Social Interactions in Captive Weasels
(Mustela nivalis)

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For my Parents

Abstract

Interactions between male, female, and male-female pairs of weasels (*Mustela nivalis*) were observed in indoor enclosures of 12m^2 and 28m^2. The experiments were designed to investigate how weasels interact and how these interactions affected their spacing. Five agonistic behaviours were described including attack, chase, follow, near approach, and far approach. Two defensive behaviours occurred both were vocalizations: squealing and hissing. All of the female pairs developed a dominant/subordinate relationship based on agonistic behaviour with the dominant females limiting the use of the area by the subordinate females. Eight of the male pairs showed a dominant/subordinate relationship based on defensive behaviour with the other five pairs showing equal amounts of agonistic behaviour. There was no relationshp between either age or weight and dominance. Males were less active than the females. Hence, the affects of dominace on spacing were less evident. Both types of male pairs tended to avoid each other. The animals did not defend areas or set up territorial boundaries, but did defend their personal space, nesting boxes and/or food stores. Agonisitc behaviour decreased over time suggesting that the animals had habituated to each other.

The male-female pairs could not be classified as dominant or subordinate initially, as the frequency and type of approaches were different. The appraoches of the males were sexual rather than agonistic. The females initially either avoided or attacked the males. Once in oestrous they approached the males trilling until copulation occurred. Both females and males continued to be active until parturition. The females then became very aggressive resulting in the confinement of the males to their nesting boxes. This continued until the young were about twelve weeks old, when the aggressive behaviour of the females lessened again. The males then became more active, renewing their approaches to test the females' receptivity.

The results of these experiments were discussed in relation to how they might affect the spacing of free-ranging weasels. The behaviours that occurred were described in an ethogram.

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Table of Contents

Introduction

In this thesis I shall describe and discuss my work on the weasel (Mustela nivalis). The weasel is a small carnivore in the family Mustelidae. In Britain this family also includes the stoat (Mustela erminea), polecat (Mustela putrious), badger (Meles meles), otter (Lutra lutra), pine marten (Martes martes), and the introduced, North American mink (Mustela vison). Weasels are widespread thoughout Britain, although they are absent from Ireland and most of the other islands except Skye. They are distributed throughout Europe from Norway to Spain, throughout Asia, and across the North American continent.

Weasels conform to the classic mustelid characteristics having long and thin bodies, short legs and a musk gland by the anus that emits droplets of a viscous and pungent substance. They are brown with a white underbelly, with the brown varying from a pale sandy colour to a dark maghogany. The patterning of the brown and white on the underbelly is unique for each weasel, and can be used to identify individuals (Linn and Day 1966). The tail is short (approximately 1/5 of the body length) and solid brown. Weasels vary in size throughout their distribution. They exhibit sexual dimorphism with the males weighing twice as much as the females. The males used in these experiments averaged 168 ± 26.5 gms. in weight, while the females averaged 86.5 ± 9.02 gms. These are larger than the average weasels weights given by either Moors (1964) or King (1975) for

Britain.

The weasel has been the subject of many studies both in the field and in the laboratory. I shall discuss many of these in more detail in the following chapters, but shall summarise the basic types of research below. There are seven main types of research on the weasel:

Field work:

1) Home range/territoriality and population dynamics (Lockie 1966, Moors 1974, Erlinge 1974, King 1975).

2) Species distribution (Parovshchikov 1963).

3) Interactions with other species (Polderboer _et al_. 1941, Rosenzweig 1966, Simms 1979, King and Moors 1979).

4) Food/prey eaten (Day 1968, Moors 1975, Tapper 1976, 1979).

Laboratory

1) Physiology (Brown and Lasiewski 1972, Iversen 1972, Moors 1977).

2) Behaviour

a) Ontogeny (Heidt 1970, Heidt _et al_. 1968, Hartman 1964, East and Lockie 1964, 1965).

b) Vocalizations (Huff and Price 1968, Heidt and Huff 1970).

c) Sexual behaviour (Hartman 1964, East and Lockie 1964, 1965).

3) Parasites (Hansson 1967, 1974, King , 1976, 1977, Lewis (1978).

The field studies have shown that weasels live within a limited area which is either a home range or a territory (Lockie 1966, King 1975). Information is available on the size and distribution of these ranges, but not on how they are established or maintained. The behavioural studies have dealt with ontogeny and sexual behaviour, but only recently with interactions between individuals (Buckingham 1979). These latter experiments were of short duration, usually around 30 minutes. Therefore, although they provided information on dominance, its affect on the use of space over a longer period could not be discussed. In order to understand the distribution of weasel ranges it is necessary to consider both the distribution of resources and the behavioural factors influencing habitation of an area. In this thesis I shall consider this second factor, the influence of behaviour on the distribution of weasels in captivity.

Chapter 1: Introduction

There are several studies on the ecology of free ranging weasels including Lockie (1966), Erlinge (1974, 1975), Moors (1974), and King (1975). These have provided good information on movements and distribution, but information on social interactions and sexual behaviour is limited. Therefore in this study I observed social interactions between single and mixed sexed pairs in captivity in order to investigate the social behaviour of the weasel. The results present information on agonistic and avoidance behaviour, spatial distribution of individuals, and the effects of the reproductive cycle on the interactions of mixed sexed pairs of weasels. They also include data on parent offspring interactions and ontogeny.

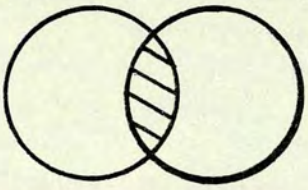
In the following pages I shall deal with what is known about weasels in the field and in captivity and the questions raised in the interpretation of the available data.

1:1.1 Territoriality

Dispersion, "the distribution of animals in space at one moment in time" (Brown and Orians 1970) has been studied by numerous researchers both in the field and in captivity. Spatially, individuals can either be clumped, randomly distributed, or regularly distributed in relation to other individuals of the same species. If distribution is regular it suggests that either the habitat is so organised to create regular distribution or that the animals are showing some form of territoriality.

The concept of territoriality has been defined and reviewed by numerous authors including Nice (1941), Noble (1939), Hinde (1956), Carpenter (1958), Brown and Orians (1970), Wilson (1975) , and Davies (1978). It was very basically defined by Noble in 1939 as "any defended area". The simplicity of this definition has been queried and other authors have qualified it by adding other criteria. Schoener (1968) agreed with Pitelka's (1959) definition of territory as an exclusive area maintained by defence. Leyhausen (1971) also considered exclusiveness, but suggested it evolved from individual distance around the animal expanding to become an exclusive area. Brown and Orians (1970) summarised their definition of territory which is a composite of all of these descriptions as : "a fixed area", defended by the resident, which eventually becomes an "exclusive area". Davies (1978) on the other hand produced a spatial definition of territory merely saying that individuals or groups are spaced more than would be expected from a random occupation of habitats. This definition although attractive in that it explicity states how territory affects the dispersion of species, fails by not stating how this random distribution is brought about.

In order to decide which of these definitions is most applicable as a general workable definition of territoriality, it is necessary to consider the practical rather than theoretical application of each. The first definition to consider is Noble's (1939) "any defended area". If an animal is defending the area immediately around itself (i.e. its personal space), is it in fact territorial? If so it has a small and very mobile territory. I would suggest in agreement with Brown and Orians that the word fixed should be added to this definition. Another important point concerns the exclusiveness of the area. According to Pitelka (1959) and Brown and Orians (1970), the area must be exclusive, in order to be considered a territory. However, these criteria were mainly based on studies on birds. When considering a less mobile animal such as a mammal, and especially a small carnivore like the weasel with a very small body size in relation to territory size, exclusiveness may be impossible. Hence, there may be some spatial overlap between members of the same sex and species , but rarely temporal overlap. Lockie (1966) suggested that some overlap is necessary for territorial behaviour to occur, as it allows neutral zone contact of individuals. These contacts may be direct with audio, visual and possibly physical contact, but may also be indirect in the form of scent posts of either urine, feces or specific gland sebum. Whichever method is employed, neighbors are aware of each other without the necessity of successive physical interactions. In the weasel we are generally dealing with territories which have two parts: an exclusive area and an area of overlap as pictured below.



The overlapping area is used by both animals, but not simultaneously. Hence each animal can leave behind signal posts so that the other animal knows that he is still in his territory. Both individuals benefit from this in that they would know who their neighbors are, and once a relationship had been established, would need to interact only occasionally. However, if one animal disappeared from his territory, the other would soon become aware of its absence, assuming the overlap area was visited regularly. This allows the surviving neighbor to have access to the now vacated area. As both weasels (Lockie 1966) and stoats (Erlinge 1977a) move around their ranges frequently, they would soon discover the absence of a neighbor (Lockie 1966). Furthermore, animals do move into areas formerly occupied by another resident, once the area becomes vacant (Lockie 1966). Hence this may be a means of acquiring a slightly larger or perhaps better territory with little output of energy. How might this system of overlap affect transient animals passing through the area? When transients settle on a vacated home range, the boundaries would remain the same as those established by the previous owner (Lockie 1966). Hence these overlapping areas may also be important in delimiting the range of the new individuals. This also suggests that the weasels are holding a certain sized area with continual pressure from neighbors keeping the boundaries stable. Therefore in the smaller carnivores the main identifiable feature of territory is defence of a fixed area. Spatial distribution must come second as the presence of overlap will vary between individuals and in different habitats.

1:1.2 Home Range

Even though an animal may not be shown to be territorial, it still inhabitats a limited area in its lifetime which is termed its home range. As defined by Burt (1943) and restated by Jewell (1966), a "home range is the area over which an animal normally travels in pursuit of its routine activities". Jewell defined the specific part of the home range that an animal would inhabitat including the life time range which is the total area with which the animal had become familiar. He also considered the areas of maximum use which included Kaufman's (1962) "core area". Hediger (1950) discussed the "living spaces" of animals and how they consisted of only certain paths and tracks including sleeping places, that were used while other areas were not entered. One question still remains. By what means are these home ranges maintained? For instance if boundaries of neighboring individuals do not overlap, if these are not the result of agonistic interactions between individuals, how do they originate? Brown and Orians (1970) suggested three reasons for the lack of overlap between home ranges including "mutual avoidance, preference for an unexploited food supply, physical barriers, or different habitat preferences". DeVore (1965) suggested that baboons employed several methods that served to keep neighboring groups apart. These included daily routines which resulted in the use of different area, social boundaries of organised groups, and loud vocal advertisement of some species. The latter characteristic is also sometimes listed under territorial defence as in the puma (*Puma concolor*) (Seidensticker *et al*. 1973). Even if home ranges may overlap spatially, they need not overlap temporally. Similarly by definition home ranges are not defended, but clearly animals must occasionally fight upon seeing an intruder. Thus when dealing with home ranges we may have to deal with degree of defence versus defence or no defence. Encounters may be scored as to whether they were a short fight resulting from suddenly encountering another individual or whether they were a long fight with one animal eventually being chased out of the range. McBride suggested in 1971 that, "we do not know whether home range systems are open or closed to entry by outsiders". The "home range pattern may be a system of recognition of neighbors closed to entry to strangers".

1:1.3 Territory versus Home Range

When considering whether an animal is territorial or merely inhabiting a home range, the definition of each is critical. By definition territory requires defence, home range generally does not.

How does the information available on mammalian distribution fall into these categories? Brown (1969) pointed out that territory requires both dispersion and defence of the area. Hence information on dispersion only is not sufficient to decide whether or not an animal is territorial. Therefore, merely noting that the ranges of several animals do not overlap or overlap very little is not sufficient without the additional knowledge of whether this is the result of behaviour or habitat features. (In captivity the reverse occurs with ranges overlapping due to space restrictions, but with boundary fights sometimes occurring when both individuals are out simultaneously). It seems most likely that territory and home range are at opposite ends of a scale with different species and species in varying habitats occurring at different levels. Therefore in order to consider whether a species is territorial or inhabiting a home range we must use means of acquiring data that focus our attentions on how individuals interact or avoid interacting in order to maintain their distribution.

1:2.1 Territory and Home Range in Some Mustelids

The social organisation of some of the mustelids has been described. However, the quantity and quality of information varies considerably because the data are a result of a mixture of straight observation, live capture-release, and more recently radio tracking.

Presently there is information on the dispersion pattern of the badger, the wolverine (Gulo gulo), the European otter, the American pine marten (Martes americana), the mink, the stoat, and the weasel.

The badger was initially reported to live in mixed and single-sexed groups and not to defend territories (Neal 1948). The females did defend the area round the set, though, and the offspring during the breeding period. On the other hand Kruuk (1978) found that in Oxfordshire badgers were territorial. He recorded border fighting and the marking of territorial boundaries with latrines. Cheeseman and Mallinson (1980) also noted territoriality by social groups of badgers (referred to as clans by Kruuk). Not all of the bordering areas were as exclusive, though, as those studied by Kruuk.

There is little information on the pine marten in Britain. There are only estimates available on home range or territory size. There have been studies on the American marten, though, with the following results. Hawley and Newby (1957) suggested that martens lived in home ranges, not territories, because territorial defence was not seen. Mech (1977) also referred to home ranges. Within the sexes there was generally little overlap of range, but between sexes overlap did occur (Hawley and Newby 1957). Juveniles were also tolerated by adults of the same sex , as they established their home ranges regardless of the sex of the occupant of the area. The size of home range varied in the different sections of the country. This presumably was the result of differing habitats and prey densities. Weckworth and Hawley (1962) also reported fluctuations in marten numbers with the cyclic changes in prey density.

Erlinge (1967, 1968) studied the European otter in Sweden which is also territorial. Transients and temporary residents made up almost equal proportions of the adult population. Between males the boundaries overlapped and in these areas, territorial conflicts were frequent. Territories were mostly maintained by signals with little evidence of fighting. In Scotland Kruuk and Hewson(1978) suggested that coastal living otters are territorial based on information about the location of holts. There was considerable overlap between territories, though, when the actual movements of otters were studied. They suggested that this may be related to the degree of defence possible of the available resources.

Gerell (1970) used radios to track free living American mink in Sweden. He referred to the area that they inhabitated as their home range, but suggested that territorial behaviour influenced the boundaries of these ranges. Although the home ranges of male and females overlapped, there was no overlap between animals of the same sex. He also suggested that the size of the home range was dependent on the population density and the available resources of the area.

There is information on three of the weasel species. The long-tailed weasel (Mustela frenata) which lives in North America has overlapping home ranges. The overlap is usually spatial not temporal (Quick 1944). In Finland Nyholm (1959) observed stoat movements by snow tracking and referred to the areas used as home ranges. Lockie (1966), on the other hand, who observed stoat distribution by live capture release, suggested that they were territorial. The most complete data available is that of Erlinge (1977a). His results showed little or no overlap within the sexes, but frequently complete overlap between sexes. Hence, he also suggested that stoats are territorial.

In the literature presently available on weasels, there are contrasting views on the social system. In Britain, Lockie (1966) stated that they were territorial because there was a small degree of overlap between neighbors of the same sex, "residents prevented other from settling " and " residents only extended their boundaries when a resident animal was removed". He also suggested that weasels were not regulating territory size in relation to food supply fluctuations, but were instead holding the largest areas possible. In Sweden Erlinge (1974) also stated that weasels are territorial, but unlike Lockie related it directly to prey density. It should be noted , however, that they were dealing with two very different habitats. Carron valley was a uniform young forestry plantation while Erlinge's study area was much more varied environment with a consequently patchy distribution of prey species. Moors (1974) also discussed territoriality, but in Aberdeenshire farmland. He suggested that the distribution of his animals was heavily dependent on the man-made distribution of stone dykes. This produced long territories following the contours of the dykes with some overlap between individuals. In contrast King (1975) stated that in her study area , Wytham woods, weasels were not territorial, but had home ranges. She went on to argue that by the strict definition of territory used by Brown and Orians (1970), territory could not have overlap zones. As the ranges of mammals generally do overlap slightly and these areas may in fact be necessary for olfactory communication (eg. sign posts) , weasels could not ever be considered territorial. Similarly, as she did not see any direct defensive behaviour as did Lockie (1966) she could not state that her animals were territorial (see Section 1:1.3). Therefore, the social system of weasels may vary in different habitats. However, the interpretation of data clearly varies depending on the definitions used for territory and home range.

Although the results of the above trapping studies suggest how weasels are distributed, the actual boundaries delineated are strongly influenced by the placement of traps. Consequently any forays out of the main areas, but not involving capture would not be recorded. Other authors have discussed the bias of the different methods of recording animal location, see (Brown and Orians 1970), so I shall only deal with it in passing. The important point is that as yet there is minimal information on how weasels interact in the field and how this might influence their distribution. Hopefully these questions will be answered once the results of some of the radio tracking work on the smaller mustelids are made available. However, until then the only means of answering these questions are through experiments on captive individuals. In this study I asked how do two weasels interact when given access to each other and how did this affect their movements within the space provided?

1:3 Dominance and Territorial Behaviour

When studying the results of a trapping or radio tracking study of a territorial species, one is immediately struck by the variation in the size of the areas. Although this could be attributed purely to ecological factors such as habitat or prey density, it may also be affected by varying degrees of aggressive behaviour, and hence the dominance exerted by the individuals involved. Dominance as used here is defined by Deag (1977). The dominant animal is the animal whose behaviour was not limited by others. The subordinate animals is the one whose behaviour was limited and showed submission.

In solitary territorial animals ,the submissive animals could be interpreted as the one who restricts its movements in response to the other animal. Watson and Moss (1970) described in detail the long term ecological effects of dominance on population limitation, but I shall deal with the effects between individuals instead of within populations.

There has been some confusion as to whether dominance is related to territory and if so in what way. Fisler (1969) suggested that dominance hierarchy and territory "were at opposite ends of a continuum of social behaviour related to density of population." Donegan (1978) suggested that in order to insure that his animals showed territorial behaviour and did not lapse into a dominance hierarchy, it was necessary to separate them when not being observed. I would disagree with this as surely under natural conditions an animal must be dominant to an intruder invading its area in order to retain its territority. Furthermore groups can be territorial. Hence they cannot be at opposite ends of a density scale.

Another problem concerning dominance and territory is that of the space limitations in captive experiments. One could suggest that as space is often too limited for animals to have a normal sized territory, they instead replace territorial behaviour with a dominance hierarchy. Hence dominance behaviour in a territorial animal is merely an artefact of captivity. Similarly dominance is usually assessed by agonistic encounters which may occur more frequently in captivity due to the close proximity of the animals and the inability to escape from each other. The increased frequency of encounter can in fact lead to the classic pariah animals as seen by Leyhausen (1965). However, I would suggest that only the degree of dominance may be magnified by the close proximity of captivity. It must also exist in free ranging individuals. Under natural conditions dominance may affect territory size (Erlinge 1974, 1977b), territory quality and consequently access to mates.

Another factor that is not often considered by laboratory researchers when discussing dominance and its relevance to the wild is the activity of the animals involved. Erlinge (1977b) clearly showed that although his animals were interacting and could be classed as dominant or subordinant, more of their time was spent avoiding each other both temporally and spatially. He suggested that this was also the case for wild individuals. Lockie (1966) and King (1975) similarly discussed non-interaction between neighboring animals. I would suggest, therefore, that when looking at a small territorial animal in captivity we must also consider the temporal use of the area as well as agonistic encounters and spatial distribution. Merely labelling then as dominant or subordinate is not sufficient. We must consider how this apparent relationship affects their overall movements. Similarly the degree of difference between dominance and subordinate may have profound affects not apparent in laboratory experiments. For instance two animals of widely varying degrees of agonistic behaviour may in the field produce widely differing territory sizes or one may be territorial, the other may not. This clearly complicates the interpretation of results collected in experiments in captivity. However, with careful consideration of what is known about wild individuals and careful planning, captive experiments can yield information not obtainable from field work.

1:4.1 Captive Studies

Behaviour between individuals of the same species has been frequently studied in captivity. The research may either consider a specialised question such as aggression and fighting behaviour (polecats, Poole 1967, 1972, 1974a, 1974b; mice* Scott 1966), maternal behaviour (dogs, Rheingold 1963), play behaviour (polecats, Poole 1966) or early behavioural development (weasels, Heidt 1970, pumas, Eaton and Velander 1977). Otherwise a more generalised view of the animal may be taken such as considering the social organisation of the species under varying density, age composition or sex (shrews, Crowcroft 1957, mice, Crowcroft and Rowe 1963, cats, Leyhausen 1965). Finally when more than one species of the same family are kept in

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* Due to the sparcity of research on captive mustelids and in order to illustrate some of the points made in the following discussion, I shall occassionally be referring to species not closely related to mustelids.

captivity, the researcher has the excellent opportunity to do cross species comparative studies (Peromyscus maniculatus and P. californicus, Eisenberg 1962, stoats and weasels, East and Lockie 1965, canidae, Kleiman 1967). Regardless of the reason for the research, one of three experimental methods is generally used.

1:4.2 Short Term Experiments

The first is short term arena observations where the animals are introduced either separately or together and usually given time to investigate the area. They are then allowed to interact for a period of time varying from five minutes to two hours. After which they are withdrawn. This method has been used to study Peromyscus (Sadlier 1965), gerbils(Swanson 1974), polecats (Poole 1966, 1967, 1972a, 1972b, 1973,1974a, 1974b), stoats (Erlinge 1977), and weasels (Buckingham 1979).

The results of this type of experiment includes detailed analysis of short term behavioural sequences such as courtship and copulation and fighting. In some cases rank order may be established, but some individuals may need a longer time to establish which is dominant (Bowen and Brooks 1978). Similarly the measures used to score dominance may also mask the real rank order from these short term experiments. Poole (1973) found that "the formation of rank order was not related to the amount of fighting which took place".

The individuals which were introduced into the arena first won more fights, hence it may have been related to prior residency as opposed to fighting prowess. Difficulties are also encountered when individuals that have had previous association are used (Poole 1973).

This technique has been the main method used to study agonistic behaviour in mustelids. Poole used it to study various aspects of polecat behaviour including aggressive play (1966), aggression(1967, 1972a, 1973, 1974a) and oestrous behaviour in relation to interactions between familiar and unfamiliar individuals(1974b). He showed that aggression and aggressive play are different with aggressive play lacking the behaviours causing intimidation of the opponent. Play, however, could turn into aggression if the level of attack became too intense (1966). Fights were extremely variable in "duration, intensity, and temporal patterning". Individual polecats varied in their degree of aggression (1972a). When looking into individual differences in fighting in more detail, he found that the order of introduction into the arena was related to fighting success as mentioned earlier. Similarily the animals who initiated the fight also had a better chance of winning (1973). In 1974a Poole described the details of fighting in polcats. The degree of aggression in polecats varied seasonally with it being more intense during the breeding season. Females showed less aggression than males and usually showed only ritual aggression to females that were strangers. When fights occurred in both sexes, there were no threats prior to attack. Similarly there was a lack of courtship behaviour prior to copulation (1967). Finally Poole considered sexual behaviour (1974b) and found that males approached females in the same manner regardless of the females' reproductive state. They varied their subsequent behaviour depending on the females receptivity, showing both sexual and aggressive behaviour. Unfamiliar females proved to be a stronger stimulus to males than did familiar females.

