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THE BEHAVIOUR AND ECOLOGY
OF THE AMERICAN MINK
MUSTELA VISON (SCHREBER)
IN A COASTAL HABITAT

by

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B.Sc. (Wales)

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ABSTRACT

The behaviour and ecology of coast-living mink were studied using a combination of dietary analysis, live-trapping, radio-tracking, and direct observation. A total of 82 mink were captured. Thirteen male and twelve female mink were fitted with radio-collars on 67 occasions. 3795 hours of radio-telemetric data were collected, approximately half of which was obtained manually by following the mink and recording its behaviour, location and habitat type at ten minute intervals. The remainder of the data were collected by remotely monitoring the presence or absence of a mink in its den.

A sample of 3007 scats were collected and analysed, 1957 of which were from known individuals, facilitating the analysis of sex differences in the diet. Lagomorphs were the major component of the diet for both sexes, accounting for 66% (bulk) of the male's and 31% of the female's diets. Females consumed more fish and crustaceans than males. There were significant changes in the contribution of lagomorphs to the diet throughout the year, and these were related to their estimated abundance. Both sexes consumed more fish in the winter, but females also showed a subsidiary peak in the consumption of fish during the summer.

Mink were found to be less active than in all freshwater habitats reported in the literature. This was attributed to the greater food availability in this coastal area. Males spent 4.6 hours per day out of their den, compared with 3.6 hours for females. The difference was due to increased levels of travel by males, particularly during the rut. Males and females spent similar lengths of time foraging (2.8 hours per day). Males were predominantly nocturnal during all seasons, 84% of their activity occurring during the hours of darkness. Their activity was closely tied with dawn and dusk. A similar relationship was not apparent for females, for which only 64% of activity was nocturnal. The activity of neither sex appeared to be related to the tidal cycle, though most of the female's shore-based foraging took place at low water. The habitats used by mink reflected to some extent their diet, females foraging primarily on the shore, males in the scrub and plantations. Both sexes used the rocky zone above the shore extensively when travelling between dens and/or foraging sites.

The social system generally conformed to the previously reported pattern of intrasexually distinct ranges. Intersexual range overlap occurred but was not found to be extensive. Males had larger home ranges than females, and home range sizes varied seasonally. The changes observed were primarily due to reproductive strategy. First matings occurred in mid-February. The mating system was promiscuous, males travelling widely during March in search of mating opportunities, with some males leaving the study area completely at this time.

Major sex-related differences in behaviour and ecology were due either to the differing reproductive roles of the sexes or to the consequences of a marked sexual dimorphism. The effects of the latter probably reduced levels of both exploitation and interference competition between the sexes. Males were more efficient at foraging than females and this may contribute to the 'extreme' levels of dimorphism in mink. Alternatively, sexual selection might have led to extreme dimorphism if the short lifespan of small mustelids led to a greater investment in body size, as an adaptation to increase mating success.

DECLARATION

I declare that this thesis is original. Any material which is not my own work has been identified as such. The analysis and interpretation of the results are entirely my own unless otherwise stated. No part of it has been submitted previously for a degree at any other university.

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Durham

1990

ACKNOWLEDGEMENTS

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DEFINITION OF TERMS

Age Classes

Bacular morphology in males, and for females, the presence of white hairs on the neck (a result of previous matings, permitted the separation of mink into two major age classes:

a. Adults; Individuals greater than one year of age.

b. Sub-adults; Individuals less than one year of age.

Kits were defined as sub-adults which were still associating with their mothers. Sub-adult mink that had dispersed from their natal area, but were less than seven months old (the age at which secondary sexual development started (Enders, 1952)), were termed juveniles.

Residential status

On the basis of trapping results and radio-tracking data, mink were divided into three classes:

a. Residents; Present for at least three successive months within a three kilometer length of coast.

b. Temporary residents; Captured or radio-tracked for two successive months within a three kilometer length of coast.

b. Transients; Captured during one month only.

This classification is based on that of Gerell (1971).

Statistics

The majority of the analyses are weighted two-way analyses of variance. The means quoted in the text are 'least square means' for the effect under consideration. These were used instead of the normal arithmetic mean because they adjust for the effects of other factors in the presence of unequal sample sizes (i.e., unbalanced designs). For further information about least square means and their calculation, see SAS Institute Inc., (1985). As a general guide, the arithmetic means rarely differed by more than 5% of the least square mean value.

Means are quoted plus or minus one standard error of the mean, whereas in the figures, the mean plus one standard error (bar) is plotted. If means are plotted without standard error bars, this indicates (unless otherwise stated) that 3-point running means have been plotted.

Figures, in general, do not have sample sizes plotted on them. Sample sizes for the trapping, dietary and radio-tracking analyses, are given in Tables 2.2, 3.1 and 4.1–2 respectively.

1. GENERAL INTRODUCTION

1.1 Background

The accidental release and subsequent establishment of feral populations of the American mink *Mustela vison* (Schreber) throughout Europe, has prompted a series of investigations, aimed at determining the niche occupied by mink, and their likely effects on native fauna (e.g., Gerell, 1968; 1970; Erlinge, 1972; Chanin and Linn, 1980; Wise *et al.,* 1981). The majority of these studies examined mink populations in riparian or lacustrine habitats. Few, until recently, have dealt in detail with coast-living mink, even though studies in North America have shown that mink densities may be very high in this type of habitat (Hatler, 1976).

In a series of papers based on mink in the present study area, the feeding ecology and some aspects of the behaviour of mink in a coastal habitat were examined (Dunstone and Birks, 1983, 1987; Birks and Dunstone, 1984, 1985). One particularly interesting finding was a marked sex-related difference in the diet (Birks and Dunstone, 1985), which they attributed to the marked sexual dimorphism in body size (1.74 : 1, male : female). Other sex-related differences, which could be related to the larger size of the male, have included greater levels of activity by males (Whitman, 1981) and larger male home range size (Gerell, 1970; Chanin, 1976; Hatler, 1976; Whitman, 1981; Birks and Linn, 1982).

These sex-related differences provided the impetus for the current study. Within the broader scope of a study of mink in a coastal habitat, the primary aim was to investigate the sex-related differences in a number of aspects of mink ecology and behaviour. An attempt was made to separate those differences due to body size dimorphism from those expected because of the differing reproductive roles of the sexes. This information might then provide clues to those factors which were responsible for the evolution of extreme sexual dimorphism in mink and other small mustelids.

1.2 The study animal : *Mustela vison* (Schreber).

1.2.1 Distribution

The American mink, a member of the family Mustelidae (Order Carnivora), is a predatory, semi-aquatic mammal native to the Nearctic. Its distribution encompasses most of North America, extending north through Canada and Alaska, but not the high arctic, and south to Florida in the east and New Mexico in the west. Its taxonomy and range have been discussed thoroughly by Hatler (1976).

Mink were introduced into the Palearctic region following their importation into Europe for the fur trade in the 1920s and 1930s. Escapes from mink farms led to the establishment of feral populations throughout many countries in Northern Europe (Wildhagen, 1956; Gudmundson, 1952; Westman, 1966; Gerell, 1967a; Thompson, 1968; Deane and O'Gorman, 1969), whilst in the USSR they were deliberately released into the wild to provide a population for hunting and trapping (Pavlov, 1970).

1.2.2 Morphology

The mink is similar in size and shape to the polecat *Mustela putorius*, having a long cylindrical body and short legs. It has partially webbed feet in association with its aquatic habits but its adaptations are not as extensive as those of the otter *Lutra lutra* (Sinclair, Dunstone and Poole, 1974). Its pelt is usually very dark brown though selective breeding has resulted in a wide variety of colours which occasionally turn up in feral populations (Birks, 1987). It also has areas of white fur on its underside. The area, shape and location of these patches vary considerably from individual to individual (Fairley 1979, Chanin 1983). Mink, like other mustelids, exhibit a marked sexual dimorphism in body size, males being heavier by a factor of 1.64 to 1.91 (Moors, 1980).

1.2.3 Diet

Investigations based on gut contents of commercially trapped individuals (Sealander, 1943; Korschgen, 1958), individuals trapped for control purposes (Gerell, 1968; Day and Linn, 1972), and based on faecal material (e.g. Gerell, 1968; Wise *et al.*, 1981) have shown that the mink is an opportunistic predator, utilizing whatever small- or medium-sized prey are available. Prey range in size from the European hare *Lepus europeus* (Birks and Dunstone, 1984), to invertebrates such as the water beetles*Dytiscus* sp. (Hamilton, 1959). Vegetable matter may occasionally be consumed (Hamilton, 1959).

In riparian habitats, aquatic prey such as fish and crayfish *Astacus astacus*, and also amphibians make up a large proportion of the diet (Hamilton, 1959; Gerell, 1968; Erlinge, 1969, 1972; Akande, 1972; Cuthbert, 1979; Melquist *et al.*, 1981). In marshes and wetlands, ground-nesting birds such as waterfowl may be selectively predated, when present (Gerell, 1968; Sargeant *et al.*, 1973; Eberhardt and Sargeant, 1975; Chanin and Linn, 1980; Wise *et al.*, 1981). Geographic differences in dietary composition are often related to the distribution of prey species. Rabbit often forms the most important prey item in the British Isles (Wise *et al.*, 1981; Dunstone and Birks, 1987) whereas in Sweden,

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crayfish were found to be the major component (Gerell, 1967b, 1968; Erlinge, 1969, 1972). In North America however, muskrats and small rodents are reported to be the species most frequently taken (Sealander, 1943; Korschgen, 1958; Hamilton, 1959).

The occurrence of different prey items in the diet also varies with seasonal changes in their abundance or vulnerability. Rodent predation peaks in the autumn (Gerell, 1968), whilst lagomorph predation is greatest in the summer when young rabbits are most numerous (Dunstone and Birks, 1987). Fish consumption usually peaks in the winter and Gerell (1968) suggested that this was due to their increased vulnerability in colder waters. Crayfish on the other hand become more vulnerable during the summer as their mobility increases with rising water temperature (Gerell, 1967b, 1968).

In coastal habitats a major part of the diet is composed of rock pool fish, and crustaceans, usually crabs (Gerell, 1968; Hatler, 1976; Cuthbert, 1979; Dunstone and Birks, 1987). Mammals, particularly lagomorphs make up a significant proportion of the diet of mink in Scotland (Cuthbert, 1979; Dunstone and Birks, 1987). The majority of the birds consumed in these latter studies were Charadriiformes, probably Laridae (gulls), and the authors suggested that they were mostly taken as carrion.

Diet studies based on the analysis of gut contents suggested that there may be sex differences in the diet (Sealander, 1943; Hamilton, 1959; Casson and Klimstra, 1983). Large mammals, principally muskrats and lagomorphs, occurred more frequently in the guts of males, as opposed to females. Dietary studies which rely on the analysis of faeces usually do not allow differentiation between the scats from males and females. Recently however, using radio-tracking to locate the dens of known individuals, Birks and Dunstone (1985) reported sex differences in the consumption of lagomorphs, fish, crustaceans and large birds. These differences were attributed to the marked sexual dimorphism in the body size of mink, allowing males to take larger prey.

1.2.4 Activity Patterns

Mink spend a large proportion of their time in their dens (Marshall, 1936) though levels of activity vary both seasonally (Whitman, 1981) and between different habitats (Gerell, 1969; Hatler, 1976; Whitman, 1981). Males tend to be predominantly nocturnal and become active around dusk, whereas females may be more diurnal (Gerell, 1969) and are less active than males in all seasons (Whitman, 1981). Crepuscular activity patterns have been reported by Marshall (1936) and Whitman (1981) in riparian habitats; in coastal

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habitats activity patterns were closely tied to the tidal cycle, as well as the day/night cycle (Hatler, 1976). It has been suggested by Gerell (1969) that activity patterns are probably guided by the activity cycles of the main prey species.

1.2.5 Habitat Utilization

Mink are invariably found distributed along aquatic habitats such as rivers and streams (Gerell, 1970; Chanin, 1976), lakes (Gerell, 1969; Birks, 1981), marshes (Errington, 1943; Eberhardt and Sargeant, 1977) or the sea coast (Gerell, 1968; Hatler, 1976, Dunstone and Birks, 1982). Marshall (1936) and Burgess (1978) reported that the majority of mink activities and dens occurred close to the water's edge, though Linn and Birks (1981) observed that activity was not unusual up to 200m from water especially where aquatic prey was scarce.

Mink generally avoid exposed or open areas (Gerell, 1970; Burgess, 1978) and tend to be associated with bushy or wooded cover adjacent to aquatic habitats (Marshall, 1936; Gerell, 1970; Allen, 1983). This behaviour is less well-defined when terrestrial foods become a significant proportion of the mink's diet (Allen, 1983). Wetlands with irregular and diverse shorelines provide more suitable mink habitat than do wetlands with straight, exposed shorelines (Allen, 1983). Habitats provided by small streams are preferred to those associated with large broad rivers (Allen, 1983). Mink are common along streams where there is an abundance of debris for cover and pools for foraging (Melquist *et al.*, 1981) and Burgess and Bider (1980) demonstrated that improving a stream by creating pools and providing cover within the channel led to an increase in mink activity. The preferred use of stream and lake edges may be due to mink not being able to forage efficiently in open water (Dunstone and O'Connor, 1979). In a coastal habitat, Hatler (1976) suggested that sheltered rocky shore is ideal for mink since the home ranges of resident animals are very much smaller than those reported for riparian and lacustrine mink. He attributed the higher mink populations to the relatively consistent food supply available throughout the year in the intertidal zone.

Mink do not use the whole of their range evenly (Gerell, 1970). Intensity of use varies because of the heterogeneity of prey distribution and because of social factors (Gerell, 1970). Birks (1981) found that a home range typically contained one or two core areas (which occupied only a small part of the range) in which most of the foraging occurred. When prey was abundant throughout the whole range, these core areas were

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not so well defined. Utilization of the home range varied in response to seasonal changes in prey availability (Gerell, 1970; Birks and Linn, 1982).

1.2.6 Den Use

Mink typically use a number of dens throughout their home range for shelter, concealment, and the rearing of young (Marshall, 1936; Schladweiler and Storm, 1969; Gerell, 1970; Melquist *et al.*, 1981; Birks and Linn, 1982). Mink usually use dens which are close to preferred foraging areas, or concentrations of prey (Linn and Birks, 1981; Melquist *et al.*, 1981), and moves between the dens typically take place at night (Birks and Linn, 1982). The most commonly used den sites in riparian habitats are cavities beneath tree roots at the water's edge, however preferred den sites were usually located in rock piles well above the water line (Gerell, 1970). Many different types of den have been recorded, ranging from the burrows of muskrats (Eberhardt, 1973) and rabbit (Chanin, 1976; Wise, 1978; Birks, 1981), to hollow trees, root systems, rock piles, birds' nests and man-made structures (Birks, 1981). Such dens can be used for less than one day (Birks and Linn, 1982) up to 40 days for a female with kits (Eberhardt and Sargeant, 1977). Thus the lack of suitable dens may limit the value of a habitat to mink (Errington, 1961; Gerell, 1970; Birks and Linn, 1982).

