT    GROUPS=INDIV (1,10)/
                VARIABLE=V2T TO V11T/
                ANALYSIS=V2T TO V11T (1)/
OPTIONS         6
```

ANALYSIS OF VARIANCE - 2+3

FACTOR	DF	SS	MS	F	SIGNIFICANCE
SEX	1	7513.9	7513.9	15.08	$P<0.005$
RESIDUAL	8	3986.0	498.2		
INDIVIDUAL MALE	4	1339.1	334.8	2.66	$P<0.041$
RESIDUAL	60	7553.4	125.9		
INDIVIDUAL FEMALE	4	2646.9	661.7	3.06	$P<0.023$
RESIDUAL	60	12962.2	216.0		

ANALYSIS OF VARIANCE - 4

FACTOR	DF	SS	MS	F	SIGNIFICANCE
SEX	1	25.5	25.5	0.02	N.S.
RESIDUAL	8	9951.7	1243.9		
INDIVIDUAL MALE	4	7384.3	1846.1	12.43	$P<0.0005$
RESIDUAL	60	8913.0	148.5		
INDIVIDUAL FEMALE	4	2567.4	641.8	6.17	$P<0.0005$
RESIDUAL	60	6242.9	104.0		

ANALYSIS OF VARIANCE - 6+7

FACTOR	DF	SS	MS	F	SIGNIFICANCE
SEX	1	6116.1	6116.1	9.22	$P<0.016$
RESIDUAL	8	5304.7	663.1		
INDIVIDUAL MALE	4	1787.1	446.8	4.19	$P<0.005$
RESIDUAL	60	6389.2	106.5		
INDIVIDUAL FEMALE	4	3517.6	879.4	4.13	$P<0.005$
RESIDUAL	60	12759.4	212.7		

ANALYSIS OF VARIANCE - 8

FACTOR	DF	SS	MS	F	SIGNIFICANCE
SEX	1	42.4	42.4	0.21	N.S.
RESIDUAL	8	1639.8	204.9		
INDIVIDUAL MALE	4	778.2	194.6	5.76	$P \leq 0.001$
RESIDUAL	60	2028.1	33.8		
INDIVIDUAL FEMALE	4	861.6	215.4	8.09	$P \leq 0.0005$
RESIDUAL	60	1598.0	26.6		

ANALYSIS OF VARIANCE - 11

FACTOR	DF	SS	MS	F	SIGNIFICANCE
SEX	1	2688.9	2688.9	2.22	N.S.
RESIDUAL	8	9700.0	1212.5		
INDIVIDUAL MALE	4	7107.3	1776.8	4.38	$P \leq 0.004$
RESIDUAL	60	24348.5	405.8		
INDIVIDUAL FEMALE	4	2592.7	648.2	5.38	$P < 0.001$
RESIDUAL	60	7223.7	120.4		

ANALYSIS OF VARIANCE - MANOVA

FACTOR	DF	PILLAIS	APPROX F	SIGNIFICANCE
SEX	5	0.981	12.00	$P \leq 0.016$
RESIDUAL	4			
INDIVIDUAL MALE	20	1.19	4.98	$P \leq 0.0005$
RESIDUAL	236			
INDIVIDUAL FEMALE	20	1.21	5.12	$P \leq 0.0005$
RESIDUAL	236			

DISCRIMINANT FUNCTION ANALYSIS

DISCRIMINANT FUNCTIONS	EIGENVALUES	PERCENT OF VARIANCE	CUMULATIVE PERCENT	CANONICAL CORRELATION
1	1.581	43.60	43.60	0.783
2	1.015	27.98	71.58	0.710
3	0.468	12.92	84.50	0.565
4	0.444	12.25	96.75	0.555
5	0.118	3.25	100.00	0.325

STANDARDISED COEFFICIENTS

VARIABLES	DF1	DF2	DF3	DF4	DF5
2+3	0.94	-0.36	0.54	-1.17	-0.01
4	-0.54	1.51	-0.10	0.24	-0.04
6+7	0.63	0.20	-0.48	0.96	0.63
8	-0.04	-0.15	0.88	0.27	-0.76
11	-0.85	-0.90	0.24	-0.02	0.73

CENTROID VALUES

INDIVIDUALS	DF1	DF2	DF3	DF4	DF5
BANDIT	-1.15	-0.04	-0.43	-0.04	-0.13
COONIE	-0.34	-0.14	-0.65	-0.11	-0.77
HOB	-1.27	-0.84	-0.40	-0.20	0.41
MALLI	-1.97	1.77	0.33	-0.10	0.28
SNARK	-0.77	-1.72	0.77	1.03	-0.04
FURO	0.56	0.13	-0.78	-0.56	0.01
JILL	1.04	1.49	0.48	0.97	-0.20
PUG	1.76	0.10	-0.11	0.02	0.29
SATHA	1.45	-0.36	-0.52	0.29	0.29
SWUZZLE	0.69	-0.38	1.31	-1.28	-0.13

APPENDIX 3

Data and analysis of variance for preliminary Y-maze tests (Chapter 5). F=familiar U=unfamiliar *=missing value. N.S.= P>0.05.

DATA

SUBJECT	TRIAL	ODOUR	TIME (s)	NORMALISED RANK
BANDIT	1	F FEMALE	14.8	-0.17
	2	F MALE	20.8	0.13
	3	U FEMALE	18.6	-0.04
	4	U MALE	158.5	1.09
HOB	1	F MALE	19.4	0.04
	2	F FEMALE	8.2	-0.82
	3	U MALE	12.2	-0.49
	4	U FEMALE	14.8	-0.17
MALLI	1	U FEMALE	4.8	-1.48
	2	U MALE	92.3	0.82
	3	F FEMALE	*	*
	4	F MALE	*	*
SNARK	1	U MALE	12.7	-0.40
	2	U FEMALE	7.7	-0.94
	3	F MALE	169.4	1.26
	4	F FEMALE	10.5	-0.59
FURO	1	U MALE	14.0	-0.31
	2	U FEMALE	196.9	1.48
	3	F MALE	86.5	0.70
	4	F FEMALE	*	*
JILL	1	U FEMALE	47.0	0.40
	2	U MALE	66.8	0.59
	3	F FEMALE	42.1	0.31
	4	F MALE	41.7	0.22
PUG	1	F MALE	286.7	1.82
	2	F FEMALE	*	*
	3	U MALE	66.4	0.49
	4	U FEMALE	145.8	0.94
SWUZZLE	1	F FEMALE	9.3	-0.70
	2	F MALE	3.7	-1.82
	3	U FEMALE	6.6	-1.09
	4	U MALE	5.3	-1.26

ANALYSIS OF VARIANCE - GENSTAT COMMANDS

```
'REFE'      YMAZE
'UNIT'      $32
'NAME'      F=FAMILIAR, UNFAMILIAR
  :         I=HOB,JILL,BANDIT,FURO,SNARK,SWUZZLE,MALLI,PUG
  :         S=MALE, FEMALE
'FACT'      RESPONDENT $I=(3...6)2,(1,2,7,8)4,(3...6)2
  :         ODOUR $I=4(1...8)
  :         O_SEX $S=4(1,2)4
  :         R_SEX $S=(1,2)16
  :         FAMILIARITY $F=2(1,2)4,2(2,1)4
  :         RUN $4=2,3,1,4,(1,4,2,3)2,2,3,1,4,3,2,4,1,
                  (4,1,3,2)2,3,2,4,1
'READ/P'    T
'GROU'      RNK=RANK(T;FLFV)
'CALC'      RKS=VARFAC(RNK)
  :         NRKS=NED(RKS/29)
'PRIN/P'    ODOUR, O_SEX, RESPONDENT, R_SEX, FAMILIARITY,
            RUN, T, RKS, NRKS $ (8,7)2,11,4,(6.1)2,8,4
'BLOC'      R_SEX/RESPONDENT+O_SEX/ODOUR
'TREA'      R_SEX*O_SEX+FAMILIARITY
'ANOV'      T, NRKS
'RUN'
```

ANALYSIS OF VARIANCE - NRKS

FACTOR	DF	SS	MS	F	SIGNIFICANCE
SEX OF SUBJECT	1	0.97	0.97	0.38	N.S.
RESIDUAL	6	15.33	2.55		
SEX OF ODOUR	1	0.36	0.36	0.90	N.S.
RESIDUAL	6	2.40	0.40		
SEX SUBJECT/ SEX ODOUR	1	4.21	4.21	10.17	$P<0.01$
FAMILIARITY	1	0.83	0.83	2.10	N.S.
RESIDUAL	11	4.56	0.41		

APPENDIX 4

General Behaviour of Ferrets in the T-maze.

The various individuals used as subjects behaved differently in the T-maze. Wild-caught adults typically had a long latency to response, and moved slowly and deliberately, in straight lines to and from the odour ports, keeping close to the walls of the arenas. They did not spend long in the arenas, often investigating each arena once only and then returning to the start-box. In contrast, the one year-old, captive-bred animals moved quickly out of the start-box and spent the whole trial exploring the arenas, including the odour ports. They often engaged in play behaviour, jumping high in the air off all four feet, batting at the light bulbs and scratching at the newspaper. These activities where interspersed with periods of odour investigation. All the animals sometimes raised themselves up on their back legs when investigating an odour port, and then slid down with their abdomen and chest touching the wall. Male Snark often scent marked by body rubbing (see Chapter 2), and all the males frequently urinated in the arenas, and would then turn round, sniff and lick the urine. Periods of grooming also occurred.

APPENDIX 5

Data for T-maze preference tests (experiments 1-7, Chapter 5).

EXPERIMENT 1

SUBJECT	TIME SPENT SNIFFING		INITIAL CHOICE
MALES	FERRET	BLANK	
BANDIT	34	0	F
HOB	103	16	F
MALLI	*	*	*
SNARK	107	58	B
FEMALES			
FURO	3	0	F
JILL	95	0	F
PUG	122	21	F
SWUZZLE	10	0	F

EXPERIMENT 2

SUBJECT	TIME SPENT SNIFFING		INITIAL CHOICE
MALES	FERRET	WEASEL	
BANDIT	57	10	F
HOB	96	21	F
MALLI	13	3	F
SNARK	29	28	F
FEMALES			
FURO	153	47	F
JILL	33	75	F
PUG	58	83	F
SWUZZLE	8	59	W

EXPERIMENT 3

SUBJECT	TIME SPENT SNIFFING		INITIAL CHOICE
MALES	SAME SEX	OPPOSITE SEX	
BANDIT	30	96	O
	20	15	O
	14	15	O
HOB	99	84	O
	6	14	O
	6	14	S
MALLI	10	11	O
	0	8	O
	0	9	O
SNARK	61	49	O
	10	14	S
	30	96	O
FEMALES			
FURO	55	47	O
	12	0	S
	37	35	O
JILL	17	33	S
	*	*	*
	*	*	*
PUG	*	*	*
	18	8	S
	9	22	O
SWUZZLE	0	15	O
	9	17	O
	17	0	S

EXPERIMENT 4

SUBJECT	TIME SPENT SNIFFING		INITIAL CHOICE
MALES	OESTROUS	ANOESTROUS	
BANDIT	16	24	O
	7	11	O
	6	30	O
HOB	173	123	A
	22	59	O
	7	13	O
MALLI	11	18	A
	1	15	O
	10	15	O
SNARK	145	187	A
	24	91	O
	4	5	A

EXPERIMENT 5

SUBJECT	SEX OF	TIME SPENT SNIFFING		INITIAL CHOICE
MALES	ODOUR	FAMILIAR	STRANGE	
AYYA	MALE	40	79	S
	FEMALE	16	32	S
BANDIT	MALE	40	16	S
	FEMALE	58	36	S
COONIE	MALE	30	64	S
	FEMALE	25	41	S
HOB	MALE	7	21	F
	FEMALE	18	21	S
MALLI	MALE	6	9	F
	FEMALE	51	23	S
FEMALES				
BESTIE	MALE	73	122	S
	FEMALE	118	139	F
FURO	MALE	*	*	*
	FEMALES	3	19	S
SATHA	MALE	9	20	S

	FEMALE	*	*	*
SWUZZLE	MALE	1	4	S
	FEMALE	0	19	S
TITI	MALE	34	86	S
	FEMALE	28	24	F

EXPERIMENT 6

SUBJECT	TIME SPENT SNIFFING		INITIAL CHOICE
MALES	OWN	FAMILIAR	
AYYA	12	62	F
BANDIT	60	31	F
COONIE	42	33	F
HOB	13	39	O
MALLI	0	19	F
ANNIE	45	55	F
BESTIE	103	43	O
DAWN	36	52	O
RAE	37	58	O
TITI	63	25	O

EXPERIMENT 7

SUBJECT	STALENESS	TIME SPENT SNIFFING		INITIAL CHOICE
MALES		FRESH	STALE	
AYYA	2HOUR	39	27	F
	1DAY	57	47	S
BANDIT	2HOUR	57	40	S
	1DAY	123	100	F
COONIE	2HOUR	42	37	S
	1DAY	105	75	S
MALLI	2HOUR	11	23	S
	1DAY	17	13	S
FEMALES				
ANNIE	2HOUR	31	35	F
	1DAY	36	33	F
BESTIE	2HOUR	87	97	S
	1DAY	107	63	S
DAWN	2HOUR	53	69	S
	1DAY	64	52	F
TITI	2HOUR	63	73	F
	1DAY	67	25	F

APPENDIX 6

Analysis of variance of normalised rank time spent sniffing data of preference test experiment 5 (Chapter 5). N.S.= P>0.05.