Erlinge (1977b) used short duration experiments for his work on the interactions between pairs of stoats in captivity . He was mainly concerned with relating how animals responded to each other in captivity and how this might relate to the social spacing of stoats in the wild. He suggested that defensive reactions were more common than offensive ones. However, this may have been due to his scoring techniques with certain behaviours which were scored for each individual (eg. chasing and fleeing) elevating the number of reactions in these action/reaction type behaviours (pers. com. S.Erlinge). He did show very clearly, though, that mutual avoidance was a major component of total numbers of behaviours and that the animals showed both spatial and temporal avoidance. These along with retreat from the resident by an intruder were effective in "dispersing individuals " in the areas and were "consistant with observations " on wild stoats (Erlinge 1977b). A third factor affecting the use of space was dominance. In males this was found to relate both to body weight and age. A similar correlation did not occur in females.

Finally Buckingham (1979) observed the interactions between single—sex pairs of weasels using short duration experiments. He used a round robin system. He found that dominance was established by display and some fighting. The subordinates showed appeasement behaviours which resulted in lowering the level of aggression that the dominant animals showed towards them. Females were more active, but the dominant females interacted less than the subordinate females. Dominance was not related to weight in the males , but possibly related to weight in the females.

1:4.3 Medium Duration Experiments

Type two experiments allow a more long term exposure of the animals to each other. Frequently they are introduced separately, often into separate parts of an area and not allowed immediate contact. They are left to explore the area and eventually are allowed access to the other animal(s). These experiments continue for several days or weeks. Lemmings (Bowan and Brooks 1978) , gerbils (Donegan 1978), Peromyscus sp. (Eisenberg 1962) and shrews (Crowcroft 1957) have all been studied in this manner. Besides the basic information gained in type one experiments , by using this method information about territorial behaviour and long term social associations is gained. If the dominance hierarchy changes with time and/or habituation this information is also acquired. Furthermore with these longer term experiments the several types of dominance which may occur can be considered. Either the achievement of dominance by prior access (ie. first one into the area Poole 1973) or dominance by superior strength or fighting ability not related to residency.

1:4.4 Long Term Experiments

The final method involves long term exposure of individuals where pairs or colonies are established, left to interact, and possibly reproduce. The information produced includes long term changes in behaviour such as changes in pair/colony relationships during breeding (weasels, Lockie 1966), ontogeny (weasels, Heidt 1970), maternal behaviour (cats, Schneirla, Rosenblatt , Tobach 1963), play behaviour(cats, pers. com. C. Lawrence), rank order and social organisation in relation to density (house mice, Crowcroft and Rowe 1963). This type of experiment has also been used to look at play and interactions between littermates of polecats (Bunnel 1979).

1:5.1 Reproduction

The sexual cycles of the Mustelidae have been studied by numerous authors using both live animals and carcassess. The mustelids can be divided into two distinct groups , those which have delayed implantation and those with immediate implantation (see Ewer 1973 for a review of these). In Great Britain the former include the stoat , mink, badger, and pine marten. The weasel, polecat, ferret, and otter are included in the latter.

The sexual cycle of the weasel was first studied in Britain by Hill (1939). She described the general condition and seasonal changes in the reproductive organs of males, mostly from carasses. Males come into breeding condition between February and March and remained in condition until the end of October. The testes then regress and are comparatively inactive until mid February. Young males born in April and May can be fully developed by four months and therefore may breed in their first year. Late born males (eg. September) stay small throughout the winter months, but come into breeding condition synchronously with the other males in February. Deansely (1944) studied the reproductive cycle of female weasels using dead specimens obtained throughout the year. She stated that weasels can be impregnated from March through to August. The early breeders (eg. March) can breed again in July/August and produce a second litter in August/September. Young born in April can become pregnant in August, but rarely do. All of the females examined were anoestrous from the end of August until the end of February. Deansely also suggested that weasels are induced ovulators.

Behaviour during oestrous and copulation are described in the ethogram in Appendix A. Gestation lasts 34-37 days (East and Lockie 1965 and this study) counting from the first mating. Table A:14 in Appendix A lists the copulation to parturition data. The number of young varies from three to ten with the mean of this study being 5.3 from ten litters. East and Lockie (1964,1965) presented a similar mean of 5.0 for four litters.

1:6 The Aims of this Study

In section 1:2.1 I discussed what is known about the social organisation and spatial distribution of weasels. This included information on home range size and distribution and density in relation to habitat and food. However, all of this information describes the results of the spacing of weasels. It does not provide any information on how interactions might cause or maintain this spacing. Part I of this study was designed to answer two basic questions. 1) How do weasels interact when allowed access to each other? 2) How do these interactions eventually affect their spatial distribution?

I chose the medium duration experimental type as described in Section 1:4.3 First of all it allowed the animals access to each other for a long enough period of time to establish a stable relationship between them. Secondly the experiments were designed so that each animal had a home area with which it was familiar. It was only allowed access to the other animal's area after a three day acclimatisation period in its own area. By being familiar with the area, the animals should be more confident and less stressed during the interaction period. This would produce more realistic interaction. Both Erlinge (1974) and Buckingham (1979) looked at interactions between weasels, but neither did a long term exposure experiment (ie. days) with a long acclimatisation period. By using this longer term method, I hoped to replicate interactions that might occur between neighboring animals under natural conditions. As my experiments were run throughout the whole twelve month period, I also considered seasonal changes on relationships.

The second series of experiments dealt with the interactions between male and female weasels. Information on how male and female weasels are dispersed in the field is scarce, but suggests that ranges between sexes can overlap from completely to not at all. This is discussed in Section 1:5.1. The effects of the sexual cycle on this spacing has been mentioned, but not dealt with in detail. Lockie (1966) suggested female(s) remained within a males range all year implying that this male would be available to mate with her/them during the breeding season. He suggested that the male tolerated the female(s) on their ranges. Lockie (1966) produced information on the male-female relationship from captive research. He suggested that there is a change in dominance between males and female weasels during pregnancy, with the female becoming dominant. This continues through lactation until the young begin to disperse. The male then resumes his former dominant position. In these experiments I looked at this relationship more closely. First of all by repeating the experiments to confirm Lockie's results, and then by more careful observations of the behaviours that occurred. The conditions of the experiments were similar except that the area used for the observations was larger. The interactions between the males and the offspring were also observed and described. Finally a behavioural ethogram was developed including postures, activities, vocalizations, and maternal behaviour.

1:6.1 Summary

In this introduction the literature on territoriality, home range, and dominance have been reviewed. Noble's (1939) definition of territory of "any defended area" was chosen as the most useful definition, but that the word fixed should be included in it to exclude examples of the defence of personal space. Dominance was discussed in relation to how it could affect territory size in wild populations and also how it could be applied to solitary species studied in the laboratory. I suggested that when considering dominance and submission in these small species , temporal use of the space was equally important to agonistic encounters and spatial distribution. The different methods used in captive studies and the type of results gained from each study were also discussed. Short term experiments are useful for some behavioural sequences, and possibly for rank order information. The latter may be more dependent on experimental technique, such as prior introduction, and so may lead to false conclusions if observed for only a short period. Medium duration experiments are useful for information on social associations. Finally long term experiments enable information to be gained on changes over time of maternal, breeding, and social behaviour including ontogeny studies. The medium and long term experiments were chosen for these studies. Finally the sexual cycle of the weasel was reviewed and the relationship between the sexes was described.

Chapter 2: Animals and Methods

2:1 Animals

A total of sixteen male and eleven female weasels were used in the experiments over the three years (see Appendix B). Fifteen of the sixteen males were born in the wild and box trapped (Figure 2:1) between January 1976 and September 1977. The remaining male was captive born in June 1975 and hand reared. Although he was more tame than most of the wild caught individuals when in close proximity to humans, there was no apparent difference in his behaviour in the observation areas.

The females used in the experiments were all captive born from captive born mothers and wild caught fathers, since all attempts to capture wild females were unsuccessful. This may have influenced the results, although no obvious differences in behaviour were apparent in the captive born versus wild caught males. Buckingham (1979) also found that there were no apparent differences in behaviour between captive and wild bred individuals. As weasels show a seasonal reproductive cycle, the animals would have been at varying stages of this cycle throughout the three years of experimentation. The effects of this on the experiments are discussed in Section 3:3.9. However, it should be noted that both animals in each pair should have been at the same point in the reproductive cycle when the observations occurred.

Figure 2.1 Wooden box trap.

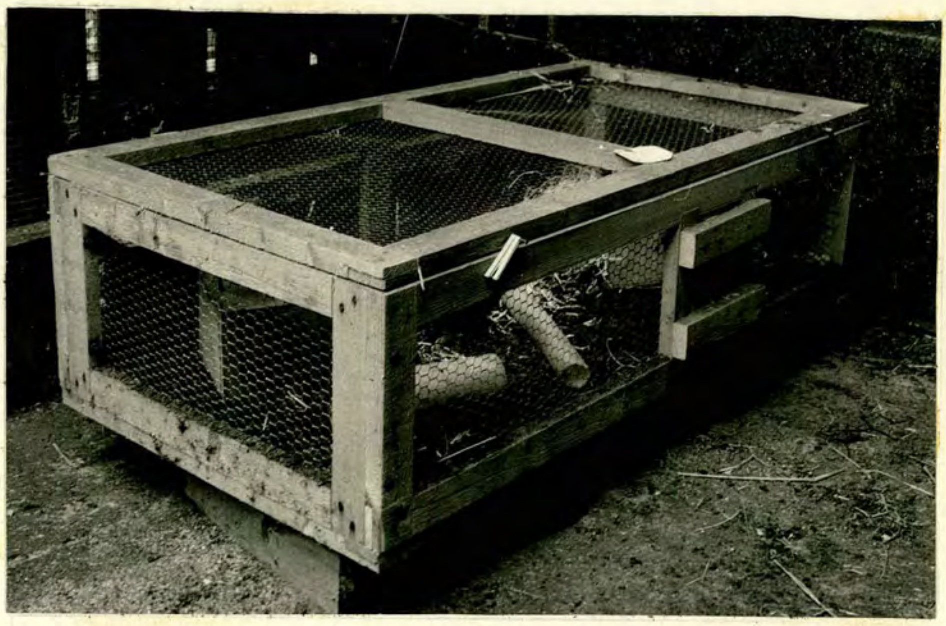

Figure 2.2 Cage used to house weasels.

2:2 Housing and Maintenance

The weasels were housed individually in 122 cm. x 61 cm. x 30.5 cm. wood frame with wire mesh cages (Figure 2.2). Each cage had two nesting boxes, several plastic or paper cyclinders for tunnels and a water bottle. Sawdust and/or peat were used as substrate with straw in the nest boxes and a free standing pile for bedding. The cages were kept in two locations inside the Department of Forestry and Natural Resources, University of Edinburgh, and outdoors in a covered aviary behind the Forestry department. Due to space limitations, both sexes were housed in each area.

The animals were fed daily on laboratory mice averaging about 35 grams each. These mice were either freshly killed or frozen and thawed. During the winter milk mixed with egg was given weekly in a bowl along with a freshly killed mouse which had been injected with cod liver oil . Fresh water was available ad libitum.

2:3 Arenas

Two separate arenas were used for the observations. The first of 28 m^2 was located in the basement of the Department of Forestry (Figures 2.3). Natural lighting provided the main source of illumination, augumented by time controlled overhead flourescent lights on a 14 hour light, 10 hour dark cycle throughout the observation period. The second arena of 12 m^2 was located in the

Figure 2.3 Left hand side of Forestry arena.

basement of the Department of Zoology nearby (Figures 2.4 and 2.5). It was lit by artificial lighting only, again on a 14-10 hour cycle.

Each of the two arenas was partitioned into halves with an adjoining door 19 cm. wide at the end of the arena closest to the observer. Both sides were provided with several nesting boxes filled with straw. There were also tunnels, rocks, trees, stone dykes, and water bottles. When in the observation areas, the animals were fed daily with one mouse per animal.

2.4 Observational Procedure

Although the methods varied slightly for the three different sets of experiments, the basic procedure was as follows. The individual variations per experiment will be listed under the individual sections.

2:4.1 Basic Procedure

On day four or five the door between the two areas was fixed open and observations commenced. The door remained open throughout the remainder of the period that the animals were in the arenas. The observations occurred between 0700 and 2200 hours over the next three days. Observations were not strictly at random, but an attempt was made to balance the number of observations made at the different times. The animals were observed for one period each day lasting from

Figure 2.4 Left hand side of Zoology arena from observation chair.

Figure 2.5 Left hand side of Zoology arena viewed from back of arena showing the doorway.

one and one-half to two and one-half hours as explained in the experimental variations below. Observations were not made between 2200 and 0700 as preliminary trials with observation occurring throughout the 24 hour period, showed that behaviour was evenly spaced throughout the 24 hour period. Other authors have given conflicting comments on activity, some reporting that weasels are arrhythmic (King 1971, Moors 1974), others that they show bursts of activity and are mainly nocturnal with a peak at dawn (Kavanau 1969, Price 1971, Kavanau _et_ _al_. 1973). Buckingham (1979) suggested that they are not absolutely arrhythmic as they have distinct patterns and cycles of activity throughout the day. The locations of these activity cycles within the 24 hour period varies seasonally for individuals as well as per individual. Hence I feel that randomly spaced observations were the most suitable way of observing the animals.

Observations were made while sitting looking into the arenas from above. A continual recording of behaviour was taken by speaking into a taperecorder (ITT Professional). Intrusions were timed with a stopwatch. A timer was incorporated into the tapes which bleepd every thirty seconds. The tapes were later transcribed verbatim with the thirty second ticks marked on the transcript.

2:4.2 Variations on the Basic Method

Male-male Interactions

Type 1: The adjoining door was opened on the fourth day that the animals were in the observation area. They were then observed for a minimum of four, 1 and 1/2 hour periods. Four days were found to be the most effective period for gathering data as the animals became inactive very quickly once the initial interacting period was over.

Type 2: The adjoining door was opened on the fourth day and the animals were observed for 3 hours on the first day and 1 and 1/2 hours per day on days two and three. The experiment was ended on day three.

Type 3: Adjoining door opened on day four with the animals being observed for 2 and 1/2 hour periods for three days.

Female-Female Interactions

As in type one experiments on the males lasting from four to seven days.

Male-Female Interactions

As in type one except that the experiment continued until the 85th or 95th day after parturition. The pairs that did not breed were used as controls and were observed from forty to fifty-five days.

At the end of the observation period the weasels were returned to Forestry and the areas were cleaned. The arena in Forestry was swept and washed with disinfectant. The arena in Zoology was only swept with any feces scraped up and the immediate area washed. The entire floor was not washed. Initially I planned to look at the deposition of feces in relation to the washed and unwashed areas. However, it was soon apparent that the weasels chose similar locations to defecate regardless of whether the areas were washed or unwashed. These areas were adjacent to their main resting places, in the corners of the arena, and along the perimeter squares. This is discussed in more detail in Section 3:3.10.

After the areas had been swept and/or washed, new sawdust was spread out over the area. The straw was replaced in the nesting boxes. The items in the arena were replaced in their original locations unless an animal was coming into the arena for the second time. For returning individuals the floor plan was altered, but the items remained the same.

Chapter 3: Female-female Interactions

3:1 Introduction

Information on the distribution of female weasels in the field in relation to other females and to males is very limited. This is mainly because female weasels are not only difficult to trap initially, but also have a lower rate of recapture. Hence there are few recorded home ranges for females. However, such information as we do have suggests that:

1) Females have smaller ranges than males , although size of range varies with habitat (Lockie 1966, Erlinge 1974, King 1975).

2) These ranges frequently overlap partially or completely with a male's range (Lockie 1966, Erlinge 1974, King 1975).

3) Female-female ranges may overlap slightly (King 1975, Erlinge 1974) or not at all (Lockie 1966, Erlinge 1974).

Erlinge's study (1977a) of the stoat showed that its social system is similar to that of the weasel. In 1977b he discussed observations on interactions between captive female stoats. He stated that the females established a rank order when tested using a round robin system. This order was not positively correlated with either age or body weight in contrast to his results for male stoats (see Section 4:1). From his work on male weasels, Erlinge (1977b) suggested that rank order was reflected in territory size. Neighboring weasels with widely differing degrees of agonistic behaviour showed a larger degree of difference in territory size.

Buckingham (1979) observed the interactions between females in captivity. He found that the dominant females were more aggressive, active, and possibly heavier than the subordinate females. While the subordinate animals had a higher number of interactions and behavioural encounters, including both aggressive and defensive behaviours, males had a much lower overall activity. He suggested that the higher amount of activity by the females may be explained by the territorial system described by Lockie (1966). As females did not come into contact with other females, they would not have enough encounters to develop ritualised postures in place of interactions. However, both Erlinge (1974) and King (1975) showed that female ranges do overlap. Hence females may interact more frequently with other females than suggested by either Lockie (1966) or Buckingham (1979). Hence in this chapter I shall attempt to produce more information on the nature of interactions between female weasels in order to discover how female weasels interact. I shall also consider how their interactions affected the use of the available space.

3:2 Animals and Methods

The animals were released into an arena, one on either side of a partition that divided the area into halves. They were allowed three days to adjust to the area and then the connecting door was fixed open for the remainder of the observation periods. The animals were observed one and one half hours per day over a period of four or more days. Throughout the observation periods, a continuous recording was made of the activity that occurred. This was then transcribed verbatim. Hence although most of the analysis involved the interactions that occurred, there is a recording of all activity.

3:3 Results

3:3.1 Description of the Behaviours Used in the Analysis of the Data

Eight main behaviours occurred frequently enough to classify. These are described in detail in the ethogram (Appendix A), but are briefly listed below. (The abbreviations used to designate the behaviours are shown in brackets.)

1) Attack (Attk) Physical aggression towards an opponent with bodily contact and biting.

2) Chase (Chs) One animal chased the other with the animal being pursued moving rapidly, closely followed by the pursuer.

3) Follow (Fllw) One animal followed the other at a greater distance than normally occurred in a chase. Both animals moved at a normal gait.

4) Near Approach (N App) One animal approached the other to within 10 cm. or less.

5) Far Approach (F App) One animal approached the other to no closer than 10 cm. but within 1/2 metre.

6) Squeal (Sql) Squeals that occurred in isolation or as a response to an attack, chase, follow, or approach.

7) Hisses (Hss) Hisses that occurred in isolation or as a response to an attack, chase, follow, or approach.

8) Intrusion (Int) One animal crossing through the doorway into the other side of the partitioned area that was normally occupied by the other animal.

Buckingham (1979) listed similar behaviours in his agonistic interactions along with several behaviours that are frequently seen in other animals in dominant/subordinate interactions, eg. cower, present, and anal sniff. I did not see any of these in my single-sex pair interactions. I would suggest that the difference is a reflection of observational circumstances. In my experiments the animals had large areas in which to interact. Similarly the animals had a number of secure hiding places where they could prevent the other animal from entering. Buckingham's experiments were done in smaller enclosures (1/10 and 1/21 the size of mine), and the animals did not have places of retreat. I would suggest that these postures were the result of the confined conditions, and are not likely to occur in animals which could move about more freely.

3:3.2 Scoring

The behaviours scored were often part of a continuous series of activities where one behaviour led into another. The following sequence is a typical example of such a series of activities.

12.05.5: Weasel A in Area 1 in Nest box 1, Weasel B approached A to within 15 cm (F App), withdrew to Tube 2 (60 cm. away), immediately approached again to within 5 cm (N App), withdrew to side of Nest box. B approached again, went into Nest box 1, attacked A. A came running out being chased by B, A ran into Tube 1. B went to other side of partition (Area 2) (Animal other side).

This sequence could be scored several ways. Taken as individual components the following behaviours occurred.

A (in House 1 at start of activity)	B (moving around in Area 1)
	F App
	N App
	Attk
Flee	Chs
	Animal to other side (AOS)

In my scoring this would be considered as one behavioural sequence. B would be scored for the behaviours that occurred at the end of the series or were the result of part of the encounter (eg. the attack and the chase with a note of B leaving and going to the other side of the arena). The approaches were not scored as they merely lead up to the attack. However, the chase occurred as a result of the attack and was scored, as chase does not always follow an attack. It actually occurs very rarely. Similarly both attack and follow are more agonistic behaviours than the approach and rarely occurred. Hence I always scored for these behaviours. Approach on the other hand was very common. Frequently a series of between 3 and 10 mixed approaches (far approach and near approach) would occur. As the complete series of behaviours was short (usually less than 30 seconds) and was continuous, this was considered as one approach series and scored only once. The series was scored for the final type of approach only and for whether the animal remained on the same side of the arena (ARS) or went to the other side of the arena (AOS) following the encounter.

Secondly I did not score doubly for action-reaction type responses. For instance, if one animal ran at another who then fled with the first continuing to follow, this was one chase-flee action. It could be scored two ways: either as one chase for the first individual and one flee for the second, or as a chase reaction with the individual doing the chase receiving a score of one, the second individual receiving no score. The fleeing behaviour by the second animal was a direct reaction to being chased. Therefore it did not actually initiate an action, but merely responded to the other animal's behaviour. In the above sequence, animal A would receive no score for the encounter. Its behaviour was purely in response to that of B. By scoring these action-reaction type behaviours for each animal the number of behaviours can be elevated and lead to a misinterpretation of events. It should also be noted that the frequency of approach is actually lowered by my scoring methods. I used this method because the animals being approached were frequently asleep. Hence the animal approaching could do so numerous times without encountering a response. Thus I decided that the actual event of the approach was the critical factor and not the number of approaches if they followed in close succession (eg. within 5 sec.).

3:3.3 Correlation and Frequency of Behaviour

Spearman rank correlation coefficients were calculated for attack, chase, follow, near approach, far approach, squeal , and hiss. Chase was chosen as the basic agonistic behaviour and the other behaviours were compared with it. Other researchers have also used chase in other species as the agonistic behaviour with which to correlate other possible agonistic behaviours including (Allin and Banks 1968, lemmings; Payne and Swanson 1970 and Donegan 1978, gerbils). Two basic classifications of behaviours resulted from this correlation: agonistic and defensive. The results of these correlations are presented in Table 3:1. There was also a positive correlation between the frequency of behaviour and the duration of activity (rho = 0.865, p = 0.01, Spearman Rank Correlation, n=9).

The frequencies of these behaviours were then tabulated for each pair for the total period of observation. In Table 3:2 the Chi ^{2} values for agonistic behaviour within each pair are shown. In five of

Table 3:1 Spearman Rank Correlation Coefficients Between Chase and the Other Behaviours.

Agonistic Behaviours	Frequency	Correlation with Chase (rho)	p value
Attack	48	0.7846	.01
Chase	57	—	--
Follow	34	0.7441	.05
Near Approach	203	0.8017	.01
Far Approach	242	0.6471	.05
Defensive Behaviours			
Squeal	124	-0.3686	NS
Hiss	38	0.1282	NS
Unclassified			
Displacement	1	NS*	
Prey Robbery	2	NS	

*NS=Not Significant.

Table 3:2 Chi^{2} Values for Agonistic Behaviour within Pairs.