1.2.7 Home range and Territoriality

The mink is a solitary carnivore (Gerell, 1970). Intrasexual and intersexual interactions are rarely seen except during the mating season (Hatler, 1976; Whitman, 1981). The mink's association with an aquatic habitat, in combination with a solitary habit, leads to a series of linear home ranges, the configuration of which reflects the shape of the water body (Gerell, 1970). Trapping studies (Gerell, 1970; Chanin, 1976) indicate that range overlap between individuals of the same sex is uncommon, whereas intersexual overlap is common. The social system thus appears similar to that of other solitary mustelids such as the weasel *Mustela nivalis* (Lockie, 1966; Erlinge, 1974; King, 1975), the stoat (Erlinge, 1977b), the otter in riparian habitats (Erlinge, 1968) and the marten *Martes americana* (Hawley and Newby, 1957).

The existence of discrete home ranges in which other individuals do not settle, suggests the influence of territorial behaviour, and Gerell (1970) suggested that the territorial system in mink seemed to be maintained by oscillatory guarding movements covering the whole territory. Territories do not appear to be completely exclusive, however. There is

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often spatial overlap at the borders of adjacent ranges. Overlap generally occurred during the incidental absence of one owner (Gerell, 1970; Whitman, 1981), thus perhaps only certain areas of the range are actively defended; or the territorial system could be defined in terms of a spatio-temporal framework rather than a strictly spatial one.

Gerell (1970) found, by simultaneously radio-tracking a number of mink, that a female could, at least temporarily, defend a territory against a male. His trapping data indicated a system where a male's range could include the range of one or more females, but he suggested that this did not preclude the females defending a smaller territory against the male in whose territory she lived. Birks (1981) found that only a third of the resident female mink had extensive territory overlap with males. Mink may therefore differ from other mustelids, for example stoats and weasels, where the female territories commonly lie totally within those of males. This type of system depends on the delicate and varying balance of aggression and dominance between the males and females (Lockie, 1966; Erlinge, 1977a). Erlinge (1977a) suggested that the avoidance of the male by the female is an important contributory strategy to ensure the female's continued residence. Birks (1981) argued that the linear home ranges of mink made it difficult for a female to avoid a male, and this made overlapping territories less feasible.

The extent of a mink's home range has been estimated by a number of authors. In early studies based on trapping data it was estimated in 2-dimensions, as an area (Marshall, 1936; Mitchell, 1961) but since mink normally travel in close association with water, most workers quote range size simply in terms of length of waterway (Gerell, 1970; Chanin, 1976; Hatler, 1976; Whitman, 1981; Birks, 1981; Dunstone and Birks, 1982). The home ranges of mink in coastal habitats were smaller than those in riparian habitats (Hatler, 1976; Dunstone and Birks, 1982), suggesting more favourable foraging conditions.

Although the length of a male mink range was always larger than that of a female, the size did not increase in proportion to the increased male body-weight (Birks, 1981). Gerell (1970) suggested that the most important factor affecting home range size was the population pressure. This in turn was a function of the population density in relation to the carrying capacity of the area. Further evidence for the importance of population pressure was reported by Birks (1981), who found home ranges in socially unstable areas (caused by mink control operations) to be much greater than that in stable areas.

Both Gerell (1970) and Chanin (1976) found that in some areas, not all of the available space in a riverside habitat was filled. Isolated territories were still formed

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in the absence of adjacent territories. Gerell (1970) considered that other factors could affect boundary delimitation in these cases, for example, topographic features such as bridges, or transitions between banks with good and sparse cover.

In addition to the resident mink occupying a system of well-defined home ranges or territories, there may also be transient individuals. Although transient individuals may be caught at most times of the year (Birks, 1981), they are essentially a seasonal phenomenon related to the mink reproductive cycle. In the autumn, the young of the year become independent of their mothers and try to set up territories for themselves (Chanin, 1976), leading to an increase in numbers of transient. During late February to early April there is another increase in the population of transients, but this is almost exclusively composed of males. Many authors have commented on the long distances moved by male mink at this time (Marshall, 1936; Gerell, 1970). Chanin (1976) and Birks (1981) both report that males desert their territories at this time of year in search of females.

1.2.8 Reproductive behaviour

The physiology of mink reproduction has been extensively studied because of its importance to the ranching of mink for their fur (Hansson, 1947; Enders, 1952; Venge, 1971). These accounts detail specific behaviours associated with mating, but apart from Hatler (1971) there have been no reports of observations of mink mating behaviour in the wild.

The mink breeds once a year (Hansson, 1947; Enders, 1952). Both males and females are fertile at nine months of age. The females become receptive at the end of February, and remain in season possibly until early April. Female mink have been known to become pregnant as early as late January on mink farms; but in the wild mink populations from higher latitudes, mating may not take place until May (Hatler, 1976). Several authors have commented on the promiscuous nature of the mink mating system (Marshall, 1936; Enders, 1952; Mech, 1965; Hatler, 1971; Birks, 1981). Male mink have been reported moving widely during the mating season (Marshall, 1936; Gerell, 1969). Chanin (1976) and Birks (1981) stated that the males vacate their territories in the mating season in their search for females, and that they rarely return to their original territories (Chanin, 1976).

Hatler (1971) described the mating season as a time of great intraspecific stress resulting in individuals in poor condition; males due to intersexual competition for females, and females due to their being unable to feed properly because of the attentions of males.

He reported the death of a female as a probable result of excessive male harrasment. On mink farms, there have been deaths reported when the male accidentally punctures the skull of the female with his incisors (Enders, 1952).

Ranch-based studies have shown that the physiology of the female reproductive cycle is quite complicated. Female mink are induced ovulators (Hansson, 1947; Enders, 1952). Ovarian follicles develop but it requires the "violent" stimulation of copulation for ovulation to occur (Enders, 1952). If ovulation does not occur, the follicles become atretic and another group or "wave" of follicles starts to develop. If stimulation occurs, then 18 hours later, the follicles show a considerable degree of enlargement, and by 50 hours most will have ruptured and development of follicles begins again. A number of "waves" result, separated by a period of between six and twelve days (Enders, 1952). There may be as many as four waves per season, but there are often fewer (Venge, 1971). Many breeders are convinced that there are periods of increased and decreased female receptivity, (presumably related to this cycle) though the scientific evidence for cyclic peaks in female receptivity is not convincing (Enders, 1952).

Mink are unusual amongst mammals in that females are capable of both superfecundation and superfoetation. The former can result in the mixed paternity of a litter resulting from a single ovulation; the latter arises because fertilization does not stop further ovulations, so even if a female becomes pregnant by one or more males, ovulations at a later date can result in kits fathered by another male(s) (Enders, 1952; Shackleford, 1952). This situation may actually be more widespread amongst mammals, but few non-domestic species have been studied in such detail.

If a female is mated more than once before ovulation, it is usually sperm from the final mating that fertilizes most eggs and is responsible all or most of the kits in that litter (Venge, 1971). Similarly, if a female has been fertilized by one or more males and six to ten days later is then mated by another male, most of the kits in the eventual litter will have been fathered by the last male. This is because another ovulation usually takes place, and blastocysts from the later ovulation appear to survive better (Enders, 1952; Shackleford, 1952).

On mink farms, females are not always receptive and may strongly resist the mating attempts of a male. Enders (1952) found that if a male managed to achieve a strong grip on the neck of the female then copulation usually followed. The very severe wounds that sometimes occur on the necks of females in the wild (pers. obs.) suggest that they

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are mated many times. These wounds do not occur on mink farms where the number of matings are controlled by man. (Enders, 1952).

Gestation of ranch mink on farms is of very variable duration (typically 35–72 days). This is due to delayed implantation. In temperate latitudes, even though fertilization takes place between February and April, implantation does not occur until early April. Its timing is remarkably uniform, being determined by the increasing length of day. This results in much less spread in the date of parturition. The time from implantation to parturition is approximately 30 days, with births occurring in late April or early May (Enders, 1952). The females bring up their kits unaided by males.

1.2.9 Population Biology

Population parameters are usually estimated from trapping studies. The first studies (Errington, 1936; Hibbard, 1955; Mitchell, 1958; Balser, 1959; Adams, 1963; Birney and Fleharty, 1966) were based on commercially-exploited populations where the material had been derived from trapping, usually during the winter season. In these studies, the age ratio (sub-adults caught per adult capture) was usually high. This occurred because high mortality, in this case caused by trapping, is reflected in a greater proportion of juvenile animals in the population.

Most of these studies, as well as some others involving live-trapping (Chanin, 1976; Hatler, 1976) show a male bias in the sex ratio. Chanin (1976) found that the sex ratio calculated from trapping results changed with the season, because male mink were caught far more often than females during the winter. Gerell (1971) found that during live-trapping studies, not only did trapping success vary with season, but the rate of recapture varied with sex, age, and the study area under investigation.

The fecundity of females has been estimated at between 5.5 and 5.8, based on uterine scars, nipple counts and numbers of embryos, (Chanin, 1976) and 3.6 to 3.8 based on direct observation (Gerell, 1971), the latter probably being a better estimate of the number of young reaching independence. Mortality has not been estimated as such but two separate trapping studies have indicated an almost complete turnover of the population in three years (Mitchell, 1961; Gerell, 1971).

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1.3 Sexual dimorphism in mustelids

Sexual dimorphism in body size is a characteristic feature of the family Mustelidae, and is particularly evident in the sub-family Mustelinae which includes weasels, stoats, mink and martens. Males are always larger, sometimes by a factor of two but the ratio varies between species and geographically within species (McNab, 1971; Moors, 1980; Ralls and Harvey, 1985).

Theoretical explanations for sexual dimorphism fall into two groups: those suggesting that it evolved as a means of reducing competition between the sexes by reducing niche overlap, and those suggesting that dimorphism arose because of selective pressures favouring large size in males and/or small size in females.

Many mustelids have evolved elongate bodies and relatively short legs, presumably as an adaptation to help them pursue fossorial prey into burrows. This shape could have substantial "costs" in terms of higher energy demands due to heat losses incurred by the resultant increase in surface area to volume ratio. Brown and Lasiewski (1972) speculated that the greater costs of the elongate shape must have been compensated for by the increased foraging efficiency resulting from the ability to enter burrows, but that it also led to an increase in the intensity of intraspecific competition for food. They suggested that sexual dimorphism could have evolved to reduce intraspecific competition by allowing each sex to exploit prey which were less available to the other sex.

The reduction in competition for food arising from size-related niche separation was also suggested by Rosenzweig (1966, 1968) to explain the coexistence of groups of sympatric predators or "hunting sets", occupying similar habitats and employing similar hunting strategies. McNab (1971) found a uniform gradation in size from the smallest to the largest of five North American mustelids, the least weasel *Mustela nivalis*, stoat *M. erminea*, long-tailed weasel *M. frenata*, American marten *Martes americana* and fisher *Martes pennanti*. Body-weight increased by a factor of two for each species, suggesting an even spacing of ecological niches, and McNab concluded that the maximum and minimum size attained by a predator was constrained by the occupation of adjacent niches by other members of "the set". Thus, for example, the stoat grew larger in the north in the absence of the larger long-tailed weasel.

Male and female mustelids frequently occupy slightly different niches. There is a consistent trend for females to consume smaller prey than do males. Intersexual differences in niche utility have been shown for weasels (Day, 1968; Erlinge, 1975; King,

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1977), stoats (Day, 1968; Brugge, 1977; Erlinge, 1979), polecats (Brugge, 1977), ferrets (Roser and Lavers, 1976), mink (Sealander, 1943; Birks and Dunstone, 1985) and martens (Yurgenson, 1947). In stoats, this has lead to differences in the habitat utilization of each sex (Erlinge, 1979).

If sexual dimorphism had evolved primarily to encourage the exploitation of different food resources, then marked sex-related differences in the feeding apparatus would be expected. In some bird species, differences in feeding apparatus as well as body size are apparent (Selander, 1966; Holyoak, 1970), and sex-related differences in the mouthparts have also been noted in the skate *Chondrichthyes rajidae* (Feduccia and Slaughter, 1974). Differences in head shape have been reported for weasels (Hall, 1951), stoats (Petrov, 1956) and mink (Wiig, 1986). The canine and carnassial teeth are larger in the male, as are anatomical features to allow the accommodation of larger and more powerful jaw muscles. These sex-related differences could lend support to the niche separation argument for dimorphism. Petrov (1956) however, found that the dimorphism in the skulls of stoats becomes especially apparent in old males and Erlinge (1979) considered that if it occurred as a result of selection for differential prey exploitation, then dimorphism should have developed in early life. He also suggested that the large size of the canine teeth in males could also be explained in terms of competitive mating.

Arguments in favour of differential niche utility as a basis for dimorphism have, however, been criticized by a number of authors (Erlinge, 1979; Moors, 1980; Ralls and Harvey, 1985). They fail to explain why, in mustelids, the male is always the larger (Moors, 1980), whilst in families of the Carnivora, such as the Viverridae and Hyenidae, reversed sexual dimorphism has occurred (Ralls, 1976). Moors (1980) pointed out that although sexual dimorphism may be an advantage for coexistence in competitive equilibrium, it can also be maintained in several other ways, for example different foraging strategies, activity patterns, or by differences in habitat utilization (Hespenheide, 1975).

Being the smaller member of a dimorphic pair may, in fact, be a disadvantage. Prey density is inversely related to prey size (Elton, 1927), and, by a reduction in size, an individual may accrue the benefits of a more abundant food supply (Storer, 1966). However, Wilson (1975) pointed out that "larger animals eat things unavailable to smaller competitors, but the reverse is much less true", and as such, small size may be a severe selective disadvantage, particularly for carnivores relying on fluctuating or unpredictable prey (Moors, 1980). Small size does not reduce competition, as competition arises when

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food is scarce or limiting. In this situation, the limited breadth of prey species available to a smaller individual is a disadvantage, the adverse consequences of which have been described for female weasels and stoats (Lockie, 1966; Erlinge, 1974), and female pine martens *Martes martes* (Weckworth and Hawley, 1962).

If dimorphism arose as an adaptation by one sex to the predation of a particular size of prey, then there should be a discernible relationship between prey size and predator size. However, sexual dimorphism is still found in mustelids, such as otters and badgers (albeit to a lesser extent), where there is little difference in the size of the prey taken by the different sexes, because their prey consist exclusively of items smaller than themselves (Moors, 1980). Although a positive relationship exists, Ralls and Harvey (1985) found that prey size was not a good, or even the best, predictor of predator size.

The arguments for character displacement (i.e., the constraint of body size imposed by sympatry with a smaller or larger competing species) as a means by which dimorphism between competing predators arose (McNab, 1971) has also been criticized by Ralls and Harvey (1985). They found that the observed geographical variations in the size of *M. erminea* in North America were not correlated with the presence or absence of either *M. nivalis* or *M. frenata*, and neither of these latter species covaried in size or degree of dimorphism with the stoat.

The problems of invoking niche utility arguments to explain the observed aspects of mustelid biology lead to alternative explanations referencing other factors that select for the size of each sex in isolation.

Sexual dimorphism is characteristic of, and most pronounced in, polygynous or promiscuous mammals (Brown, 1975, Gittleman, 1984). Evidence that intersexual selection favours larger males is only indirect, and is based on observations of fighting during the mating season. This has been reported for polecats and ferrets *Mustela furo* (Poole, 1970, 1972), mink (MacLennan and Bailey, 1969), pine martens (Weckworth and Hawley, 1962), and weasels *Mustela nivalis* (King and Moors, 1979). A dominance hierarchy is thought to exist which depends in part on body size (Poole, 1972; Erlinge, 1977a; Birks, 1981). As many male mustelids are thought to have a polygynous or promiscuous mating system (Erlinge, 1979; Birks, 1981; Sandell, 1986), greater dominance by virtue of size is likely to lead to a greater number of matings.