ANALYSIS OF VARIANCE - GENSTAT COMMANDS

```
'REFE'          ANOVA
'UNIT'          $40
'NAME'          IN=COONIE, MALLI, AYYA, HOB, BANDIT,
                   BESTIE, SWUZZLE, SATHA, TITI, FURO
  :             FA=FAMIL, UNFAMIL
  :             OS=MALE_ODR, FEMALE_ODR
  :             RS=MALE_RES, FEMALE_RES
'FACT'          RESPONDT $IN=4(1...10)
  :             ODOUR_SEX $OS=2(1,2)10
  :             RESP_SEX $RS=20(1,2)
  :             FAMILITY $FA=(1,2)20
  :             TRIAL $2=2(1,2)10
'READ/P'        TIME
'GROU'          DI=RANK(TIME;FLEV)
'CALC'          NRTIME=NED((VARFAC(D1)-0.5)/
                (NVAL(TIME)-NMV(TIME)))
'PRIN/P'        RESP_SEX,RESPONDT,ODOUR_SEX,TRIAL,FAMILITY,
                TIME,NRTIME$5(9.0),1(6.0),1(8.3)
'BLOC'          RESPONDT/TRIAL
'TREA'          FAMILITY*RESP_SEX*ODOUR_SEX
'ANOV'          TIME, NRTIME
'RUN'
```

ANALYSIS OF VARIANCE - NRTIME

FACTOR	DF	SS	MS	F	SIGNIFICANCE
SEX OF SUBJECT	1	0.47	0.47	0.14	N.S.
RESIDUAL	8	26.27	3.28		
SEX OF ODOUR	1	0.06	0.06	0.10	N.S.
SEX OF ODOUR/ SEX OF SUBJECT	1	0.13	0.13	0.20	N.S.
RESIDUAL	6	4.04	0.67		
FAMILIARITY	1	2.27	2.27	9.15	$P \leq 0.01$
FAMILIARITY/ SEX OF SUBJECT	1	0.81	0.81	3.27	N.S. ($P \leq 0.1$)
FAMILIARITY/ SEX OF ODOUR	1	0.00	0.00	0.01	N.S.
FAMILIARITY/ SEX OF ODOUR/ SEX OF SUBJECT	1	0.06	0.06	0.26	N.S.
RESIDUAL	14	3.45	0.25		

APPENDIX 7

Data and analyses of variance for bioassay experiments (Chapter 7). Odours are listed in the order of testing for each subject. COV= covariate for age/tameness. *=missing value. N.S.=P>0.05.

BIOASSAY EXPERIMENT 1

DATA

SUBJECT	COV	ODOUR	TIME SPENT SNIFFING(s)	NORMALISED RANK TIME	SPEED OF RESPONSE(s)	NORMALISED RANK SPEED
MALES						
AYYA	1	234	36	0.08	107	0.53
		23	27	-0.22	23	-0.30
		49	31	-0.06	11	-0.98
		239	17	-0.53	101	0.38
		4	72	0.72	9	-1.19
		9	31	-0.06	9	-1.19
BANDIT	0	9	0	-1.76	122	0.72
		4	22	-0.34	79	0.28
		239	17	-0.53	170	0.95
		49	12	-0.70	129	0.78
		23	12	-0.70	101	0.38
		234	36	0.08	35	-0.02
COONIE	1	49	67	0.53	14	-0.67
		9	58	0.44	16	-0.58
		23	96	1.23	34	-0.10
		4	91	1.08	15	-0.63
		234	89	0.98	115	0.65
		239	92	1.15	51	0.20
HOB	0	239	0	-1.76	900	1.42
		234	13	-0.63	115	0.65
		4	9	-1.08	42	0.10
		23	5	-1.42	37	0.04
		9	7	-1.27	246	1.08
		49	0	-1.76	900	1.42
MALLI	0	23	10	-0.95	180	1.01
		239	10	-0.95	686	1.23
		9	10	-0.95	270	1.15
		234	17	-0.53	35	-0.02

		49	0	-1.76	900	1.42
		4	11	-0.80	103	0.44
SNARK	0	4	51	0.32	11	-0.98
		49	19	-0.44	13	-0.78
		234	40	0.18	8	-1.53
		9	7	-1.27	9	-1.19
		239	11	-0.80	19	-0.40
		23	8	-1.15	67	0.24
FEMALES						
BESTIE	1	4	119	1.53	13	-0.78
		9	60	0.49	46	0.16
		49	69	0.67	13	-0.78
		234	68	0.60	4	-2.15
		239	68	0.60	9	-1.19
		23	97	1.32	8	-1.53
DAWN	1	239	89	0.98	17	-0.49
		49	82	0.83	34	-0.10
		4	44	0.24	25	-0.24
		23	30	-0.12	42	0.10
		234	54	0.40	28	-0.18
		9	21	-0.40	154	0.90
PUG	0	9	*	*	*	*
		234	*	*	*	*
		239	*	*	*	*
		4	*	*	*	*
		23	*	*	*	*
		49	*	*	*	*
RAE	1	49	22	-0.34	141	0.83
		23	40	0.18	17	-0.49
		9	27	-0.22	85	0.32
		239	25	-0.28	23	-0.30
		4	28	-0.16	21	-0.36
		234	84	0.89	8	-1.53
SWUZZLE	0	234	*	*	*	*
		4	*	*	*	*
		23	*	*	*	*
		9	*	*	*	*
		49	*	*	*	*
		239	*	*	*	*
TITI	1	23	79	0.78	7	-1.86

239	51	0.32	28	-0.18
234	98	1.42	17	-0.49
49	33	0.00	105	0.49
9	36	0.08	112	0.58
4	51	0.32	12	-0.89

ANALYSIS OF VARIANCE - GENSTAT COMMANDS

```
'REFE'          EXPT 1
'UNIT'          $72
'NAME'          SX= MALE, FEMALE
  :             OD= 2+3, 2+3+4, 2+3+9, 4, 4+9, 9
  :             RE= BANDIT, SNARK, HOB, MALLI, AYYA, COONIE,
                    BESTIE, TITI, RAE, DAWN, SWUZZLE, PUG
'FACT'          RESPONDT $RE= 6(1...12)
  :             ODOUR $OD= (1...6)12
  :             SEX $SX= 36(1,2)
  :             ORDER $6= 5,6,3,2,4,1,6,3,5,1,2,4,
                          4,2,1,3,6,5,1,4,2,6,5,3,
                          2,1,4,5,3,6,3,5,6,4,1,2,
                          6,4,5,1,3,2,1,3,2,6,4,5,
                          2,6,4,5,1,3,4,5,1,3,2,6,
                          3,1,6,2,5,4,5,2,3,4,6,1
'EQUA'          COVAR= 24 (0), 36 (1), 12 (0)
'READ/S'        TIME, SPEED
'GROU'          RT= RANK (TIME;FLR)
  :             RS= RANK (SPEED;FLL)
'CALC'          NRT= NED (VARFAC (RT)/64)
  :             NRS= NED (VARFAC (RS)/64)
'PRINT/P'       SEX, COVAR, RESPONDT, ODOUR, ORDER,
                TIME, NRT,SPEED, NRS, $ 7.0, 7.0,
                9.0, 6.0, 9.0, 5.0, 7.3, 8.0, 7.3
'BLOC'          ORDER*RESPONDT
'TREA'          SEX*ODOUR+POL (ORDER,2)
'COVAR'         COVAR
'ANOV/PYRU=13' TIME, NRT, SPEED, NRS
'RUN'
```

TABLE OF MEANS - NRT

GRAND MEAN	-0.006					
SEX	MALE	FEMALE				
	0.006	-0.018				
ODOUR	2+3	2+3+4	2+3+9	4	4+9	9
	0.015	0.443	-0.053	0.212	-0.212	-0.443
SEX/ODOUR	2+3	2+3+4	2+3+9	4	4+9	9
MALE	-0.094	0.465	-0.131	0.423	-0.259	-0.371
FEMALE	0.123	0.421	0.025	0.001	-0.164	-0.515
ORDER	1	2	3	4	5	6
	0.020	0.100	0.194	-0.279	-0.105	0.033

ANALYSIS OF VARIANCE - NRT

FACTOR	DF	SS	MS	F	SIGNIFICANCE
RESPONDT STRATUM					
SEX	1	0.01	0.01	0.01	N.S.
COVARIATE	1	13.94	13.94	13.82	$P \leqslant 0.01$
RESIDUAL	7	7.06	1.01		
ORDER.RESPONDT STRATUM					
ODOUR	5	5.82	1.16	7.33	$P \leqslant 0.0005$
SEX/ODOUR	5	0.83	0.17	1.05	N.S.
ORDER	5	1.65	0.33	2.09	N.S.
RESIDUAL	35	5.56	0.16		

TABLE OF MEANS - NRS

GRAND MEAN -0.149

SEX	MALE	FEMALE
	-0.099	-0.199

ODOUR	2+3	2+3+4	2+3+9	4	4+9	9
	-0.362	-0.510	0.021	-0.456	0.169	0.245

SEX/ODOUR	2+3	2+3+4	2+3+9	4	4+9	9
MALE	-0.012	-0.180	0.405	-0.553	-0.027	-0.225
FEMALE	-0.711	-0.839	-0.363	-0.360	0.365	0.714

ORDER	1	2	3	4	5	6
	-0.054	-0.144	-0.282	-0.230	0.030	-0.213

ANALYSIS OF VARIANCE - NRS

FACTOR	DF	SS	MS	F	SIGNIFICANCE
RESPONDT STRATUM					
SEX	1	0.09	0.09	0.04	N.S.
COVARIATE	1	3.61	3.61	1.77	N.S.
RESIDUAL	7	14.28	2.04		
ORDER.RESPONDT STRATUM					
ODOUR	5	6.66	1.33	4.22	$P \leqslant 0.005$
SEX/ODOUR	5	7.57	1.51	4.79	$P \leqslant 0.0025$
ORDER	5	0.83	0.17	0.53	N.S.