Pair*	ACFAA** for Animal one	ACFAA** for Animal two	p Value
Mg Er	39	18	.01
Mg Il	82	72	NS (.065)
Sk Il	15	96	.001
Ls Ss	30	16	.05
Il Fo	42	60	NS (.10)
Fo Ky	29	75	.001
Ss Ho	3	26	.001

*All pairs will be referred to by a four letter code. The first two letters refer to the first animal in the pair, the other two to the second individual.

**ACFAA is all of the agonistic behaviours added together including Attack, Chase, Follow, Near Approach, Far Approach.

the seven pairs there were significant (.05) differences between the amount of agonistic behaviour shown by each animal. The other two had p values of .065 and .10. The animals were then classified as more agonistic (MAA) or less agonistic (LAA) according to their scores. The animal showing the higher score was classified as the more agonistic animal of that pair. The lower scoring animals were then labelled the less agonistic animals. I avoided using the terms dominant and subordinate until I was convinced that the behaviour met the criteria defined by Deag (1977) (see Section 1:3). The weasels in these experiments did not show some of the more typical dominant/subordinate postures as discussed in Section 3:3.1. Hence dominance as is shown later, could only be assessed by area usage and some interaction behaviour . The final classification of each animal was not related to either weight (Sign test n=7, x=3, p=0.500) or age (Sign test n=6, x=2, p=0.344). It should be remembered that my interest was in the difference in agonistic behaviour within the pairs, not the overall rating of each animal with response to every other animal. This would have required a round robin system with every animal being tested against every other animal.

3:3.4 Use of the Area

As I have established that in the majority of cases one female was more agonistic than the other, how did this affect their use of the areas? The frequency of intrusions through the connecting doorway and into the other side of the arena normally occupied by the other weasel were considered. The amount and type of activity of the animal intruding into the other area was studied. In Table 3:3 the distribution of the numbers and types of intrusions for the more or less agonistic animals is presented. There were no significant differences between the total number of intrusions for the MAA and LAA. Similarly the duration of intrusions was not significant.

The intrusions were divided into three types. 1) Intrusions where one animal intruded into the other side of the arena when the resident was present and both were active similutaneously. 2) Intrusions where one animal intruded into the other side of the arena when the resident was present, but only one animal of the pair was active. 3) Intrusions where each animal entered the other's area at the same time, so that they were on opposite sides of the arena.

The frequency of each of these types of intrusions was tested for the pairs using a Sign test. There were no significant differences between the MAA and the LAA in these intrusion types.

The MAA and LAA were also tested as groups for trends in behaviour in relation to intrusions. Both groups had a significantly higher number of active intrusions (intruder spent greater than 50% of her time moving about) than passive intrusions (intruder spent greater than 50% of her time in a house). The active intrusions were then broken down into two categories. First of all when both animals were active and on the same side of the arena. Secondly when only one

Table 3:3 The Distribution and Type of Intrusions for the MAA and LAA (Sign test, n=7).

	No. of MAA with Higher Score	No. of LAA with Higher Score	Equal Pairs	p=	Sig.
Number of Intrusions	3	3	1	0.656	NS
Duration of Intrusions	4	3	0	0.500	NS
Type of Intrusions					
Both Active	3	3	1	0.656	NS
One Active	5	2	0	0.227	NS
Animal Other Side	2	4	1	0.334	NS

animal was active or when they were on opposite sides of the arena. The MAA had significantly more one active or animal other side (x=0, p=.008, n=7 Sign test). The LAA had similar results only the difference was only nearly significant at x=1, p=.062, n=7 Sign test). Finally I considered whether the resident tended to remain on the same side of the arena when the other individuals entered, or whether she left and went to the other area. The MAA remained on the same side (x=0, p=.016,n=6 Sign test), while the LAA left or stayed equally (x=3, p=.500, n=7 Sign test).

3:3.5 Location of Encounters

The location of encounters was also considered in relation to whether the animal was on its home side or the other animal's side of the arena. The frequency of encounters in each area was also considered. The the animals were categorised as either having more encounters on their home side or more on the opposite side. Seven of the seven MAA had the higher number of encounters on the opponents side of the arena (Chi^{2}=7, p=.01). Five of the seven LAA had a higher number on their home side. This difference was not significant, however (Chi ^{2}=1.29, p=.30).

3:3.6 The Change in Behaviour Over the Four Observation Periods

Figure 3:1 shows examples of the frequencies of ACFAA behaviours occurring per pair per day over the four day period from four of the

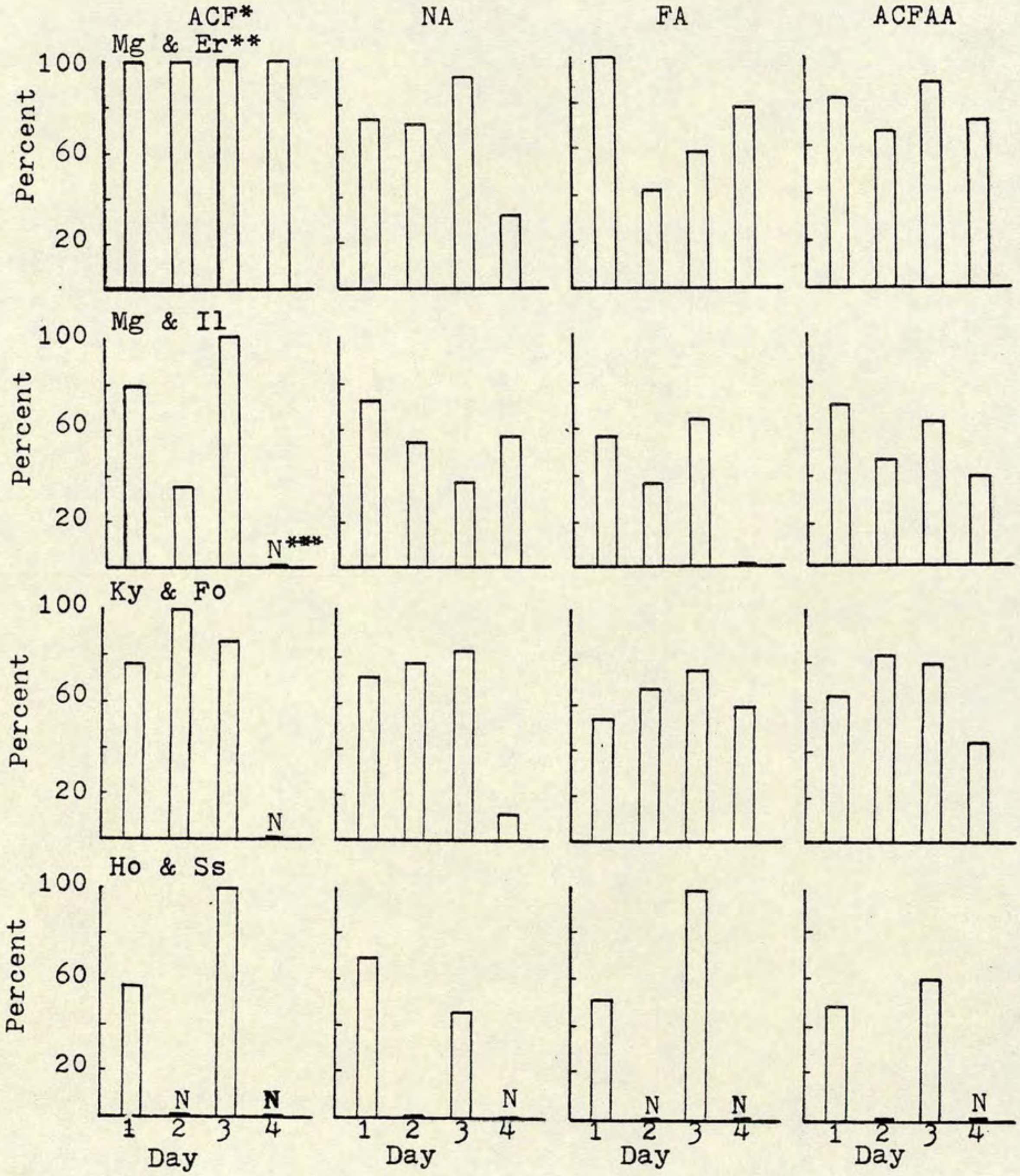

Figure 3:1 The frequency of ACF*, NA, FA, and ACFAA behaviour shown by the MAA as a percentage of total behaviour shown by the MAA plus LAA.

*ACF (Attack, Chase, and Follow), NA (Near Approach), FA (Far Approach), and ACFAA (Attack, Chase, Follow, Near Approach, and Far Approach).

*** * Name of Pair** ***N=Nil No ACFAA behaviour by either

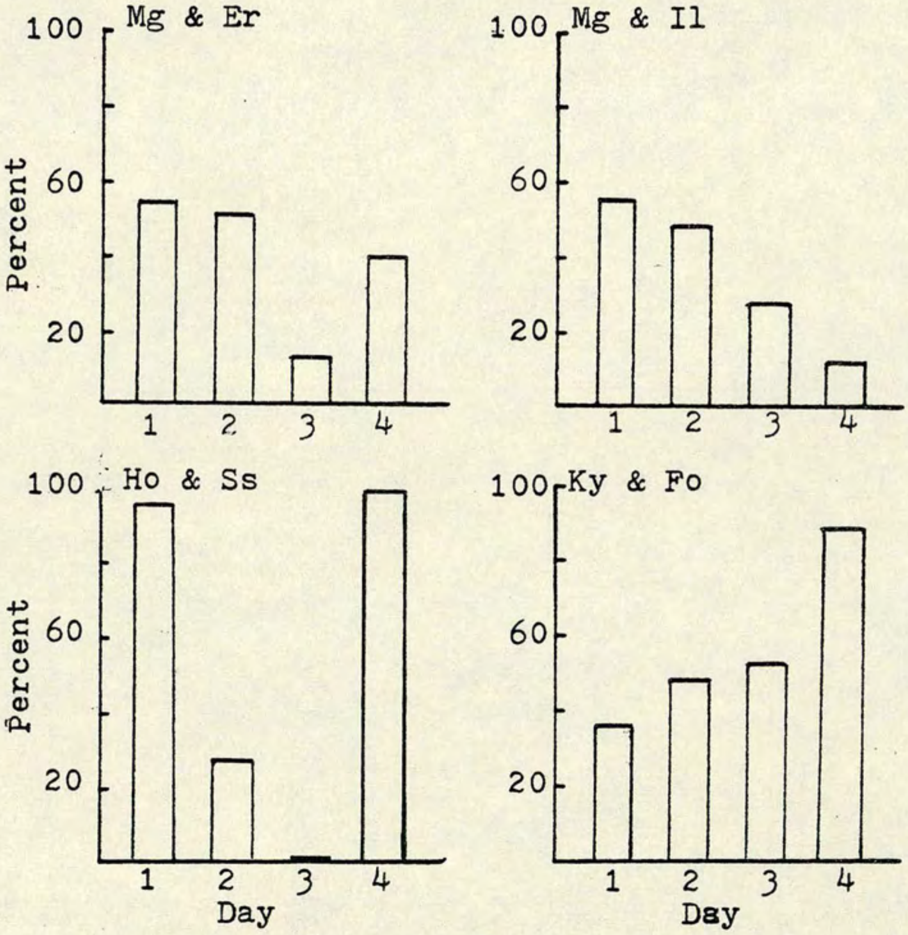

Figure 3:2 The duration of activity of the MAA as a percentage of total activity by the MAA plus LAA.

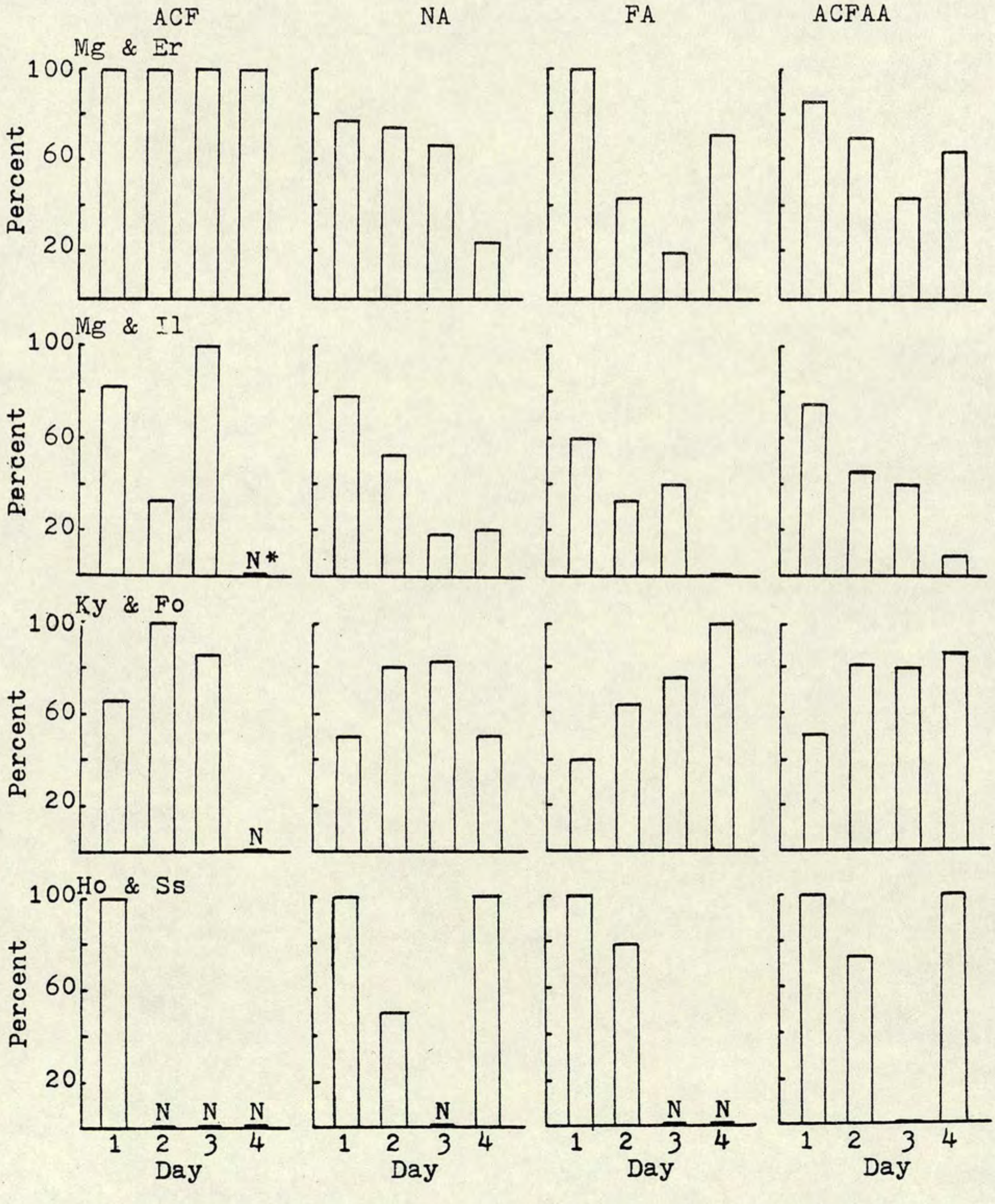

Figure 3:3 The frequency of ACF, NA, FA, and ACFAA behaviour divided by the duration of activity shown by the MAA as a percentage of total behaviour by the MAA and the LAA.

*N=Nil No ACFAA behaviour by either.

seven pairs. The frequency is expressed as a percentage of the frequency of agonistic behaviour by the MAA divided by the frequency of agonistic behaviour of the MAA and the LAA. The agonistic behaviour was divided into four categories: 1) Attack, chase, and follow (ACF) 2) Near approach (NA) 3) Far approach (FA) 4) Attack, chase, follow, near approach, and far approach (ACFAA).

$$\frac{\text{Freq. of Agonistic Behaviour of the MAA}}{\text{Freq. of Agon. Behav. MAA + Freq. of Agon. Behav. LAA}}$$

In Figure 3:2 the duration of activity by the MAA as a percentage of duration of activity of the MAA and the LAA is shown.

$$\frac{\text{Dur. of Act. MAA}}{\text{Dur. Act. MAA + Dur. Act. LAA}}$$

Finally Figure 3:3 is a composite of the two previous Figures. It shows the frequency of ACFAA behaviour of the MAA divided by the duration of activity of the MAA on that day which was then divided by the total MAA and LAA score.

$$\frac{\dfrac{\text{Freq. of Agon. Behav. MAA}}{\text{Dur. of Act. MAA}}}{\dfrac{\text{Freq. of Agon. Behav. MAA}}{\text{Dur. Act. MAA}} + \dfrac{\text{Freq. of Agon. Behav. LAA}}{\text{Dur. Act. LAA}}}$$

This produces a score of agonistic behaviour in relation to the activity of the animal. Hence, if the animal was only active for two minutes and did one ACFAA behaviour, it would have a score of .500 divided by the total of the MAA plus the LAA (.500/MAA +LAA). If it was active for ten minutes and did one ACFAA behaviour, its score would only be .100/MAA + LAA.

As mentioned earlier, each group was observed for four periods, one per day for four days. The frequency of agonistic behaviour over the four day period was tested for the MAA and the LAA using a Friedman two way analysis of variance. Attack, chase, and follow were totalled and tested as one behaviour (ACF). Near approach (NA) and far approach (FA) were tested singly. All five agonistic behaviours were then grouped and tested as a total (ACFAA) score. These results can be seen in Table 3:4. The MAA animal showed a significant change in both ACF and NA behaviour over the four days . The changes in FA and total behaviour were not significantly different for the MAA. None of the frequencies of behaviour changed significantly over the four day period for the LAA. The direction of behavioural change was then checked using a Sign test for Day 1 and Day 4 (see Table 3:5). For the MAA the amount of ACF and NA behaviour decreased significantly ($p=0.008$). The total number of ACFAA behaviour also decreased with the difference being nearly significant ($p=.062$). There was no change in the number of far approaches. The LAA showed no significant differences between Day 1 and Day 4 for any of the agonisitic behaviours.

3:3.7 Duration of Time Active Over Four Day Period

The durations of time active over the four day period and the

Table 3:4 The Change in Agonistic Behaviour Over the Four Day Period (Friedman two way analysis of variance).

More Agonistic Animals (n=7)

Behaviour	Xr^2	p=
Attack, Chase, Follow	12.39	.01
Near Approach	11.23	.02
Far Approach	1.07	NS
All	4.76	NS

Less Agonistic Animals (n=7)

Behaviour	Xr^2	p=
Attack, Chase, Follow	2.87	NS
Near Approach	2.57	NS
Far Approach	3.04	NS
All	5.01	NS

Table 3:5 The Change in ACFAA Behaviour Between Day 1 and Day 4 (Sign test).

More Agonistic Animals

Behaviour	p=	Direction of Change
Attack, Chase, Follow	.008	Decreased
Near Approach	.008	Decreased
Far Approach	.500	No Change
All	.062	No Change

Less Agonistic Animals

Behaviour	p=	Direction of Change
Attack, Chase, Follow	-------*	--
Near Approach	.656	No Change
Far Approach	.109	No Change
All	.109	No Change

* $n<5$, so the score could not be tested.

intrusion duration were also tested using the Friedman two way analysis of variance. The duration of time active decreased significantly for the MAA , but the intrusion duration did not change. The LAA did not show significant changes for either activity or intrusion duration. Day 1 and Day 4 were also tested using the Sign test, in order to discover whether there was a difference in these behaviours between the beginning and the end of the observation period. The results from the intrusion duration were nearly significant (p=0.062) for the MAA while the duration of activity did not alter significantly. Neither the change in duration of activity nor the intrusion duration changed significantly for the LAA.

3:3.8 The Location of Encounters Within Each Area

The location of the ACFAA behaviours in the arenas was considered. It was found that 68% of all encounters occurred while one of the animals was in a nest box or tunnel. However, the percentage of time spent in each area by the animals during the observation period must be considered in order to interpret this figure correctly. In Section 3:3.4 I discussed the two classifications 1) both active on one side or 2) both animals on one side of the arena, but only one active or one on each side of the partitioned arena. When both animals were on one side of the arena, 56% of the time was spent with one animal in a nest box. [redacted]

(The percentage of encounters occurring at the nest box and elsewhere are listed in Table 3:6). These figures are similar suggesting that the frequency of ACFAA activity occurring around the nest boxes was related to duration of activity at those locations. However, as the animals in the nest boxes were rarely chased from them as a result of these behaviours (only 2 out of 400 encounters at the nest box), I would suggest that the animals were able to defend themselves in a nest box. Simlarly when considering all of the other behaviours, more occurred at the nest box (400) than in the open arena (127). This difference was significant (p=.008, Chi ^{2}=34.9). This similarly suggests that the animals were more easily displaced when not in a nest box.

It should also be noted that very few encounters occurred at the doorway between the two areas. Frequency of time spent in the doorway squares is known, but duration is not. Hence it is impossible to assess how frequency of encounter relates to duration of time in those squares. The animals did not patrol these doorway areas, though, and did not prevent the other individuals from entering their section.

3:3.9 Effects of the Seasonal Reproductive Cycle on the Frequency of Interactions

Weasels are seasonal breeders as discussed in Section 1:5.1. The females are capable of breeding from March until August. They then become anoestrous until February. The seven pairs of females were tested in seven different months. During three of these the months,

Table 3:6 The Location of Encounters

Encounter Type	Nest Box	Tunnel	Doorway	Water	Grass	Centre Square	Perimeter Square
Attack	36	1	0	0	1	2	2
Chase	27	4	5	1	3	2	12
Follow	6	1	2	2	0	2	5
Near App	170	5	13	1	3	0	11
Far App	188	10	15	10	3	0	16
Squeal	66	17	9	3	0	3	18
Hiss	16	4	5	0	0	1	7
Total	509	42	49	17	10	10	71
Percent	68	06	07	02	01	01	10

October, November, and December, they should have been anoestrous. While during the other three, May, July, and August, they were capable of breeding. (September was deleted from the data as it is a transitional period between oestrous and anoestrous.) In order to test the effects on aggression of being in oestrous, the total aggression scores were compared for the two periods, oestrous versus anoestrous using Chi ^{2}. There were no significant differences in the frequency of agonistic behaviour between the oestrous and anoestrous animals (Chi $^2 = 0.292$).

3:3.10 The Distribution of Feces

The distribution of feces in the arena was recorded for all three sets of observations, but will not be discussed any detail. The weasels tended to defecate in latrines and these latrines were located around the perimeter of the arena. When defecating weasels usually stand with their back to an object such as a wall, nest box, rock or pot and defecate looking out over the area (see Appendix A). This presumably facilitates defence if the animal is approached while defecating. However, even though the animals were clearly depositing scent posts at the perimeter of the observation area, the area was too small to interpret this in any meaningful way. Furthermore the location of feces was probably related to areas of more intense activity, so even if the arenas were very large, interpretation would be complicated. Hence no conclusions were made about the use of feces as sign posts.

3:4 Discussion

These experiments were devised in order to discover how weasels spaced themselves in an open area of moderate size? How might such behaviour relate to their social system under natural conditions? In order to decide whether the animals were showing some form of territorial behaviour four questions must be answered:

1) What type of relationship was established between each pair of weasels?