An increase in male size may also carry with it a number of other benefits related to mating opportunities. It could lead to an increased speed of movement and therefore a

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higher encounter rate with females. A larger size could also lead to an increase in range size, as home range size is related to metabolic requirements (McNab, 1963; Gittleman and Harvey, 1982; Mace *et al.*, 1983) and a larger range will probably contain more females. Large male size may also be useful in subduing females (Simms, 1979).

Factors promoting large male size may not be sufficient to account for the magnitude of the sexual dimorphism observed in mustelids (Ralls and Harvey, 1985). Erlinge (1979) and Moors (1980) suggested that the smaller females might be selected to reduce their energy demands, especially during the breeding season when the demands on the female will be the greatest as she rears the young without male assistance. The energy requirements of female mammals may increase by approximately 25% during gestation, and can double during lactation (Migula, 1969). East and Lockie (1964) found that a female weasel increased her food consumption by 127% during lactation when she had a litter of four offspring. Any savings the female can make in her own requirements could be channelled into reproduction. Moors (1980) calculated that a hypothetical, male-sized female weasel would have to catch an extra half a vole each day to meet her own increased metabolic needs, and Powell and Leonard (1983) similarly calculated that it would be difficult for a male-sized female fisher to find the extra 300-500 KJ/day it would need.

Ralls and Harvey (1985) argued that small females would only be favoured if hunting efficiency remained constant for individuals of different sizes, and as nothing was known about the relationship between weasel size and hunting efficiency, they considered further speculation worthless. They suggested that a more profitable way of viewing the size differences would be to seek the selective pressures which have operated to make males so large and energetically inefficient. However, a little was known about intersexual differences in mustelid foraging efficiency. For example, Powell and Leonard (1983) had found that the foraging strategy employed by female fishers during lactation was similar to that of males. The maximum daily energy expenditure was also very similar, suggesting that the reduced maintenance requirements of females almost exactly compensated for the higher costs of reproduction, and that there was an energetic advantage to being smaller whilst lactating.

The food available to growing young can have significant effects on their adult size. East and Lockie (1964) raised a weasel litter in captivity, feeding the kits *ad libitum*. The female kits grew approximately 40% larger than their wild counterparts whilst males showed a 90% increase. Powell (1979a) reported that males from a population of fishers,

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translocated to an area where the food supply was unexploited by other predators, were significantly heavier than the original males, whereas females were not. Laboratory studies revealed that the size attained by adult males was much more dependent on the plane of nutrition than was female size (mink : Sinclair et al., 1962; other mammals : Widdowson, 1976). Adult male size is particularly dependent on food resources during the initial growth period, whereas the size a female attains is largely unaffected (Sinclair *et al.*, 1962). Kits of a high initial weight are more affected by energy restriction than are smaller individuals (Jørgensen et al., 1962), and so food restriction will have a greater consequence in males. Ralls and Harvey (1985) used these facts to explain the large geographic variations in sexual dimorphism they found throughout North America, suggesting that local environmental conditions affected the amount of food that was available during the critical male growth period.

No one theory propounded so far is likely to explain all the observed diversity in dimorphism within the mustelids. Theories evoking differential niche utility as a basis for dimorphism have largely been superseded by those calling upon differing selective pressures acting on the sexes during the reproductive cycle, though Moors (1980) commented that a reduction of intersexual competition could be a valuable side-effect of dimorphism, and as a secondary benefit, could augment the main selective pressures favouring the trait. Intrasexual competition favouring large size seems to have gained acceptance as the factor primarily responsible for sexual dimorphism, and although further pressure, selecting for small females has been proposed, it remains to be proved that the costs of reproduction are any easier to meet in a small animal.

1.4 Scope of the present study

In this study, I have attempted an integrated approach to the investigation of sexual dimorphism in mink. It is based on observations of a population of coast-living animals that preliminary studies had shown to be living at high density. The open nature of the habitat, and the lack of persecution, permitted extensive long-term study, with the possibility of direct observation of some aspects of the mink's behaviour. The dataset comprises approximately 2500 hours of radio-tracking data collected by myself between October 1982 and April 1985, and in addition a further 1300 hours of radio-tracking data collected by Dr J.D.S. Birks, post-doctoral research assistant to Dr. N. Dunstone between October 1982 and March 1984.

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Chapter 2 describes the study area and details the main methods on which the study relied.

Chapter 3 examines the seasonal and sex-related differences in the diet of mink, and examines, in detail, the way these differences are related to the availability of the prey types to each sex. Seasonal and sex-related differences in the level and nature of activity, and its distribution throughout the circadian and tidal cycles, are examined in Chapter 4, whilst Chapter 5 looks at the mink's utilization of different habitats within the study area. It also examines mink denning behaviour, as the availability of suitable den sites is thought to affect the suitability of habitats for mink (Allen 1983).

The interrelationships between individual mink in terms of their spacing patterns and reproductive behaviours are examined in Chapter 6.

Finally, in Chapter 7, sex-related differences in ecology and behaviour in mink are summarised and examined for relevance to the continuing discussions regarding the extreme levels of dimorphism found in the family Mustelidae.

2. GENERAL METHODS

2.1 Study Area

The study area was centred on the Ross Peninsula (O.S. grid reference NX6543) on the west coast of the Dee Estuary, near Kirkcudbright, Dumfries and Galloway Region, in south-west Scotland (Plate 2.1). The study area consisted of 12 km of rocky coastline though the majority of the research took place in the central 6 km of coastline (Figure 2.1).

The study area provided a heterogenous habitat. Each mink home range comprised a stretch of shoreline with a littoral zone. This ranged from sheer rock face below the cliffs, for example to the west of Slack Heugh, to wide rock shelves with numerous rock pools, such as the Bents, very long boulder beaches again with many rock pools, like the shore below the Fauldbog or Fox Craig, to shallow sloping sandy bays, i.e., Ross and Brighouse Bay (Figure 2.1). The rocky shore was exposed and macrophytic algal cover was low. The different types of shore varied in utility to mink because of differences in exposure, number of rock pools, and seaweed cover, all of which probably affected the abundance of aquatic prey. In addition, the degree of exposure affected the chances of carrion being washed up.

Above the high tide level there was usually an area of rock (Silurian greywacke) which provided an abundance of den sites. Along part of the coast the rocky zone comprised high sea cliffs (for example Slack Heugh, Figure 2.1) which supported quite high numbers of nesting sea birds during the summer months. There were also sea cliffs to the extreme west of the study area. Above the rocky zone in most areas, there was a region of scrub comprising hawthorn *Crateagus monogyna*, gorse *Ulex europaeus*, and bracken *Pteridium aquilinum*. This scrub provided cover for many terrestrial prey species including lagomorphs, birds, mice and voles.

Inland, the major part of the study area comprised farmland, principally unimproved and improved pasture bounded by dry stone walls. Barley *Hordeum* sp., and kale *Brassica oleracea* were grown in some of the fields. Good populations of hare *Lepus europaeus* and rabbit *Oryctolagus cuniculus* were found within the pasture and arable land. The dry stone walls provided some cover in an otherwise very open area. The mink were generally too large to get inside the walls, though the cover provided alongside the walls did provide a less exposed route across the fields.

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Plate 2.1

Aerial photograph of the Ross Peninsula
and surrounding area

Figure 2.1 The study area

Ross Island

Ross Bay

Brighouse Bay

Fauldbog

The Bents

Slack Heugh

Fox Craig

1

2

3
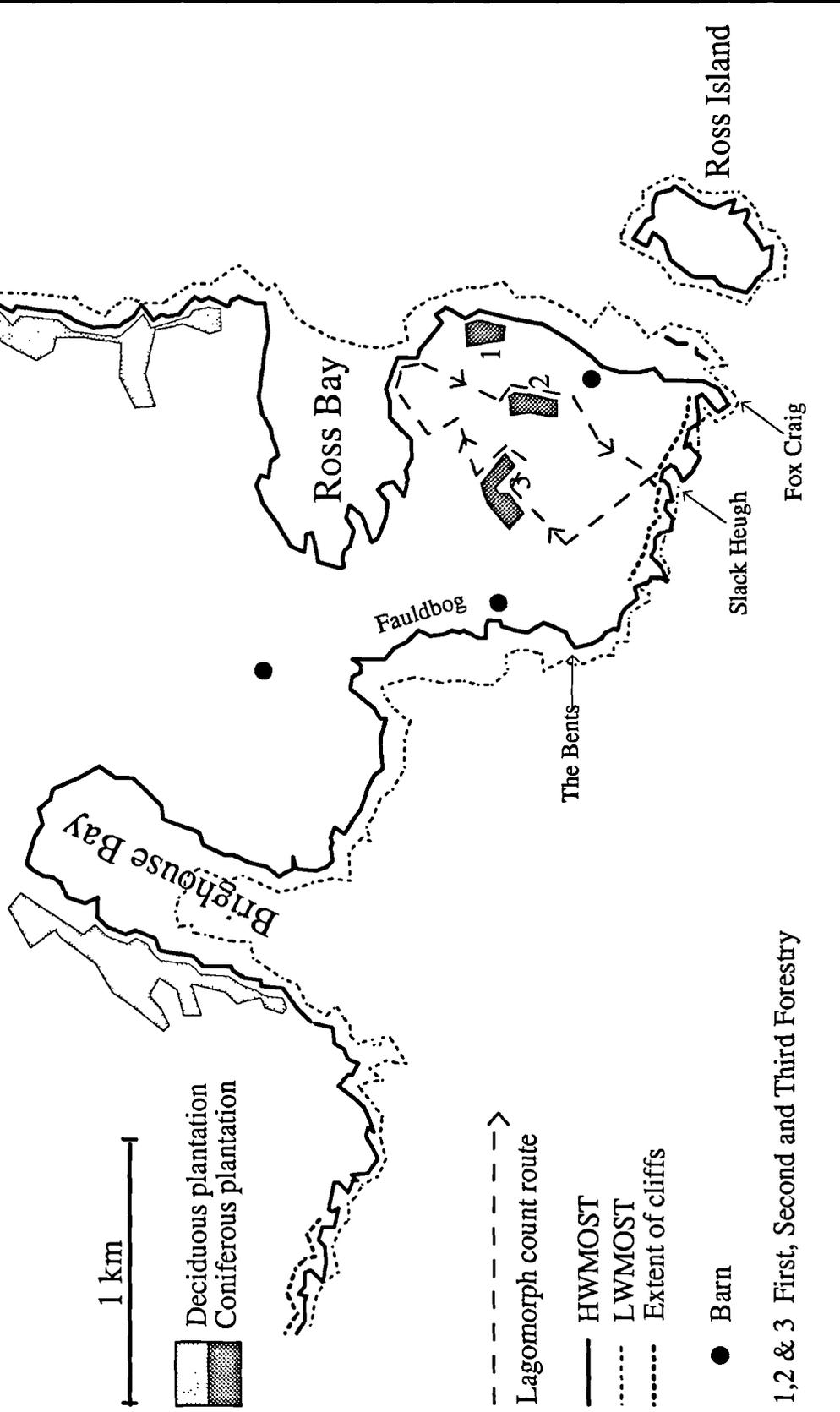
1 km

Deciduous plantation
Coniferous plantation

Lagomorph count route
HWMOST
LWMOST
Extent of cliffs
Barn

1,2 & 3 First, Second and Third Forestry

On the Ross peninsula there were three small conifer plantations, (named First, Second and Third Forestry), only one of these being mature. First Forestry was situated on the coast (Figure 2.1) and constituted Norway spruce *Picea abies* 2–3m high. Where tree density was low there were thickets of gorse and dog rose *Rosa canina*, otherwise the understorey was mainly composed of grasses (Gramineae). Second and Third Forestry were both situated on hillsides. Second Forestry was again a Norway spruce/gorse/dog rose mixture, whereas Third Forestry was more dense, mature and comprised of Norway spruce and Japanese larch *Larix kaempferi* with very little understorey. Outside the main study area (i.e., to the north of Ross Bay and the west of Brighouse Bay) there were more extensive areas of mature and immature plantation. To the west was Graplin plantation which screened a caravan site from direct view, and comprised mainly deciduous trees and some boggy areas. To the north another deciduous wood extended for some distance along the coast, and was then replaced by an immature and quite open coniferous plantation (Senwick wood). These plantations extended down to the rocky zone above the shore.

Ross Island was bounded by a rocky zone and exposed rocky shore. It had been ungrazed for many years and the grass had grown extremely thick and deep making it equivalent to scrub in terms of cover. It differed from the rest of the study area in that no lagomorphs were present, but it was home to a large sea bird colony.

2.2 Dietary analysis

2.2.1 Scat collection

Mink scats were collected on a monthly basis, both from dens and from open areas. These were placed individually in plastic bags labelled with the date, site of deposition and, if known from radio-tracking evidence, the identity of the individual from which it was obtained. General collections of scats were made each month between September 1981 and January 1983, thereafter scats were only collected from the dens of known individuals.

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2.2.2 Scat analysis

The faecal samples were soaked in a detergent solution (1% Teepol) overnight prior to sieving. The undigested remains were dried at 50°C for 24 hours and then weighed.

Remains of mammalian and avian prey were identified using hair and feather characteristics (Day, 1966) and using jaws and teeth of small mammals when present. Fish remains were identified using keys (particularly that of Watson, (1986)) and by means of reference collections. Crustacean prey were identified from carapace fragments. It was frequently possible to distinguish between Decapoda, Amphipoda and Isopoda on the basis of the shape and texture of carapace fragments and the shape of the appendages when they were present.

2.3 Prey Distribution

Interpretation of the mink's diet is greatly facilitated by a knowledge of the distribution and relative abundance, and changes in abundance, of prey species. Time precluded the detailed study of the abundance of most of the available prey species although presence/absence was noted and a certain amount of detailed monitoring of key groups was undertaken.

A quantitative assessment of rabbit and hare abundance was attempted via counts along a set route (Figure 2.1), 30 minutes before sunset. Three counts were made each month for the duration of the study. These counts did not give any indication of the absolute abundance of lagomorphs but gave a measure of the relative changes in abundance throughout the year.

Rabbits were present throughout the study area but were seen in highest numbers near Third Forestry though numbers were also high in Second Forestry and in Slack Heugh (Figure 2.1). Hares were usually observed in the pasture and crops, for example wheat and root crops, but were often observed in the coastal scrub and even on the shore.

The main avian prey group were the Charadriiformes. These occurred in large numbers on the sea cliffs around the centre of the study area, particularly at Slack Heugh (Figure 2.1). They were also particularly abundant on Ross Island. By far the most abundant bird was the herring gull *Larus argentatus* but large numbers of guillemots *Uria aalge*, razorbills *Alca torda* and cormorants *Phalacrocorax carbo* also nested in the study area. Data on the numbers of these birds were kindly provided by local ornithologists.

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Large flocks of waders, principally lapwing *Vanellus vanellus*, curlew *Numenius arquata*, oystercatcher *Haematopus ostralegus* and redshank *Tringa totanus* fed in Ross Bay and Brighouse Bay before dispersing to breed in the spring. Flocks of passerines aggregated in the vicinity of the kalefields during the winter months but the abundance of these species was not estimated.

Details of seasonal changes in the abundance of aquatic prey, principally rock pool fish and the shore crab, were obtained from the available literature.

Sample catches of small mammals were occasionally made in a variety of habitats to examine species composition.

The amount of carrion available to the mink was assessed by monthly counts along a set route which included a long stretch of exposed shoreline on which a variety of carcasses were regularly washed up.