RESIDUAL	35	11.05	0.32		

BIOASSAY EXPERIMENT 2

DATA

SUBJECT	COV	ODOUR	TIME SPENT SNIFFING(s)	NORMALISED RANK TIME	SPEED OF RESPONSE(s)	NORMALISED RANK SPEED
MALES						
AYYA	1	234	48	0.76	67	0.51
		B	15	-0.10	37	0.15
		234Q	36	0.57	13	-1.07
		234I	12	-0.28	219	1.27
		I	35	0.48	20	-0.37
		Q	38	0.70	15	-0.90
BANDIT	0	Q	22	0.23	29	-0.03
		I	20	0.18	52	0.34
		234I	14	-0.18	90	0.83
		234Q	6	-0.66	119	1.16
		B	2	-1.13	763	1.74
		234	11	-0.37	28	-0.08
COONIE	1	234Q	111	2.04	105	0.98
		Q	57	1.16	17	-0.69
		B	25	0.28	78	0.63
		I	53	1.023	27	-0.154
		234	59	1.394	80	0.691
		234I	27	0.339	225	1.394
HOB	0	234I	*	*	*	*
		234	*	*	*	*
		I	*	*	*	*
		B	*	*	*	*
		Q	*	*	*	*
		234Q	*	*	*	*
MALLI	0	B	*	*	*	*
		234I	*	*	*	*
		Q	*	*	*	*
		234	*	*	*	*
		234Q	*	*	*	*
		I	*	*	*	*
SNARK	0	I	35	0.48	16	-0.76
		234Q	2	-1.33	45	0.28
		234	19	0.10	55	0.39
		Q	5	-0.76	97	0.90

		234I	0	-2.04	900	2.04
		B	3	-0.98	361	1.54
FEMALES						
BESTIE	1	I	51	0.90	6	-1.74
		Q	19	0.10	65	0.45
		234Q	58	1.27	7	-1.54
		234	66	1.74	3	-2.04
		234I	61	1.54	18	-0.57
		B	53	1.02	74	0.57
FURO	0	234I	*	*	*	*
		234Q	*	*	*	*
		I	*	*	*	*
		B	*	*	*	*
		234	*	*	*	*
		Q	*	*	*	*
PUG	0	Q	*	*	*	*
		234	*	*	*	*
		B	*	*	*	*
		I	*	*	*	*
		234Q	*	*	*	*
		234I	*	*	*	*
SATHA	0	234Q	3	-0.98	15	-0.90
		B	10	-0.45	43	0.23
		Q	8	-0.57	23	-0.28
		234I	9	-0.51	20	-0.37
		I	13	-0.23	8	-1.39
		234	15	-0.10	18	-0.57
SWUZZLE	0	234	6	-0.66	15	-0.90
		I	4	-0.83	27	-0.15
		234I	3	-0.98	10	-1.17
		Q	1	-1.74	24	-0.23
		B	2	-1.33	19	-0.45
		234Q	2	-1.33	9	-1.27
TITI	1	B	16	-0.03	18	-0.57
		234I	28	0.39	110	1.07
		234	49	0.83	87	0.76
		234Q	18	0.03	37	0.15
		Q	11	-0.37	31	0.03
		I	37	0.63	33	0.08

ANALYSIS OF VARIANCE - GENSTAT COMMANDS

```
'REFE'          EXPT 2
'UNIT'          $72
'NAME'          SX= MALE, FEMALE
  :             OD= 2+3+4, 2+3+4+Q, 2+3+4+I, Q, I, B
  :             RE= BANDIT, SNARK, HOB, MALLI, AYYA, COONIE,
                    SWUZZLE, SATHA, FURO, PUG, BESTIE, TITI
'FACT'          RESPONDT $RE= 6(1...12)
  :             ODOUR $OD= (1...6)12
  :             SEX $SX= 36(1,2)
  :             ORDER $6= 6,4,3,1,2,5,3,2,5,4,1,6,
                          2,6,1,5,3,4,4,5,2,3,6,1,
                          1,3,4,6,5,2,5,1,6,2,4,3,
                          1,6,3,4,2,5,6,1,4,3,5,2,
                          5,2,1,6,3,4,2,5,6,1,4,3,
                          4,3,5,2,1,6,3,4,1,5,6,1
'EQUA'          COVAR= 24 (0), 12 (1), 24 (0), 12 (1)
'READ/S'        TIME, SPEED
'GROU'          RT= RANK (TIME;FLR)
  :             RS= RANK (SPEED;FLL)
'CALC'          NRT= NED (VARFAC (RT)/64)
  :             NRS= NED (VARFAC (RS)/64)
'PRINT/P'       SEX, COVAR, RESPONDT, ODOUR, ORDER,
                TIME, NRT, SPEED, NRS, $ 7.0, 7.0,
                9.0, 6.0, 9.0, 5.0, 7.3, 8.0, 7.3
'BLOC'          ORDER*RESPONDT
'TREA'          SEX*ODOUR+POL (ORDER,2)
'COVAR'         COVAR
'ANOV/PYRU=13' TIME, NRT, SPEED, NRS
'RUN'
```

TABLE OF MEANS - NRT

GRAND MEAN	0.001					
SEX	MALE	FEMALE				
	0.071	-0.068				
ODOUR	2+3+4	2+3+4+Q	2+3+4+I	Q	I	B
	0.389	-0.104	-0.189	-0.119	0.381	-0.351
SEX/ODOUR	2+3+4	2+3+4+Q	2+3+4+I	Q	I	B
MALE	0.400	0.118	-0.535	0.360	0.616	-0.535
FEMALE	0.379	-0.327	0.157	-0.599	0.147	-0.166
ORDER	1	2	3	4	5	6
	0.154	-0.120	0.284	-0.165	-0.170	0.023

ANALYSIS OF VARIANCE - NRT

FACTOR	DF	SS	MS	F	SIGNIFICANCE
RESPONDT STRATUM					
SEX	1	0.35	0.35	0.31	N.S.
COVARIATE	1	22.38	22.38	20.00	$P \leqslant 0.01$
RESIDUAL	5	5.60	1.12		
ORDER.RESPONDT STRATUM					
ODOUR	5	5.77	1.15	6.94	$P \leqslant 0.005$
SEX/ODOUR	5	5.51	1.10	6.62	$P \leqslant 0.001$
ORDER	5	2.10	0.42	2.53	N.S.
RESIDUAL	25	4.16	0.17		

TABLE OF MEANS - NRS

GRAND MEAN 0.000

SEX	MALE	FEMALE
	0.451	-0.450

ODOUR	2+3+4	2+3+4+Q	2+3+4+I	Q	I	B
	-0.063	-0.221	0.564	-0.147	-0.585	0.452

SEX/ODOUR	2+3+4	2+3+4+Q	2+3+4+I	Q	I	B
MALE	0.484	0.369	1.410	-0.260	-0.312	1.014
FEMALE	-0.609	-0.810	-0.281	-0.035	-0.858	-0.109

ORDER	1	2	3	4	5	6
	-0.164	0.269	-0.374	0.152	0.053	0.063

ANALYSIS OF VARIANCE - NRS

FACTOR	DF	SS	MS	F	SIGNIFICANCE
RESPONDT STRATUM					
SEX	1	14.62	14.62	11.31	$P \leqslant 0.025$
COVARIATE	1	0.07	0.07	0.06	N.S.
RESIDUAL	5	6.47	1.29		
ORDER.RESPONDT STRATUM					
ODOUR	5	11.28	2.26	4.73	$P \leqslant 0.005$
SEX/ODOUR	5	6.54	1.31	2.74	$P \leqslant 0.05$
ORDER	5	3.23	0.64	1.35	N.S.
RESIDUAL	25	11.93	0.48		

BIOASSAY EXPERIMENT 3

DATA

SUBJECT	COV	ODOUR	TIME SPENT SNIFFING(s)	NORMALISED RANK TIME	SPEED OF RESPONSE(s)	NORMALISED RANK SPEED
MALES						
AYYA	1	1	38	0.063	12	-1.036
		1234	43	0.363	38	0.126
		67	49	0.501	27	-0.363
		167	106	1.834	6	-1.834
		23467	57	0.728	29	-0.210
		234	102	1.501	80	0.842
BANDIT	0	234	17	-0.573	35	0.021
		23467	42	0.253	30	-0.147
		167	2	-1.440	84	0.967
		67	7	-1.111	30	-0.147
		1234	12	-0.967	55	0.477
		1	13	-0.872	35	0.021
COONIE	1	67	53	0.674	39	0.168
		234	68	0.903	121	1.192
		1234	62	0.784	50	0.363
		23467	80	1.036	18	-0.648
		1	38	0.063	27	-0.363
		167	75	0.967	195	1.383
HOB	0	1234	36	-0.021	737	1.645
		167	0	-1.834	900	2.128
		234	30	-0.168	69	0.674
		1	0	-1.834	900	2.128
		67	0	-1.834	900	2.128
		23467	2	-1.440	155	1.282
MALLI	0	167	17	-0.573	35	0.021
		1	5	-1.192	44	0.253
		23467	23	-0.431	91	1.036
		1234	8	-1.036	65	0.598
		234	26	-0.319	82	0.903
		67	3	-1.282	77	0.755
FEMALES						
ANNIE	1	234	144	4.957	14	-0.784
		67	17	-0.573	41	0.210

		23467	43	0.363	18	-0.648
		167	50	0.573	26	-0.454
		1234	18	-0.477	28	-0.275
		1	14	-0.755	200	1.501
BESTIE	1	167	82	1.111	4	-2.128
		234	116	2.128	24	-0.524
		1234	97	1.383	12	-1.036
		67	95	1.282	15	-0.728
		1	41	0.147	12	-1.036
		23467	84	1.192	11	-1.383
DAWN	1	1	36	-0.021	46	0.297
		1234	67	0.842	26	-0.454
		167	52	0.623	53	0.431
		23467	105	1.645	8	-1.645
		67	49	0.501	35	0.021
		234	42	0.253	92	1.111
RAE	1	1234	29	-0.210	50	0.363
		23467	48	0.431	13	-0.842
		234	13	-0.872	12	-1.036
		1	14	-0.755	28	-0.275
		167	26	-0.319	23	-0.573
		67	16	-0.674	77	0.755
TITI	1	1234	26	-0.319	12	-1.036
		1	34	-0.126	34	-0.084
		67	42	0.253	11	-1.383
		1234	35	-0.084	65	0.598
		234	41	0.147	56	0.524
		167	26	-0.319	11	-1.383

ANALYSIS OF VARIANCE - GENSTAT COMMANDS

```
'REFE'          EXPT 3
'UNIT'          $60
'NAME'          SX= MALE, FEMALE
  :             OD= 2+3+4, 1, 6+7, 1+2+3+4, 1+6+7, 2+3+4+6+7
  :             RE= AYYA, COONIE, BANDIT, HOB, MALLI,
                    BESTIE, DAWN, RAE, TITI, ANNIE
'FACT'          RESPONDT $RE= 6(1...10)
  :             ODOUR $OD= (1...6)10
  :             SEX $SX= 30(1,2)
  :             ORDER $6= 6,1,3,2,4,5,2,5,1,3,6,4,
                          1,6,4,5,3,2,3,4,5,1,2,6,
                          5,2,6,4,1,3,2,5,4,3,1,6,
                          6,1,5,2,3,4,3,4,6,1,5,2,
                          5,2,3,4,6,1,1,6,2,5,4,3
'EQUA'          COVAR= 12 (0), 18 (1), 30 (0)
'READ/S'        TIME, SPEED
'GROU'          RT= RANK (TIME;FLR)
  :             RS= RANK (SPEED;FLL)
'CALC'          NRT= NED (VARFAC (RT)/60)
  :             NRS= NED (VARFAC (RS)/60)
'PRINT/P'       SEX, COVAR, RESPONDT, ODOUR, ORDER,
                TIME, NRT, SPEED, NRS, $ 7.0, 7.0,
                9.0, 6.0, 9.0, 5.0, 7.3, 8.0, 7.3
'BLOC'          ORDER*RESPONDT
'TREA'          SEX*ODOUR+POL (ORDER,2)
'COVAR'         COVAR
'ANOV/PYRU=13' TIME, NRT, SPEED, NRS
'RUN'
```

TABLE OF MEANS - NRT

GRAND MEAN 0.08

SEX	MALE	FEMALE
	0.27	-0.10

ODOUR	2+3+4	1	6+7	1+2+3+4	1+6+7	2+3+4+6+7
	0.80	-0.53	-0.23	0.06	0.06	0.35

SEX/ODOUR	2+3+4	1	6+7	1+2+3+4	1+6+7	2+3+4+6+7
MALE	0.78	-0.24	-0.10	0.34	0.30	0.54
FEMALE	0.81	-0.82	-0.36	-0.22	-0.18	0.15

ORDER	1	2	3	4	5	6
	0.53	0.07	-0.03	0.31	-0.22	-0.16

ANALYSIS OF VARIANCE - NRT

FACTOR	DF	SS	MS	F	SIGNIFICANCE
RESPONDT STRATUM					
SEX	1	1.20	1.20	0.79	N.S.
COVARIATE	1	21.07	21.07	13.97	$P \leqslant 0.01$
RESIDUAl	7	10.56	1.51		
ORDER.RESPONDT STRATUM					
ODOUR	5	10.47	2.10	3.23	$P \leqslant 0.025$
SEX.ODOUR	5	0.65	0.13	0.20	N.S.
ORDER	5	3.92	0.78	1.21	N.S.
RESIDUAL	35	22.72	0.65		

TABLE OF MEANS - NRS

GRAND MEAN 0.041

SEX	MALE	FEMALE
	0.223	-0.141

ODOUR	2+3+4	1	6+7	1+2+3+4	1+6+7	2+3+4+6+7
	0.292	0.141	0.142	0.240	-0.144	-0.424

SEX/ODOUR	2+3+4	1	6+7	1+2+3+4	1+6+7	2+3+4+6+7
MALE	0.471	-0.055	0.253	0.386	0.278	0.007
FEMALE	0.113	0.336	0.030	0.094	-0.566	-0.856

ORDER	1	2	3	4	5	6
	-0.264	0.151	-0.085	-0.200	0.096	0.549

ANALYSIS OF VARIANCE - NRS

FACTOR	DF	SS	MS	F	SIGNIFICANCE
RESPONDT STRATUM					
SEX	1	1.14	1.14	0.59	N.S.
COVARIATE	1	5.21	5.21	2.71	N.S.
RESIDUAL	7	13.46	1.92		
ORDER.RESPONDT STRATUM					
ODOUR	5	3.74	0.75	1.56	N.S.
SEX/ODOUR	5	2.68	0.54	1.12	N.S.
ORDER	5	4.22	0.84	1.76	N.S.