2) Did the animals restrict their activities to one side of the arena more than the other?

3) Where did the encounters occur in the arena? For example: Did the animals prevent each other from entering into their half of the arena? Were animals chased out of their opponents half if they had entered when the resident was sleeping or otherwise occupied? Did the animals patrol the areas?

4) Did the frequency of behaviour change over the four day observation period?

3:4.1 The Relationship Between the Weasels

When allowed access to each other, the interactions that occurred were mostly agonistic. This enabled one individual of each pair to be termed the MAA, and the other the LAA. The two classes of animals used the arena space similarly. There were no significant differences in intrusion types. Both groups crossed over to the other side of the arena during the intrusion of the other animal. However, the LAA had an equal frequency of staying or leaving, while the MAA stayed significantly more than she left. This suggests that the MAA were less easily displaced by the intrusions of the LAA, than vice versa.

3:4.2 Use of the Area

The duration of time spent on one side of the arena or the other varied considerably between animals. The longest duration of the observation time spent on the home side was 357.87 minutes out of 360 minutes total. The shortest was 66.85 out of 360 minutes. However, the weasels were rarely active on the same side of the area at the same time. Only 25% of their time was spent with both animals on one side of the arena with both being active. This again suggests that the weasels were avoiding each other by spatial and temporal distribution of activity. Erlinge (1977b) found that avoidance was common in mixed and single sexed pairs of stoats observed in captivity. In free ranging animals the avoidance of neighbors is also common in territories or home range dispersion patterns. Erlinge reported it for otters (1968) and for stoats (1977a). King (1975) stated that it was important in weasel distribution. The avoidance of other individuals or groups has also been reported for several species of felids including cats (Leyhausen 1965), cheetahs (Eaton 1970), and mountain lions (Seidensticker *et al*. 1973). Schaller (1972) stated that individual lion prides wandered around areas normally occupied by others without being molested. This could be a form of avoidance by design or chance.

3:4.3 Defence Behaviour

It is clear that the weasels were avoiding each other both spatially and temporally, but were they showing territorial behaviour? In order to answer this question it is necessary to consider the location of encounters. Most encounters occurred while one animal was in a nest box. However, the percentage of the frequency of encounters occurring at the nest boxes was closely related to the percentage of time spent in the nest box compared to other locations. Hence this may have been defence of personal space. Similarly as nest boxes were also used as food stores, the animals may have been defending food not nest boxes or personal space. There were a few cases when one animal prevented another from entering a nest box that was vacant at that time, but normally used by that animal. Only these could be considered actual defence of nest box. However, these were too few to provide any definite answers. Hence defence appeared to relate to either housing, food or personal space. All defence was oriented around the immediate vicinity of the individual.

Although the number of encounters at the doorway was small compared to total encounters (7%) , it was the second most frequent type of encounter after nest boxes . It again is impossible to interpret without knowledge of the duration of time spent in the doorway squares. The animals did not noticeably defend the doorway areas, though, and did not prevent the other individuals from entering their half of the arena. When active the animals moved around the perimeter of the arena or between areas providing cover. This was probably due to space limitations rather than to territorial type patrolling behaviour.

Although the animals had different degrees of agonistic behaviour, each individual could have defended an area. The size of the area may have been related to status, but the shape of the observation area would aid an animal trying to defend its home ground. There were differences between the two classes with the LAA generally being more agonistic in their own areas, but showing some agonistic behaviour on both sides. The MAA on the other hand had higher agonistic behaviour on the opponents side. As there was no significant difference in the number of intrusion, the LAA was definitely initiating fewer agonistic encounters in the MAA home area. On the other hand the MAA was initiating more on the LAA side. This suggests that the behaviours of the LAA was limited by that of the MAA. Hence, the animals were clearly showing a dominance hierarchy (see Section 1:3), with the dominant individual limiting the behaviour of the subordinate.

3:4.4 Frequency of Encounters Over Time

Finally, did the frequency of encounters change with time? It is generally suggested that under natural conditions once an animal has established a territory, the amount of fighting that it is actually involved in is reduced and other methods are used for territorial defence. These include scent posts, vocalizations, and visual displays. Therefore if territorial behaviour occurred in these experiments, the frequency of fighting should have decreased with time. The results varied between pairs, but overall there was a decrease in ACFAA behaviour over the four day period. This might suggest that they had established territories and only needed periodic interactions to confirm them. However, when examined more closely, it was found that the duration of activity also decreased. Hence the decrease in frequency of behaviour may have been related to the decrease in duration of activity rather than to a general decrease in agonistic behaviour. It may also have been due to the increasing familarity of animals resulting in a weaker stimulus to fight. Poole (1973) noted differences in attack intensities of familar versus unfamilar individuals in polecats. Finally a hierarchy could have been established and only needed to be reinforced occasionally. Since there is so little data available on the daily activities of free ranging weasels, it is difficult to interpret this information fully.It may be the result of confinement or may represent territorial behaviour. On present knowledge I would suggest that the weasels in this case were not defending their areas in any meaningful sense. They were instead defending either their personal space or their resources (nest boxes and the food contained within them).

3:4.5 Effects of the Reproductive Cycle on Behaviour

The effects of the reproductive cycle on interactions between female weasels was also considered. The little information available on female weasels does not deal with the possible seasonal effects of breeding on the spacing in female weasels. Buckingham (1979) found that the seasonal cycle affected activity, but he did not discuss how this would affect spacing. Erlinge (1974) discussed the movements of males during the breeding season and Lockie (1966) mentioned the effects of breeding on the male-female relationship, but neither dealt with females alone. In these experiments that there was no significant difference in agonistic behaviour as shown by the number of encounters initiated by the anoestrous or anoestrous animals. Similarly if the months occurring during the transitional period from breeding to non-breeding condition (eg. September, October) are excluded, there is still no significant difference. Even when animals that could possibly be approaching breeding condition are contrasted against those who are definitely not in breeding condition, there is no apparent affect.

How might this information relate to free-living weasels? King (1975) showed two female ranges in her distribution map. One was a single female's range from August to October. The other included this female's range and that of an additional female whose home range overlapped with the first taken from November to March trapping results. If breeding state affects the spacing of weasels, it would be apparent at these two stages. One might expect that the anoestrous females would be more tolerant of each other than the breeding females , hence more overlap of home ranges may be evident. Female weasels towards the end of pregnancy and during lactation are more agonistic towards males than at other times of the year (see Section 5:4.2). Unfortunately, the relationship between pregnancy and non-pregnant females was not observed nor was that of two pregnant females considered. However, the pregnant weasels were also more aggressive towards humans (personal observation) than normally, so they may be more agonistic towards everything at that period. Hence, I might expect tolerance of all other individuals to be lowered during pregnancy and lactation and this would limit overlap within the same or opposite sex. Clearly there is not enough data on wild weasels to make any conclusions. If the captive weasels were acting similarly to wild females, the seasonality of breeding condition may not affect the degree of agonistic behaviour amongst females, but actual pregnancy and lactation may. In any case the females were showing a high degree of agonistic behaviour throughout the year even with the added effects of pregnancy.

3:5 Summary

Two major categories of behaviour occurred, agonistic and defensive. These were then used to classify the individuals of each pair as either more agonistic or less agonistic. Although basically the animals tended to avoid each other and hence be active alternatively, some differences in behaviour were evident in relation to the two classifications. After an encounter the MAA tended to remain on the side where the encounters occurred. The behaviour of the LAA varied in that they left as frequently as they remained. The MAA initiated more encounters on the side of the arena in which the other weasel usually stayed. While the LAA initated more encounters on their home side. The frequency of behaviour of the MAA decreased over the four day period, while that of the LAA did not. Similarly the duration of activity of the MAA decreased, although the number of intrusions did not. Neither behaviour decreased for the LAA. The location of encounters was also considered. The weasels did not defend their areas, but merely defended their personal space/food store/ resting place. Finally the seasonal condition of the females did not affect their behaviour.

Chapter 4: Male-male Interactions

4:1 Introduction

In this chapter I shall present and discuss the results of my experiments on the social interactions of male weasels in captivity. As in the female-female experiments, the purpose of these experiments was to study how male weasels interact and how this affects their spatial distribution.

There is quite detailed information available on the distribution of male weasels from field studies which suggests that:

1) The home ranges of male weasels may be contiguous but overlap is small or non-existant (Lockie 1966, Erlinge 1974, King 1975).

2) The range size varies with habitat (King 1975), food supply (Lockie 1966, Erlinge 1974), and season (Moors 1974, Erlinge 1974).

There are some ideas on how male weasels might establish a home range or territory. Lockie (1966) suggested that it may be opportunistic. If a resident died or was removed, any transients passing through the area would have the option of settling there. Hence, acquisition of a territory may be more by chance rather than the result of a direct competition. The area taken would be similar to that used by the previous resident due to the presence of neighboring animals. Lockie found that if no transients were available then the neighbors might eventually encroach on the area and thereby enlarge their present holdings. On the other hand King (1975) described the immediate assumption of a range by a neighboring male in response to the resident male's death. She suggested that his movements around the area prevented other neighbors and transients from trying to move into the area.

Erlinge (1974) considered another aspect of territoriality and asked how dominance and territory size are related. He assessed the relationship between pairs of males who had been captured on adjacent territories. The member of one pair showed very different amounts of agonistic behaviour and the individuals could be classified as either dominant or subordinate. In the field the dominant individual had a larger range presumably at the expense of the subordinate, because when the dominant animal was removed, the subordinate took over his area. The second pair was of equal dominance which was reflected in the size of territories that they maintained and the amount of overlap between the ranges.

In the my experiments I considered how weasels interacted when placed in an enclosure and what the results were of these interactions.

4:2 Animals and Methods

The basic method was as used for the female-female experiments. The animals were placed into the partitioned arena, one on either side of the partition and given four days to adjust to the areas. The doorway joining the two areas was then opened and the observations began. The animals were observed on three different regimes of observation:

1) 1 and 1/2 hours per day for four or more days

2) 3 hours on day one and 1 and 1/2 hours on days two and three with the experiment ending on day three.

3) 2 and 1/2 hours on days one, two, and three with the experiments finishing at that time.

For the analysis only the first 1 and 1/2 hours of data from the observation periods was used. This meant that some data had to be discarded from the longer observation periods, but eliminated the need to convert the data into standardised time periods. As the males were generally inactive, very little data other than sitting in the houses was actually discarded. However, some of the weasels were only observed for three days while others were observed for four. Hence the data had to be analysed separately as three or four day periods in some cases and analysed as means in others.

4:3 Results

4:3.1 The Description of Behaviour Used in the Analysis of Data

The behaviours used in the analysis of the male-male interactions were similar to those used in the female-female analysis. These included attack, chase, follow, approach, squeal, and hiss. Note that in the female-female experiments approach was subdivided into near and far approach. This was not done for the males.

4:3.2 The Classification of Pairs in Relation to Their Interaction Behaviour

The behaviours were classified as either agonistic or defensive using a Spearman rank correlation test. In the female-female experiments, all of the behaviours were compared with chase. This was not possible for the males, however, as chase occurred very infrequently. Only four out of the fourteen males performed a chase as opposed to seven of the ten females. Hence attack was chosen as the main agonistic behaviour for the comparison. Attack was compared with chase, approach, squeal and hiss. The results are shown in Table 4:1. None of the behaviours were significantly correlated with attack. However, chase and approach were positively correlated with attack while the correlations between squeal , hiss, and attack were negative. Hence chase and approach were classified as agonistic while squeal and hiss were labelled defensive. Thus the classification of behaviour is in accordance with that of the female-female experiments, although the relationship is not as strong.

As in the female experiments, the behaviours within pairs were

Table 4:1 Spearman Rank Correlation Test Between Behaviours

Behaviour	Frequency	Correlation with Chase	Significance
Agonistic			
Attack* with	24		
Chase	8	0.4376	NS
Approach	105	0.2772	NS
Defensive			
Attack* with			
Squeal	101	-0.0012	NS
Hiss	22	-0.1764	NS

*Attack was used for the correlation as there was not a sufficient number of chases to use in the comparison.

considered next. Chi^2 scores were calculated for each animal of each pair for both agonistic and defensive behaviour. The results are presented in Table 4:2. Only two of the fourteen pairs showed a significant difference in agonistic behaviour between the two individuals. However, nine of the fourteen showed a significant difference in defensive behaviour. Hence, males could be classified as either less or more defensive on that basis. The animal with the lower number of squeals and hisses was labelled the less defensive animal (LDA), while the one with more such vocalizations was designated the more defensive animal (MDA).

The remaining five of the fourteen pairs did not show a significant difference in defensive behaviour. When re-examining the results of the Chi^2 test for agonistic behaviour it was found that the members of these pairs also failed to show a significant difference in their agonistic behaviour scores. They did in fact have tied scores for agonistic encounter. Therefore all of the pairs could either be classified as containing more or less defensive males or with both males equal for agonistic behaviour. One pair had both a tied score for agonistic behaviour and a significant difference in its defensive behaviour. It was excluded from this part of the analysis.

The behaviour of these two groups of pairs was examined. The less defensive animals were compared with the more defensive animals. In the pairs with tied scores one member of the pair was randomly

Table 4:2 The Comparison of Agonistic and Defensive Behaviours within Pairs Chi^2.

Agonistic Behaviours

Pair	Score of Animal 1	Score of Animal 2	Chi2	Significance
IG PG*	29	0	29.0	.001
AR FS	22	0	22.0	.001
WO CL	5	8	0.69	NS
WO IG	4	4	0	NS
JM AN	4	2	0.67	NS
DL DD	4	4	0	NS
JM AL	0	6	2.0	NS
JY DL	12	6	2.0	NS
WO JY	1	6	3.57	NS
UN PG	4	4	0	NS
AN GO	1	1	0	NS
IG DD	2	6	2.0	NS
DL AN	3	0	3.0	NS
UN JM	0	0	0	NS

Defensive Behaviours

IG PG	2	26	20.57	.001
AR FS	0	4	4.0	.05
WO CL	1	12	9.31	.01
WO IG	1	1	0.33	NS
JM AN	4	0	4.0	.05
DL DD	13	0	13.0	.001
JM AL	3	0	3.0	NS
JY DL	0	24	24.0	.001
WO JY	4	0	4.0	.05
UN PG	3	2	0.20	NS
AN GO	0	3	3.0	NS
IG DD	13	1	10.29	.01
DL AN	5	0	5.0	.05
UN JM	0	0	0	NS

*All pairs will be referred to by a four letter code. The first two letters refer to the first animal in the pair, the other two to the second individual.

assigned as x, the other as y. The two members of the x,y pair were compared. A Sign test was used to test the pairs. It was hypothesized that there would be a difference in the behaviour of the less and more agonistic individuals while the equal pairs would not show a difference. The mean frequency per day was used in the analysis of intrusions and number of agonistic behaviours. Three intrusion types were classified as described in Section 3:3.4. The results are presented in Table 4:3. There was a significant or nearly significant difference between the less and more defensive animals in four of the five behaviours. These included the mean number of intrusions/day, mean duration of intrusions/ per day, the frequency of intrusions with both animals active, and the frequency of intrusions when only one animal was active. The behaviour of leaving and going to the other side during an opponent's intrusion could not be tested statistically, but the results are shown.

4:3.3 The Distribution of Activity

The distribution of activity was also considered for the LDA and the MDA alone. The results are shown in Table 4:4. Two basic categories were considered. The first was when both animals were active simultaneously on the same side of the arena. The second included instances when the animals were on opposite sides of the arena or when only one was active, but both were on the same side of the arena. The latter category was then divided into two: when only

Table 4:3 The Comparison of the Behaviours of the Less and More Defensive pairs (LD/MD, n=8) and of the Equal Pairs (XY, n=5) (Sign test).

Behaviour	LD/MD x=	LD/MD p=	LD/MD sig.	Animal with Higher Score	XY x=	XY p=	XY sig.
Mean # of Intrusions/Day	1	.062	NR sig.	LD	2	.500	NS
Mean Dur. of Intrusions/ Day	1	.035	sig.	LD	2	.500	NS
Type or Intrusion							
Both Active	0	.004	sig.	LD		* ---------	
One Active	1	.062	NR sig.	LD		* ---------	
A nimal Other Side		* ---------		MD		* ---------	
Where the Animals Go After an Encounter							
Remains on the Same Side of the Arena	1	.062	NR sig.	LD		* ---------	
Goes to the Other Side of the Arena	2	.334	NS	LD		* ---------	

* The test could not be applied in these cases as n was less than five.

Table 4:4 The Activity of Each Group of Animals in Relation to the Activity of the Other Animals (LD/MD, n=8, XY n=5) (Sign test).

Less Defensive Pairs	x=	p=	Significance	Most Frequent Activity
Both Active versus One Active or AOS	0	0.400	Sig.	One Active or AOS*
One Active versus AOS	0	0.008	Sig.	One Active
Where the Animal Goes After an Encounter (Same Side or Other Side)	0	0.008	Sig.	Same Side
More Defensive Animals				
Both Active versus One Active or AOS	0	0.016	Sig.	One Active or AOS
One Active versus AOS	2	0.500	NS	Equal
Where the Animal Goes After an Encounter (Same Side or Other Side)	1	0.109	NS	—
Equal Pairs				
Both Active versus One Active or AOS	1	0.062	NRS*	One Active or AOS
One Active versus AOS	1	0.016	Sig.	One Active
Where the Animal Goes After an Encounter (Same Side or Other Side)	0	0.031	Sig.	Same Side

* AOS= Animal Other Side
** NRS=Nearly Significant

one animal was active, but both are on the same side of the arena and when the animals were on opposite sides of the arena. All three classifications of animals showed a significant or nearly significant tendency to be active when alone as opposed to being active when the other animal was also active on the same side of the arena. Activity alone was then broken down into active alone with both on one side versus activity with the other animal on the other side. Both the less defensive and the equal (x, y) animals were significantly more active when both animals were on one side of the arena, but one was inactive. The more defensive animal, however, showed an equal tendency to be active alone with both animals on one side or when the animals were on opposite sides of the arena. The movements of the initiator of an encounter after the encounter were also considered. The animal would either remain on the same side of the arena or go to the other side. Both the LDA and the equal pairs stayed on the same side significantly more times. The MDA animals showed an equal tendency towards either.

4:3.4 Weight and Dominance

Only one of the pairs of male weasels was weighed before a trial. The animals, Ar and Fs, weighed 155g and 197g respectively. In the trial Ar showed significantly more agonistic behaviour. Hence in this case, dominance was inversely related to weight. Although the other pairs were not actually weighed, they were assessed by eye when the animals were put into the observation areas. Each animal was classified as either large, medium, or small. (Regular weighing commenced at a later date, but the results were not used to classify individuals due to the possible increase in size with age and captivity.) The assigned size categories of small, medium, and large, are listed in Table 4:5 along with the dominance classifications of the MAA or LAA. The animals are separated into two classes, those with a difference between agonistic/defensive scores, those with equal scores. The animals with a difference between agonistic scores are presented twice, once under agonistic and once under defensive socre. The relationships within pairs according to their weight classes were tested using a Sign test. Animals were given a positive score if:

1) the more agonistic animal was the larger of the two.

2) the less defensive animals was the larger of the two.

3) they were equal in rank and there was no difference between their sizes.

Clearly the categories are very rough, but I do not feel that they are unrealistic for weasels. The weight of a weasel can vary between 10 to 12 grams depending on whether it has just eaten or has an empty stomach (King 1980). Thus if one is dealing with small differences in weight, assigning dominance rank according to weight may be equally inaccurate. Furthermore the data presented Appendix B

Table 4:5 The Relationship Between the ACFAA Score of the Members of Each Pair and the Weight Classification of Each Individual.

Classified According to Agonistic Behaviour				Classified According to Defensive Behaviour			
MAA	LAA	MAA	LAA	MAA	LAA	MAA	LAA
Ig	Pg	L	M	Ig	Pg	L	M
Ar	Fs	M	L	Ar	Fs	M	L
Cl	Wo	M	L	Wo	Cl	L	M
Jm	An	M	M	An	Jm	M	M
Jy	Dl	L	M	Jy	Dl	L	M
Wo	Jy	L	L	Wo	Jy	L	L
Dd	Ig	L	L	Dd	Ig	L	L
Dl	An	M	M	An	Dl	L	L

Equal Agonistic Scores

X	Y	X	Y
Wo	Ig	L	L
Jm	Al	M	M
Un	Pg	S	M
An	Go	M	L
Un	Jm	S	M

Table 4:6 Location of Encounters between Weasels

Behaviour	Nest Box	Grass	Perimeter Square	Centre Square	Doorway
Attack	6	0	1	0	0
Chase	3	0	0	0	0
Approach	48	1	0	0	0
Approach OS	21	0	0	0	0
Squeal	26	0	1	2	0
Hiss*	14	0	0	0	1
Total	118	1	2	2	1
Percent	95	.008	.016	.016	.008

* This vocalization was very quiet so may not have always been recorded.

in in Figures B:1 and B:2 support my three weight classifications. I hypothesised that if dominance was related to weight, pairs of the same weight class should be of equal dominance ranks. Therefore I would expect the animals of the less and more defensive groups to be of different weight classes, and those of equal agonistic scores to be in the same class. In the agonistic groups only four of the eight were of different size categories. There was no apparent relationship between weight and agonistic behaviour for these four, although the number of animals was too small for statistical analysis. Of the defensive pairs, again three of the four were positive, one negative. This sample size was also too small for statistical analysis. Finally in the pairs of equal agonistic scores, two of the five were of equal weight ($n=5$, $x=2$, $p=0.500$).

Age must also be considered as a factor that may influence dominance. In these experiments the animals were between four months and 1 and 1/2 years as aged by tooth wear (Lockie 1966) when tested. As the animals were selected at random for the observations, by chance the greatest age difference within any pair was six months. Taking this into consideration age did not affect dominance in these experiments.

4:3.5 The Location of Encounters

The location of encounters was also considered. The results are shown in Table 4:6. Only seven of the fourteen pair results were used as the floor was not properly grid-marked until half way through the experiments. The encounters occurred in five basic area types.

1) Nest box squares-the squares in which nest boxes were located. There were two nest boxes in each area, thus four nest box squares in total.

2) Perimeter squares, those along the edge of each area, excluding nest box squares.

3) Centre squares- those in the centre of the arena.

4) Doorway squares- The two squares adjacent to the doorway, one on either side of the partition.

5) Grass squares- Those squares with a box of grass in them.

The encounters were divided up as follows: 95% occurred at the nest boxes or tunnels, 1.6% occurred in the perimeter squares, 1.6% at the centre squares, 0.8% in the grass or tree squares, and 0.8% at the doorway.

In order to analyse this data properly, it is necessary to consider the location of encounters in relation to the amount of time spent in those locations. As stated above, 95% of the encounters occurred at the nest box, while 87.5% of the time was spent in or by a nest box. These scores are not significantly different ($\text{Chi}^2 = 1.658$). This suggests that the encounters occurred at these places because the animals spent most of their time there.

4:3.6 Behaviour Over the Four Day Period

The frequency of male-male encounters did not decrease over the four day period. These results are shown in Table 4:7. The animals were first tested as one group then broken down into less defensive, more defensive, and equal. Only the less defensive showed a change in frequency that was nearly significant at p=.079 (Friedman one-way analysis of variance). When the animals observed for the four days were analysed alone, there was again no significant difference in behaviour.