2.4 The trapping study

Live-trapping fulfilled three roles :

a) the collection of basic biometric data
b) it allowed attachment of radio transmitter packages
c) it gave indications of the status of untagged mink, such as the movements of other resident individuals within the study area and the arrival of new individuals into the area.

2.4.1 Trapping methodology

The mink were trapped in cage traps, constructed from "Weldmesh" with stainless steel triggering and locking mechanisms to prevent corrosion. The traps were baited with either day-old chicks, rabbit flesh or dead laboratory rats. Chicks were favoured as they were of appropriate size and needed no preparation. Mink were occasionally caught in unbaited traps. Traps were disguised using a variety of materials including grass, bracken, thrift *Armeria maritima*, hay, drift wood, rocks and sacking or fertilizer bags. This also served to make them less obvious to passers-by. Care was always taken whilst setting the trap as the locking mechanism was prone to malfunction and this was aggravated by the use of covering materials.

Traps were not laid out at regular intervals on a grid or trap line. The majority were placed along the coast well away from the high tide line so there was little danger of inundation with water during gales or extreme high tides. They were positioned at sites along routes a mink would normally use whilst moving through its home range. These were mostly in the rocky band just above the shore and often corresponded to sites of regular deposition of faeces. Obstacles to easy movement such as dry stone walls were used as trap sites since movement would be directed round the obstacle rather than over it. Radio-tracking revealed that mink often travelled along or next to walls rather than cutting across open areas. Traps were often placed in the vicinity of known dens.

Successful traps remained *in situ* whilst unsuccessful ones were moved to different positions. This resulted in traps being unevenly distributed along the coastline (Figure 2.2). Occasionally traps were placed inland in plantations or barns where mink were known to visit (from scat deposition or radio-tracking evidence).

Initially, trapping was carried out for up to eight days per month to capture individual mink for radio-tracking. Later on in the study trapping effort increased, especially during the winter months prior to the mating season when the large influx of males into the area was studied more closely. Although the original study area comprised only the Ross Peninsula, trapping became more and more difficult (the reasons for which are unknown but were perhaps due to resident individuals becoming trap-shy) and the inability to catch females resulted in the trapline being extended well beyond its original boundaries (Figure 2.2).

Within each month the effort put into trapping depended on the ease with which the resident mink could be captured and on the radio-tracking load. Normally all traps were set until one or more known resident mink were captured and a collar fitted. Thereafter traps were closed in the radio-tagged minks home-range but left open elsewhere in the study area to monitor the status of the other residents and any visiting transients.

Eighty-two mink, forty-nine males, and thirty-three females, were captured a total of 431 times in 4412 trap nights. A marked sexual dimorphism was observed in the body weights of these mink. Males were 1.75 times the weight of females (Table 2.1).

Table 2.2 gives a breakdown by month, of trapping effort, and success in terms of mink captured, whilst Figure 2.3 shows how trapping success, adjusted for trapping effort, varied throughout the year for each sex. A two-way analysis of variance revealed a significant interaction between the effects of sex and month on trapping success

Figure 2.2   The distribution of traps throughout the study area.

Traps on Ross Island only in place during July and August
Traps to north and west of Brighouse Bay first used in 1985

MHWS

1km

◿ Approximate locations of traps placed in the coastal strip
○ Positions of traps placed inland
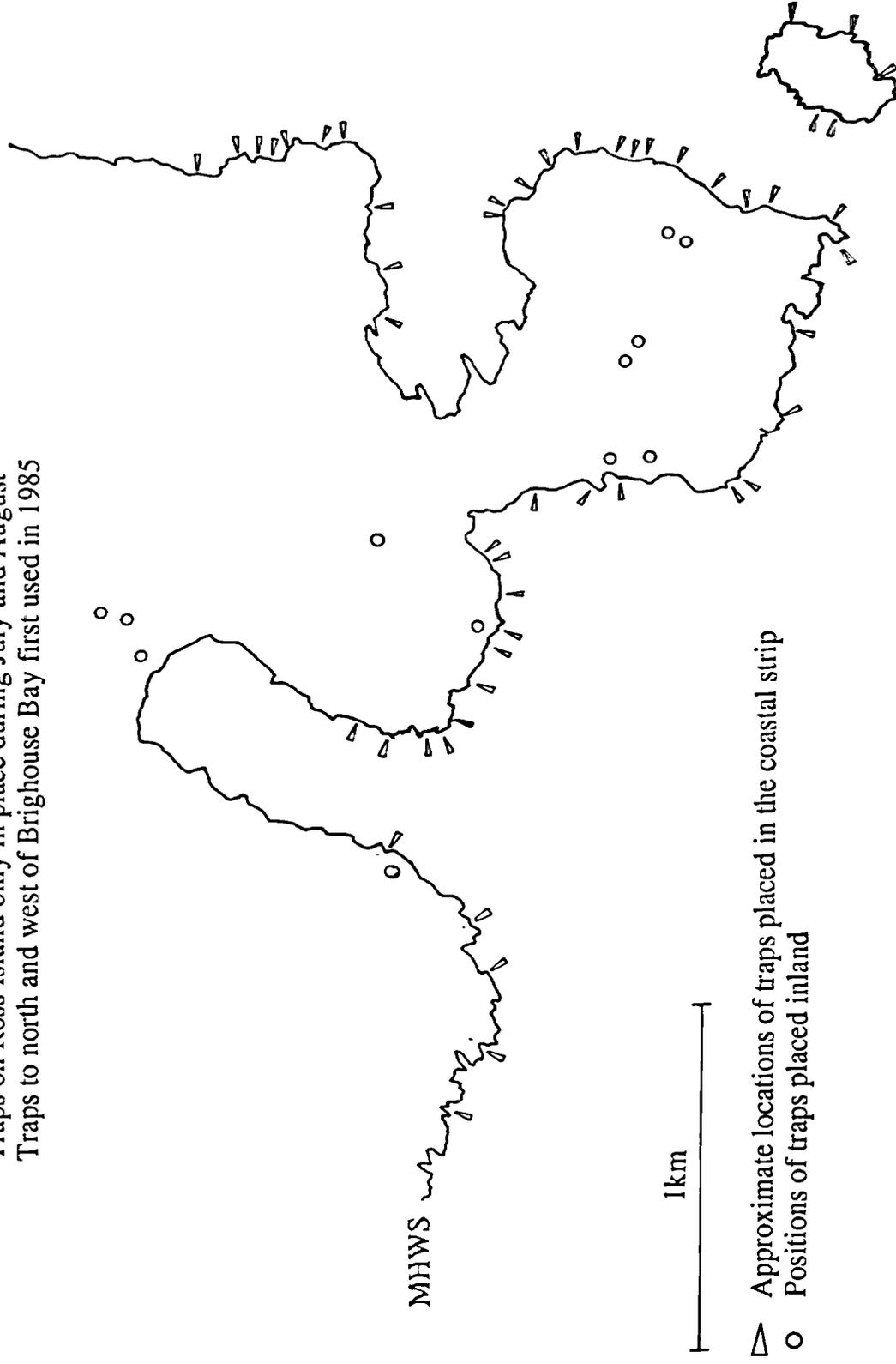
Table 2.1 The weights (in grams) and sexual dimorphism ratio of all mink captured throughout the whole study period. The total sample was based on 192 weighings of 49 male mink and 101 weighings of 33 female mink (adult sample: 90 of 20 males, 43 of 12 females).

Sex	All mink			Adults only		
	mean	SE	range	mean	SE	range
male	1047	9.6	690–1530	1148	16.5	860–1530
female	599	11.2	410–800	656	11.5	560–800
S.D. ratio	1.75:1			1.75:1		

Table 2.2 Breakdown of trapping effort and success, the latter in terms of total number of mink caught and total number of different individuals captured, throughout the year. Data for each month is summed over the whole study period.

MONTH	Trap nights	CAPTURES			
		Total		Individual	
		male	female	male	female
January	294	35	6	11	5
February	448	38	17	16	9
March	550	86	15	31	8
April	439	20	3	13	2
May	247	7	0	4	0
June	306	3	0	2	0
July	390	13	13	8	6
August	546	21	33	14	22
September	356	16	11	7	11
October	171	14	9	8	7
November	324	18	12	9	8
December	341	31	10	10	7
TOTALS	4412	302	129	49	33

($F=3.24$, $df=(11,70)$, $p<0.01$), suggesting that seasonal changes in trapping success differed between the sexes. Differences between months were significant for males ($F=5.79$, $df=(11,35)$, $p<0.001$), mainly due to a peak in trapping success during the rut in March, but not for females ($F=1.56$, $df=(11,35)$, N.S.). Though males were caught significantly more often than females (males, 6.9 ± 0.81 captures per 100 trap nights: females 3.5 ± 0.54: $F=12.18$, $df=(1,92)$, $p<0.001$), Figure 2.3 shows that differences only occurred between

Figure 2.3   Variation in trapping success throughout the year
Based on monthly means for each sex throughout the whole study period
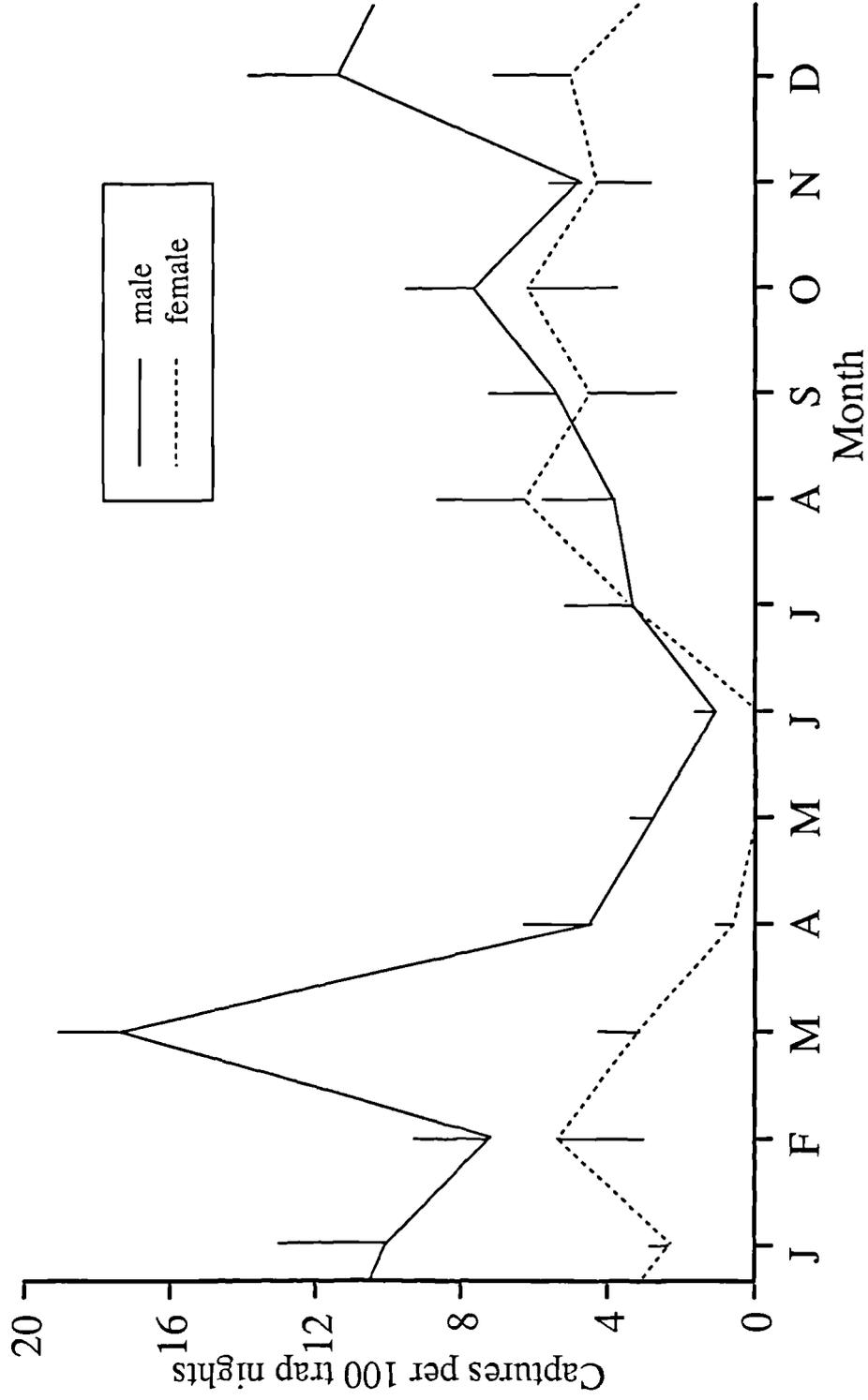
December and the following May. Trapping success was similar at all other times.

In order to reduce the stress to trapped mink, the traps were visited as early as was feasible during the morning (as mink were usually caught at night), and pains were taken to ensure that mink were stressed as little as possible during handling. It was hoped that this would also reduce the risk of mink becoming trap-shy. Traps were also checked early to reduce the risk of the mink being found by passers-by. Captured mink were identified from an ear tag if present (see below) or from their ventral spot pattern (see below). If the mink had been captured and biometric data collected in the previous four or five days, it was released immediately, otherwise it was anaesthetized.

2.4.2 Procedure for handling mink

The mink was transferred from the trap to a perspex-sided anaesthetizing box (Chanin, 1976). If this proved impossible, the cage was placed in a plastic bag and anaesthesia accomplished within the trap. A dried ether/air mixture was passed into the box until it could be seen that the mink was unconscious. The mink was then allowed to breath the mixture for varying lengths of time (usually 20 seconds to two minutes depending on size and ambient temperature). The depth of anaesthesia could also be varied in this way depending on which procedures were required. This gave anaesthesia for 2–4 minutes after which the mink was placed back in the trap to recover. After a suitable recovery period (usually less than 10 minutes), the mink was released at the site of capture.

Measurements and other details were recorded whilst the mink was under anaesthesia. The full procedure was as follows.

a) All mink captured were fitted with a numbered alloy (Monel) ear-tag (supplied by ≪America≫, Sweden). The tag was fitted well down at the base of the pinna to prevent it from being pulled out. If the tag had been shed, another one was fitted.

b) A sketch was made of the ventral spot pattern (VSP). This is a variable area of white fur on the minks underside. The VSP was especially useful for identification if a mink had shed its tag and for identifying mink in the trap since reading the tag number of an unanaesthetized mink was sometimes very difficult.

c) Body lengths, measured from nose to anus and nose to tip of tail were recorded to the nearest centimetre.

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d) The mink was sexed. Routinely, the genital area was examined for the presence or absence of a baculum. Unanaesthetized mink could usually be sexed on the basis of size or length although problems could be encountered in distinguishing between young or juvenile males and adult females, especially during late summer.

e) An attempt was made to age the mink.

i) Males. Since the width of the baculum increases with age (Mitchell 1961), it was usually possible to tell if a mink was in its first year or was an adult. In cases of uncertainty, differential growth of the bones in the skull with age leads to different facial characteristics which, with experience, may be used tentatively to back up any decision.

ii) Females. The presence of white hairs on the back of the neck (which are derived from mating bite wounds (Chapter 6)) indicated that the female was older than 10 months.