RESIDUAL	35	16.81	0.48		

BIOASSAY EXPERIMENT 4

DATA

SUBJECT	COV	ODOUR	TIME SPENT SNIFFING(s)	NORMALISED RANK TIME	SPEED OF RESPONSE(s)	NORMALISED RANK SPEED
MALES						
AYYA	1	2348	28	-0.046	28	-0.282
		234	45	0.380	55	0.704
		8	10	-0.896	107	1.593
BANDIT	0	8	21	-0.380	23	-0.482
		2348	11	-0.704	29	-0.140
		234	19	-0.589	92	1.325
COONIE	1	234	75	1.325	17	-0.967
		8	30	0.187	204	2.085
		2348	64	1.128	31	0.000
MALLI	0	2348	5	-1.446	32	0.093
		8	10	-0.896	58	0.828
		234	50	0.590	86	1.128
SNARK	0	234	7	-1.128	36	0.187
		2348	5	-1.446	29	-0.140
		8	1	-2.085	19	-0.704
FEMALES						
ANNIE	1	2348	28	-0.046	17	-0.967
		8	25	-0.234	10	-1.593
		234	20	-0.482	22	-0.590
BESTIE	1	2348	88	2.085	15	-1.325
		234	84	1.593	48	0.380
		8	49	0.482	8	-2.085
DAWN	1	8	52	0.704	17	-0.967
		2348	25	-0.234	53	0.590
		234	59	0.828	25	-0.380
RAE	1	234	*	*	*	*
		2348	*	*	*	*
		8	*	*	*	*
TITI	1	234	43	0.282	40	0.282
		8	29	0.093	66	0.967
		2348	62	0.967	50	0.482

ANALYSIS OF VARIANCE - GENSTAT COMMANDS

```
'REFE'      EXPT 4
'UNIT'      $30
'NAME'      IN= COONIE, AYYA, BANDIT, MALLI, SNARK,
  :             BESTIE, TITI, DAWN, RAE, ANNIE
  :         OD= 2+3+4, 8, 2+3+4+8
'FACT'      INDIV $IN= 3(1...10)
  :         ODOUR $OD= (1...3)10
  :         SEX $SX= 15(1...2)
'EQUA'      COVAR= 6 (1) 9 (0), 15 (1)
'READ'      TIME, SPEED
'HEAD'      H1= ''IN SECONDS''
  :         H2= ''AS NORMALISED RANKS''
'FOR'       AA= TIME, SPEED; AB= FL(1,2);AC=(1,2)
'GROU'      AB=RANK (AA;AC)
'REPE'
'FOR'       AA= FL(1,2); AB= NTIME; NSPEED
'CALC'      AB=NED((VARFAC (AA)-0.5)/27)
'REPE'
'SET'       S1= TIME, NTIME, SPEED, NSPEED
'PRIN/P'    SEX, INDIV, ODOUR,S1 $3(7.0); (8.0, 9.4)2
'DESC'      S1 $2; H1, H2
'BLOC'      INDIV/ODOUR
'TREA'      SEX*ODOUR
'COVAR'     COVAR
'ANOV'      S1
'RUN'
```

TABLE OF MEANS - NRT

GRAND MEAN 0.05

SEX	MALE	FEMALE	
	-0.03	0.13	
ODOUR	2+3+4	8	2+3+4+8
	0.34	-0.28	0.10
SEX/ODOUR	2+3+4	8	2+3+4+8
MALE	0.49	-0.44	-0.13
FEMALE	0.18	-0.11	0.32