4:4 Discussion

The purpose of these experiments was to discover how male weasels interact in captivity, and what the effects of these encounters were on the use of the available space. How do these results correspond to what is known about the social system of free-living male weasels? Did the animals show signs of territorial behaviour? Four questions must be answered in order to decide what type of social organisation was shown by the captive animals.

1) How did the individuals within a pair respond to each other?

2) Were the activities of the animals restricted more to one side of the area than the other?

3) Where did the encounters occur in the area?

4) Did the frequency of interactions change over the four day observation period?

Table 4:7 The Change in the Frequency of Behaviour Over the Observation Period (Friedman Two-way Anovariance, n=3).

Three Day Observation Period

Pair Group	Xr^2	p=	Significance
All Pairs	2.625	$.30 < p < .20$	NS
Less Defensive	5.25	.079	NR Sig.
More Defensive	.0625	$.967 < p < .794$	NS
Equal Pairs	0.35	$.967 < p < .794$	NS
Four Day Observation Period			
All Pairs	4.538	$.149 < p < .120$	NS
Less Defensive	2.5	$.528 < p < .361$	NS
More Defensive	0.90	$.944 < p < .528$	NS

4:4.1 The Relationship Between the Animals

The responses of the males to each other were either agonistic, defensive, or avoidance. Two basic types of relationships occurred, one where the animals had a different status with regards to defensive behaviour and one where they were of equal status as determined by agonistic behaviour. These results are in agreement with those found by Erlinge (1974).

4:4.2 The Use of the Area

How then does this affect the use of the area by the individuals? There was no difference in area use by the pairs of equal status. The less and more defensive animals did show a difference, however. The less defensive animals had a nearly significantly higher number of intrusions per day and significantly longer intrusions per day. This suggests that a less defensive animal was more free to use the area than the more defensive member of its pair. This is supported by the breakdown of intrusion types. The LDA had a significantly higher number of intrusions where both animals were active. There was no difference between the two when only one was active suggesting that the LDA tended to avoid being active simultaneously with the MDA. When considering the frequency of leaving and going to the other side of the area during an intrusion of the other animal, three of the four MDA had a higher score.

Although this was not significant, it appears that the MDAs are avoiding the LDAs by going to the other side during intrusions by the latter. Similarly the MDA may be free to investigate the LDA's area during his absence, if the behaviour of the MDA is limited by that of the LDA. In either case the animals were avoiding each other both spatially and temporally. Avoidance was also apparent in the analysis of intra-group behaviours. These results are in agreement with those of the female-female trials. In both cases the animals were either avoiding the more dominant individual or were more freely able to investigate the dominant individual's area when he/she was not present.

4:4.3 Factors Affecting Dominance

As discussed in Section 3:3.3, dominance can be dependent on several factors. In this study I considered two of these, age and weight. Neither was significantly related to dominance although there were complications in the interpretation of both measurements. Other authors have also suggested that age and size have no affect in dominance in weasels. Buckingham (1979) found that weight did not affect dominance in his captive weasels. Lockie (1966) stated that there was no difference in age or size between residents and transient weasels. This suggests that dominance as evinced by the establishment of a territory was not related to either age or weight. King (1975) suggested that the mean lifespan of weasels in Marley wood, Oxfordshire was ten to eleven months, suggesting that they were fairly short lived. If this is indeed the a case, I would not expect age to affect dominance as the animals would all be of a similar age class. Similarly as weight is age related to a certain point, it would be unlikely to affect dominance. In stoats, however, rank order or dominance was related to age and weight (Erlinge 1977). Unfortunately there is little information on longevity of either stoats or weasels in the wild other than kill trapping results. Stoats may be longer lived in the wild than weasels, hence their dominance may be age and weight dependent. In Section 3:4.2 I discussed the effects of avoidance in wild female weasels. There are several advantages to avoiding neighbors, but these are probably more important for the males with their larger degree of territorial overlap. Spatial and temporal avoidance enables the animals to use overlapping areas without contact, thus preventing encounters. It also prevents direct competition for resources, although competition is still present. Pounds (1979) stated that the home ranges of the weasels and stoats that he studied did not overlap within the same sex and species, but did overlap temporally and spatially between sexes and species.This might suggest that behaviour within sexes was preventing overlap as opposed to competition for resources.

4:4.4 The Change in Behaviour Over the Observation Period

The results of the change of behaviour over the four day period were similar to those of the females. The frequency of defensive behaviour of the less defensive males changed with the result being nearly significant in agreement with the MAA females who were of a comparable status. This again suggests that the males established a relationship and only needed periodic contact to confirm it. The lack of change in the MDA males may be related to a generally lower amount of activity. Similarly it could also mean that the animals habituated to each other, so were less motivated to initiate encounters with each other.

4:5 Summary

Interactions between male weasels were observed in order to assess their relationships and the influence of these on the use of the areas. The males were first of all classified according to the amount of agonistic behaviour that they showed. There was no relationship between weight or age and dominance. There were significant differences in the behaviour of the LDA and MDA animals while those pairs classified as equal did not show a behavioural difference. All groups tended to avoid each other. The animals did not defend their areas, although they did defend their personal spaces/nest boxes or food stores. The behaviour of the LDA encounters decreased over the four day period suggesting that the animals either habituated to each other or had established a relationship which needed to be renewed only occasionally.

Chapter 5: Male-female Interactions

5:1 Introduction

This chapter deals with a description of how male and female weasels interact during the various stages of the sexual cycle. It includes a discussion of how these results might affect the distribution of wild weasels.

The present information on male and female weasel distribution suggests that:

a) Female weasels inhabit home ranges that are generally smaller than those of the males. The mean weight of females is about 40% of that of the males, therefore, they require less area to meet their food requirements. Territory size is not directly proportional to weight, though, suggesting that other factors are involved (King 1975).

b) The degree of overlap between male and female ranges varies from complete (Lockie 1966) to none (Erlinge 1974, King 1975) and depends on territory shape (Moors 1974).

c) This overlap may vary with season and reproductive condition of the female (Lockie 1966, Erlinge 1974).

The means by which weasels maintain their distribution is not known. Although recent radio tracking studies (C. Pounds, University of Aberdeen, pers. commun.) have provided some information on this subject, how individuals actually interact is not yet clear. Part three of my research, therefore, considered how male and female weasels respond to each other and how this may affect their spatial and temporal distribution.

5:2 Animals and Methods

The procedure was similar to that used in the previous experiments. The animals were put into the enclosures, one on either side of the partition and left for three to four days. The door between the two areas was then opened and observations commenced. The pairs were observed for 1 and 1/2 hour/day for the first four days. They were then observed approximately three to four times per week until the experiments were terminated. A total of six male-female pairs were used in the experiments. Four pairs bred and were observed for up to 150 days. Two pairs did not breed, and served as controls.

5:3 Results

5:3.1 The Description of the Behaviours Used in the Analysis of the Data

Although the basic ACFAA behaviours described in Section (3:3.1) were shown by the male-female pairs , slight variations occurred. These and some additional behaviours are described below.

Approach Behaviour: In the single-sex pairs it could be described as investigative, basically testing the degree of agonistic response by the animal who was being approached. The approaches were generally face to face without contact (eg. no body sniffing occurring as in other species: cats, Leyhausen 1966, canids, Kleiman 1966, and polecats, Poole 1974). Although fights did occasionally occur, the approacher usually withdrew without contact.

In the mixed pairs the anoestrous females behaved as in single-sex encounters making short approaches to the males and responding agonistically towards them. The behaviour of the males was slightly different, however. When approaching the females, they would trill, a vocalization used by males during courtship. They would also try to sniff the females' perineal region and attempt to secure a neck-bite, the first step in copulation (see ethogram, Appendix A). Sniffing or neck-biting were never seen between single-sex pairs. When the females were not in oestrous, the males would eventually cease to approach them and retire to the nest boxes.

Throughout the period of non-oestrous, the males would periodically approach the females and test their readiness to mate. When the females were not in oestrous their responses were either to avoid the males by fleeing or to attack them then flee. Although the males would often try to follow the females, they soon lost track of them with the females' greater speed and abrupt changes in direction.

Oestrous females behaved very differently. They would often run up to the males trilling and rubbing against them. (Females only trill to males other than their young when in oestrous or during the early stages of pregnancy.) They would repeatedly approach them then flee. When in oestrous the females would remain comparatively still when approached by the males and submit to a neck-bite (see description of copulation in ethogram for further details).

Run-at: This behaviour was only seen by females to males. The females would approach the males with a running gait as opposed to the more common walking approach. Their mouths were open as if in preparation to bite the males. If contact was made the behaviour was labelled:

Face nipping: as above or with the approach in a walking gait. This behaviour was also described in polecats.

5:3.2 The Behaviour Over the First Four Days of Observation

The relationships between chase and attack, follow, near approach, far approach, and squeal were tested for four of the male-female pairs for the first four days of observation. As in the female-female pairs, chase was found to be correlated with attack and near approach (Table 5:1), but not with follow, far approach, or squeal. Similarly as in the female-female groups, squeal was negatively correlated with chase, but not significantly so. The data was then broken down into male and female categories (four of each group). The males had a significant correlation between follow and

Table 5:1 Correlation Coefficient with Chase and Other ACFAA Behaviours (n= 4 Pairs).

Chase with	Frequency	rho	p=	Significance Level
Attack	60	0.864	.01	Sig.
Follow	96	0.500	---	NS
Near Approach	397	0.733	.05	Sig.
Far Approach	218	0.024	---	NS
Squeal	13	-0.183	---	--
Males only (n=4)				
Attack	9	0.816	---	NS
Follow	40	1.000	.05	Sig.
Near Approach	88	0.775	---	NS
Far Approach	83	0.258	---	--
Squeal	7	0.272	---	NS
Females Only (n=4)				
Attack	49	0.816	---	NS
Follow	54	0.800	---	NS
Near Approach	302	0.775	---	NS
Far Approach	128	0.258	---	NS
Squeal	6	-0.949	---	NS

Table 5:2 The Frequency of Agonistic and Defensive Behaviour per Pair (n= 4 Pairs).

Pair	Agonistic Behaviour		Defensive Behaviour	
	Female	Male	Female	Male
Ho & Ar	21	34	0	0
Er & Dl	7	26	0	0
mg & JM	23	1	0	7
Ss & Jy	2	18	0	0
Fo & Ra	40	4	0	0

chase. None of the other behaviours were correlated. There was no correlation between any of the female ACFAA behaviours in the mixed-sex pairs and squeal are negatively correlated with chase. This is in complete contrast to the female-female experiments where attack, follow, near approach, and far approach were correlated with chase while squeal was not.

The frequency of encounters in relation to total duration of activity (out and moving around versus sitting in the house) was also compared for the first four days. Unfortunately it was not possible to test any of the results statistically, due to the small sample size (n=4). However, in three of the four cases the females tended to be out and active for longer periods than the males. However, although the males were out for a shorter duration, three out of four had more encounters per period active. In both cases the fourth group had the least difference between their scores.

The mean of the ACFAA scores were very similar for the mixed pairs for the four day period. The mean of the females ACFAA behaviour was 14.5, that of the males 12.5. However, the adjusted mean in relation to amount of behaviour per period active of the males was 0.311 compared to 0.165 for the females. Although one animal in each pair showed a higher number of ACFAA behaviours (Table 5:2), it did not appear to be related to sex.

In Figure 5:1 the frequency of ACFAA behaviour over the four

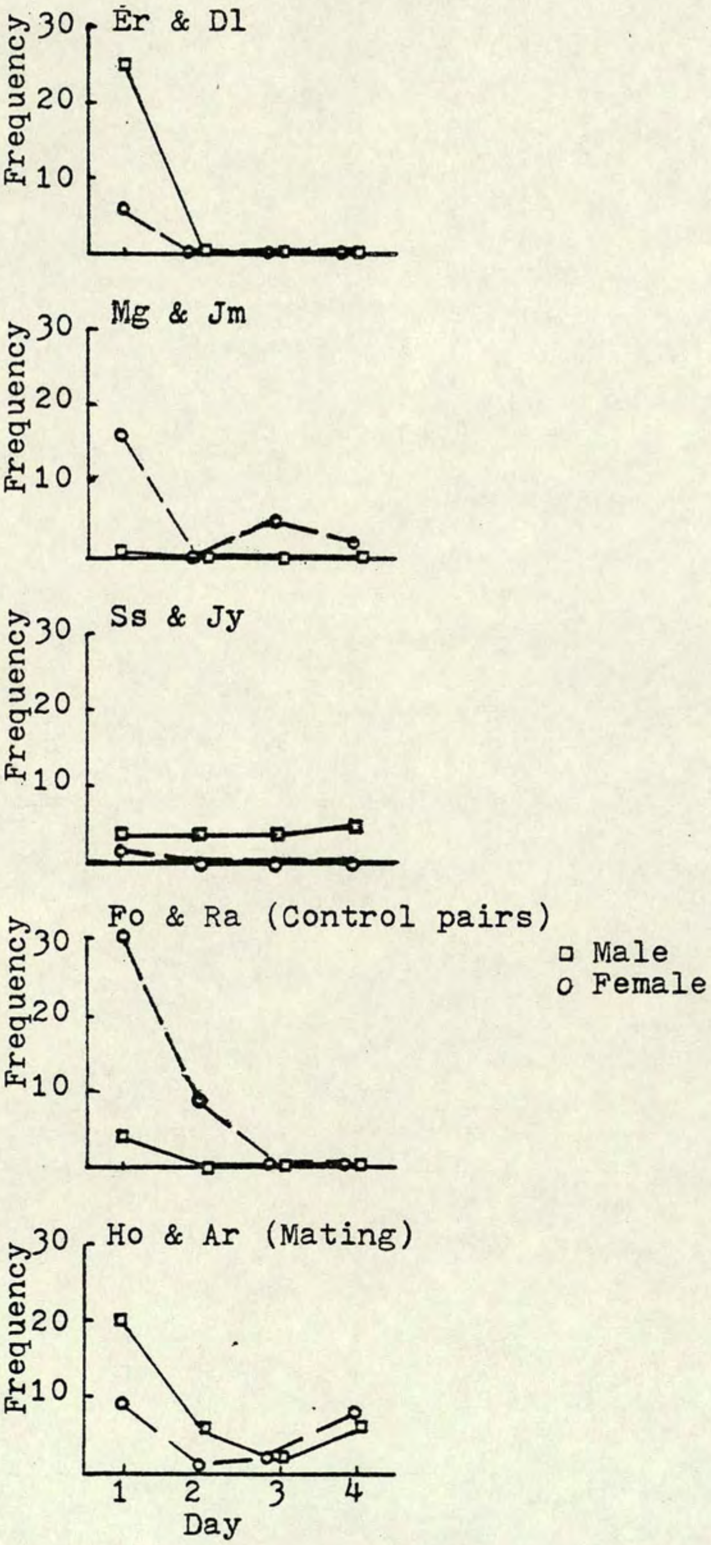

Figure 5:1 The frequency of ACFAA behaviour per day by the male and female pairs.

day period is shown. In four of the five pairs, the frequency of ACFAA behaviour either went to zero very quickly or one animal continued being active while the other remained inactive. One pair (Ho & Ar) showed a more similar pattern of behaviour. This was attributed to the fact that they were mating during the observation period. The other females were not in oestrous during the four days.

5:3.3 The Behaviour During the Breeding Cycle

In Figures 5:2, 5:3, 5:4, the ACFAA behaviour of the breeding pairs is shown for the experimental period which varied from 100 to 150 days. The durations are divided into ten day periods for comparison. Mating occurred between days -36 and -34.

Figure 5:2 presents the mean number of ACFAA behaviours per 10 day period over the 150 days. Figure 5:3 presents the mean duration of activity per 10 day period. While Figure 5:4 presents the mean frequency of behaviour divided by the mean duration of activity per 10 day period (see Section 3:3.6). The frequency of behaviours per minute of activity was similar for the females before and after parturition (0.338/min. before parturition compared with 0.306/min. after parturition. The frequency of agonistic behaviour of the males did change, though, from 0.259/min. to 0.041/min.

Note that Er & Dl were not observed for the full 150 days because the male was continually harassed by the female. He was found with a bad cut on his right hind leg and highly excited (eg.

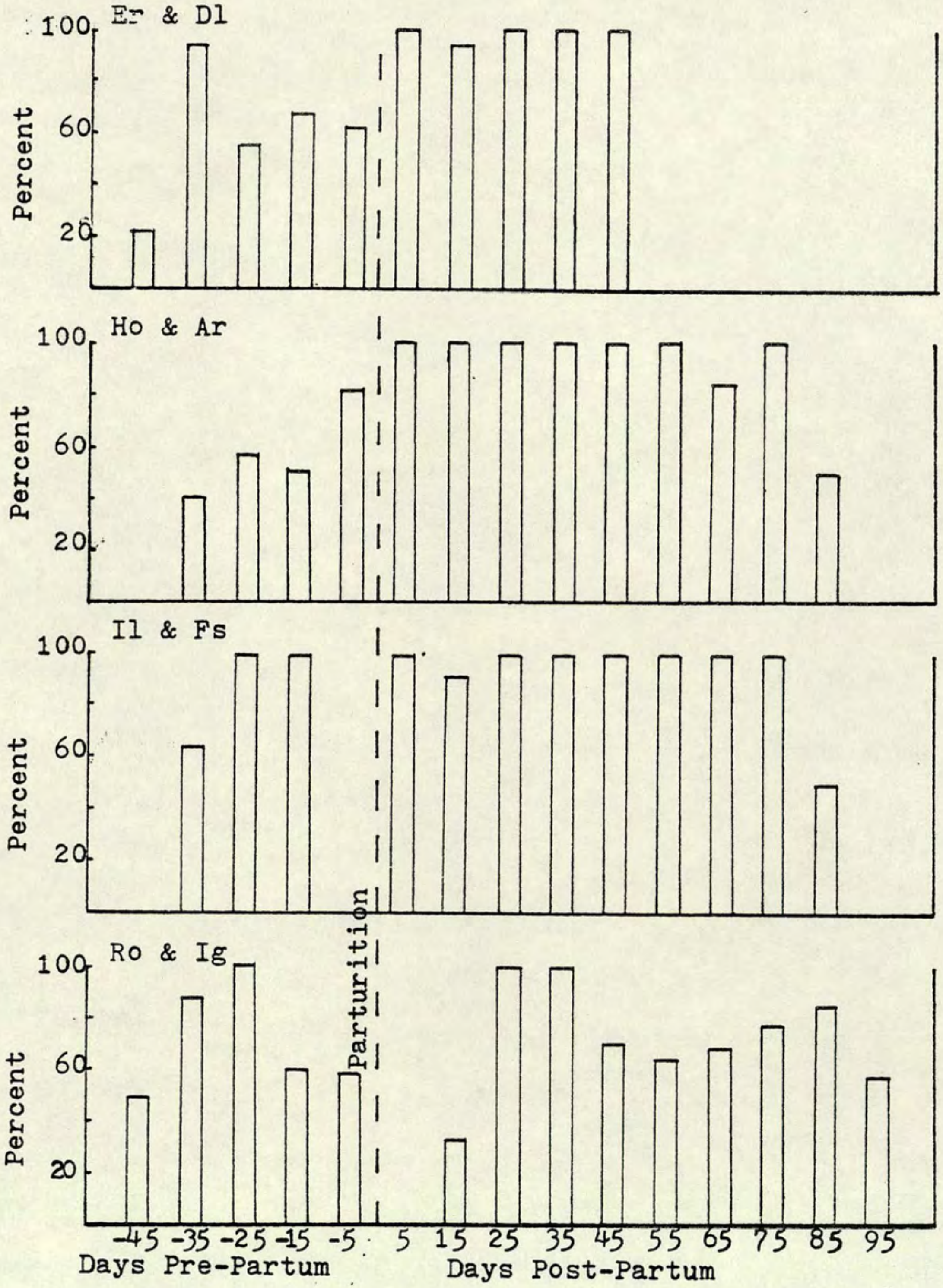

Figure 5:2 The frequency of ACFAA behaviour shown by the female as a percentage of total behaviour shown by the female plus male.

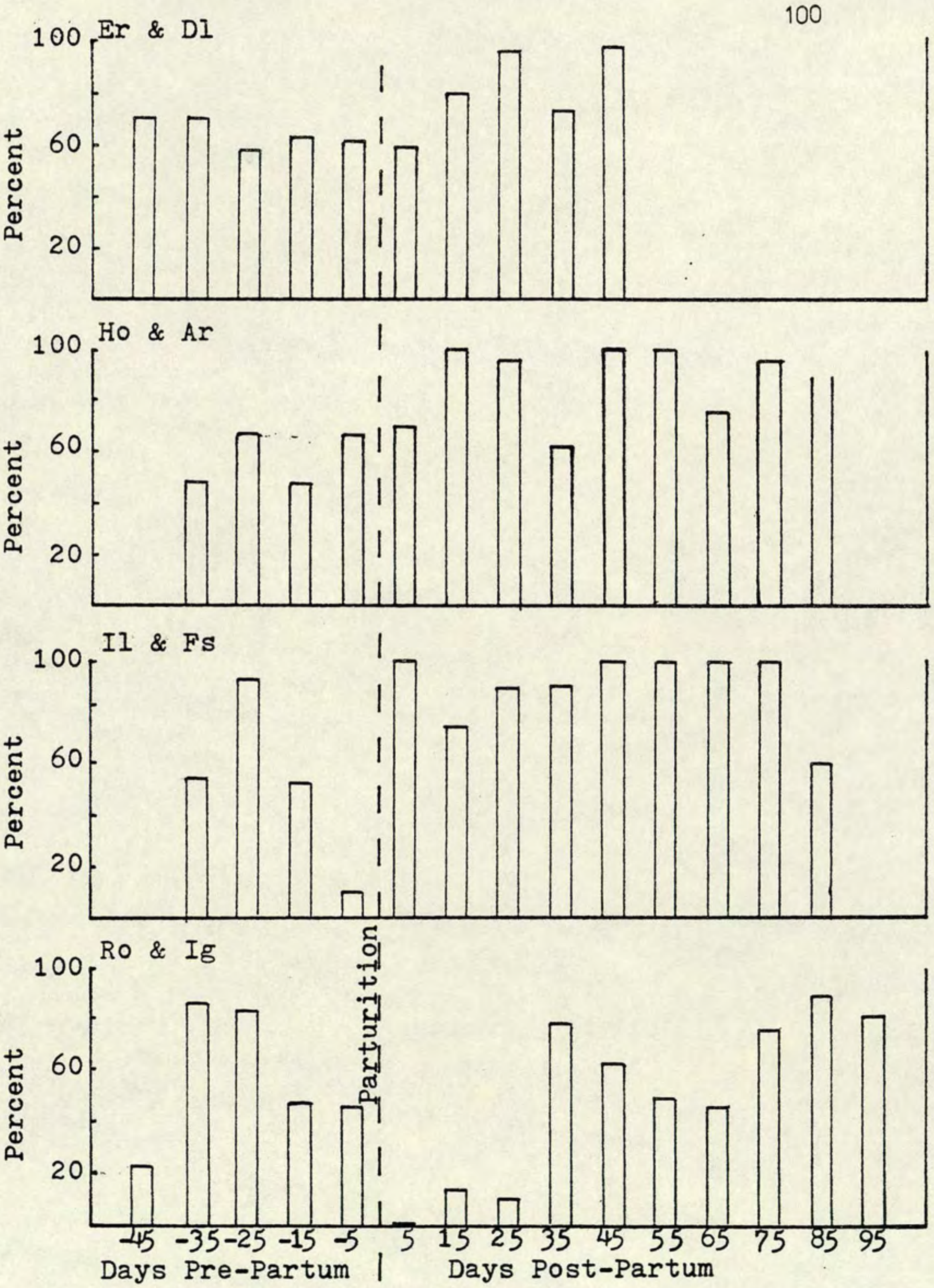

Figure 5:3 The duration of activity shown by the female as a percentage of total behaviour shown by the female plus male.