These two methods only allowed adults and young to be distinguished. Adults were defined as individuals aged one year or older. Although dentition was always noted when examining a mink, this was not used in determining age, since young mink could have badly worn teeth (pers. obs.), and old mink occasionally had teeth with very little wear. This was also noted by Chanin (1976), who suggested that tooth wear could have been influenced by diet or genetic factors. With age, the mink's coat did become lighter as more and more grey hairs appeared in the pelage (pers. obs.) but this change was not obvious until three years of age or more and so it was not used as an ageing criterion. The best way to age mink was to capture them as kits. On subsequent recaptures, ages were known to within a month. Trapping effort was therefore increased during August so as to maximize the number of kits caught.

f) Reproductive condition.

i) Males. The mink were examined to see if the testes were scrotal and if so, they were measured using calipers.

ii) Females. When the female is receptive, the vulva may evert. The nape of the neck was examined for the presence of any scabs under the fur. This would indicate whether or not a male had mated with her or had attempted to do so. Later in the season the mating scar was very obvious and often became an open

wound. On the rare occasion that a pregnant female was trapped, the foetuses could be felt. After parturition, the number of nipples was counted.

g) Dentition. The wear on the mink's teeth was categorized (none, slight, fair or heavy). If any of the mink's teeth were missing, broken or rotten, (particularly common with the long canines), this was also noted.

h) Body condition. An indication of condition was judged from the amount of fat in the inguinal region. Condition was categorized into excellent, good, fair or poor.

j) Body weight. The mink was placed in a bag and weighed to the nearest 10 grams, using a Salter spring balance.

The complete procedure was carried out only on newly captured individuals. More commonly, once identification had been established, the mink was weighed, its reproductive and body condition ascertained and its teeth examined. These observations could be carried out quickly under mild anaesthesia.

2.5 The radio-tracking study

Radio-collars were only fitted to mink that were known to be temporarily or permanently resident and for the purpose of tracking this was defined as a mink having been trapped in two consecutive months.

2.5.1 Receiving equipment

During the study, two different receiver/aerial combinations were in use, all operating in the 173Mhz waveband. The major part of the radio-tracking was accomplished using a Mariner Radar M57 receiver, though an AVM LA12 receiver was also used occasionally. The receivers were used with three-element Yagi antennae.

2.5.2 Transmitters

In the course of the study, several different collar types were tried. The electronics, waterproofing, packaging and method of attachment to the mink were constantly modified and updated.

All transmitters were attached to a collar and had either a loop antenna or a wire antenna encased in the material of the collar. The devices transmitted at a rate of between

60 and 200 pulses per minute. Theoretical transmitter life based on different design and battery types should have been between eight weeks and nine months for different models but they rarely achieved their theoretical maximum life.

a) Loop antenna transmitters

These consisted of a transmitter package attached to a stainless steel metal loop which also formed the basis of the collar. The antenna was coated with rubber and leather to stop it rubbing on the mink's neck. The steel loop was shortened to the correct size for the neck and the two halves were bolted together, completing the transmitter circuit. The problem with this design was that due to the small difference in diameter between the mink's neck and head, the collar had to be fitted reasonably tightly to ensure that the transmitter stayed on. This could cause rubbing and abrasion to the neck if the collar was left on for too long. For these reasons their use was discontinued in favour of a less permanent form of attachment.

b) Whip antenna transmitters

These collars were made of a double thickness of leather into which a wire aerial was incorporated. The idea was that the leather would wear and the collar would break and fall off at some unspecified time. Cases of abrasion decreased dramatically, some mink having collars on for four months with no ill-effects. Two old males were prone to neck abrasion and collars were always removed from them when they were not being radio-tracked. A method was eventually perfected whereby the collar was glued to the guard-hairs of the mink's neck using contact adhesive (Evostik). This was particularly useful for attaching collars to growing kits, to individuals susceptible to abrasion and to transient individuals or individuals that might leave the area. The collar was adjusted so that it could easily be pulled off over the head by the mink once the adhesive had worn off. The period of retention was somewhat unpredictable but the collars remained *in situ* for long enough to collect useful data and none of the mink with glued collars ever developed neck abrasion.

c) Transmitter circuitry and packaging

The original transmitter circuitry was designed in the Applied Physics laboratory, University of Durham. The components were wrapped in plastic, coated in silicone jelly and potted in a two-component epoxy putty. These proved quite unreliable. Failure usually resulted from water getting into the components via the metal aerial loop. The potting

material was also relatively soft and wore quite quickly as it was slung under the neck of the mink and probably knocked and scraped on the rocks. With the advent of leather collars, the potting medium was replaced by epoxy resin. The entrance hole for the wire aerial was much smaller thus reducing the chances of water working its way down to the electronic components.

In 1983 a new transmitter circuit was tried based on a design by Mariner Radar. This used microcomponents on a small printed circuit board. It had a better range and was also smaller. Rather than reduce the physical size of the package, the components were encased in a small plastic tube sealed with epoxy and then potted in further layers of resin. The air gap surrounding the components resulted in a more stable frequency emission, less susceptible to the slight changes caused by a mink's changing body position relative to the transmitter. This made it somewhat more difficult to detect changes in the activity of the mink as one then had to rely on slight changes in amplitude of the signal rather than more noticeable shifts in frequency. The constancy and predictability of the frequency did however make locating the transmitter easier and the interpretation of chart recordings of mink activity was also more accurate. The plastic tube was also less susceptible to abrasion. Even if the epoxy resin wore away it was still difficult for the water to get into the electronic circuitry.

Finally unpotted transmitter packages were purchased from Biotrack Ltd. These had been tested with the aid of a frequency spectrum analyser and had a much greater signal strength (range) and a longer life than previous designs. They were potted in epoxy-resin and plastic tubes as before.

The weight of the transmitter packages and collar combined was typically 20–30g, approximately 5% of the weight of a female mink and 2–3% of a male.

2.5.3 Radio-tracking technique

Radio-tracking is a usually means of locating the animal so that it may be observed. In practice, for a small nocturnal mainly fossorial carnivore, this is rarely possible and the radio-signal becomes the means of study itself. A thorough account of radio-tracking in practice can be found in Kenward (1987). The methods used in the present study and their associated problems are as follows:

a) Location of the subject

In ideal situations, line of sight and preferably overlooking the subject, the mink transmitter could have a range of over 1km. The mink however was too small to carry a reasonably-sized loop aerial and a whip antenna could not be used without interfering with the animal's behaviour. The top of the antenna was thus only 5–7cm above the ground when the mink was active. All these factors reduced the strength of the transmitted signal relative to that which was theoretically possible. Added to this, the terrain was such that when the mink was foraging there were usually rocks between the mink and the observer, and when the mink was in its den it was usually within crevices in the rocks or deep within a rabbit burrow which further attenuated the signal. Under such circumstances the receiver had to be within 50–100m of the transmitter to guarantee picking up any signal. Fortunately, the mink occupied a virtually linear habitat and so a walk around the coast was often sufficient to locate the animal.

b) Location of the den

Triangulation is often used to locate a radio-signal (Birks, 1981). With a Yagi antenna, the amplitude of the signal is greatest when it is pointing in the direction of the source. Two or three fixes are taken from different locations, and the intersection of these fixes gives the approximate position of the source. In the field however, the habitat topography had a marked effect on the ease with which the radio-source could be located because the signal was reflected off cliff faces and rocks. The signal of greatest amplitude often appeared to come from a position which bore little relation to the actual signal source. Familiarity with the study area was therefore a great advantage. The operator learned how the radio-signal behaved in particular areas.

The problem of location was confounded when the mink was active. Directional cues were ascertained using signal amplitude variation, but as the signal from an active mink was constantly varying, a directional fix could be very vague. Following the signal until it did not get any louder ultimately led to the den. Unfortunately, the presence of an observer outside the den could disturb the mink. However, during the day the animal was unlikely to come out and would settle down as soon as the observer left the immediate vicinity.

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c) Following mink movements

Gross changes in signal strength due to the changing orientation of the transmitter aerial, compounded by the effects of the intervening habitat on the signal strength and attenuations caused by entering burrows, swimming and moving behind boulders indicated that the mink had left its den.

The precise grid coordinates of the mink for each 10-minute fix and often intermediate times were recorded on a 1:2500 scale map of the study area. More important to the analysis than the precise location of the mink was the habitat it was using. Unlike locating a den, the observer could not get close to an active mink for fear of changing its behaviour. At night, the radio-signal gave only an approximate idea of a mink's location so another means of location was often needed. Betalights (Macdonald, 1978), fitted to the collar, allowed a much more accurate determination of a mink's location and habitat type. In practice, it was often easier to see the beta light at night than to see the mink itself foraging in the open during the day. An image intensifier was available to watch the mink at night but proved to be only of limited use due to its bulk and its effect on the observer's night vision.

d) Remote monitoring

This was used to monitor the presence/absence of a mink in its den. The information gained was useful in that it gave the time of leaving and re-entering a den and, if one den was being used predominantly, the duration of the "foraging bout". However, the equipment gave no indication what the mink might be doing whilst out of den and the information had to be interpreted with care.

A Grant Instruments Type DB9–U mini chart recorder was used at first. This made a 20 second record of the radio-signal every 10 minutes. With care, it was possible to tell whether the mink was active or inactive in its den but this information was not used due to the fair degree of uncertainty inherent. The main problem with this equipment was that although the chart recorder could function for two weeks whilst recording at 10-minute intervals, the receiver batteries only lasted for 6–10 hours. To overcome this problem, a relay was fitted into the chart recorder which closed when the recorder started its trace. The receiver was then switched on only during the trace every 10 minutes enabling its batteries to last for up to a week.

Later in the study, a Grant Instruments Squirrel meter/logger Type SQ2 IV2 was used. This gave a digital readout of the signal strength at programmable intervals. The data logger switched on the receiver for five seconds during each time interval, and the peak voltage from the receiver was recorded. Only one reading was taken by the data logger so it was not possible to tell whether the mink was active or not. More care had to be taken with positioning the aerial because the data logger was more likely to pick up a radio-signal from a mink foraging in the vicinity of its den. Further problems included the lack of a permanent record and difficulties transcribing the data in the field without access to a microcomputer. It was however far more portable than the chart recorder and so it could be carried around routinely. The short duration of signal measurement also resulted in increased life of the receiver batteries.

2.5.4 Data collection and analysis

Radio fixes were taken at 10-minute intervals. The duration of the tracking period varied with weather conditions. Where possible, the mink were tracked for a continuous 24-hour period by two or more workers on a shift basis. Usually however tracking was carried out discontinuously by one worker whose aim was to collect data for at least one complete 24-hour cycle on each mink radio-collared each month, albeit split over a number of days. After this had been achieved, the mink was tracked when it was thought likely to be foraging. It was often not possible to collect data over the whole 24-hour cycle, usually because the mink shed its collar or the collar stopped transmitting. When more than one mink was radio-collared simultaneously, an attempt was made to get at least one fix on each collared animal each day.

Mink with collars which were not being tracked for activity studies were trapped at regular intervals to check that the collar was not causing neck abrasion. When a mink was being tracked however, all the traps in its normal home range were closed.

Radio fixes were divided into four categories:

a) **Inactive in den** - The mink was in one place and the signal did not fluctuate.
b) **Active in den** - The mink was in one place but the signal strength fluctuated constantly.
c) **Foraging** - The mink was out in the open and moving through its home range slowly enough to be searching for food. The signal strength fluctuated widely.
d) **Travelling** - The mink was out of its den and moving through its home range at a speed which precluded searching for prey.

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These four categories cannot include all the mink's activities, but they represented four states which could be determined purely by the nature of the radio-signal and its movement. Where more details about the activity were known they were recorded as such. These included 'rutting' when either the male or the female is engaged in the act of copulation, 'eating' and 'drinking' and occasionally 'fighting'.

Activity, location, habitat and other relevant information were recorded on a dicta-phone. After the tracking session the tape was transcribed and each fix transferred to a 1:2500 map of the area. The data were coded and transferred via coding sheets on to the mainframe computer at the University. Climatic details for the area were supplied by the Meteorological Office. Details of prey densities, levels of human disturbance, mink biometric data and trapping records were also held in separate computer disc files and subsequently merged with the tracking data. Analysis of the data was carried out using a number of proprietary software packages (such as SPSSX, SAS, MIDAS, GENSTAT, GHOST, GINO F, GIMMS, SPIRES) and many programmes written in FORTRAN and PASCAL by the author.

3. DIET

3.1 Introduction

A thorough knowledge of the composition of a mink's diet is an invaluable if not essential aid to the interpretation of radio-tracking data, yet radio-tracking such a small, essentially nocturnal carnivore, does not allow an investigator to say, with any certainty, which prey are being hunted or how successful the mink has been at catching them.

Analysing a sample of 1024 faeces (scats) from known mink on the present study area, Birks and Dunstone (1985) found evidence of differences in the diet and attributed this to differences in body size between the sexes. That sample of 1024 scats has now been increased substantially, by a further 933, allowing a more detailed examination of the seasonal trends in the consumption of different prey items, and the differences related to sex and size. In addition, by using on-site and literature based estimates of prey availability, the relationship between availability and consumption has been examined.

3.2 Methods

Details of scat collection and identification of prey remains have been given in Chapter 2. A percentage bulk method was employed (see Wise *et al.*, 1981) to estimate the relative proportions of prey remains in the diet, since other methods, based on the percentage occurrence of different items in the scats, overestimate the contribution of small prey to the diet (Section 3.4.1). After sorting and identifying the different prey items in each scat, the relative volume of each prey item was estimated by eye to the nearest 10%, and subsequently used to calculate the dry weight of items in each scat. These were summed for each item, and for all items (total bulk), for the derivation of percentage bulk.

3.3 Results

In total, 1957 scats were collected from known individuals, and analysed. Table 3.1 shows how many scats were collected from each sex, for each month, and the number of individuals upon which each month's sample was based.

For the sake of convenience, the proportion of undigested prey remains in material collected for a sample, was equated with the the prey's contribution to the "diet". Any errors or assumptions inherent in this "conversion" will be considered in the discussion.

Table 3.1 A monthly breakdown of the number of individuals, number of scats, and dry weight (g) of faecal material on which the dietary analysis is based.

Month	Male			Female		
	No. of animals	Scats	Total dry wt	No. of animals	Scats	Total dry wt
January	4	101	78	1	30	22
February	6	84	45	3	26	16
March	3	86	64	5	193	179
April	1	17	12	1	11	12
May	1	13	11	2	60	76
June	2	48	36	4	285	136
July	1	28	19	5	296	201
August	1	9	6	6	95	33
September	2	138	95	2	25	5
October	2	15	9	0	0	0
November	4	119	86	3	59	38
December	5	88	81	4	131	86
Total	32	746	461	36	1211	804

In addition to the scats from known individuals, a further 1050 scats, collected from open areas and the dens of unidentified mink, were included for an assessment of the diet as a whole. Mink were found to prey upon a wide variety of species, both aquatic and terrestrial. A complete breakdown of the diet by prey species is given in Table 3.2. Mammals accounted for approximately 46% of the bulk of the diet (undigested faecal material). Seven mammalian categories were identified in the diet, but by far the most abundant category was the lagomorphs, totalling 41%. The next most important group was fish (26%), comprising more than seven species. The fish most heavily preyed upon was the blenny or shanny *Lypophris pholis*. Birds accounted for 17% of the diet, the major order being the Charadriiformes. Apart from the occasional occurrence of an amphibian, the rest of the diet comprised invertebrates (11%), in particular the shore crab *Carcinus maenas* (9%).

Within one taxonomic class, the predation of different species may involve different strategies. For this reason, in the analysis of mammal consumption, two groups were recognized: lagomorphs and small mammals. Birds were also split into small and large species. Small species comprised the Passeriformes and Columbiformes; large birds, all other bird orders recorded (Table 3.2).