ANALYSIS OF VARIANCE - NRT

FACTOR	DF	SS	MS	F	SIGNIFICANCE
RESPONDT STRATUM					
SEX	1	0.10	0.10	0.08	N.S.
COVARIATE	1	5.58	5.58	4.33	N.S.
RESIDUAL	6	7.73	1.29		
ORDER.RESPONDT STRATUM					
ODOUR	2	1.91	0.95	3.14	N.S.
SEX/ODOUR	2	0.82	0.41	1.36	N.S.
RESIDUAL	14	4.25	0.30		

TABLE OF MEANS - NRS

GRAND MEAN -0.04

SEX	MALE	FEMALE	
	0.44	-0.52	
ODOUR	2+3+4	8	2+3+4+8
	0.20	-0.13	-0.20
SEX/ODOUR	2+3+4	8	2+3+4+8
MALE	0.56	0.75	-0.01
FEMALE	-0.16	-1.01	-0.39

ANALYSIS OF VARIANCE - NRS

FACTOR	DF	SS	MS	F	SIGNIFICANCE
RESPONDT STRATUM					
SEX	1	3.92	3.92	3.53	N.S.
COVARIATE	1	0.30	0.30	0.27	N.S.
RESIDUAL	6	6.66	1.11		
ORDER.RESPONDT STRATUM					
ODOUR	2	0.91	0.46	0.55	N.S.
SEX/ODOUR	2	2.57	1.28	1.56	N.S.
RESIDUAL	14	11.56	0.82		

APPENDIX 8

Capture sites of resident ear-tagged ferrets caught during live-trapping experiments at Pukepuke Lagoon (Chapter 8). Superscripts refer to number of captures at any trap site.

MALES		FEMALES	
M1.	6288	F1.	8284
2.	6297	2.	6286
3.	6138	3.	6295
4.	6142	4.	6131
5.	6142	5.	6134
6.	6144	6.	6136
7.	6104	7.	6103
8.	6101	8.	6112
9.	6107		
10.	6110		
11.	6113		

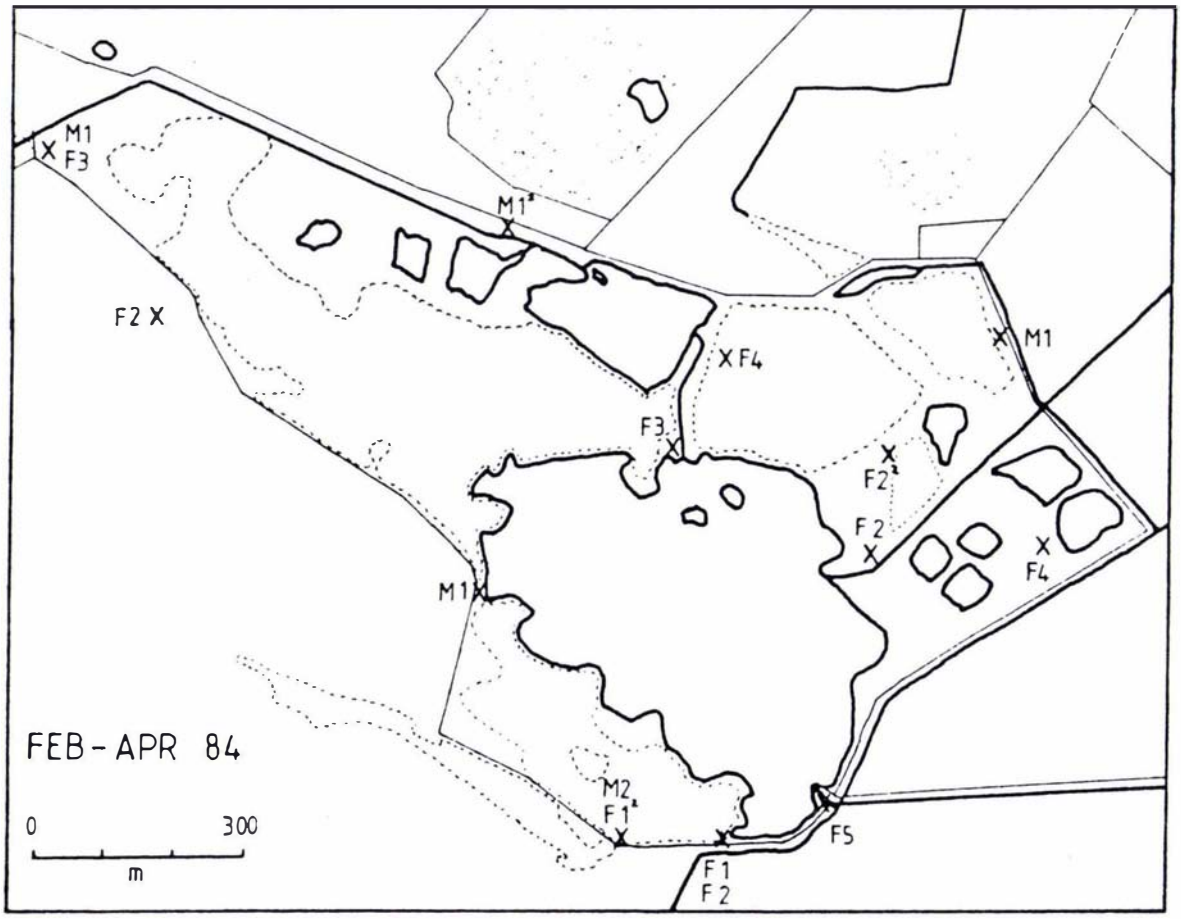
= water

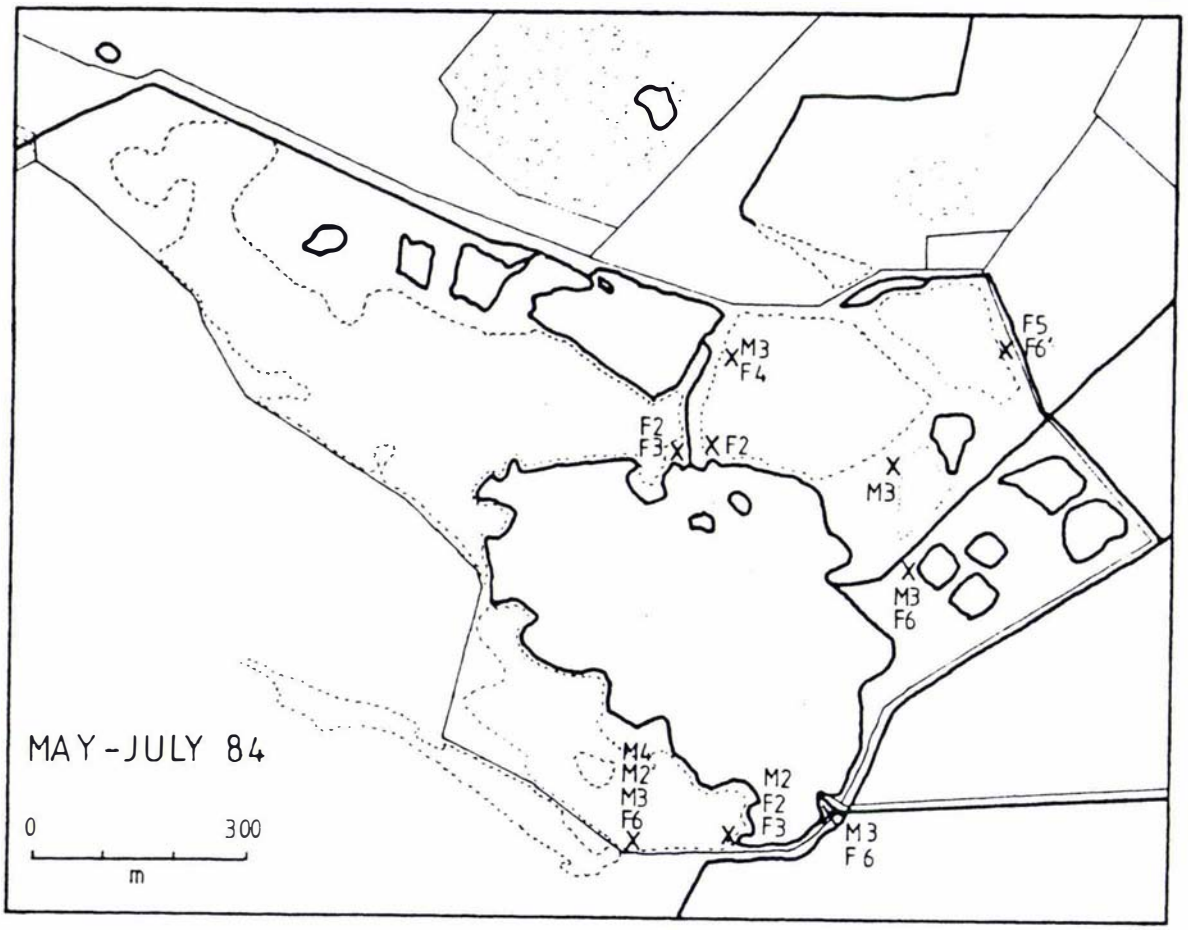
= swamp

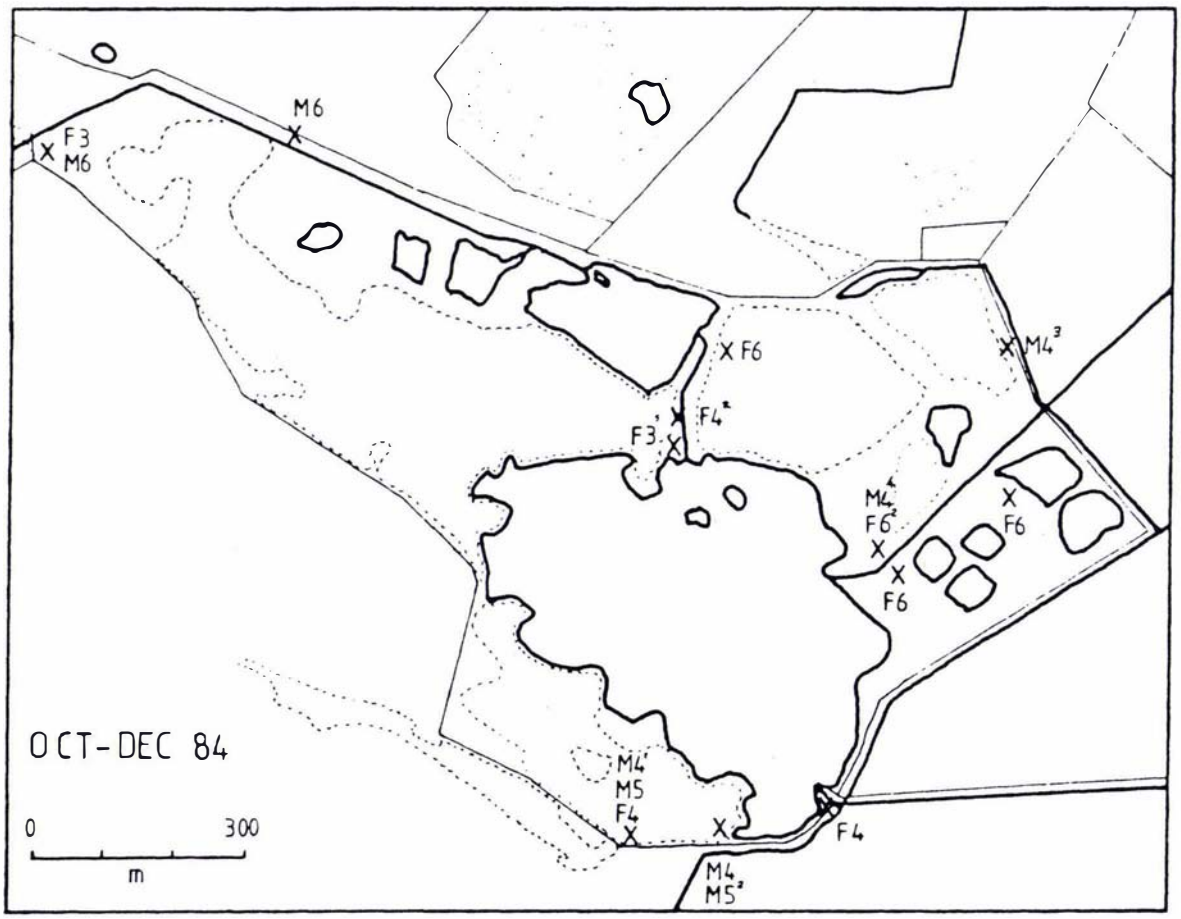
X = trap site

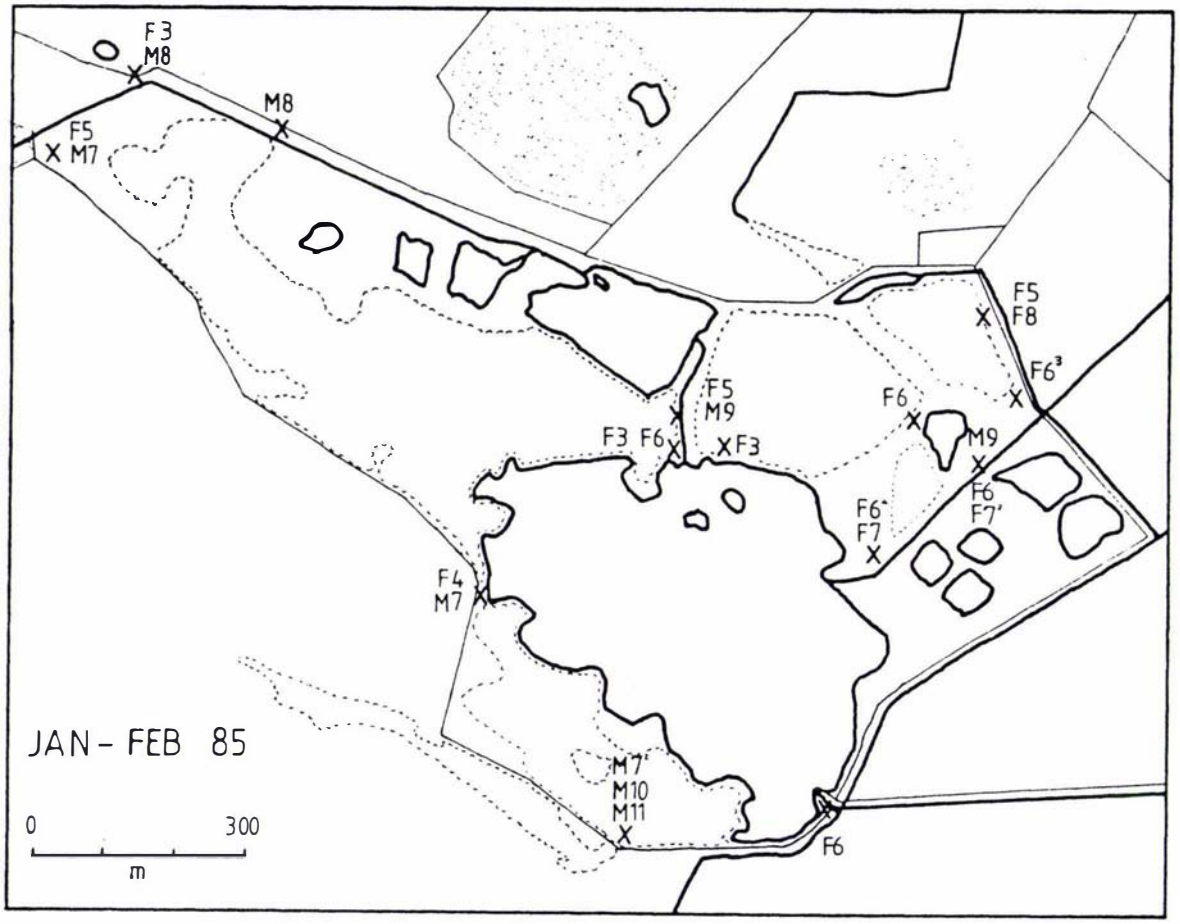
= fenceline

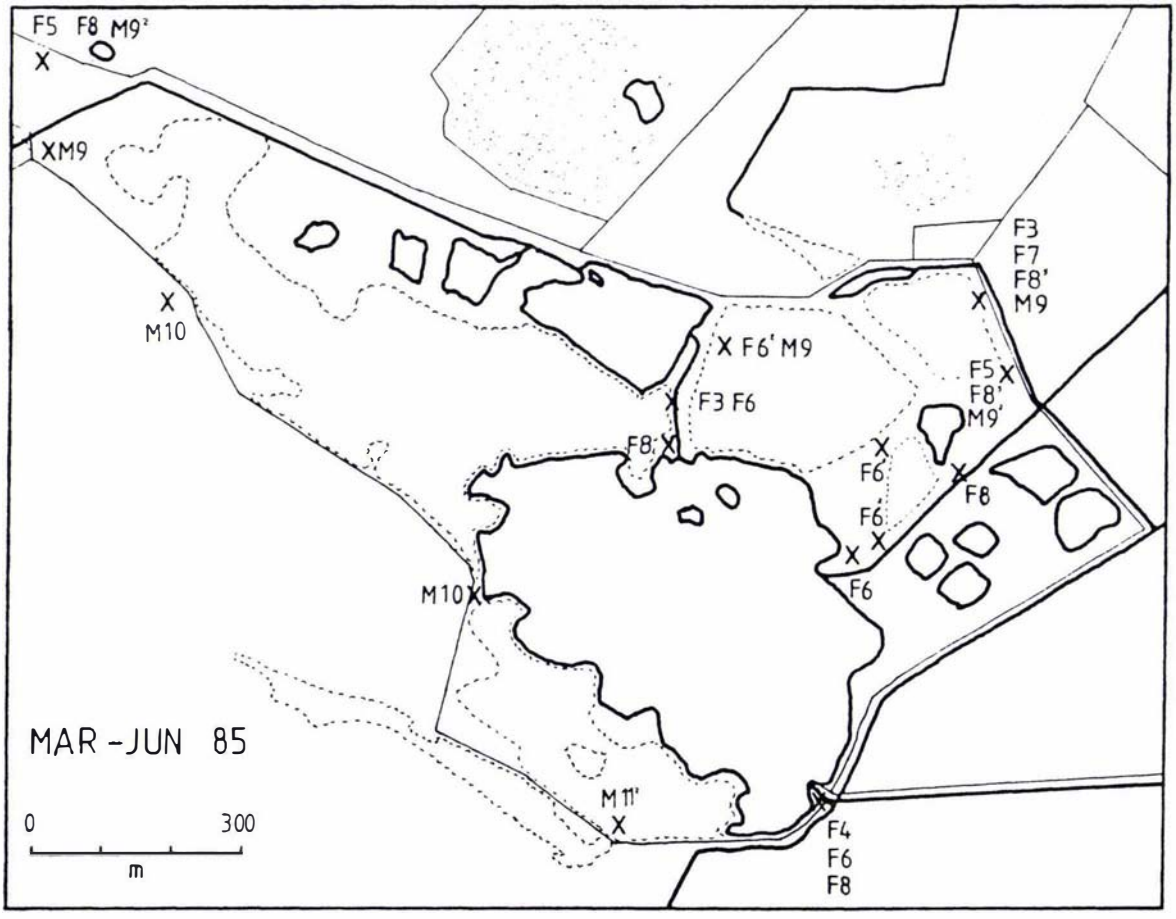
= pine forest




F5
F6
M3
F4
F2
F3
F2
M3
M3
F6
MAY-JULY 84
M4
M2
M3
F6
M2
F2
F3
M3
F6
0
300
m


M6
F3
M6
F6
M4
F3
F4
M4
F6
F6
F6
OCT-DEC 84
M4
M5
F4
F4
M4
M5
0
300
m


F3
M8
M8
F5
M7
F5
F8
F6³
F5
M9
F6
F3 F6
F3
M9
F6
F7'
F6*
F7
F4
M7
JAN - FEB 85
M7'
M10
M11
F6
0
300
m


F5 F8 M9²
XM9
X
M10
F3
F7
F8'
M9
X F6' M9
F5
F8'
M9'
F3 F6
F8
F6
F8
F6
M10
F6
MAR - JUN 85
M11'
F4
F6
F8
0
300
m

APPENDIX 9

Data from live-trapping experiments at Pukepuke Lagoon – sex, age (adult/juvenile), weight, choice of trap treatment and release of anal gland secretion during handling for each identified ferret.