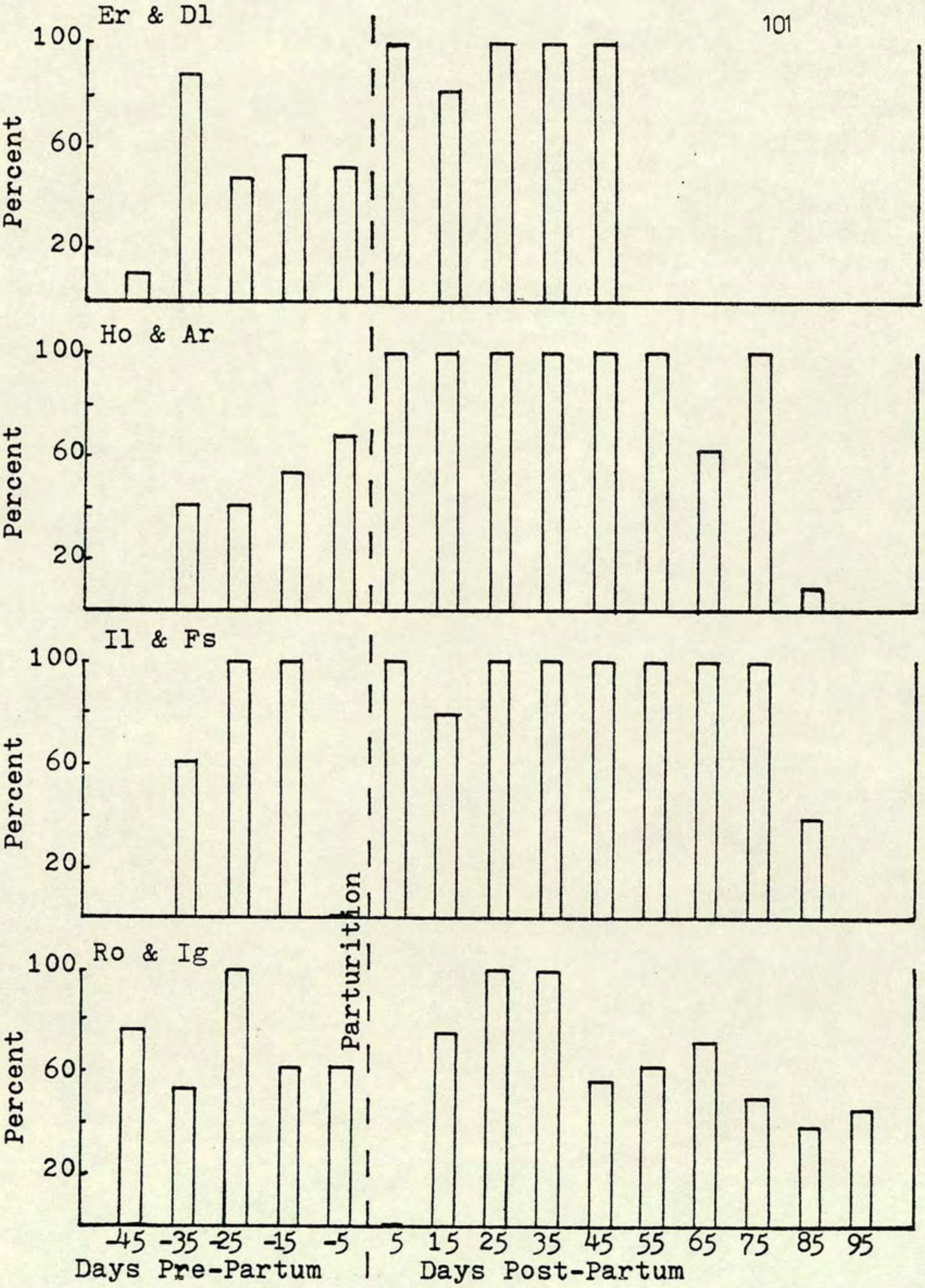

Figure 5:4 The frequency of ACFAA behaviour divided by the duration of activity shown by the female as a percentage of total behaviour shown by the female plus male.

squealed loudly when approached by the female or myself, which was not his usual behaviour). I ended the experiment at that time.

On 24 April 1979, 57 days after parturition, I introduced a strange male into the fourth family grouping (Ro & Ig). My hypothesis was that the female would attack and try to drive the strange male away, while the resident male would remain inactive. This was based on the high degree of agonistic behaviour shown by the female during lactation and the generally higher amount of attacking behaviour shown by the female. The intruding male was placed in a cage on the side of the arena with the resident female and two kittens. The resident male was confined to the other side of the arena. The following describes the events that followed the introduction:

13.15.0 The resident female (RF) approached the intruding male (IM) which squeaked and went between the partition and the doorway. The resident male (RM) was scratching at the doorway dividing the two arenas and squealing loudly. (This continued until 13.25.0.) The RF occassionally approached the doorway between the two arenas and scratched at it , but did not approach the IM 13.20.0 The RM forced his way into the arena moved about it and at 13.26.0 went in between the partition and the doorway and attacked the IM. THe fight continued until 13.30.5 when I separated the males. Both were covered with cuts and bleeding. This fight were notable not only for its duration, but also for the ferocity of attacks. Similarly neither animal broke away and fled as in a normal fight.

Although this experiment was only done once, I think that the results suggest some interesting points. First of all in this pair, remembering that they did not show the same types of interactions as the other groups, the male served a useful function of attacking an intruder into the family's living space. Whether the attack was purely defence of the area (not previously seen in the single-sex pairs), or defence of family or both cannot be concluded. The attack was noteworthy, however, as the force with which it was carried out was unlike any previously seen for either males or females. It would be interesting to repeat these experiments in larger areas and deal more with introduced individuals at all points in the breeding cycle including oestrous. The competition between neighboring males for breeding females would be a question worth investigating.

Two of the pairs who did not breed served as controls for the breeding experiments. Figures 5:5, 5:6, 5:7, show data for mean frequency of ACFAA behaviour, mean duration of activity, and mean frequency of ACFAA behaviour/ duration of activity for these pairs over a period of 50 or 60 days. Note that the females are still quite active, the males less so.

When comparing these scores with those for the breeding pairs, the females behaved similiarly to pre- and post- partum breeding females. The males were intermediate between the two. They lacked the continuous approaching behaviour as seen to females in oestrous and in early pregnancy, but did not show the extreme submissiveness and

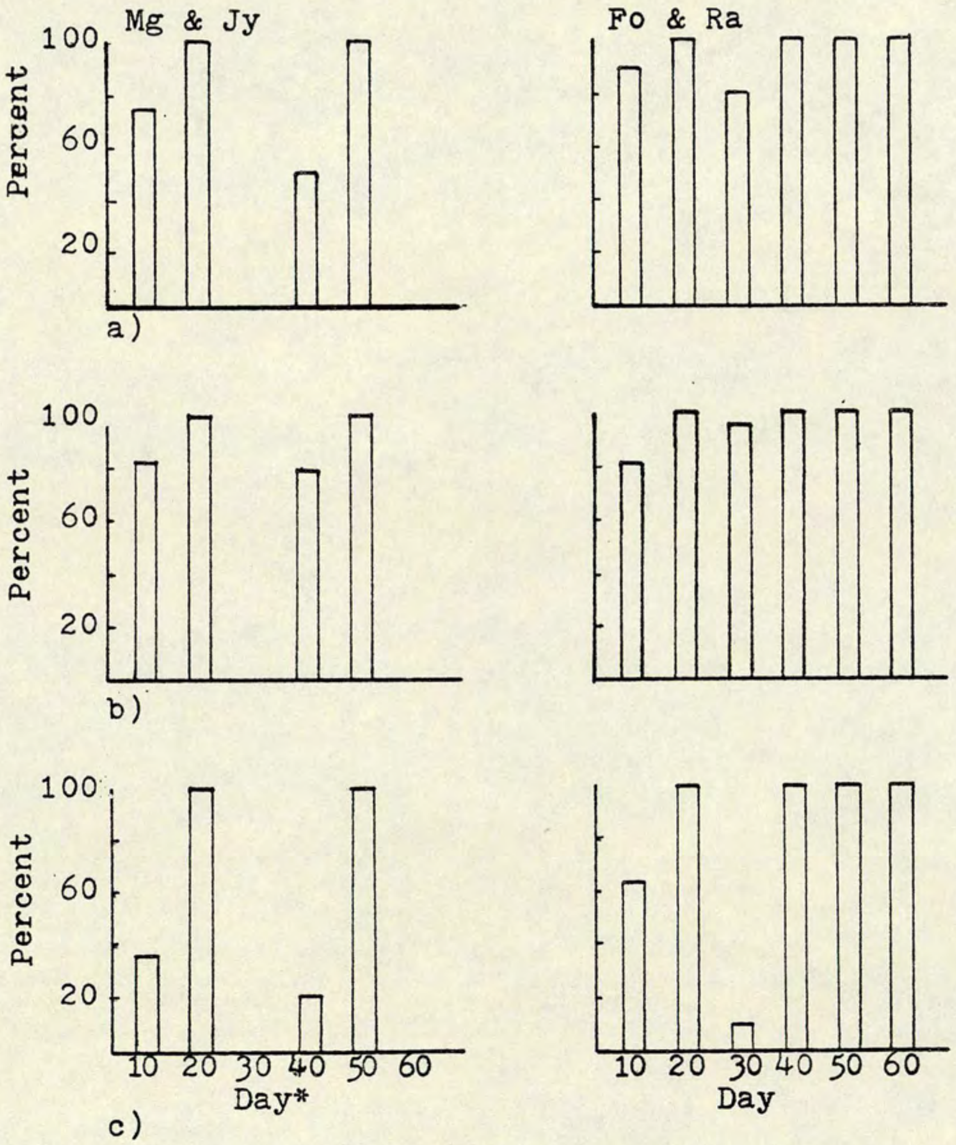

Figure 5:5 The mean frequency of ACFAA behaviour of the Control pairs (Female behaviour as a percentage of male plus female behaviour per 10 day period.

a) Frequency of ACFAA behaviour
b) Duration of Activity
c) Frequency of ACFAA behaviour divided by duration of activity.

strict confinement to the nest boxes as in the post partum males. This would suggest that the males were being basically inactive as seen in the male-male interactions with occasional approaches to the females to assess their reproductive state.

5:4 Discussion

5:4.1 The Behaviour Over the First Four Days

The types of behaviour seen in the male-female experiments were similar to those seen in the single-sex pairs. The additional ones were sexually oriented including the neck bite, copulation and face nipping (shown in females only). Poole (1967) reported a similar behaviour for polecats. It was, however, oriented towards the neck and thus classified as neck nipping.

The frequency of agonistic behaviour decreased over the four day observation period in three of the four pairs. (Five pairs were actually observed, but the female was in oestrous in the fifth pair, so this pair was excluded from the analysis.) The agonistic behaviour also decreased in the female-female pairs, but did not change in the male-male pairs. Similar decreases in interactions with time have been reported for weasels (Buckingham 1979), mice (Mackintosh 1970, Poole and Morgan 1972), and gerbils (Donegan 1978). It could be argued that the decline was due to increasing familiarity with the other animal so that it was a weaker stimuli for attack. In captive polecats Poole (1973) noted differences in attack intensities of familiar versus unfamiliar individuals. Similarly a hierarchy may have been established and only required occasional reinforcement. It could also be a combination of the two. Another factor must be considered, though, and that is the sexual aspect of the male-female interactions not present in the single-sex pairs. This is discussed further in Section 5:4.2.

The fifth pair as mentioned above (Ho & Ar) did not show the decrease in interactions over the period. Their frequency of interactions decreased and then increased again. Furthermore the number of behaviours per animal is very similar over the period. The immediate cause for this was that the pair were mating, but this does bring out an important point. That is that the female actively participates in initiating copulatory activity in weasels (see ethogram, Appendix A). Rowe-Rowe (1978) describes females initiating copulation in African weasels (Poecilogale albinucha). It has also been reported in polecats (Eibl-Eibesfeldt 1956, as cited by Poole (1964)), but appears to occur only when the animals are given a large area in which to interact (Poole 1964). Female approach has also been reported in shrews (Crowcroft 1957), another solitary species.

5:4.2 The Change in Behaviour Over the Breeding Cycle

In 1966 Lockie reported that during the latter part of pregnancy a female became dominant to the male with whom she was housed. Erlinge (1977) reported a similar incidence in stoats, as did and Crowcroft (1957) for shrews. In these experiments the females also became dominant during late pregnancy or early lactation, but I would like to elaborate on the description given by Lockie (1966). Of the four groups observed, the first three as seen in Figure 5:2 showed approximately equal numbers of ACFAA behaviours by the male or female before parturition. After parturition the males showed considerably less ACFAA. However, the interpretation of these behaviour and especially the approach behaviour had to be redefined as stated in Section 5:3.1. Payne and Swanson (1970) found a similar reclassification was necessary in their work on gerbils. Towards the end of pregnancy, however, the aggression of the females towards the males increased and eventually became true dominance as defined earlier. The components of dominance shown included squealing by the male (squealing alone as opposed to squealing during an encounter), food stealing by the females from the males, and the eviction of the males from their nest boxes by the females. Similarly when the males left their nest boxes, the females would frequently leave theirs, go across to where the males were and chase them back into the males' nest boxes.

Finally around the 12th week of lactation the males again became active and showed an increase in ACFAA behaviours. The females then ceased to steal their food or nest boxes and to chase them. This coincided with when the young would have been dispersing in the wild (Lockie 1966).

The fourth group behaved very differently from the other three. The male continued being active throughout the cycle. In the wild pairs of weasels are occasionally seen together complete with offspring (pers. commun. S. Erlinge). This pair may be an example of such a case where the antagonism between the pair was not strong enough to drive the male away. He did not at any time feed either the young or the female. He did allow the young to sleep with him, though, and occasionally played with them. There was also the introduction experiment where he either defended the areas or his offspring.

5:4.3 The Interpretation of the Experiments in Relation to Knowledge of Wild Weasels.

When comparing the agonistic behaviour of the control pairs with that of the breeding pairs, the females behaved similarly to the breeding females. The males, however, behaved more like the males in the single-sex pair experiments. They neither frequently approached the females as in the pre-partum groups or remained in their nest boxes behaving submissively as in the post-partum animals. In captivity this agonistic behaviour was seen as a means of allowing the males to make occasional contact with the females to assess their reproductive condition, and to allow both of them to use the area with minimal interaction (mutual avoidance).

During the non-breeding and early breeding season, a similar interpretation could also apply to those wild weasels living in overlapping home ranges. First of all the males could indirectly assess the females' reproductive state by contact with feces and/or urine. Captive males regularly inspected females' feces/urine. The males could also make periodic assessment of the females' reproductive condition by entering the females' ranges. Approaching the females and then withdrawing with minimal contact if they were not ready to mate. It should be remembered that in captivity the approaches were sexual rather than aggressive. The fighting that occurred was mostly defensive and initiated by the females. Weasels like many of the mustelids (Moors 1974) show sexual dimorphism. As the males can often be twice as large as the females, the sexual versus aggressive approaches by the males are significant. If males were treating females as males, and fighting with them as they do with males, the females could easily be injured in the interactions.

Mutual avoidance both temporal and spatial was another common behaviour in the non-breeding animals. Erlinge (1977a,b) stated that mutual avoidance played a major role in the dispersion of stoats. It has also been shown in cheetahs (Eaton 1970) and cats (Leyhausen 1965). I would suggest that in weasels with overlapping home ranges it is also a crucial factor in distribution.

During late pregnancy/early lactation the captive females became dominant over the males. If in the wild this dominance was manifested as exclusion of the males by the females as suggested by Lockie (1966), how might this affect the success of rearing a litter? In rodents during pregnancy energy demands increase by 30% (Migula 1969 and Myrcha _et_ _al_. 1966). During lactation they increase to 112% (Migula 1969 and Myrcha _et_ _al_. 1966). East and Lockie (1964) showed that female weasel also increased their food consumption during lactation to 150-200%. Therefore a female has to capture between two and three times as many prey or larger prey during this period. As females concentrate on smaller prey items (King 1971), the former is probably the case. How might this be affected by the exclusion or lack of exclusion of the males? Male and female weasels consume significantly different types of prey (King 1971, Tapper 1979). They also hunt in different areas (Pounds 1979). Erlinge (1979) stated that non-breeding female stoats are less successful hunters than the males. Although direct observational data is not available, there is some data that suggest that there may be a difference in hunting success and certainly that female weasels compete less well with males (Lockie 1966). When food declined in his study area, the females disappeared first followed by the males. This suggests that males were able to survive probably by switching to larger prey, but possibly by also being more efficient at prey catching. This competition for prey is obviously crucial at certain stages of the vole cycle. Similarly when the females have higher nutritional demands such as during lactation,it is also important. By excluding males from their home ranges, females have more prey available to themselves.

Another point to be considered is actual defence of the young by the female. Other species do occasionally prey on weasels including short-eared owls (Lockie pers. commun.), cats (own observation), and in North America long-tailed weasels (Polderboer *et al.* 1941). Weasels preying on other weasels has not been reported to my knowledge, but is obviously not impossible, especially if young ones are available. In captivity, however, the males never harmed the young and would in fact let them enter their nest boxes and sometimes played with them. It could be argued that this was because the female was always within easy reach of the males and this prevented them from harming the young. I would suggest, however, that there is no reason for male weasels to harm young weasels within their home ranges. Any young in their area are likely to be their own. If maximum reproductive success is desirable, killing them would be counter productive. Female weasels in these experiments, however, still were very defensive of their young both against males and against humans.

5:5 Summary

In this chapter I discussed the relationship between male and female weasels in captivity and how it may relate to wild weasels. Although the ACFAA behaviours were similar to the single-sex pairs, the approaches of the males to the females were generally sexually oriented rather than aggressive. It was found that the frequency of activity decreased over the initial four day period, if the animals were not breeding. During oestrous the females would continually approach the males trilling until copulation eventually occurred. Both the males and the females continued to be active and have a high frequency of interaction before parturition. After parturition, though, the males became inactive and usually stayed in their nest boxes. It was suggested that this was the result of the increased dominance behaviour shown by the females after they gave birth. When the young were around twelve weeks old, the males again became active and the females became less aggressive. This is normally when the young begin to disperse in the wild. In one pair the male did not show a large decrease in activity as shown by the other three males. In the field pairs of weasels are occasionally seen complete with offspring. It was suggested that this pair might be an example of such a case.

The control pairs showed spatial and temporal mutual avoidance. It was suggested that this may be a means of dispersion in the field where weasels have overlapping home ranges.

The results were interpreted with regards to wild weasels. It was suggested that as the males' continual approaches to the females were sexual rather than aggressive, they could periodically assess the females reproductive state without entering into fights. As males are much larger than females, this would decrease the risk of a female being injured in an interaction. The change in dominance was suggested to occur in the wild in the form of the females excluding the males from their home ranges. This would decrease competition for food and enable the female to meet her increased nutritional demands encountered during lactation. It was also a means of protecting the young.

Chapter 6: Final Discussion

6:1 Comments on Weasels as Experimental Animals

Before I begin the final discussion, I would like to comment on the problems involved in using weasels in behavioural experiments. First of all one has to deal with the obvious difficulty of producing suitable food and housing for a non-laboratory species. This was easily managed with the use of the wood-wire cages provided with several objects in which the weasels could hide and sleep. Food was easily acquired in the form of laboratory mice.

Greater difficulties were encountered when it came to designing the actual experiments and the experimental set up. Care was taken to provide a varied and thus hopefully stimulating habitat by placing in the arenas trees up to one metre tall, large boxes of grass, stone dykes, and tunnels. This gave the animals a three dimensional habitat. Ideally it would be more satisfactory to have an outdoor enclosure with natural vegetation, but this was not feasible at the time.

By varying the cages and experimental habitat I feel that I was able to provide the animals with more stimulating surroundings. Consequently I had no trouble with stereotypic behaviour in any of the wild individuals and only three of my captive reared animals showed any of this behaviour. None of these were subsequently used in the experiments.

However, there are limitations to the use of weasels for captive experiments. The main problem encountered throughout the three years was the lack of activity by the animals while under observation. Buckingham (1979) found a similar lack of activity with his animals being active for less than 20% of the time. The inactivty was not I am sure due to my presence as activity recorders placed in the arenas in the Department of Zoology showed that they remained in their nest boxes for long periods of time.The inactivity may have been a sign of boredom or of being too well fed, hence lacking any food seeking drive. This lack of activity did severely limit the amount of data that could be collected and thus the conclusions that could be drawn from the behaviour of the animals. Similarly besides the obvious limitations placed upon interpreting the behaviour of captive animals, one very soon ends up with a lot of hours of observation and limited information derived from it.

I do feel that there are studies that can be done on captive weasels, such as feeding studies or observations on family interactions. If large natural enclosures are available, intruder experiments could be done as discussed in Chapter 5:3.3. These experiments would, however, have to be based on firm knowledge of how and under what conditions wild weasels interact. Interspecific relationships between weasels and stoats would also be an interesting and useful subject of study. Unfortunately there is little information on this subject presently available. Finally more information on intraspecific relationships is required as mentioned in Section 6:6. Therefore I would recommend anyone wishing to continue with research on captive weasels to consider these problems and enter into the work only after careful consideration of the questions to be asked.

6:2 Final Discussion

There are many factors that could affect the way that individuals of a species are dispersed. These include physical characteristics such as habitat and food supply, or those factors that the individuals themselves control through behaviour, such as territoriality, mutual avoidance, or habitat preference. In these experiments I asked how does behaviour influence the spacing of captive weasels and how might the responses revealed operate in the wild to affect free ranging weasels.

The results of the single-sex pair experiments will be considered in Sections 6:3 and 6:4 and then compared with those of the mixed-sex pairs in Section 6:5.

6:3 The Comparison Between the Pairs of Males and Pairs of Females

The results of the male-male and female-female experiments were similar in most of the actions observed. Both sexes showed a significant correlation between frequency of behaviour and duration of activity. Five basic behaviours occurred which could be used to classify the animals into two categories, agonistic or defensive. The agonistic behaviours included attack, chase, follow, and approach. The defensive behaviours included two vocalizations: squeal and hiss. The relative aggressiveness of the individuals within each pair was assessed using these behaviours. Individuals could either be classified as more of less aggressive or equal. The classification of each animal was also evident by its use of the area. Neither age nor weight influenced the classification of the animals. Although none of the animals defended the areas in which they lived, individuals defended their nest boxes, food supply or personal space. The animals avoided each other both spatially and temporally.