Table 3.2 The overall diet of the mink on the Ross peninsula, expressed as the bulk of different items in proportion to the total amount of faecal material collected.

		% bulk
Eel	Anguilla anguilla	1.1
Salmonid	Salmo sp.	.0
Blenny (shanny)	Lipophrys pholis	8.3
Butterfish (Gunnel)	Pholis gunnelus	.9
5–Bearded Rockling	Ciliata mustela	4.1
Seascorpion	Taurulus bubalis	3.7
Goby	Gobius sp.	.5
Seasnail	Liparis liparis	.2
3–Spined Stickleback	Gasterosteus aculeatus	.1
15–Spined Stickleback	Spinachia vulgaris	.1
Flatfish		.1
Unidentified fish		6.9
TOTAL FISH		**26.0**
Shore crab	Carcinus maenas	8.7
Other Decapoda		.9
Isopoda		1.0
Amphipoda		.1
Other Crustacea		.3
TOTAL CRUSTACEA		**11.0**
Lagomorph		41.0
Rat	Rattus norvegicus	.9
Field Vole	Microtus agrestis	2.4
Bank Vole	Clethrionomys glariolus	.4
Woodmouse	Apodemus sylvaticus	.5
Shrew	Sorex sp.	.1
Sheep		.0
Squirrel	Sciurus sp.	.3
Unidentified mammals		.0
TOTAL MAMMALS		**45.5**
Charadriiformes		7.7
Galliformes		.4
Passeriformes		3.3
Anseriformes		.9
Columbiformes		.5
Unidentified birds		4.6
TOTAL BIRDS		**17.4**
TOTAL AMPHIBIANS		**.1**

Number of scats	3007
Number of prey occurrences	4433
Dry weight of faecal material	2064g

An analysis using one scat as one sample (for example Birks and Dunstone, 1985) was considered to suffer from problems of independence. This was because many scats were collected from the same individual, more than one scat may result from a meal, (captive males produce about ten scats a day, females, five (Robinson, 1987)) and there is a differential rate of passage of different prey items through the gut (Sealander, 1943). To test whether this independence problem could be alleviated to some extent by treating all the scats from one individual mink, from one month as a sample, the variation between months to within a month was compared for the two major prey categories (lagomorph and fish) using a nested analysis of variance. The analysis used all individuals for which there was more than one monthly sample and for which there were two consecutive months of data, to reduce any seasonal effects.

The variance between scats in the same month was significantly less than the variance between the bulked monthly samples for males (lagomorph, $F=8.48$, df=(7,398), $p<0.001$; fish, $F=5.72$, df=(7,398), $p<0.001$) and for females (lagomorph, $F=7.28$, df=(7,610), $p<0.001$: fish, $F=11.05$, df=(7,610), $p<0.001$), probably because the individual scats for one mink in one month were correlated, the lack of independence reducing the variance. There was therefore a greater independence between bulked monthly samples. This does not mean that the monthly samples were independent, just more independent than individual scats. Therefore the F values based on monthly samples had to be treated as guides rather than exact measures. The variance between different mink was not significantly greater than variance between months for the same mink, (males: lagomorph, $F=0.708$, df=(6,7), N.S; fish, $F=1.053$, df=(6,7), N.S.: females: lagomorph, $F=1.120$, df=(6,7), N.S; fish, $F=1.267$, df=(6,7), N.S.), and so it was considered reasonable to treat separately, different monthly samples for the same individual, rather than having to pool them.

The effects of sex and month on the diet were analysed using two-way analysis of variance. Since samples varied in size, each sample was weighted in the analysis by its dry weight.

The results are given in Table 3.3. The diet, as measured by changes in faecal prey remains, changed significantly throughout the year for two of the six prey groups, lagomorphs and fish. There were significant intersexual differences in the consumption of three of the six prey groups, males consuming relatively more lagomorphs whilst females consumed relatively more fish and crustaceans (Table 3.4). When comparing prey consumption with availability, it was the trend in consumption of a prey type throughout

the year, rather than the absolute consumption of a prey type in a particular month, that was important. In order to emphasize these trends, three point running means were used to represent seasonal changes in relative consumption of different prey, to help overcome the problems caused by the small sample sizes in each month, which resulted from the use of individual mink months as a sample (Figures 3.1–3.6).

Table 3.3 Results of a two-way analysis of variance examining the effects of sex and month on the consumption (% bulk) of different prey groups in the diet.

| Prey group | Effects (error df=45) | | | | | |
| | Sex (df=1) | | Month (df=11) | | Interaction (df=10) | |
	F	sig	F	sig	F	sig
Fish	4.94	*	2.44	*	0.67	NS
Crustacea	4.46	*	1.88	NS	0.81	NS
Lagomorph	34.37	***	4.82	***	0.64	NS
Small mammals	2.81	NS	2.74	**	2.18	*
Large birds	1.29	NS	0.43	NS	0.26	NS
Small birds	3.39	NS	1.53	NS	0.74	NS

Table 3.4 Sex differences in the consumption (% bulk) of the six major prey groups in the diet.

| Prey group | Male | | Female | |
	Mean	SE	Mean	SE
Fish	13.8	6.1	28.7	5.6
Crustacea	6.6	3.9	15.7	3.6
Lagomorph	66.3	6.5	30.7	6.0
Small mammals	5.1	1.6	6.1	1.5
Large birds	5.7	6.2	15.0	2.3
Small birds	2.5	2.3	3.8	2.1

3.3.1 Fish

Visual observations revealed that aquatic prey were hunted in a variety of different ways. Female mink were observed swimming in open water and diving in search of prey. Dive durations were recorded from two up to a maximum of 30 seconds. Often, mink were observed standing on rocks in open water or next to a rock pool, 'peering intently' into the water before diving in. Occasional sampling of rock pools revealed that fish were often found hidden in small rocky crevices in the sides of the pool. Littoral

Figure 3.1 Monthly changes in the consumption of fish

based on the % bulk estimate, meaned
over all individuals in any one month

———	male
············	female

a. mean and standard errors

b. 3-month running mean

Figure 3.2   Monthly changes in the consumption
of three fish species

based on the % bulk estimate
of all scats collected in the month

————	male
- - - - - - -	female

a. blenny

b. 5-bearded rockling

c. seascorpion
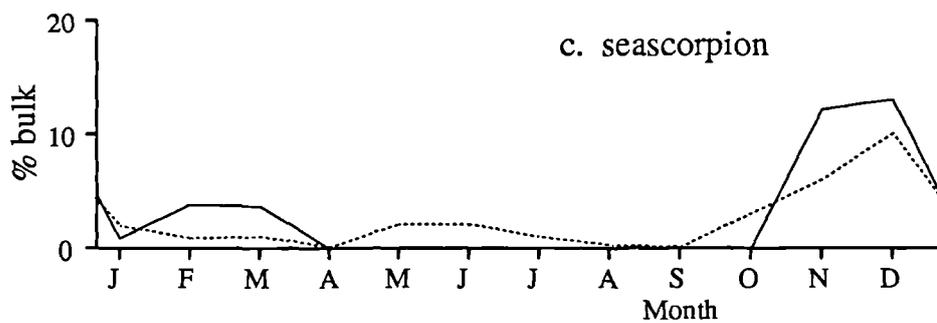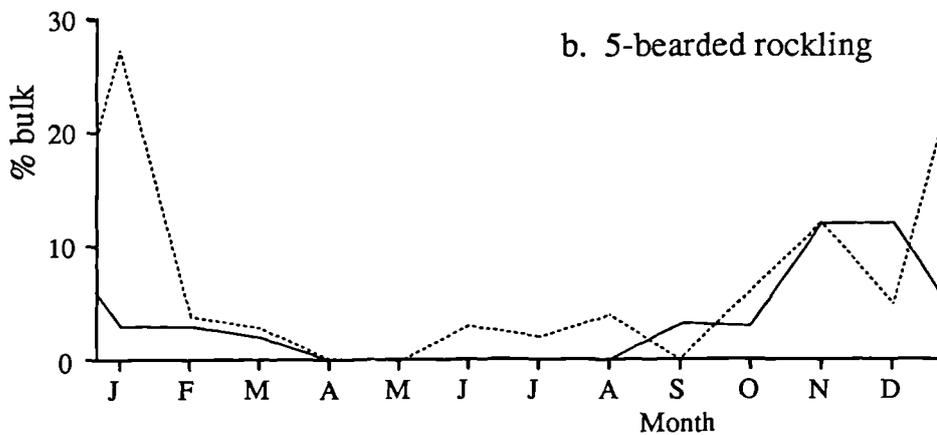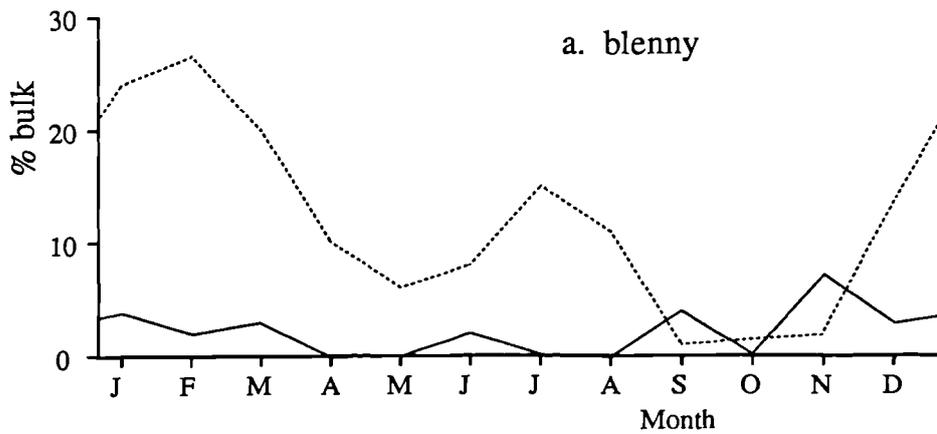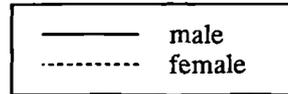
Figure 3.3a Monthly changes in the consumption of lagomorphs

based on the % bulk estimate, meaned
over all individuals in any one month
(3-month running means)
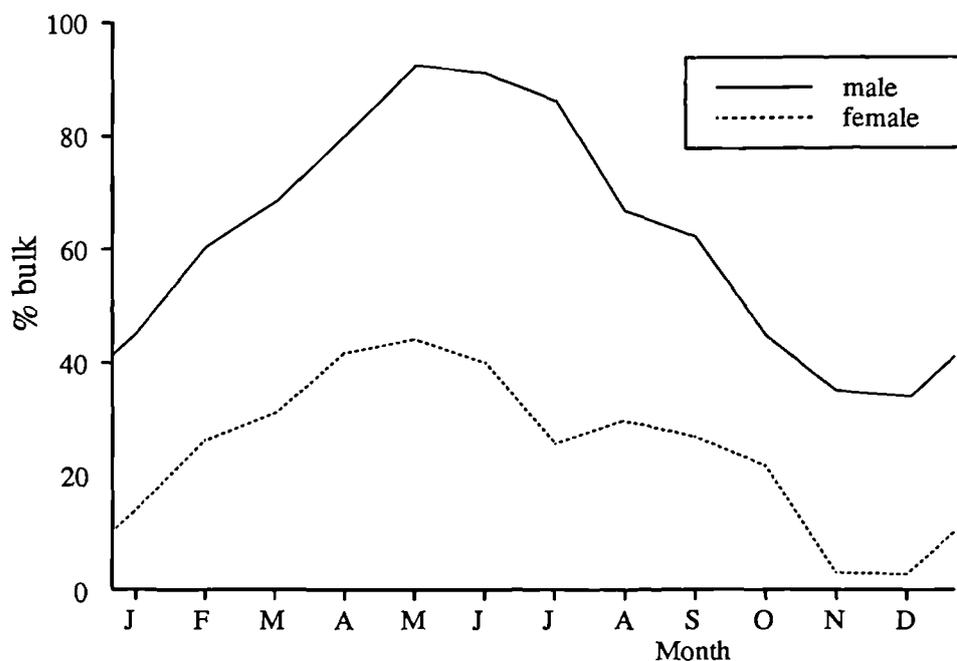
Figure 3.3b Monthly changes in lagomorph abundance

means and standard errors of all lagomorph
counts combined over all years
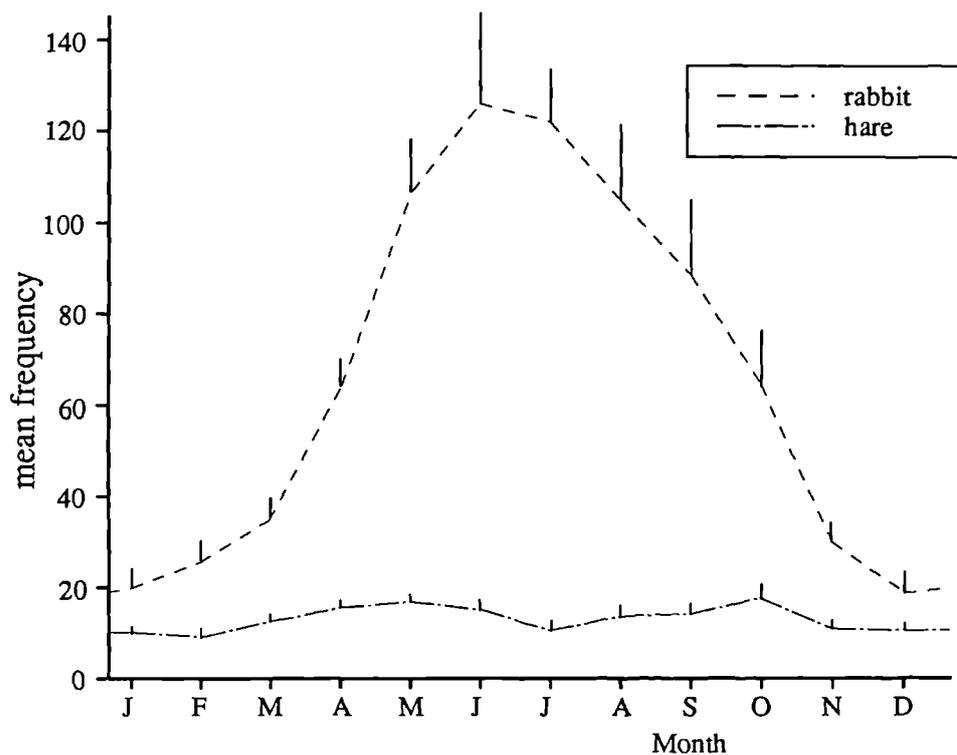
Figure 3.4 Monthly changes in the consumption of minor prey items

(3-month running means)
based on the % bulk estimate, meaned
over all individuals in any one month