TRAPPING DATA

EARTAG NO.	CAPTURE DATE	SEX	AGE	WEIGHT (g)	CHOICE OF TRAP	ANAL ODOUR RELEASE
6101	JAN 85	M	A	---	LURE 1	✓
	JAN 85			1120	LURE 1	✓
6102	JAN 85	M	J	---	LURE 4	X
6103	JAN 85	F	J	400	LURE 1	✓
	FEB 85			440	LURE 4	✓
	FEB 85			500	LURE 1	✓
	APR 85			600	LURE 1	✓
	APR 85			600	LURE 1	X
	JUN 85			750	LURE 3	✓
6104	JAN 85	M	A	980	LURE 4	✓
(6147)	JAN 85			850	BAIT	✓
	JAN 85			900	LURE 1	✓
	JAN 85			880	LURE 1	X
6105	FEB 85	F	J	480	BAIT	✓
6107	FEB 85	M	A?	500	BAIT	✓
	FEB 85			650	BLANK	✓
	MAR 85			880	BAIT	✓
	MAR 85			900	LURE 4	X
	MAR 85			900	BLANK	✓
	MAR 85			880	LURE 1	✓
	APR 85			920	LURE 1	✓
	APR 85			900	BAIT	X
	JUN 85			1250	BAIT	X
6108	FEB 85	M	A	800	BLANK	✓
6109	FEB 85	F	A	550	LURE 4	✓
6110	FEB 85	M	A	950	BAIT	✓
	MAR 85			1000	LURE 4	✓
	MAR 85			950	LURE 1	✓

6111	FEB 85	F	J	480	LURE 1	✓
6112	MAR 85	F	J	420	LURE 4	✓
	MAR 85			500	LURE 1	✓
	MAR 85			480	LURE 4	✓
	MAR 85			---	LURE 1	X
	APR 85			550	LURE 3	✓
	APR 85			520	BAIT	✓
	APR 85			500	LURE 1	X
	JUN 85			550	LURE 1	X
	JUN 85			550	LURE 4	X
	JUN 85			550	LURE 1	X
	JUN 85			550	LURE 2	X
	JUN 85			---	LURE 2	X
6113	MAR 85	M	A	1150	LURE 1	X
	MAR 85			1200	LURE 4	X
	APR 85			1500	BAIT	✓
6130	MAR 84	M	A	1120	BAIT/LURE 1	✓
6131	MAR 84	F	A	550	BAIT/LURE 1	✓
(6139)	APR 84			490	BAIT/LUTE 1	✓
	MAY 84			800	BAIT	X
	OCT 84			600	BAIT	X
	OCT 84			580	BAIT	X
	OCT 84			---	BAIT	X
	NOV 84			650	LURE 1	✓
	JAN 85			450	LURE 4	✓
	APR 85			600	LURE 1	✓
6132	MAR 84	F	A	650	BAIT	X
6133	APR 84	F	A	510	BAIT/LURE 1	X
6134	APR 4	F	A	800	BAIT	✓
	JUN 84			---	LURE 3	X
	JAN 85			600	LURE 1	✓
	JAN 85			600	LURE 1	X
	MAR 85			700	BAIT	✓
	MAR 85			700	LURE 1	✓
	MAR 85			840	LURE 4	X
6135	MAY 84	M	A	1280	LURE 1	✓
6136	MAY 84	F	J	670	BAIT	✓
	MAY 84			---	LURE 3	✓
	JUN 84			680	LURE 2	X
	JUN 84			---	LURE 1	X

	JUN 84			---	LURE 2	✓
	OCT 84		A	730	BAIT	✓
	NOV 84			500	BAIT	✓
	NOV 84			500	LURE 1	✓
	NOV 84			400	LURE 1	✓
	DEC 84			550	LURE 3	✓
	JAN 85			500	BAIT	✓
	JAN 85			500	BAIT	✓
	JAN 85			480	LURE 1	✓
	JAN 85			480	BAIT	X
	JAN 85			---	LURE 4	✓
	JAN 85			500	LURE 4	✓
	FEB 85			500	LURE 4	✓
	FEB 85			470	LURE 1	✓
	FEB 85			480	LURE 1	✓
	MAR 85			500	LURE 4	✓
	MAR 85			500	LURE 1	X
	MAR 85			550	LURE 4	✓
	MAR 85			500	BAIT	✓
	MAR 85			500	BAIT	✓
	MAR 85			500	BAIT	✓
	MAR 85			500	LURE 4	X
	APR 85			570	LURE 1	✓
	APR 85			550	LURE 4	X
	APR 85			570	LURE 4	X
	APR 85			550	LURE 2	✓
	JUN 85			650	BAIT	✓
6137	MAY 84	F	A	680	LURE 1	✓
6138	MAY 84	M	A	1100	BAIT	✓
	MAY 84			---	LURE 3	X
	JUN 84			1100	LURE 1	X
	JUN 84			---	BAIT	✓
	JUN 84			---	LURE 1	✓
6139	- SEE 6131					
6140	JUN 84	M	A	1030	BAIT	✓
6141	JUN 84	M	A	1280	LURE 1	X
6142	JUL 84	M	A	1150	LURE 1	✓
	OCT 84			1100	LURE 2	X
	OCT 84			1080	LURE 2	✓
	OCT 84			---	LURE 1	X

	NOV 84			980	LURE 1	✓
	NOV 84			1000	BAIT	✓
	NOV 84			1080	LURE 2	✓
	DEC 84			1200	LURE 3	✓
6143	OCT 84	M	A	1150	LURE 1	✓
	NOV 84			1200	LURE 1	✓
	DEC 84			1000?	LURE 1	✓
6144	OCT 84	M	A	1050	LURE 3	✓
	NOV 84			720	LURE 1	X
6147	- SEE 6104					
6148	JAN 85	M	A	1150	LURE 4	✓
6149	JAN 85	M	J	750	LURE 1	✓
6150	JAN 85	M	J	500	LURE 1	✓
6281	FEB 84	F	J	650	BAIT	✓
	FEB 84			---	BAIT/LURE 1	X
	FEB 84			---	BAIT	✓
	FEB 84			---	BAIT	X
6282	FEB 84	M	A	980	BAIT	X
	FEB 84			---	LURE 1	X
	FEB 84			---	LURE 1	X
6284	FEB 84	F	A	620	BAIT	✓
(6293)	FEB 84			570	BAIT	✓
	MAR 84			630	LURE 1	X
6285	FEB 84	F	J	550	LURE 1	✓
	FEB 84			---	BAIT/LURE 1	X
6286	FEB 84	F	A	670	BAIT/LURE 1	✓
	FEB 84			---	BAIT	✓
	MAR 84			620	BAIT/LURE 1	✓
	APR 84			550	BAIT/LURE 1	✓
	APR 84			---	BAIT	✓
	MAY 84			830	LURE 3	✓
	JUN 84			800	LURE 3	X
	JUN 84			---	LURE 3	X
6287	FEB 84	F	J	500	BLANK	X
	FEB 84			---	LURE 1	✓
6288	FEB 84	M	A	880	BAIT	X
	FEB 84			---	LURE 1	✓
	FEB 84			---	BLANK	X
6289	FEB 84	M	J	740	BAIT	X
6290	FEB 84	F	J	520	BLANK	X

6291	FEB 84	F	J	370	BAIT/LURE 1	✓
	FEB 84			---	LURE 1	✓
6292	MAR 84	F	A	620	BAIT	✓
	MAR 84			---	BAIT/LURE 1	✓
6293	- SEE 6284					
6295	MAR 84	F	A	590	LURE 1	X
	MAR 84			---	LURE 1	X
	MAY 84			830	LURE 2	X
	JUN 84			---	LURE 1	✓
	OCT 84			680	BAIT	✓
	OCT 84			680	BAIT	✓
	OCT 84			---	LURE 3	✓
	DEC 84			490	LURE 3	✓
	DEC 84			500	LURE 3	✓
	DEC 84			---	BAIT	✓
	JAN 85			600	LURE 1	✓
	JAN 85			480	BAIT	X
	MAR 85			580	BAIT	✓
	MAR 85			670	LURE 4	X
	APR 85			700	BAIT	X
6297	MAR 84	M	A	1120	LURE 1	✓
(6298)	MAY 84			1300	LURE 1	✓
	JUN 84			1200	LURE 3	✓
	JUL 84			1850	LURE 1	✓
6298	- SEE 6297					
6299	MAR 84	F	A	590	BAIT	✓

BIBLIOGRAPHY

Adams, M.G. 1980. Odour-producing organs of mammals. In Stoddart, D.M. (Ed.) Olfaction in mammals. Symp. Zool. Soc. Lond. 45:57-86.

Albone, E.S. 1984. Mammalian semiochemistry. The investigation of chemical signals between mammals. Wiley, Chichester.

Albone, E.S., Gosdern, P.E. and Ware, G.C. 1977. Bacteria as a source of chemical signals in mammals. In Müller-Schwarze, D. and Mozell, M.M. (Eds.) Chemical signals in vertebrates. Plenum Press, New York. pp. 35-43.

Alexander, A.J. and Ewer, R.F. 1959. Observations on the biology and behaviour of the smaller African polecat (Poecilogale albinucha). Afr. Wildl. 13:313-320.

Altmann, J. 1974. Observational study of behavior: sampling methods. Behav. 49:227-267.

Anon. 1980. Flavour and fragrance chemicals. Chemalog Hi-lites 4:1.

Asa, C.S., Peterson, E.K., Seal, U.S. and Mech, L.D. 1985. Deposition of anal sac secretions by captive wolves. J. Mammal. 66:89-93.

Banks, W.J. 1981. Applied Veterinary Histology. Williams and Williams, Baltimore.

Beauchamp, G.K., Doty, R.L., Moulton, D.G. and Mugford, R.A. 1976. The pheromone concept in mammalian chemical communication: a critique. In Doty, R.L. (Ed.) Mammalian olfaction, reproductive processes and behavior. Academic Press, London. pp. 143-160.

_____ 1979. Response by Beauchamp et al. J. Chem. Ecol. 5:301-305.

Bedoukian, P.Z. 1970. Purity, identity and quantification of pheromones. In Johnston, J.W.Jr., Moulton, D.G. and Turk, A. (Eds.) Communication by chemical signals. Adv. Chemoreception Vol. 1. Appleton-Century-Crofts, New York. pp. 19-34.

Beroza, M. (Ed.). 1976. Pest management with insect sex attractants and other behavior-controlling chemicals. ACS symposium series no. 23. American Chemical Society, Washington.

Boonstra, R. and Krebs, C.J. 1976. The effect of odour on trap response in Microtus townsendii. J. Zool., Lond. 180:467-476.

Bowers, J.M. and Alexander, B.K. 1967. Mice:individual recognition by olfactory cues. Science 158:1208-1210.

Brinck, C., Erlinge, S. and Sandell, M. 1983. Anal sac secretions in mustelids - a comparison. J. Chem. Ecol. 9:727-745.

Brinck, C., Gerell, R. and Odham, G. 1978. Anal pouch secretion in mink Mustela vison. Oikos 30:68-75.

Brown, L. 1976. British birds of prey. A study of Britain's 24 diurnal raptors. The New Naturalist. Collins, London.

Brown, R.E. 1979. Mammalian social odors: a critical review. Adv. Study Behav. 10:103-162.

Claus, R. 1975. Neutralization of pheromones by antisera in pigs. In Nieschlag, E. (Ed.) Immunization with hormones in reproduction research. North-Holland, Amsterdam. pp. 189-197; not seen, cited in Mykytowycz 1979.

Corbet, G.B. and Hill, J.E. 1980. A world list of mammal species. British Museum (Natural History), Cornell University Press, London.

Corbet, G.B. and Southern, H.N. 1977. The handbook of British mammals. 2nd ed. Blackwell Scientific Publications, Oxford.

Crawley, M.C. 1982. Wildlife conservation in New Zealand. N.Z. J. Ecol. 5:1-5.

Creed, J.C. and Kainer, R.A. 1981. Surgical extirpation and related anatomy of anal sacs of the ferret. J. Am. Vet. Med. Assoc. 179:575-577.

Crump, D.R. 1980a. Thietanes and dithiolanes from the anal gland of the stoat (Mustela erminea). J. Chem. Ecol. 6:341-347.

_____ 1980b. Anal gland secretion of the ferret (Mustela putorius forma furo). J. Chem. Ecol. 6:837-844.

Crump, D., Swigar, A.A., West, J.R., Silverstein, R.M., Müller Schwarze, D. and Altieri, R. 1984. Urine fractions that release flehmen in black-tailed deer, Odocoileus hemionus columbianus. J. Chem. Ecol. 10:203-215.

Daly, M., Wilson, M.I. and Behrends, P. 1980. Factors affecting rodents' responses to odours of stangers encountered in the field: experiments with odour-baited traps. Behav. Ecol. Sociobiol. 6:323-329.

Daly, M., Wilson, M.I. and Faux, S. 1978. Seasonally variable effects of conspecific odors upon capture of deer mice (Peromyscus maniculatus gambelii). Behav. Biol. 23:254-259.

Doty, R.L. 1975. Determination of odor preferences in rodents: a methodological review. In Moulton, D.G., Johnston, J.W.Jr. and Turk, A. (Eds.) Methods in olfactory research. Academoc Press, London. pp. 395-406.

Eibl-Eibesfeldt, I. 1950. Über die Jugendentwicklung des Verhaltens

eines männlichen Dachses (Meles meles L.) unter besonderer Berucksichtigung des Spiels. Z. Tierpsychol. 7:327-355; not seen, cited in Goethe 1964.

_____ 1956. Zur Biologie des Iltis (Putorius putorius L.). Zool. Anz. (Suppl. Verh. Dtsch. Zool. Ges., Erlangen) 19:304-314.

Eisenberg, J.F. and Kleiman, D.G. 1972. Olfactory communication in mammals. Ann. Rev. Syst. Ecol. 3:1-32.

Erlinge, S. 1977. Agonistic behaviour and dominance in stoats (Mustela erminea L.). Z. Tierpsychol. 44:375-388.

Erlinge, S., Sandell, M. and Brinck, C. 1982. Scent-marking and its territorial significance in stoats Mustela erminea. Anim. Behav. 30:811-818.

Ewer, R.F. 1973. The carnivores. The world naturalist. Weidenfeldt and Nicolson, London.

Fitzgerald, B.M. 1964. Ecology of mustelids in New Zealand. MSc. thesis, University of Canterbury.

Fitzgerald, B.M., Johnson, W.B., King, C.M. and Moors, P.J. 1984. Research on mustelids and cats in New Zealand. WRLG Research Review No. 3. Wildlife Research Liaison Group, Wellington.

Frank, H.R. 1940. Die Biologie des Dachses. Z. Jagdk. 2:1-25; not seen, cited in Goethe 1964.

_____ 1962. Biologies des Mauswiesels (Mustela nivalis L.) nach Beobachtungen an einer Gefangenschafts-Population. Manuskr; not seen, cited in Goethe 1964.