6:4 The Differences Between the Pairs of Males and Females

There were some differences between the interactions of the males and females, though. First of all the males had a lower frequency of ACFAA behaviour. A Mann-Whitney U test was used to compare mean frequency between the sexes. The difference was very significant at $z=4.546$ and $p=0.00003$, with the male mean being 1.32, and the female mean being 10.03. Buckingham (1979) found similar differences in his male and female weasels. When the mean frequencies of all agonistic behaviour per activity duration were compared, the males had a higher mean frequency of behaviour. The difference was only nearly significant, though, ($z=1.414$ and $p=0.0793$, male mean = 0.080, female mean= 0.037 Mann-Whitney U test). I would suggest then that the females were generally initiating encounters while they were already out and moving around, while the males were actually leaving their resting places in order to initate encounters.

The types of relationships between the pairs of males were more varied than those between pairs of females. In the females there was a clear dominant/ subordinate relationship in six of the seven cases. However, in the males, only eight of the thirteen pairs showed a clear dominant/ subordinate relationship which again was based on defensive and not agonistic behaviour. The other five pairs were of equal status. These results indicate that there is a difference between the relationships of males and those of females. The difference in the male-male interactions was the use of defensive behaviours (squeal and hiss) in place of agonistic behaviour to settle encounters. Males are heavier, stronger, have larger teeth, and a larger bite, hence males have more risk of serious injury during a fight. Therefore, defensive behaviour may serve as a warning against beginning a fight. Similarly, once in a fight the techniques used by males are different than those used by females. Males grasp each other and roll around biting at each other's neck and face region, while kicking with their hind legs. Although females do some wrestling and mouth fighting, they use a striking movement more frequently where they rear up on their prostrate opponent aand strike at it with the mouth opened widely. It is quite similar to a snake striking a prey. The different relationships may be representative of the difference in the distribution of the male and female ranges. Males ranges are generally larger than female ranges, contiguous, with areas of overlap. Females have smaller ranges with some overlap, but probably have fewer contacts with both known and unknown individuals. If neighboring males have regular contact it is to their advantage to quickly establish a stable relationship in order to decrease any possible fighting. This relationship can either be one of equal pairs or of a more and less dominant individual which might then affect the territory size on that boundary (Erlinge 1974). When transients pass through an area, more agonistic encounters may occur. On the other hand females may not have as frequent contact with other animals, hence they would not establish the less aggressive relationships. Furthermore many of these encounters will be with individuals larger than themselves. Finally if female ranges are smaller, they may be more tenacious when defending them.

The explanation for the higher amount of activity in the females may be found in these encounters. As discussed earlier, females are smaller than males. Although this size differential may be advantageous for rearing young (Erlinge 1979, Moors 1980), it may be disadvantageous in territorial encounters with larger animals. However, if females are more aggressive and more actively defend their ranges, this may counteract their lack of size.

Another factor to consider is the relative abilities of males and females to capture prey. Erlinge (1975) studying weasels in captivity found that females averaged one capture per 50 minutes, while males averaged one per 12.5 minutes during the initial activity period with the same number of prey available. Over the 24 hour period, the males caught 5.1 prey while the females only caught 1.5. The difference was not due to the time spent hunting, but was the result of a greater hunting intensity and ability on the part of the males. Therefore under natural conditions, females may need to spend more time hunting in order to feed themselves. This would be even more time consuming when they had offspring unless hunting efficiency improves during lactation. Erlinge (1979) reported a female stoat with young who caught four times as many prey as non-breeding females over the same hunting period. Therefore it could be selectively advantageous to be more active in order to catch more food , assuming an increase in activity means that more prey are likely to be encountered and captured. Higher activity may also enable more successful territorial defence. Hence the increased activity of the females in my experiments may have been based on an inherent activity drive of wild females. Clearly in order fully to understand this relationship it is necessary to have more information on the movements and interactions of free-living weasels. Spacing can also be influenced by the lack of encounters. In these experiments weasels used both mutual avoidance and dominance when establishing their use of the area. Both Moors (1974) and King (1975) discussed mutual avoidance as a means of dispersion in free ranging weasels. Spatial and temporal avoidance have also been described in martens (Mech 1977).

The relevance of the agonistic side of dominance can be clearly seen, but the aspect of vocal defence should also be considered. This was particularly noticeable in the males. The use of vocalizations versus encounters to defend an area has been noted for martens (Hawley and Newby 1957). Similarly in the weasel vocalizations were used in place of fighting as described above.

These experiments did not consider how territories are established, but some of the results did provide some information relevant to this subject. Neither age or size of the individual had any affect on dominance. Hence it may not affect the establishment of a territory either. Lockie (1966) suggested that establishing a territory may be related to being in the right place at the right time rather than to fighting prowess.

In the experiments, the weasels did not defend whole areas, but only the area they were in when approached. As this was generally a nest box, it was difficult to differentiate between defence of resources and defence of personal space. However, as the weasels did not defend boundaries, in this instance food supply may have been the only thing worth defending.

6:5 The Male-Female Pairs

As in the male-male experiments, the male-female pairs showed very few chase or attack behaviours over the first four days of observations. There was also no correlation between chase and the other behaviours. This was especially noticeable in the females, who in the single-sex experiments showed a high correlation between the agonistic behaviours. None of these were significant in the mixed pairs. This could be the result of several factors. First of all the number observed was very low (n=4) possibly making the number of behaviours too low for comparison. However, it is more likely that the females were actually behaving differently in the mixed sex encounters. The difference was undoubtedly related to the sexual aspect of the behaviours observed. This is supported by the fact that a dominance hierarchy did develop at a later stage in the experiments. Approaches labelled as agonistic in the single-sex pairs were used by the males to test the receptivity of the females as described in Section 5:3.1. Therefore, they were not agonistically oriented. Hence I would not expect them to correlate with agonistic behaviour. Dominance behaviour did occur during late pregnancy and lactation, though, on the part of the female. Free-living females at this time would presumably be enlarging their home ranges or territories at the expense of neighboring males.

There were also differences between the mixed and single-sex pairs in the mean number of behaviours occurring over the first four days. In the mixed pairs the males were nearly as equally as active as the females while in the single-sex pairs their activity was almost ten times less. This again would be due to the sexual interactions. The number of behaviours per period of activity were in agreement with the single-sex pairs results, though, with the males having a higher mean.

6:5.1 The Change in Agonistic Behaviour over the Four Day period

In the female-female pairs, the agonistic behaviour of the MAA decreased significantly over the four day period. Similarly, in the male-male pairs the behaviour of the LDA also changed. . In the mixed pairs, both increased & decreased. In three of the four pairs, both individuals decreased their behaviour, while in the other pair one decreased while the other increased. As the male was the one who did not decrease, I would again suggest that the lack of decrease was sexually related.

What behaviours influenced spacing in the mixed pairs, therefore? First of all avoidance was again a common and useful means of ensuring dispersion. The encounters were not so fierce as to damage the other individual , but they would cause avoidance. (The introduction of the strange male discussed in Section 5:3.3 should be remembered here as an example of how strange individuals may be treated.) However, contact between the sexes must be frequent enough to enable the males to mate with females who may be living within their ranges. It is notable that the females did not use any loud vocalizations to attract the males like those occurring in some of the felids during oestrous (domestic cats and pumas, Pers. obs.). The only sexually oriented vocalization was the trill, a softer vocalization that can only be heard at short distances. Both males and females give this vocalization during courtship. This suggests that some other means of communication (eg. scent), or direct confrontation must be used in order for the animals to remain in contact with each other.

6:6 Conclusions

Although it is difficult to compare the behaviour of captive animals with that of free-ranging individuals, in these experiments several behaviours occurred that would influence the spacing of wild weasels. Spatial and temporal avoidance were the major factors influencing the spacing of single-sex pairs. When the animals were active together agonistic encounters occurred, but were frequently avoided by the used of threatening vocalizations. In wild weasels these vocalizations may also deter interactions. Finally the effects on weasels of the differences between the amount of activity of the females should be considered. Assuming that females are more active than males it may conteract the size disadvantage in encounters with larger individuals. If the higher activity level is also a real difference and not an artefact of captivity, they may be able to retain territories by persistance in fighting rather than by strength. Similarly it may make up for their lower efficiency in catching prey.

The mixed-sex pairs interacted differently than the single-sex pairs. Although they also avoided each other spatially and temporally, when they did interact the interactions were sexually rather than aggressively oriented. They may also need to keep in closer contact, possibly by more overlap, in order to assess the reproductive condition of the females. Other methods of advertisement must be used such as urine or sebaceous gland secretions.

Clearly the interpretaion of the above results are merely suggestions about how the spacing of weasels could be influenced by social interactions. Although they are based on information about free-ranging weasels, only tentative conclusions can be made due to the sparcity of data on wild individuals. Furthermore, so many questions arise from this data that still need to be answered. Some of these can be answered through research on captive animals, but more information is required on wild weasels to support captive research. In these experiments I only considered the three basic group types, male-male, female-female and male-female. The effects of age and reproductive condition should be looked into in more detail. The male-female relationship should be examined more carefully, possibly considering the relationship between hormones and the changes in behaviour that I observed during lactation. The interactions between male-female groups and other individuals of both sexes could be considered also. The introduction of the strange male in these experiments produced some very curious results. It would be worthwhile discovering whether this was a valid result or a chance occurrence. The social system of wild weasels should also be considered in more detail. Information on the establishment and maintenance of territories is limited. The responses of like and opposite-sex neighbors to each other is not known. Similarly the effects of juveniles and transients on the retention of a territory should be considered. Finally the effects of the seasonal cycle of both sexes on the interactions between individuals is unknown. These questions could probably be answered with a mixture of research on captive animals and radio tracking studies on wild weasels. Both types of research are necessary and fruitful when studying a small carnivore, but only if the results of both are considered when interpreting information gathered from either source.

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Appendix A: Ethogram for Mustela nivalis

A:1 Locomotion: Gaits

Run: This is the fastest gait. The body is elongated with the head extending forward at the level of the back. It is used when the animals are frightened or disturbed in order to reach cover quickly. It is also used prior to an attack, although a slow approach is more commonly used. Two speeds of running are illustrated in Figures A:1.8 and A:1.9, run and dash.

Lope: This is the most common gait used when moving around the arena. It is slower than the run. The back is arched as the animal moves. The two hind feet hit the ground almost simultaneously closely followed by the front feet which fall almost together. This gait is illustrated in Figure A:1.28.

Bounding: This gait is similar to the lope, with the exception that the arch in the back is even more exaggerated. It is commonly used in play.

Trot: Footfall pattern; R rear, L front, L rear, R front. The trot is a medium speed gait. The head is slightly raised above the level of the back. It is smoother than the lope as the back is not arched.

Walk: The head is held up and the animal may look around as it moves. The body is relaxed. This is the slowest gait used for normal movement. The walk is illustrated in Figure A:1.7.

Slow walk: Used when investigating something or when approaching a conspecific in an antagonist encounter. The body is stretched, tense, and sometimes lowered slightly.

Slink: The body is lowered causing the shoulders to be raised slightly. The face and body are tense. This gait is used when fleeing from an opponent or when in a stressed situation.

Snake: The body is stretched with the chin flat on the ground. The front legs remain loose at the sides of the body with the rear legs providing the propulsion. It occurs when going through low or small openings (eg. tunnels) or sometimes after eating. It also occurs in conjunction with marking (see Section A:5 and Figure A:1.15).

Jump: Weasels jump from a variety of positions including: a) In rear-up position often balancing the front feet against something. The animal pushes off with its hind legs while clawing with its front legs and feet. It then lands on its rear legs with the body still erect. b) From a standing position: the animals frequently leaps onto objects. The body is arched. The rear legs are used for propulsion with the front legs aiding to secure a landing (see Figure A:1.10). c) In the air: When in the low cages, the animals occasionally lept into the air from a standing position and turn around falling back to the ground. The body is initially raised slightly as if to rear-up (see section A:3). The animal pushes off with its rear legs, turns in mid air, and falls to the ground (see Figure A:1.11).

Crouch: The front and rear legs are bent slightly with the front elbows close to the body. The back is humped slightly. The head can be in a variety of position depending on the reason for crouching. If the animal is avoiding another weasel or another animal, it will turn its head away from the animal, but continue to make quick glances at the individual. Under these circumstances the body is tense. This posture can also be used when eating. The animal eating looks up frequently, but the body is not tense.

Scratch-at: This action is similar to digging except that it is used to refer to digging actions made towards objects that could not be affected by digging, such as wooden nesting boxes, cement floors, walls, and wire (see Figure A:1.24).

A:2 Stationery Postures

Sit: 1) The haunches are curved under so that the back is humped slightly. The front feet are together, the body is normally elongated (see Figure A:1.1). 2) Hump sit: The rear legs are brought forward within 4-6 cm. of the front legs. The back is extremely humped.

Curl: This is the normal resting posture. The body is curled so that the nose is near the tail or resting on the flanks (see Figure A:1.2). The animals usually sleep in this posture.

Sit Curl: Like the sit, except that the body is resting more on one haunch than the other.

Lie flat: The body is extended full length with the weasel lying on its ventral side. The rear legs are either stretched out posteriorly, or drawn up underneath the body. The front legs are either loose on either side of the body or partially tucked underneath. The head remains on the ground with the chin lying flat on the ground (see Figure A:1.3).

Stretch: 1) The hindlegs remain stationary. The animal walks forward with the front legs, lengthening the body as it walks. It then pushes the head and neck forward so that the legs are at a 135^{o} angle with the body. 2) A variation of the above occurs with the back arched and the shoulders pushed forward.

Stand: The animal is stationary with all four legs straight and the feet on the ground. The head is in various positions depending on whether the animal is looking, sniffing, or in transition between postures (see Figure A:1.4, A:1.5).

A:3 Investigation

Investigating: The animal lopes or walks around the enclosure looking into and sometimes entering the various objects. Sniffing of the various objects is an important component of investigation.

Rear-up: While standing on the hind legs, the upper torso is raised vertically and held there while the animal looks around. The front feet are held in the air (see Figure A:1.6).

Head-up: The animal is in any of the postures listed above, but with its head raised. The weasel uses this and the previous posture to survey an area (see Figure A:1.4).

Response to novel object: New objects are approached cautiously with the animal moving a little closer each time. Eventually it touches and sniffs the object and then runs away. The weasels continues these hesitant approaches and sniffing until it no longer runs away.

A:4 Eating and Drinking

Eating: 1) Sit eat: The animal is in a sitting position. It looks up periodically as it chews. Occasionally the mouth is opened wide and the rim of the mouth is licked. It sometimes rubs its chin against the ground after the meal (see snake, section A:1). This may be a marking behaviour. The molars are used to tear off pieces of meat.

Methods of Eating Prey: 1) Mouse: The weasel begins at the head and eats the head, thorax, etc. It sometimes leaves the skin from the haunches. The tail is rarely eaten. When given several mice, it eats all the heads first with the rest of the carcasses being left until later. Most food is consumed in the nesting boxes. Food is also stored for indefinite periods in the nesting boxes.

Cacheing: Mice are stored in tunnels, nesting boxes, pots of grass, under rocks, etc. In other words wherever hiding places were available. Caches are not defended unless the animal is actually present.

Behaviour with dead prey: 1) While holding the prey in the mouth, the weasels roll from side to side scratching at the mouse with the rear feet. 2) Sometimes play behaviour follows with somersaultts, leaping in the air and rolling from side to side. Buckingham (1979) described behaviours similar to these by weasels oriented towards live prey items. One of my hand tame weasels acted similarly to a live robin. Although the robin watched the young weasel, it easily remained outwith striking distance and soon flew away.

Drinking: From dish: The weasel sits in a crouched position and laps at the water with its tongue. 2) From a bottle: While standing it laps at the spout with the tongue. The front feet are sometimes placed against the spout of the bottle.

A:5 Defecation, Urination, Use of Sebaceous glands

Defecate: The tail is held vertically in the air. The feet remain stationary. The rear end moves up and down (see Figure A:1.12). The weasels usually use specific sites for defecation (latrines) located adjacent to their houses or in areas of high use.

Urinate: Similar posture to defecation. Usually occurs in conjunction with defecation.

Urine marking: In males when the animal is walking along he quickly drops his abdomen and places one small drop of urine on the substrate (see Figure A:1.13 through A:1.16). Males marked throughout the arena. Tame males that I have hand-reared marked various places, but frequently marked articles of clothing, books or papers that had been handled by me and presumably had my odor on them. Urine marking in the females is seen less frequently and could be confused with the anal drag (see below). The females had to touch their ano-genital region to the ground or object being marked. The movement is neither as quick or easy as that of the males.

Anal drag: This is occasionally seen for males, but more often seen in the females. They would drag their anus against the ground using their front legs for propulsion. This may be confused with urine marking as mentioned above. The purpose of the anal drag is presumably to distribute sebum from the musk gland located by the anus. This is not to be confused with the forceful evacuation of the musk gland used by a frightened weasel (see below).

Musk Gland: The forceful use of the musk gland has only been noted in two cases: 1) When the animals were frightened by human disturbance. 2) When a fight betwen two animals became very rough. This suggests that the musk gland is used defensively rather than offensively.

A:6 Miscellaneous

Sniff: A quick inhalation of air via nostrils, scenting as it inhales (see Figures A:1.5 and A:1.6).

Sneeze: A quick inhalation of air followed by a quick expulsion of air.

Inspect: Weasels of oposite sexes would sniff the side of each others faces and the perineal regions during courtship (see Figures A:1.25 through A:1.28). This is not seen in the single-sex pairs in these experiments, although Buckingham (1979) reported it in his encounter experiments.

Scratch: 1) Side or head: The animal adopts a sit curl position on the right or left side, scratching from its lower torso to head with its right or left rear foot depending on the side that is being scratched. 2) Abdomen: A sitting posture is taken with the legs being raised to scratch an area.

Groom: The fur and skin are cleaned by licking, which may be interspersed with biting. When grooming the side, from the mid-torso to the rear, the animal adopts a sit curl posture reaching its head back to the areas being groomed.

Climbing: Weasels are very agile and avid climbers of trees, walls, stone blocks, etc. The movement consists of pushing with the rear legs, feet, claws, and pulling with the front legs, feet, claws.

Digging: Weasels dig at dirt, sawdust, and any other substrate either as a means of escape or possibly for entertainment. When given large tubs of grass (1 m x .60m x .40m), they dug tunnels throughout the container. These tunnels are used as resting places and as food caches. The action of digging mainly involves the front feet and claws to loosen and push away the dirt or other substance. The shoulders are hunched slightly and the body is in a crouching position. The head is down, close to the feet.

A:7 Encounter Behaviour

Attack: This includes all types of physical fighting. One animal leaps at the other with its mouth open. The other animal responds by biting and vocalizing (chirps, squeals, hisses). The degree of attack varies. Most frequently it is left at mouth sparring with the animals preventing contact by fending off the thrusts with their mouths. Sometimes grappling results with the animals grasping each other with their front legs and scratching with their rear legs. Rolling over together in this position sometimes occurs. Buckingham (1979) referred to this position as rolling-over. Fights are generally of short duration, eg. less than 20 seconds.

Chase: Chases occurred alone or after some other approach behaviour. One animal chases another with both moving very rapidly.

The animal being pursued generally heads for cover or to another part of the arena where the other animal can not follow.

Follow: Follows are similar to chases except that neither animal is moving rapidly and both individuals seemed very casual about the behaviour.

Approach: The body is extended and lowered slightly. The neck is stretched forward with the head even with the back. The tail is either curved with the tip pointing downwards or straight and pointing slightly downwards. A slow hesitant walking gait is used in the approach (see Figures A:1.19 and A:1.20). These are classified as near or far approaches in the experiments (see Section 3:2).

Face to face encounter: Two weasels face each other and squeal. One animal is usually in a nest box. The animal on the outside of the house stands with its rear legs spread apart slightly and the front feet braced. The tail is curled up slightly. Both of the animals squeal and hiss. The animal who initiates the encounter (the one outside of the house) usually leaves first.

Retreat: The weasel reverses backwards a little, turns its head away and slowly turns around. The body is lowered slightly and the weasel slinks off (see Figures A:1.21 through A:1.23). After a few steps it resumes a normal stance with the head raised slightly, the body relaxed. It walks away in a normal posture.

Look-at: A common encounter between two animals. It may occur anywhere in the enclosure. One animal looks at the other, who turns its head to avoid eye contact. The roles are then reversed and the procedure is repeated numerous times.

Run-at: This behaviour was shown only by females towards males. The females run towards the males and veer off without touching them.

Bite-at: As for run-at, except that the females mouths are open and they bite at the males when they are close enough.

Thrust: The animal pushes its body forward quickly either squealing, hissing, or chirping at the end of the forward thrust and then withdraws quickly. This threat gesture is used towards anything or any animal in the proximity of the animal. Buckingham (1979) labelled this as the lunge.

A:8 Reproductive Behaviour

Mating behaviour: When the females are not in oestrous, all sexual approaches are made by the male towards the females. The females then rebuff the males. However, when the females are in oestrous, either animal may make the approach. Both animals trill and mating quickly follows the intial encounters. In Figure A:1.29 the male is following the female prior to mounting.

Neck bite: The male grasps the female by the back of the neck with his front legs on either side of her body. In some cases the males drag the females to another location such as a nest box or tunnel, before copulation commences. The neck bite is generally very strong so that females are unable to break away. Intromission follows shortly after the neck bite is secured. Thrusts are very rapid, too rapid to count without being filmed and replayed in slow motion. The pairs stay together for 20 or more minutes with the longest copulation during these experiments lasting for 45 minutes. Copulations always begin with the male on top and both weasels crouching with their ventral side down. However, periodically the animals fall over as the copulation progresses, so that they are both on their sides, but tthe male is still dorsal to the female. There is no copulatory tie as seen in the canids. The moment the male releases the female she moves off rapidly. Periodically the female forcibly breaks away from the male. On breaking away the female frequently turns around attacking the males, before running away squealing or chirping loudly. After leaving the male the female drags her anogenital region against the ground and often will lick herself. Both animals groom themselves concentrating on their anogenital regions after copulation (Figures A:31 through 35 illustrate the various stages of copulation).

Front-feet on: The mixed-sex pairs interact frequently while the female is in oestrous. Besides sharing resting places they frequently approach each other to test readiness to mate. The male's approahes are generally forceful, oriented towards grasping the female's nape. The females make more playful approaches to the males, rubbing against them and biting at them. Frequently they rear up against the males and leap at them putting their front feet onto the male's back or neck (see Figure A:1.30). This posture also occurs in play between mothers and offspring or in sibling play. Rowe-Rowe (1978) described a similar behaviour in female African weasels as "dancing" in front of the male during courtship.

A:9 Vocalizations

Hiss: A slow exhalation of air from the back of the throat. No harmonics* were apparent, it basically consisted of white noise. It varies in duration according to circumstances. The hiss serves as a warning vocalization.