——— male
---------- female

% bulk

a. crustaceans

b. large birds

c. small birds
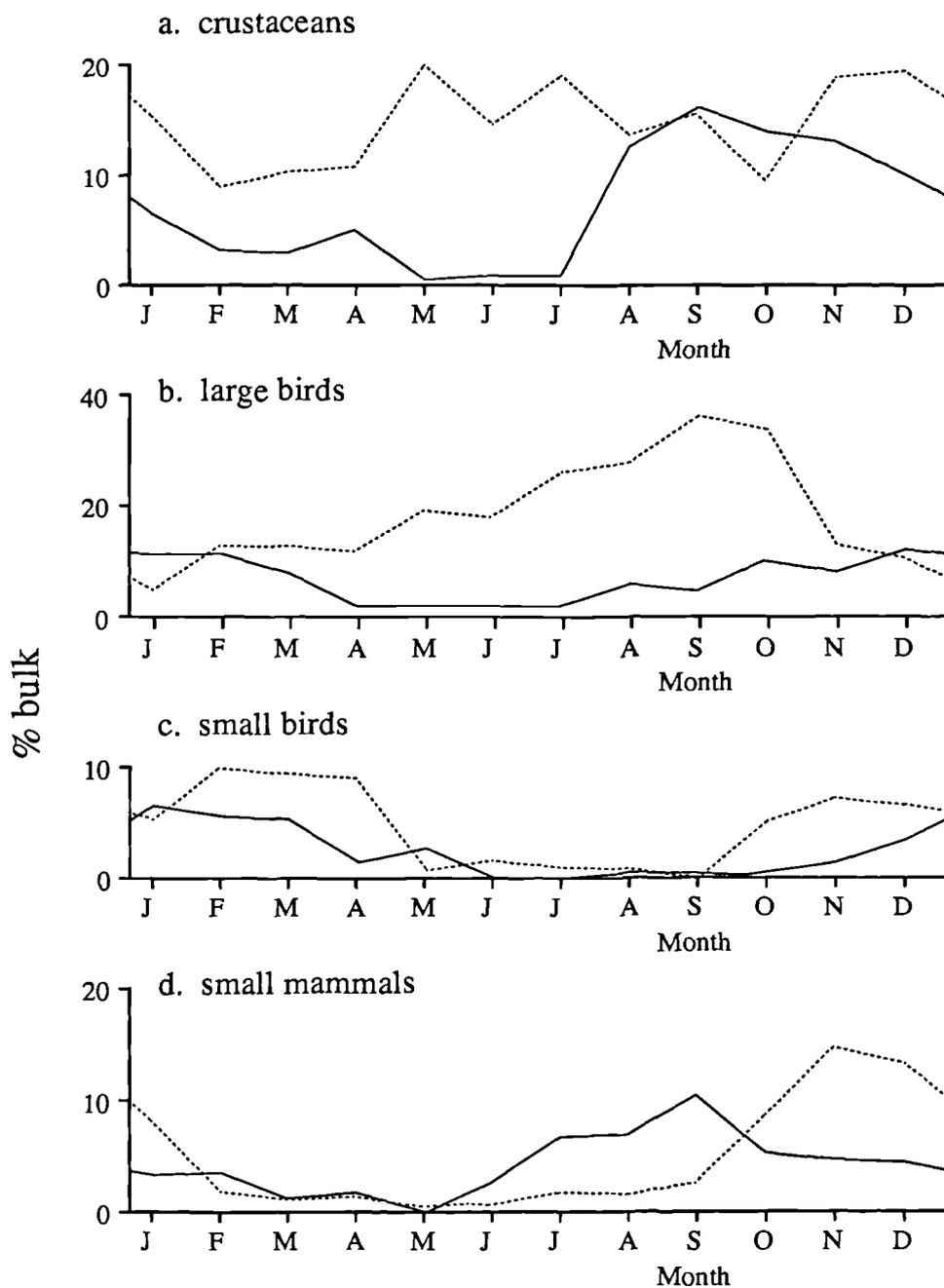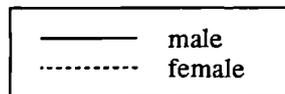
d. small mammals

Figure 3.5   Monthly changes in the consumption of the two major bird categories

based on the % bulk estimate
of all scats collected in the month

————	male
··········	female

a. Charadriiformes

% bulk

50
40
30
20
10
0

J F M A M J J A S O N D
Month

b. unidentified bird

% bulk

30
20
10
0
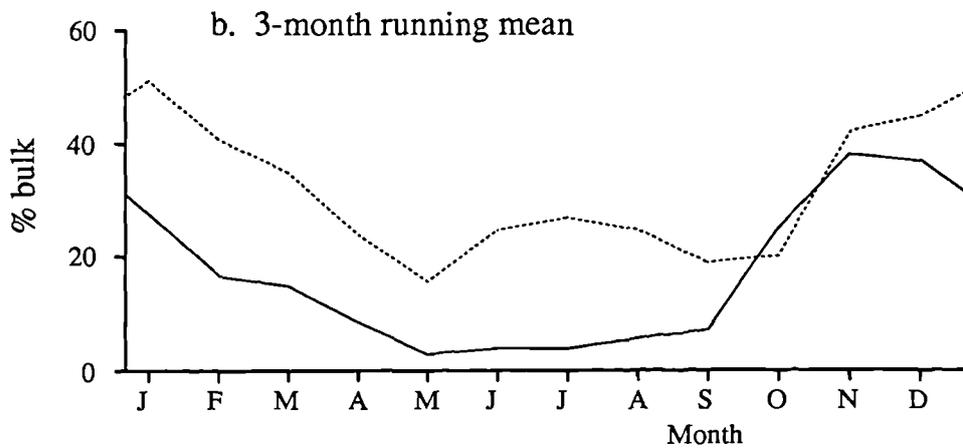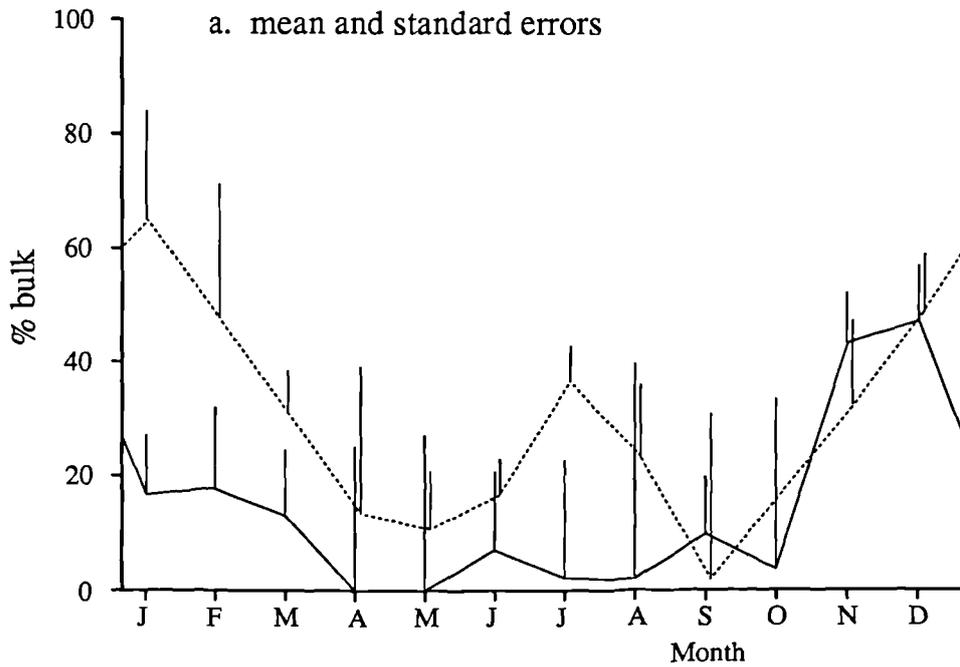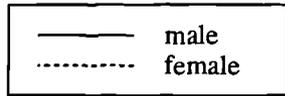
J F M A M J J A S O N D
Month
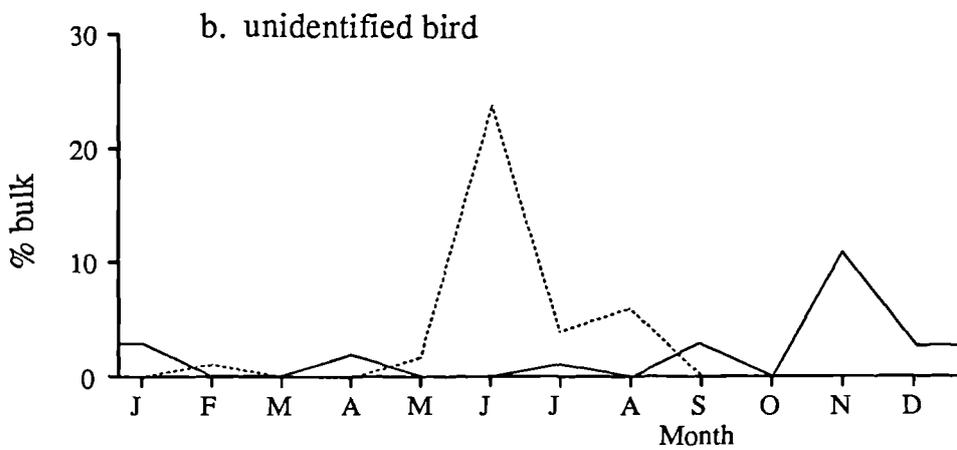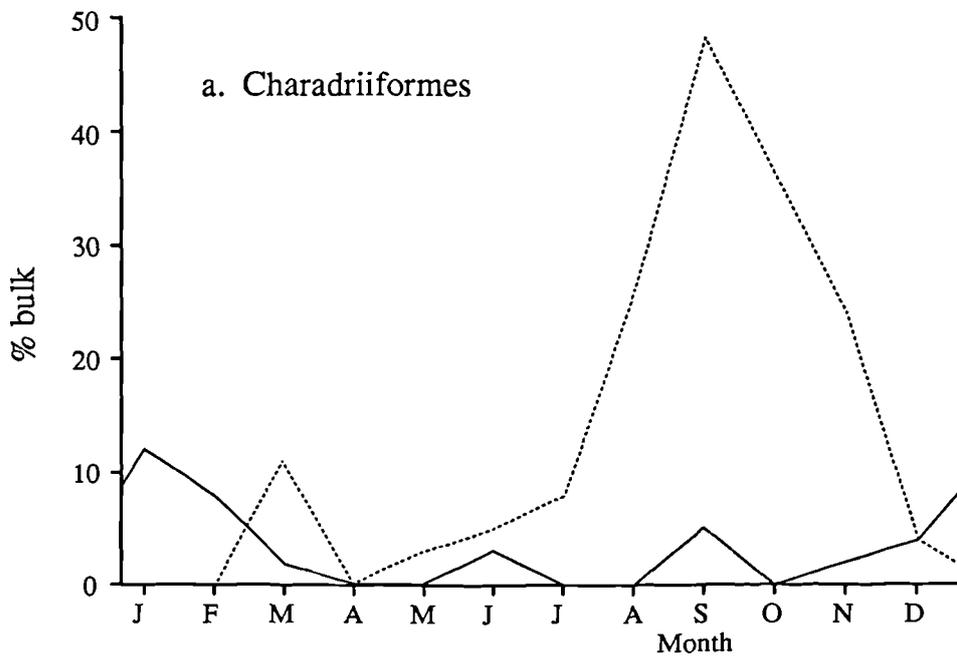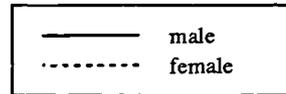
Figure 3.6   Monthly changes in the consumption of small bird and mammal species

based on the % bulk estimate
of all scats collected in the month

————	male
--------	female

a. Passeriformes

b. field vole

c. bank vole

d. wood mouse

% bulk
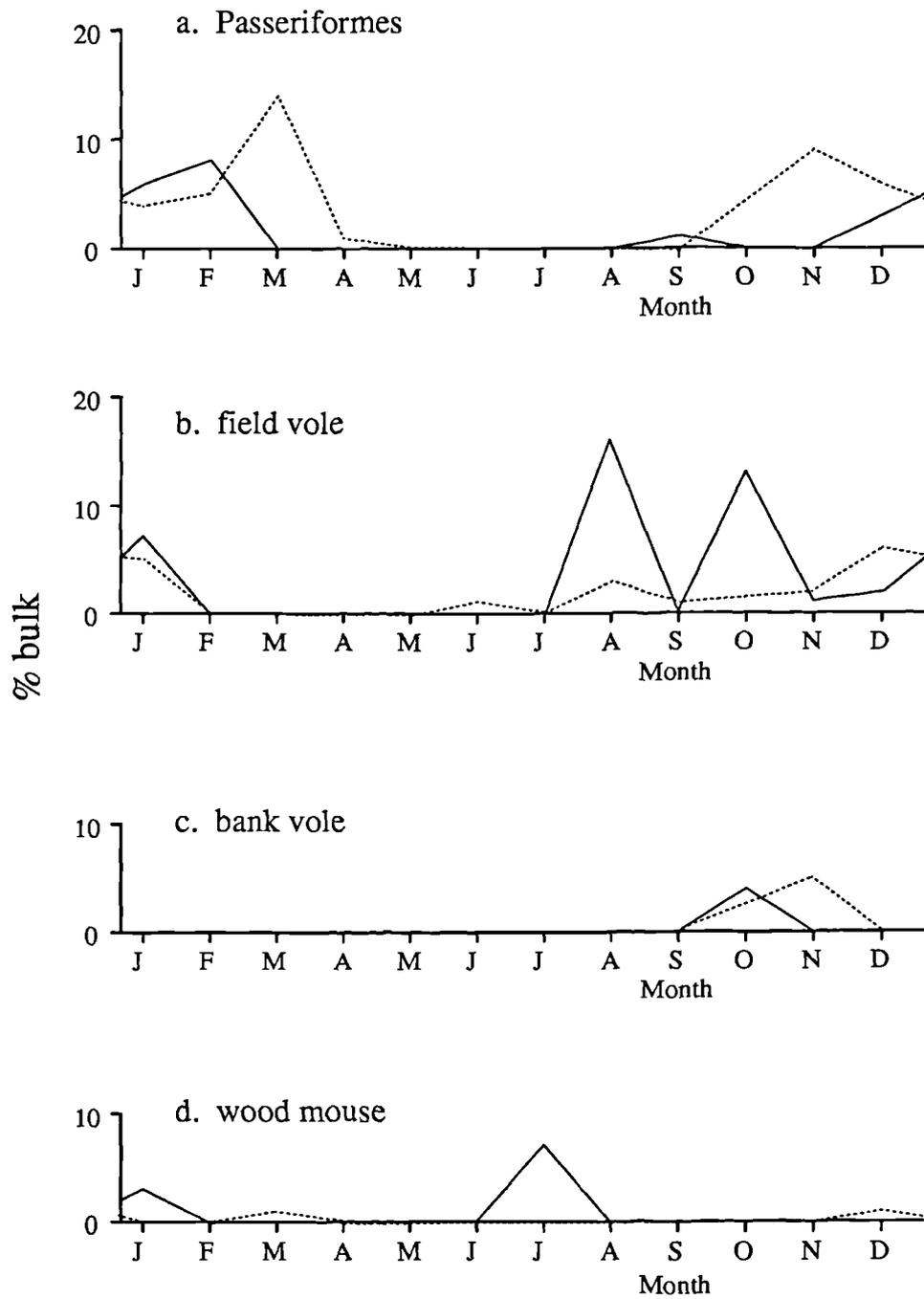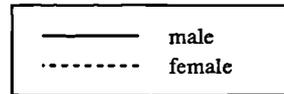
zone foraging did not only occur in association with water. Mink were observed foraging in exposed intertidal boulder fields, where they went from rock to rock, looking under seaweed and into cracks in the rock. However, observations of this type were rare and not quantified.