Gibb, J.A. and Flux, J.E. 1973. Mammals. In Williams, G.R. (Ed.) The natural history of New Zealand - an ecological survey. Reed, Wellington.

Gibb, J.A., Ward, C.P. and Ward, G.D. 1978. Natural control of a population of rabbits Oryctolagus cuniculus (L.), for ten years in the Kourarau enclosure. DSIR Bulletin 223. DSIR, Wellington.

Goethe, F. 1938. Beobachtungen über das Absetzen von Witterungsmarken beim Baummarter. D. Dtsch. Jaüger. 60:211-213; not seen, cited in Goethe 1964.

_____ 1940. Beitrage zur Biologie des Iltis. Z. Säugetierk. 15:180-223; not seen, cited in Goethe 1964.

_____ 1964. Das Verhalten der Musteliden. Handb. Zool. 8:1-80.

Goodrich, B.S. and Mykytowycz, R. 1972. Individual and sex differences in the chemical composition of pheromone-like substances from the skin glands of the rabbit, Oryctolagus cuniculus.

J. Mammal. 53:540-548.

Gorman, M.L. 1976. A mechanism for individual recognition by odour in Herpestes auropunctatus (Carnivora:Viverridae). Anim. Behav. 24:141-145.

_____ 1984a Scent marking and territoriality. Acta Zool. Fenn. 171:49-53.

_____ 1984b. The response of prey to stoat (Mustela erminea) scent. J. Zool., Lond. 202:419-423.

Gorman, M.L., Jenkins, D. and Harper, R.J. 1978. The anal scent sacs of the otter (Lutra lutra). J. Zool., Lond. 186:463-474.

Gorman, M.L., Kruuk, H. and Leitch, A. 1984. Social functions of the sub-caudal scent gland secretion of the European badger Meles meles (Carnivora:Mustelidae). J. Zool., Lond. 204:549-559.

Gorman, M.L. and Mills, M.G.L. 1984. Scent marking strategies in hyaenas (Mammalia). J. Zool., Lond. 202:535-547.

Gosling, L.M. 1982. A reassessment of the function of scent marking in territories. Z. Tierpsychol. 60:89-118.

Gossow, H. 1970. Vergleichende Verhaltensstudien an Marderartigen. Z. Tierpsychol. 27:405-480.

Hall, E.R. 1926. The abdominal skin gland of Martes. J. Mammal. 7:227-229.

Halonen, J. and Denny, M.R. 1979. Defense against predation. In Denny, M.R. (Ed.) Comparative psychology: research in animal behaviur. John Wiley and Sons, New York. pp. 400-413.

Halpin, Z.T. 1974. Individual differences in the biological odors of the Mongolian gerbil (Meriones unguiculatus). Behav. Biol. 11:253-259.

Ham, A.W. 1974. Histology. 7th edn. Lippincott, Philadelphia.

Harrington, J.E. 1976. Discrimination between individuals by scent in Lemur fulvus. Anim. Behav. 24:207-212.

Henry, J.D. 1977. The use of urine marking in the scavenging behavior of the red fox (Vulpes vulpes). Behav. 61:82-105.

Herman, T. and Fuller, K. 1974. Observations of the marten, Martes americana, in the Mackenzie district, Northwest territories. Can. Field-Nat. 88:501-503.

Herter, von K. and Ohm-Kettner, I-D. 1954. Über die Aufzucht und das Verhalten zweier Baummarder (Martes martes L.). Z. Tierpsychol. 11:113-137.

Howell, A.H. 1920. The Florida spotted skunk as an acrobat. J. Mammal. 1:88.

Hughes, R.N. 1964. Responses by the ferret to stimulus change. Br. J. Psychol. 55:463-468.

_____ 1965. Spontaneous alternation and response to stimulus change in the ferret. J. Comp. Physiol. Psychol. 60:149-150.

Jenkinson, D.McE. 1967. On the classification of sweat glands and the question of the existence of an apocrine secretory process. Br. vet. J. 123:311-316.

Jenkinson, D.McE., Montgomery, I. and Elder, H.Y. 1979. The ultra structure of the sweat glands of the ox, sheep and goat during sweating and recovery. J. Anat. 129:117-140.

Jensen, B. 1978. Resultater af fangst med kassefaelder. Nat. Jutlandica 20:129-136.

Johnson, C.E. 1921. The 'handstand' habit of the spotted skunk. J. Mammal. 2:87-89.

Johnson, R.P. 1973. Scent marking in mammals. Anim. Behav. 21:521-535.

Johnston, R.E. 1977. Sex pheromones in golden hamsters. In Müller-Schwarze, D. and Mozell, M.M. (Eds.) Chemical signals in vertebrates. Plenum Press, New York. pp. 225-249.

Johnston, R.E. and Schmidt, T. 1979. Responses of hamsters to scent marks of different ages. Behav. Neural Biol. 26:64-75.

Karlson, P. and Lüscher, M. 1959. Pheromones. A new term for a class of biologically active substances. Nature (London) 183:55-56.

Katz, R.A. and Shorey, H.H. 1979. In defense of the term "pheromone". J. Chem. Ecol. 5:299-301.

King, C.M. 1973. A system for trapping and handling live weasels in the field. J. Zool., Lond. 171:458-464.

_____ 1975. The sex ratio of trapped weasels Mustela nivalis. Mammal Review 5:1-8.

_____ 1980. Field experiments on the trapping of stoats (Mustela erminea). N.Z. J. Zool. 7:261-266.

_____ 1981. Studies on the control of stoats (Mustela erminea) in the National Parks of New Zealand. In Chapman, J.A. and Pursley, D. (Eds.) The worldwide furbearer conference proceedings. pp 1862-1874.

_____ 1983. The life-history stategies of Mustela nivalis and M. erminea. Acta Zool. Fenn. 174:183-184.

_____ 1984. Immigrant killers. Introduced predators and the conservation of birds in New Zealand. Oxford University Press, Auckland.

King, C.M. and Edgar, R.L. 1977. Techniques for trapping and tracking

stoats (Mustela erminea); a review, and a new system. N.Z. J. Zool. 4:193-212.

King, C.M. and Moody, J.E. 1976. Progress and problems of a survey of the biology of stoats in national parks. Seminar on science in national parks proceedings Lincoln College. National Parks Authority, Wellington.

King, C.M. and Moors, P.J. 1979. The life-history tactics of mustelids, and their significance for predator control and conservation in New Zealand. N.Z. J. Zool. 6:619-622.

Koehler, G.M., Hornocker, M.G. and Hash, H.S. 1980. Wolverine marking behavior. Can. Field-Nat. 94:339-341.

Korytin, S.A. and Solomin, N.N. 1969. Materialy po etiologii psovaykh. Sb. Trud. vses. nauchno-issled Inst. Zhivotnogo Syr'ya Puttniny. 22:235-270; not seen, cited in Henry 1977.

Krott, P. 1959. Der Vielfrass (Gulo gulo L. 1758). Monogram. Wildsäug. 13-Jen; not seen, cited in Goethe 1964.

Kruse, S. McK. and Howard, W.E. 1983. Canid sex attractant studies. J. Chem. Ecol. 11:1503-1510.

Kruuk, H. 1978. Spatial organisation and territorial behaviour of the European badger Meles meles. J. Zool., Lond. 184:1-19.

Kruuk, H., Gorman, M. and Leitch,A. 1984. Scent-marking with the subcaudal gland by the European badger, Meles meles L. Anim. Behav. 32:899-907.

Lavers, R.B. 1973a. Aspects of the biology of the ferret, Mustela putorius forma furo L. at Pukepuke Lagoon. Proc. N.Z. Ecol. Soc. 20:7-12.

_____ 1973b. Results of a live-trapping study on a population of ferrets at Pukepuke Lagoon. Unpublished report to Controller of Wildlife, Wellington.

Lavers, R.B. and Clapperton, B.K. in prep. Ferret. In King, C.M. (Ed.) Mammals of New Zealand. Oxford University Press.

Lavers, R.B. and Mills, J.A. 1978. Stoat studies in the Murchison mountains, Fiordland. Proc. Seminar on the Takahe and its Habitat. Fiordland National Park Board, Invercargill. pp. 222-232.

Leyhausen, P. 1965. The communal organisation of solitary mammals. Symp. Zool. Soc. Lond. 14:249-263.

Leyhausen, P. and Wolff, R. 1959. Das Revier einer Hauskatze. Z. Tierpsychol. 16:666-670.

McCabe, R.H. 1949. Notes on live-trapping mink. J. Mammal. 30:416-423.

McCann, C. 1955. Observations on the polecat (Putorius putorius Linn.) in New Zealand. Rec. Dom. Mus. (Wellington) 2:151-165.

Macdonald, D.W. 1985. The carnivores: order Carnivora. In Brown, R.E. and Macdonald, D.W. (Eds.) Social odours in mammals. Vol. 2. Oxford University Press, Oxford. pp. 619-722.

Marshall, W.H. 1963. The ecology of mustelids in New Zealand. DSIR Information Series No. 38. DSIR, Wellington.

Matthews, L.H. 1971. The life of mammals. Vol. 2. The Weidenfeld and Nicolson Natural History, London.

Maynard-Smith, J. and Parker, G.A. 1976. The logic of assymetric contests. Anim. Behav. 24:159-175.

Mazder, E., Capone, M.R. and Drickamer, L.C. 1976. Conspecific odors and trappability of deermice (Peromyscus leucopus noveboracensis). J. Mammal. 57:607-609.

Mech, L.D. and Peters, R.P. 1977. The study of chemical communication in free-ranging mammals. In Müller-Schwarze, D. and Mozell, M.M. (Eds.) Chemical signals in vertebrates. Plenum Press, New York. pp. 321-332.

Merton, D.V. 1978. Controlling introduced predators and competitors on islands. In Temple, S.A. (Ed.) Endangered birds. Croom Helm, London. pp. 121-128.

Moors, P.J. 1983. Predation by mustelids and rodents on the eggs and chicks of native and introduced birds in Kowhai Bush, New Zealand. Ibis 125:137-154.

Moors, P.J. and Lavers, R.B. 1981. Movements and home range of ferrets (Mustela furo) at Pukepuke Lagoon, New Zealand. N.Z. J. Zool. 8:413-423.

Müller-Schwarze, D. 1969. Complexity and relative specificity in a mammalian pheromone. Nature (London) 223:525-526.

_____ 1977. Complex mammalian behavior and the pheromone bioassay in the field. In Müller-Schwarze, D. and Mozell, M.M. (Eds.) Chemical signals in vertebrates. Plenum Press, New York. pp. 413-433.

_____ 1983. Scent glands in mammals and their functions. In Eisenberg, J.F. and Kleiman D.G. (Eds.) Recent advances in the study of mammalian behavior. Spec. Publ. No. 7, Amer. Soc. Mammalogists. pp. 150-197.

Müller-Schwarze, D., Müller-Schwarze, C., Singer, A.G. and Silverstein, R.M. 1974. Mammalian pheromone: identification of active component in the subauricular scent of the male pronghorn.

Science 183:860-862.

Müller-Schwarze, D., Silverstein, R.M., Müller-Schwarze, C., Singer, A.G. and Volkman, N.S. 1976. Responses to a mammalian pheromone and its geometric isomer. J. Chem. Ecol. 2:389-398.

Murphy, E.L., Flath, R.A., Black, D.R., Mon, T.R., Teranishi, R., Timm, R.M. and Howard, W.E. 1978. Isolation, identification, and biological activity assay of chemical fractions from estrus urine attractive to the coyote. In Bullard, R.W. (Ed.) Flavor chemistry of animal foods. ACS symposium series no. 67. American Chemical Society, Washington. pp. 66-77.

Mykytowycz, R. 1965. Further observations on the territorial function and histology of the submandibular cutaneous (chin) glands in the rabbit, (Oryctolagus cuniculus L.). Anim. Behav. 13:400-412.

_____ 1970. The role of skin glands in mammalian communication. In Johnston, J.W.Jr., Moulton, D.G. and Turk, A. (Eds.) Communication by chemical signals. Adv. Chemoreception Vol. 1. Appleton-Century-Crofts, New York. pp. 327-360.

_____ 1975. Activation of territorial behaviour in the rabbit, Oryctolagus cuniculus, by stimulus with its own chin gland secretion. In Denton, D.A. and Coghlan, J.P. (Eds.) Olfaction and taste, V. Academic Press, New York. pp. 425-432.

_____ 1979. Some difficulties in the study of the function and composition of semiochemicals in mammals, particularly wild rabbits, Oryctolagus cuniculus. In Ritter, F.J. (Ed.) Chemical ecology: odour communication in animals. Elesvier North Holland, Amsterdam. pp. 105-115.