Squeak: A high pitched exhalation of air. It may occur at several different pitches. The strongest harmonics are from 500 to 1600 kHz.

Squeal: Similar to the squeak, but longer in duration. Both are used during fights between individuals (see Figure A:1.17). Squeals also occur when an animal is startled.

Cluck: It arises from deep in the throat and increases in intensity as it continues. Clucks are of a medium pitch, similar to human clucking. They only occurred several times and under the following circumstances. 1) Once they were given by a male weasel in response to a mouse sitting outside of his cage. 2) They have been used by a male weasel after he had been trying to court a female who repelled him. (C. Pounds- University of Aberdeen, pers. commun.).

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* These vocalizations were recorded on a Uher tape recorder and reproduced on a Kay Sona-Graph. The Sonagrams were analysed to describe the harmonics and frequencies.

They were given by a male weasel after he and another had been together on one side of the arena for one hour with no interactions. Both animals were sitting in the houses during the hour. 4) Finally they were used by a male while sitting in a tunnel in response to the approach of another male. The male in the tunnel clucked again and then squealed.

Trill: A soft low vocalization consisting of a series of paired clicks. No harmonics are apparent as it is given through a closed mouth. The clicks are .005 seconds apart with a .013 second duration between pairs of clicks. It is used by courting animals and betwen mother and young.

Chirp: A high pitched short vocalization. No harmonics are visible, but they are probably obscured by the white noise. The vocalization is given in a series with hisses interspersed before and/or after it. It serves basically as a threat. The animal lunges forward when giving the vocalization and then quickly withdraws (see Figure A:1.18).

A:10 Facial Expressions

Weasels have very limited facial expressions other than expressions that occur when giving a vocalization. When giving chirps and squeals the mouths are opened wide and the lips are drawn back slightly. When hissing the lips are drawn back slightly, but the mouth is hardly opened. However, as these expressions are an intregal part of making the noise I do not consider them as facial expressions. The main facial expression that did occur not associated with vocalizations is the:

Yawn: The mouth is opened widely and the lips are pulled back. The tongue is frequently brought up and sometimes curled. Yawning is usually seen when the animal is in a nest box with its head poking out of the box. This is generally after a period of the animal being quiet and therefore probably asleep in the nest box.

A:11 Maternal Behaviour

Late pregnancy-During the last week of pregnancy the female begins to cache mice in the nest box. Previously she left them scattered about the arena, so that I could remove them when desired. Accompanying the cacheing behaviour is an increase of defensive behaviour at the nest box with threat postures and vocalizations directed towards any approachers.

Parturition: Parturition was not observed.

Defense of the nest: The female continues to defend the nest box while the young are present. After 5-6 weeks when the young become more independent and active outside the nest box, the defense lessens.

A:11.1 Mother Young Interactions

Lactation: The duration of lactation varies. The young begin to eat meat around 3 to 4 weeks of age, but lactation continues for a longer period. All of the females showed at least one functional nipple when the observations were concluded 10 to 12 weeks after parturition. This was attributed to security/comfort nursing rather than nursing to obtain nourishment.

Grooming: The mother grooms and licks the young using the same movements described in Section A:6.

Carrying behaviour: The neck grasp is used to carry the young. The scruff of the neck is held between the female's teeth. The young animal remains limp while being carried. The female continues to carry the young throughout the period that they are in the enclosure together. This includes the carrying of young males who are larger than the mother. The females grasped the males by the neck thereby raising the young animal's front legs off of the ground. The males then run along on their back legs following the female.

Controlling the Young: When the eyes of the young begin to open at 24 to 30 days and they become more mobile, they begin straying from the nest box. The female either physically retreives them or trills and they follow her back to the nest box. The females continually retreived the young during the third to fifth week post-partum. Afterwards they let them roam about the enclosure more freely. The young often went into the nest box inhabited by the male. The females always removed them from the male's nest boxes.

Play: Social, self and object play occur. Social play consists of rolling and biting, chasing, and king of the mountain type games. The mothers joined in on these games. Self play consists of biting at the rear feet or tail while rolling around. Object play occurs with mice, bits of plant, stones, straw, or any objects that had fallen into the arena. Items are generally treated as prey in that they are attacked and bitten. Very little manual dexterity is involved such as batting at items with paws which occurs in other carnivores.

Contact Behaviour: Piling: The mother and young usually sleep in groups of two to three layers of animals. These heaps occur even when there is enough room to sleep individually with less contact. Piling is still seen at 134 days after birth.

A:12 Ontogeny of Young Vocalizations

1 to 6 days old: The young are very vociferous initially, but quiet down after about a week. During the first week they squeak regardless of whether the female is present or not. Later they only squeak when she is absent or in response to discomfort (see 6-20 days). I would suggest that the intial squeaking may be a means of

imprinting the mother on to the young in order to reinforce the fact that she has young and must return to the nest.

6 to 20 days old: A medium pitched squeaky sound with slight variations in pitch for each vocalization. It increased in frequency and became higher pitched with age. The vocalization is no longer given by mother-reared young at 20 days of age. The vocalization is basically a response to discomfort, presumably to discomfort of cold or handling during the recordings.

27 Days: The hiss response as described in adults is given at 27 days. It occurs concurrently with the eyes opening and in response to the presence of a human or other novel object. The young could not focus their eyes well at this time, but may have been responding to the size of the observer by amount of light blacked out.

31 Days: The chirp first occurs at this time. The animal lunges forward while giving the vocalization as in adults. As it is not very steady on its feet, this lunge caused it to fall over.

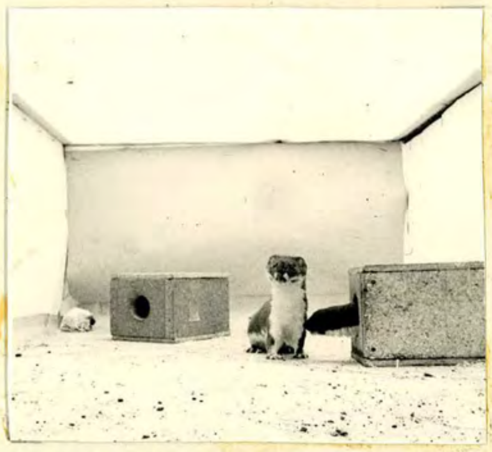
40 Days: The squeal as given by adults appears at this stage.

Photographs of Postures and Behaviours: Figures 1.1 - 1.35

1.1 Sit

1.2 Curl

1.3 Lie Flat



1.4 Head-Up Alert Stand

1.5 Stand, Sniff Ground

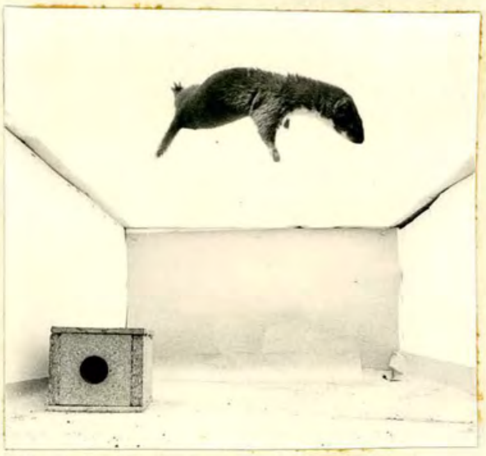
1.6 Rear-Up, Sniff Air

1.7 Walk

1.8 Run

1.9 Dash

1.10 Jump Onto (House)



1.11 Turn In Air

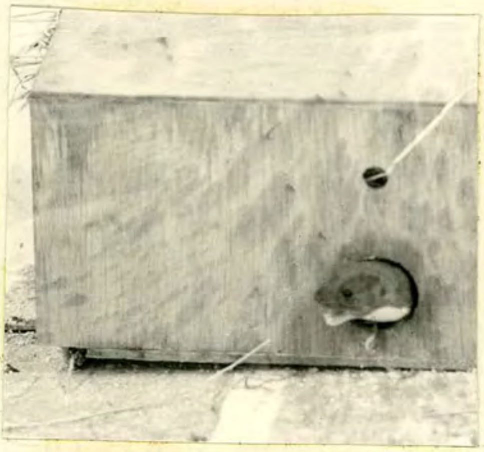
1.12 Defecate

1.13 Marking Sequence (MS)

1.14 MS Cont'd

1.15 MS Cont'd, Snake Posture

1.16 MS Cont'd



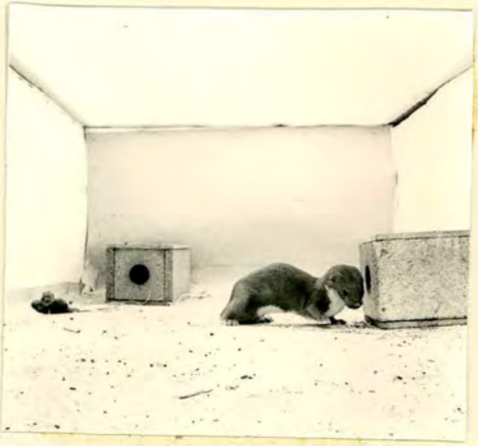
1.17 Squeal

1.18 Chirp

1.19 Approach, Look In-Stretched

1.20 Approach, Look In-Hunched

1.21 Turn Head Away



1.22 More Advanced Turn Head Away

1.23 Flee

1.24 Dig-At

1.25 Male Approach Female from Top of House

1.26 Female Approach Male, Sniff Side of Face

1.27 Female and Male Sniff Head to Tail

1.28 Female Approach Male Using Loping Gait

1.29 Male Follow Female

1.30 Male Front Feet Onto Female

1.31 Neck Bite

1.32 Male Drag Female

1.33 Male Drag Female Into House

1.34 Copulation

1.35 Copulation

A:13 Litters

Father & Mother	Date of Birth	Males	Females
Nk and Dd	14/2/77	3	3
Nk and Ch	15/7/77	2	1
Sk and Dd	31/7/77	3	2
Er and Dl	29/9/77	2	2
Mg and Jm	25/5/78	2	1
Il and Fs	21/6/78	2	8
Il and Fs	4/6/79	2	5
Ho and Ar	14/9/78	3	4
Ro and Ig	25/2/79	1	2
Or and Ar	30/7/79	1	2
	Total Young	22	30
	Percentage of each sex	41.2	58.8

A:14 Copulation to Parturition Dates

Pair	First Seen Copulating	Parturition	Gestation Days
Sk DD	27/6/77	31/7/77	34
Il Fs	16/5/78	21/6/78	36
Ho Ar	9/8/78	14/9/78	36
Ro Ig	23/1/79	25/2/79	33
		Mean	35

Appendix B

A total of 26 weasels were observed between 5/3/76 and 10/6/79. The histories of each animal are presented in Table B:1. In Figure B.1 the weights of the males are plotted over a 19 month period. Figure B:2 shows the weights of the females. Finally in Figure B:3 the weasels are classed into weight categories by the mean weight over the period of weighings. It can be seen that the females fall into continuous categories of weights, while the males separate into three distinct categories. This was discussed in Section 4:3.4. Note that once the males reached adult weight, they did not change weight classes.

Moors (1974) also found a large variation in the weights of wild caught male weasels in Northeast Scotland. He suggested that sexual selectivity affects females strongly, so that they remain small and can produce offspring with lower energy requirements than a theoretically male-sized female (Moors 1980). However, males are not so strongly affected. Hence variability is greater.

Table B:1 Notes on the Animals Used in the Experiments

Name	Date Acquired	Captive or Wild Born	Acquired from Whom/ Where
David	9/12/75	Captive	David Stephen
Alec	20/1/76	Wild	Cloich
Jerry	3/2/76	Wild	Cloich
Andy	18/2/76	Wild	Eskdalemuir
Dalgleish	28/2/76	Wild	Eskdalemuir
Goliath	21/3/76	Wild	Eskdalemuir
James	2/4/76	Wild	Eskdalemuir
Uncas	12/7/76	Wild	Cloich
Wotan	14/7/76	Wild	Cloich
PG	20/7/76	Wild	Cloich
Ignauton	21/8/76	Wild	Cloich
Cloich	29/8/76	Wild	Cloich
Arran	20/8/76	Wild	Lamancha
Feshie	30/9/77	Wild	Lamancha
Rannoch	17/6/78	Wild	East Craigs
Females			
Neko	11/11/76	Captive	Ian Linn
Morag	11/11/76	Captive	Ian Linn
Skirlie	11/11/76	Captive	Ian Linn
Eriska	14/2/77	Captive	Neko and David
Ilsa	14/2/77	Captive	Neko and David
Sasha	14/2/77	Captive	Neko and David
Lisa	15/7/77	Captive	Neko and Charlie
Fiona	31/7/77	Captive	Skirlie and David
Kirsty	29/9/77	Captive	Eriska and Dalgleish
Hoy	29/9/77	Captive	Eriska and Dalgleish
Rona	21/7/78	Captive	Ilsa and Feshie

* Only the weasels used in the observation chambers are listed above, other individuals were not used and not listed.

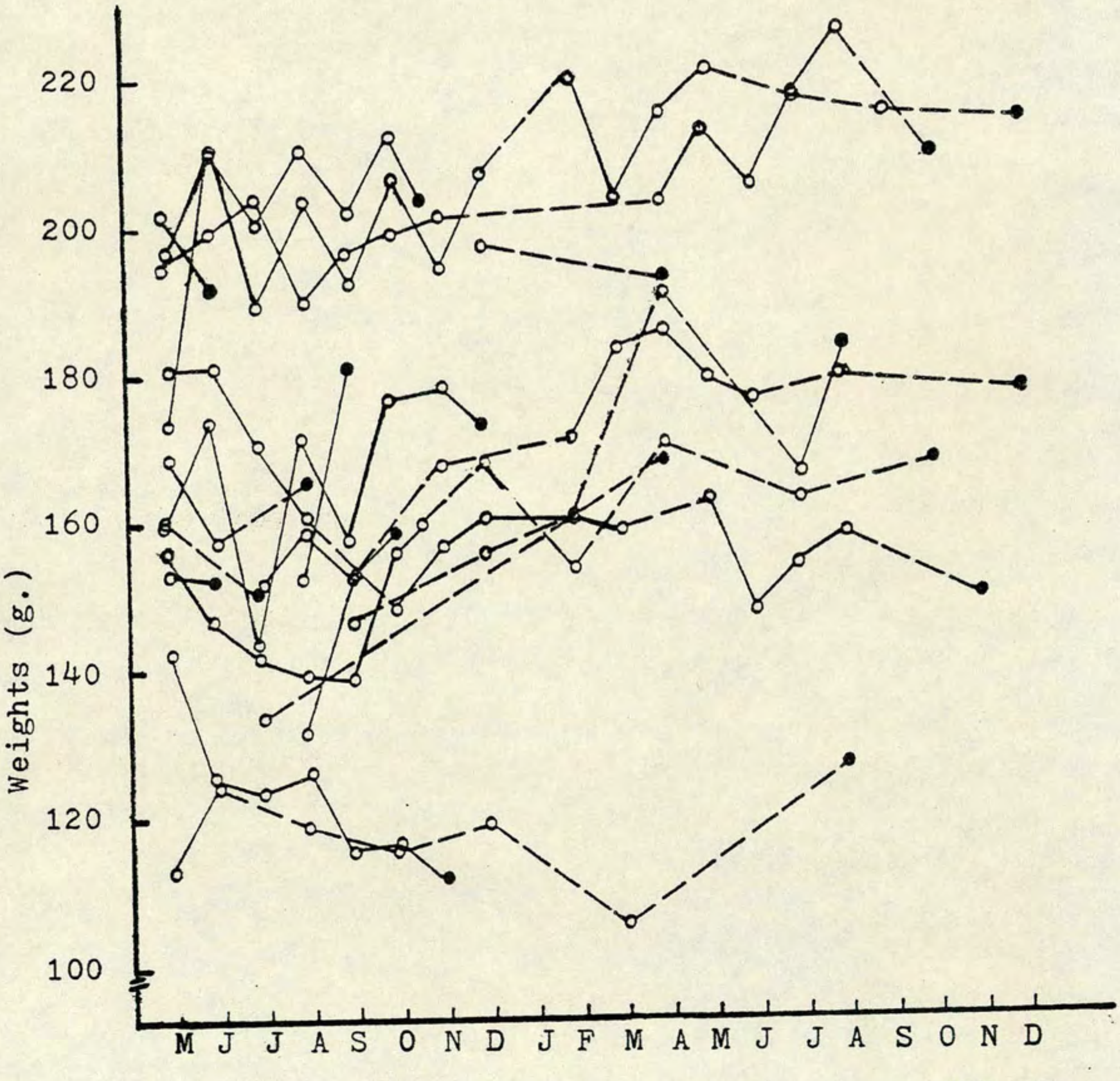


Figure B:1 Monthly Weights of Males (May 1977 through December 1978).

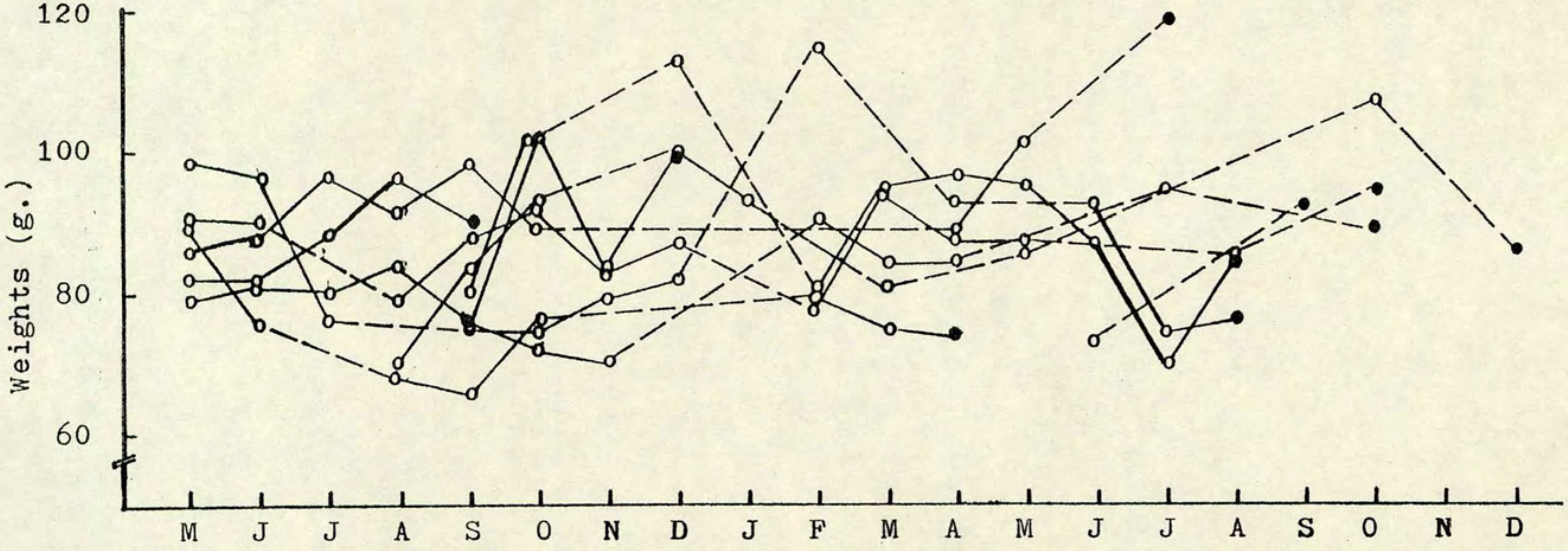


Figure B:2 Monthly Weights of Females (May 1977 through December 1978).

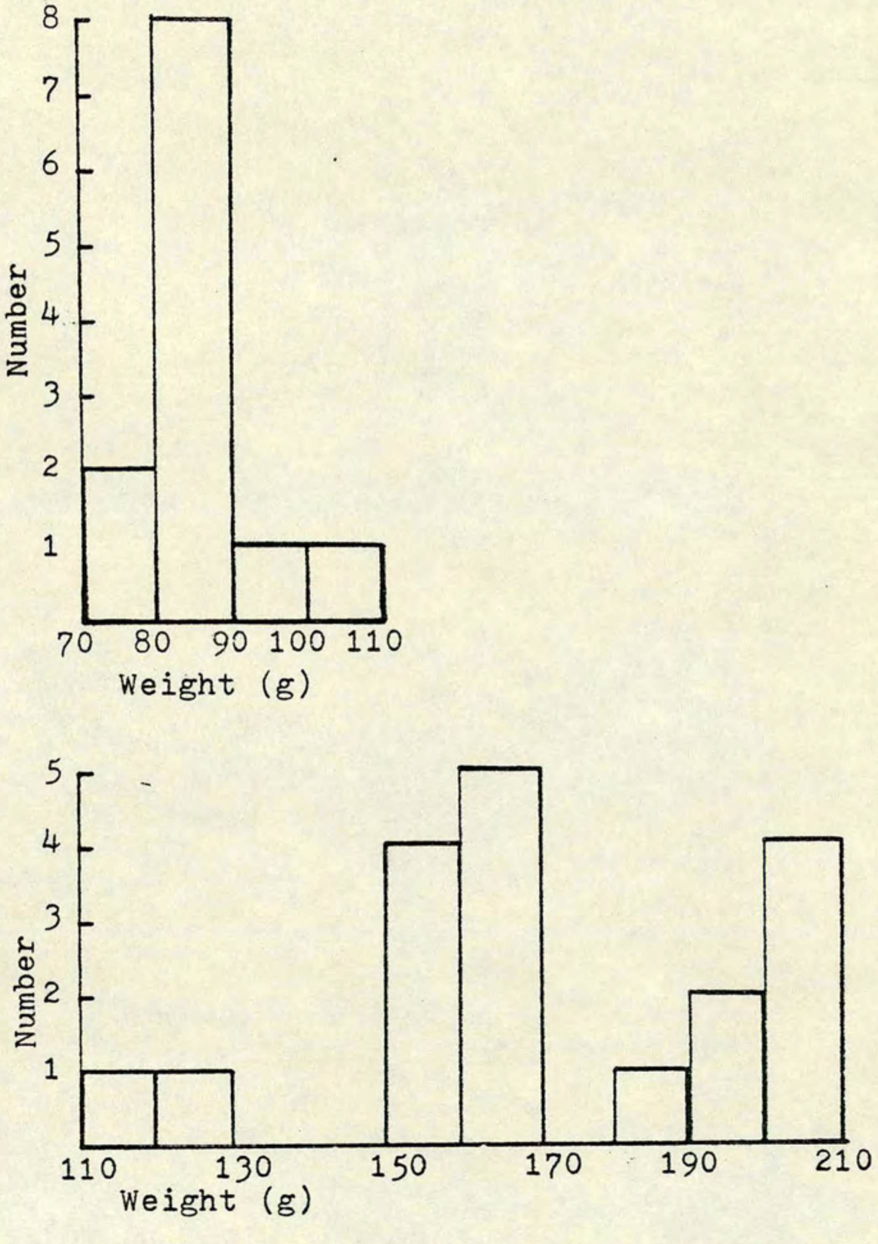


Figure B:3 The number of weasels whose mean weight falls between each 10 g. category.