Mykytowycz, R., Hesterman, E.R., Gambale, S. and Dudziński, M.L. 1976. A comparison of the effectiveness of the odors of rabbits Oryctolagus cuniculus in enhancing territorial confidence. J. Chem. Ecol. 2:13-24.

O'Connell, R.J. 1977. From insect to mammal: complications of the bioassay. In Müller-Schwarze, D. and Mozell, M.M. (Eds.) Chemical signals in vertebrates. Plenum Press, New York. pp. 377-390.

Ogden, J. and Caithness, T.A. 1982. The history and present vegetation of the macrophyte swamp at Pukepuke Lagoon. N.Z. J. Ecol. 5:108-116.

Parker, G.A. 1974. Assessment strategy and the evolution of fighting behaviour. J. Theor. Biol. 47:223-243.

Pierce, R.J. 1982a. A comparative ecological study of pied and black stilts in South Canterbury. PhD. thesis, University of Otago.

_____ 1982b. A good nesting season for black stilts at Lake Tekapo. Forest and Bird 14:30-32.

Pirie, W.R. and Hamden, M.A. 1972. Some revised continuity corrections for discrete data. Biom. 28:693-701.

Pocock, R.I. 1920. On the external and cranial characters of the European badger (Meles) and of the American badger (Taxidea). Proc. Zool. Soc. Lond. 1920:423-436; not seen, cited in Macdonald 1985.

_____ 1925. On the external characters of an American badger (Taxidea taxus) and an American mink (Mustela vison), recently exhibited in the Society's gardens. Proc. Zool. Soc. Lond. 1925:17-27.

Poole, T.B. 1967. Aspects of aggressive behaviour in polecats. Z. Tierpsychol. 24:351-369.

_____ 1972a. Diadic interactions between pairs of male polecats (Mustela furo and Mustela furo x M. putorius hybrids) under standardised environmental conditions during the breeding season. Z. Tierpsychol. 30:45-58.

_____ 1972b. Some behavioural differences between the European polecat, Mustela putorius, the ferret, M. furo, and their hybrids. J. Zool., Lond. 166:25-35.

_____ 1973. The aggressive behaviour of individual male polecats (Mustela putorius, Mustela furo and hybrids) towards familiar and unfamiliar opponents. J. Zool., Lond. 170:395-414.

_____ 1974. Detailed analysis of fighting in polecats (Mustelidae) using ciné film. J. Zool., Lond. 173:369-393.

Powell, R.A. 1979. Mustelid spacing patterns: variations on a theme by Mustela. Z. Tierpsychol. 50:153-165.

Preti, G., Smith, A.B. and Beauchamp, G.K. 1977. Chemical and behavioral complexity in mammalian chemical communication systems - guinea pigs (Cavia porcellus), marmosets (Saguinus fuscicolis) and humans (Homo sapiens). In Müller-Schwarze, D. and Mozell, M.M. (Eds.) Chemical signals in vertebrates. Plenum Press, New York. pp. 95-114.

Pulliainen, E. and Ovaskainen, P. 1975. Territory marking by a wolverine (Gulo gulo) in Northeastern Lapland. Ann. Zool. Fenn. 12:268-270.

Quay, W.B. 1977. Structure and function of skin glands. In Müller-Schwarze, D. and Mozell, M.M. (Eds.) Chemical signals

in vertebrates. Plenum Press, New York. pp. 1-16.

Ralls, K. 1971. Mammalian scent marking. Science 171:443-449.

Rasa, O.A.E. 1973. Marking behaviour and its social significance in the African Dwarf Mongoose, Helogale undulata rufula. Z. Tierpsychol. 32:293-318.

Rempe, U. 1970. Morphometrische Untersuchungen an Iltisschädeln zur Klärung der Verwandtschaft von Steppeniltisfi, Waldiltis under Frettchen. Analyse eines "Grenzfalles" zwischen Unterart und art. Z. Wissenschaft. Zool. 180:183-367.

Robertson, L.N. 1976. Mustelids on the Otago Peninsula. Dip. Sci. thesis, University of Otago.

Ropartz, Ph. 1977. Chemical signals in agonistic and social behaviour of rodents. In Müller-Schwarze, D. and Mozell, M.M. (Eds.) Chemical signals in vertebrates. Plenum Press, New York. pp. 169-184.

Roser, R.J. and Lavers, R.B. 1976. Food habits of the ferret (Mustela putorius furo L.) at Pukepuke Lagoon, New Zealand. N.Z. J. Zool. 3:269-275.

Salmon, T.P. and Marsh, R.E. 1977. Equipment and methods available for measuring the behavioral response of rodents to odors. Special Technical Publication 625. American Society for Testing and Materials, Philadelphia. pp. 86-95.

Schaller, G.B. 1973. Golden shadows, flying hooves. Alfred A. Knopf, New York.

Schildknecht, von H. and Birkner, C. 1983. Struktur und Wirkung der Musteliden-Ökomone, III. Analyse der Analbeutelsekrete Mitteleuropäischer Musteliden. Chem-Zeitun. 107:267-270.

Schildknecht, von H., Wilz, I., Enzmann, F., Grund, N. and Ziegler, M. 1976. Mustelan, the malodorous substance from the anal gland of the mink. Angew. Chem. Int. Ed. Engl. 15:242-253.

Shumake, S.A. 1977. The search for applications of chemical signals in wildlife management. In Müller-Scharze, D. and Mozell, M.M. (Eds.) Chemical Signals in Vertebrates. Plenum Press, New York. pp. 357-376.

Singer, A.G., Agosta, W.C., O'Connell, R.J., Pfaffmann, C., Bowen, D.V. and Field, F.H. 1976. Dimethyl disulphide: an attractant pheromone in hamster vaginal secretion. Science 191:948-950.

Sokolov, V.E., Albone, E.S., Flood, P.F., Heap, P.F, Kagan, M.Z., Vasilieva, V.S., Rozhnov, V.V. and Zinkevich, E.P. 1980. Secretion and secretory tissues of the anal sac of the mink

Mustela vison. Chemical and histological studies. J. Chem. Ecol. 6:805-825.

Sokolov, V.E., Chikil'din, B.S. and Zinkevich, E.P. 1975. Free volatile aliphatic acids of the anal gland secretion of the mink (Mustela vison). DoKl. Akad. Nauk SSSR Ser. Biol. 220:288-290.

Sokolov, V.E. and Rozhnov, V.V. 1983. Information value of scent markers of mustelidae: urine and excrement of Mustela putorius and Mustela vison. DoKl. Akad. Nauk SSSR Ser. Biol. 269:220-222.

Stevens, D.A. 1975. Laboratory methods for obtaining olfactory discrimination in rodents. In Moulton, D.G., Turk, A. and Johnston, J.W.Jr. (Eds.) Methods in olfactory research. Academic Press, London. pp. 375-394.

Stoddart, D.M. 1976. Mammalian odours and pheromones. Arnold, London.

_____ 1980a. Some responses of a free living community of rodents to the odors of predators. In Müller-Schwarze, D. and Silverstein, R.M. (Eds.) Chemical signals. Vertebrates and aquatic invertebrates. Plenum Press, New York. pp. 1-10.

_____ 1980b. The ecology of vertebrate olfaction. Chapman and Hall, London.

_____ 1982a. Demonstration of olfactory discrimination by the short-tailed vole, Microtus agrestis L. Anim. Behav. 30:293-294.

_____ 1982b. Does trap odour influence estimation of population size of the short-tailed vole Microtus agrestis? J. Anim. Ecol. 51:375-386.

Stoddart, D.M. and Smith, P.A. 1984. Woodmice (Apodemus sylvaticus) can distinguish conspecific from heterospecific odors in the field. J. Chem. Ecol. 10:923-928.

Stubbe, M. 1969. Die analen Markierungsorgane der Martes-Arten. Acta Theriol. 14:303-312.

_____ 1970. Zur Evolution der analen Markierungsorgane bei Musteliden. Biol. Zentralbl. 89:213-223.

_____ 1972. Die analen Markierungsorgane der Mustela-Arten. Zool. Gart. 42:176-188.

Sullivan, T.P. and Crump, D.R. 1984. Influence of mustelid scent gland compounds on suppression of feeding by snowshoe hares (Lepus americanus). J. Chem. Ecol. 10:1809-1821.

Thomson, G.M. 1922. The naturalisation of animals and plants in New Zealand. Cambridge University Press, London.

Trowbridge, B.J. 1983. Olfactory communication in the European otter (Lutra l. lutra). PhD. thesis, University of Aberdeen.

Turkowski, F.J., Popelka, M.L., Green, B.B. and Bullard, R.W. 1979. Testing the responses of coyotes and other predators to odor attractants. In Beck, J.R. (Ed.) Vertebrate pest control and management materials. Special Technical Publication 680. American Society for Testing and Materials, Philadelphia. pp. 255-269.

Turkowski, F.J., Popelka, M.L. and Bullard, R.W. 1983. Efficacy of odor lures and baits for coyotes. Wildl. Soc. Bull. 11:136-145.

Uexküll, J.V. and Kriszat, G. 1934. Streifzüge durch die Umwelten von Tieren und Menschen. Berlin; not seen, cited in Gosling 1982.

Van der Berk, J. and Müller-Schwarze, D. 1984. Responses of wild muskrats (Ondatra zibethicus L.) to scented traps. J. Chem. Ecol. 10:1411-1415.

Veitch, C.R. 1982. Eradication of cats from Little Barrier Island. Landscape 11:27-29.

Walker, A. 1930. The 'handstand' and some other habits of the Oregon spotted skunk. J. Mammal. 11:227-229.

Wemmer, C. 1971. Scent marking and anointing: behavioral parallelism in mammals. Amer. Zool. 11:623 (Abstr.).

Wheeler, M.E. 1978. Olfactory communication in ferrets and mink. MSc. thesis, Humboldt State University.

Wildhaber, C.A. 1984. Chin rubbing behaviour in ferrets (Mustela putorius furo). BSc. Hons. dissertation, Massey University.

Wodzicki, K.A. 1950. Introduced mammals of New Zealand. An ecological and economic survey. DSIR Bulletin No. 98. DSIR, Wellington.

Wuensch, K.L. 1982. Effect of scented traps on captures of Mus musculus and Peromyscus maniculatus. J. Mammal. 63:312-315.

Yamaji, T., Manabe, N., Sato, E., Watanabe, S. and Ishibashi, T. 1981. Distributions and histo-chemical characteristics of sebaceous and sweat glands in Siberian weasels (Mustela sibirica coreana and Mustela sibirica itatsi). J. Mammal. Soc. Japan 8:194-200.

Zima, J. and Král, B. 1984. Karyotypes of European mammals III. Acta Sc. Nat. Brno 18:1-51.

EMENDATION 1

This concept of "territorial confidence" (often referred to simply as confidence) is an abstract one. It is reflected in an animal's behaviour. A detailed knowledge of the behaviour of a species allows the quantification of responses in various stimulus situations. The effects stimuli have on the animal's inner state can thus be determined (Mykytowycz et al. 1976). Similar terms like "self-assurance" (von Richter 1972) and "sense of ownership or possession" (Joubert 1972) express the same concept. The related concept of "intimidation" can also be viewed in this light, and is demonstrated by submissive behaviour in the animal. These concepts gain intuitive support from the reversal of dominance as a pair of residents in adjoining territories are experimentally shifted back and forth across a common boundary (Tinbergen 1953). The relationship between scent marking and territorial confidence has already been recognised in mustelids. Erlinge et al.(1982) stated that: "marking frequency was influenced by the [stoat's] self-confidence...There seemed to be a feedback between marking and self-confidence." They saw this as being important in the settlement of asymmetric contests between resident and intruder.

Joubert, S.C.J. 1972. Territorial behaviour of the tsessebe (Damaliscus lunatus Burchell) in the Kruger National Park. Zool. Afr. 7:141-156; not seen, cited in Gosling 1982.

Richter, W. von. 1972. Territorial behaviour of the black wildebeest. Zool. Afr. 7:207-231; not seen, cited in Gosling 1982.

Tinbergen, N. 1953. Social behaviour in animals. Methuen, London.

EMENDATION 2

The hypotheses yield a number of specific predictions about the behaviour of the animal that are testable by experiment or critical field observation (Gosling 1982). Some of these predictions are easily quantified and falsification comes down to a statistically significant criterion. Others are of an empirical nature and are not as strong tests of the hypotheses. They provide valuable supportive or non-supportive information.

EMENDATION 3

The lack of differentiation by males between odours of oestrous and anoestrous females can be explained in terms of the biology of the ferret, and evolutionary strategies of males and females. As discussed in section 9.1.2, the breeding system of the ferret, with females all in oestrus at the same time, requires little need for olfactory recognition of oestrus. The solitary way of life of the ferret suggests that a successful stategy for the male would be to mate with any female he encounters during the breeding season. If this is true then there is no selective advantage to the female to signal her oestrous state.