Twelve categories of fish were recorded in the diet (Table 3.2). 23% of the fish remains could not be identified, usually because the characteristic vertebrae (used for identification) had been fragmented. Figure 3.1a shows the mean consumption of fish in each month, with its associated standard error. Figure 3.1b shows the results smoothed using a 3-month running mean. As a proportion of the diet, females usually consumed more fish than males, though in the late autumn the difference was not marked. Both sexes consumed most fish in the late autumn and winter, though females showed a subsidiary peak in the summer.

Figure 3.2 shows how the proportions of the three main fish species in the scats changed throughout the year. The blenny was the fish most commonly taken by both males and females. Rocklings and seascorpion were also common in the diet, with eels and butterfish taken in smaller amounts; other species were consumed only occasionally. All these species were taken in greatest quantity during the winter. The subsidiary summer peak in fish consumption by females was caused by an increased consumption of blennies (Figure 3.2a), and was not evident for other species which were mainly consumed in winter (Figure 3.2b-c). Only in respect of blennies was there evidence of a sex difference in the consumption of an individual fish species, females consuming more than males.

3.3.2 Lagomorphs

The two lagomorph species in the study area were hare and rabbit. The distinction between species from hair remains in the scats was not attempted. Lagomorph counts suggested that the abundance of hares was relatively constant throughout the year (Figure 3.3b). The abundance of rabbits changed dramatically throughout however, being highest during early summer.

Figure 3.3a shows the seasonal change in lagomorph consumption through one yearly cycle. Males consumed significantly more lagomorph than females, but the trend in consumption over the year was similar for both sexes. Both sexes consumed least lagomorph in November and December, and most in May; whereas the abundance of rabbits was

lowest in December and January, and highest in June (one month after the equivalent trough and peak in consumption, respectively).

The correspondence between lagomorph consumption and abundance suggests that rabbits were the main prey type. However, male mink were observed to kill hares on two occasions, both times when the hares were in dense vegetation rather than open pasture. Hare remains were found in female dens, possibly collected as carrion.

Rabbit density was highest in the conifer plantation, Third Forestry, which contained many rabbit burrows but little understorey vegetation (Chapter 2). Radio-tracking revealed that mink foraged in the plantation, but not in the pasture where the rabbits grazed (see also Chapter 5), suggesting that rabbits were possibly hunted down their burrows. Struggles between mink and rabbit were observed above ground, in dense scrub or rocky habitat. The mink was never seen to kill its prey, the rabbit broke free of the mink's grip, though one mink was observed pursuing, and keeping up with, a bolting rabbit in an open field for almost 50m before the rabbit escaped.

3.3.3 Crustacea

Crustaceans formed the fourth most important component of mink diet, and mainly comprised the shore crab. Decapods, mainly the common shrimp *Crangon vulgaris*, and isopods, mainly the sea slater *Ligia oceanica*, occurred in small amounts (less than 5% in most months). Isopods seemed to occur in the diet most frequently in autumn and winter. No seasonal trends in consumption were apparent for females, there being considerable variation in consumption of crustaceans from month to month. There was a suggestion that males may have consumed them mainly during the late summer and autumn (Figure 3.4a). However, the sex difference (male: 6.7%, female: 15.7%) was significant, crustaceans accounting for a significantly greater proportion of the diet of females.

3.3.4 Birds

Figure 3.4b shows that females consumed relatively more large birds than did males. Females took relatively more birds in early autumn, whilst males fed on these prey more commonly during the winter months. 26% of the avian prey could not be identified (Table 3.2), and these unidentified birds occurred in greatest quantity during June (Figure 3.5b). This may have resulted from the consumption of juvenile individuals, the feathers of which did not possess the diagnostic downy barbules of the adult birds. Of the

identifiable bird remains in all scats, 60.2% comprised Charadriiformes and 25.8% were Passeriformes. Anseriformes, Columbiformes and Galliformes were taken only rarely (7%, 3% & 4% respectively).

Figure 3.5a shows changes in the proportion of Charadriiformes occurring in the diet throughout the year. Female mink consumed Charadriiformes mainly during the bird breeding season (summer), whereas males took most during the winter. Passeriformes were taken mostly during the winter and early spring by both sexes (Figure 3.6a). It should be noted however that the values presented were strongly influenced by the diet of particular individuals. For females, the great majority of all of the Charadriiformes was consumed by one female, (F11) which raised kits on Ross Island (which supported a herring gull breeding colony). Those faeces collected between May and September, consisted almost exclusively of bird remains. Table 3.5 shows this female's consumption of birds during the nesting season, and the switch in dietary composition from unidentified (probably unfledged) birds in May and June, to fledged ones from July onwards.

Numerous visual observations suggested that F11 was making extensive use of the abundant sea bird carrion available found on the island. However, observations were limited to daylight hours and it was uncertain as to how many, if any, of the birds she consumed were killed by her.

Table 3.5 A breakdown of the bird composition in the diet of F11. The percentages indicate proportions relative to all bird remains in the sample, not relative to all remains of every species in the sample as a whole.

Month	Scats	Dry wt.	Percentage of bird type in diet	
			Charadriiformes	Unidentified
May	7	1.4	14	86
June	111	60.9	15	85
July	24	7.3	98	2
August	27	17.2	91	9
September	14	5.0	100	0
December	7	4.4	–	–

3.3.5 Small mammals

Small mammals accounted for a very low proportion of the diet (4% in males and females, Figure 3.4d). There were however significant variations in the amounts consumed by different individuals: small mammals accounted for 20% of the diet of some individuals in some months, whereas other mink consumed none at all. These large variations made it difficult to generalize, but the majority of the predation was directed towards the field vole (Table 3.2). The rest were taken irregularly in the decreasing order: wood mouse, rat, bank vole and finally shrew. There were no obvious seasonal trends in consumption (Figure 3.6b-d), though taken as a group, males consumed most small mammals in late summer and autumn, whilst females had a higher consumption in the winter (Figure 3.4d).

3.3.6 Carrion

Figure 3.7a shows the number of hare carcasses found during the carrion counts. Hare carrion was low in abundance during the summer and early autumn, but high in the winter, especially during January and February.

Figure 3.7b shows the number of bird carcasses found in the carrion counts. Most carcasses were washed up during the winter but numbers were also high in July. The majority of the carcasses were of Charadriiformes (83%), mostly herring gull (45%). The summer peak was composed almost entirely of this species. A fair proportion of the birds were auks (20%), washed up on the shore during the winter.

Ross Island, not included in the carrion count route, has a large gull colony, from which 30–50 gull carcasses (60% of them from juvenile birds), were found each year. Many of these were apparently untouched by mink and presumed to be the result of natural mortality in the colony. Some were in the vicinity of, or had been dragged into, mink breeding dens. Many had not even been partially consumed.

It was impossible to assess the contribution of carrion to the diet as the most carrion species also inhabited the study area and were potential live prey.

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Figure 3.7 Carrion counts

Based on the mean number of carcasses found per
month on set walks. Data from two consecutive years,
one count per month. Vertical lines on bars
indicate standard errors.

a. Hares

b. Birds
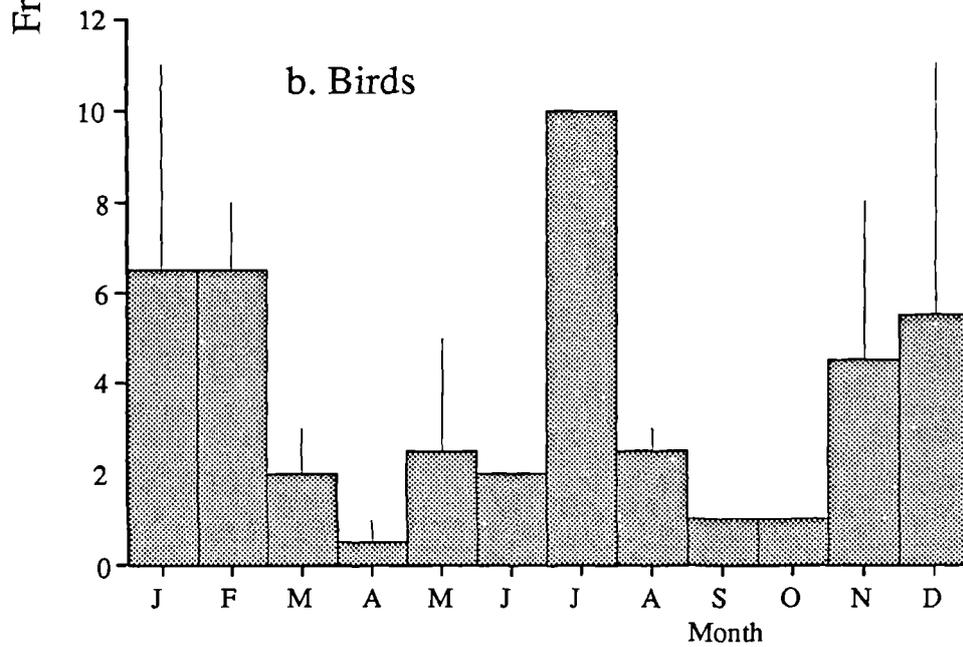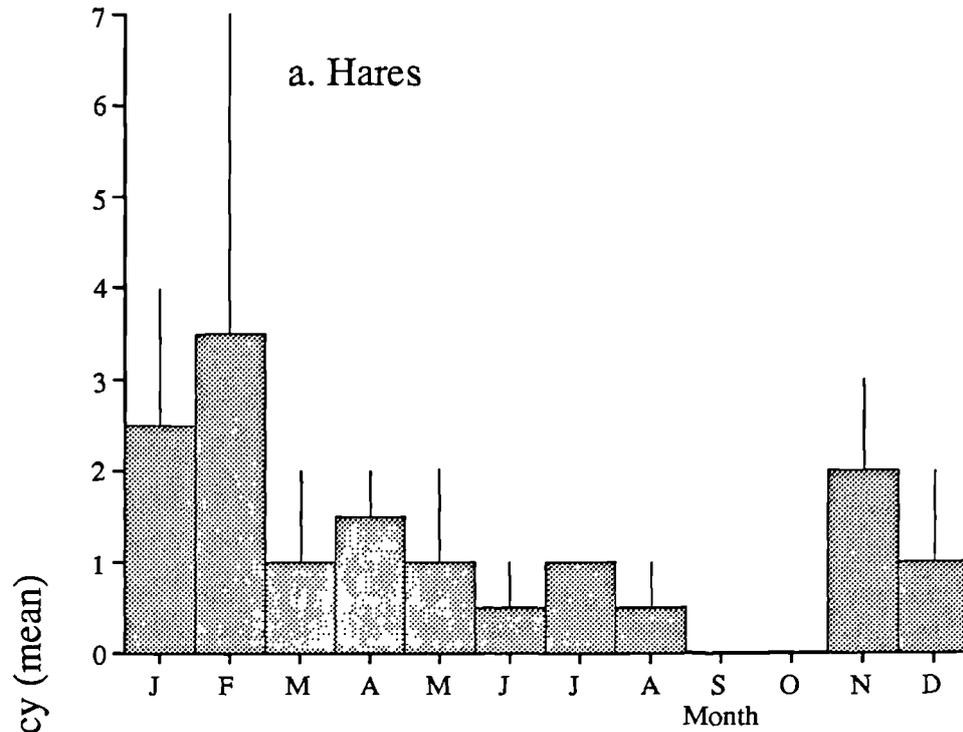
3.3.7 The effect of body size on mink diet

One suggestion by Birks and Dunstone (1985) was that sex differences in the diet were due to the ability of male mink to subdue lagomorphs more easily, by virtue of their greater size and weight. The mean weights of individual mink were calculated for each month when a scat sample was collected. The correlation between mink weight and the contribution of different prey groups in the diet was calculated using Spearman's rank correlation coefficient (one-tailed).

As expected, there was a significant positive correlation between mink size and lagomorph contribution to the diet ($\tau=0.299$, n=65, p<0.01) and a significant inverse one for fish ($\tau=-0.253$, n=65, p<0.05) None of the other correlations were significant (crab $\tau=-0.094$, n=65, N.S: small mammal $\tau=0.067$, n=65, N.S: large bird $\tau=-0.074$, n=65, N.S: small bird $\tau=-0.015$, n=65, N.S).

When correlations were calculated between prey contribution and weight for each sex separately, none were significant, for any prey group for either sex. This was not so surprising for females which were all within a narrow weight range (565–750g) but males exhibited a wide range of weights (870–1380g). In case the significant seasonal changes in diet could have been masking a weight effect (as samples came from all months), an analysis of covariance was performed. This removed the monthly effect, then the seasonal effect (as sex and weight were correlated) and finally examined the relationship between mink weight and the relative consumption of the two major prey groups, lagomorphs and fish.

Mink body weight did not account for the variation in consumption of either lagomorph (F<0.01, df=(1,39), N.S.) or fish (F<0.01, df=(1,39), N.S.) suggesting that the observed differences in the diet are simply due to sex and month.

3.3.8 The degree of association between different prey types in faeces

Many mink scats were often polyspecific. Figure 3.8 shows frequency distributions of the contribution of different prey groups in individual scats (measured on a 1–10 scale by volume: Chapter 2). Lagomorph was the only constituent in the majority of scats in which it occurred. The same was true for scats containing large and small birds. Fish and small mammals occurred regularly as traces in scats, whereas crustaceans occurred more often as traces than as major components.

Figure 3.8 The contribution of different prey items to the scat as a whole

For each prey group, the relevant figure shows the number of scats in which that particular prey group constituted a specified proportion of the scat (scored 1-10 by volume.)

As the gut transit time in mink is relatively short, (in the order of 2 hours (Slawinski *et al.*, 1962, Waller 1962)), any one scat produced is likely to contain the remains from only one foraging bout, or at the most one night's foraging. Thus polyspecificity enabled an indirect examination of the variety of prey a mink encountered during a foraging bout.

Table 3.6 shows whether a particular prey type co-occurred more or less often than expected with all other prey types in individual scats. The majority of fish species were positively associated with each other, suggesting that particular species were not hunted to the exclusion of others. The negative association between unidentified fish, and nearly all the other fish suggested that the inability to identify the fish vertebrae was due to damage, rather than difference in species. The positive association between fish and sheep, and fish and squirrel, probably occurred because these mammals were obtained as carrion washed up on the shore, as squirrels were never observed on the Ross Peninsula. Dead sheep were however washed up relatively frequently. Lagomorphs, rats and the larger birds were negatively associated with most other prey items, probably because they were large, and constituted at least an entire meal. They would therefore be expected to be the only prey item in the majority of scats in which they occurred (see also Figure 3.8).

3.3.9 Niche overlap between the sexes

A simple measure of intersexual niche overlap was worked out from the dietary data. Prey was split into five categories: aquatic, lagomorph, rodent, large bird and small bird. The extent of dietary overlap in each of these prey groups was summed, to give a measure of the overlap in dietary terms (Colwell and Futuyma, 1971; Southwood, 1978).

$$\text{niche overlap} = \sum_{i=1}^{5} \min\left(p_{mi}, p_{fi}\right)$$

where i represents the prey category (above)

p_{mi} represents the proportion of ith prey item in the diet of the male

p_{fi} represents the proportion of ith prey item in the diet of the female

$\min(x, y)$ represents the minimum value of the two arguments.

Figure 3.9 shows how this index varied throughout the year. Overlap was generally high over the winter, but also in May, when both sexes preyed on lagomorphs to a great extent. Overlap was lowest between June and August.

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Prey items (numbered):

1 eel
2 3-spined stickleback
3 blenny
4 butterfish
5 rockling
6 seascorpion
7 seasnail
8 goby
9 15-spined stickleback
10 unidentified fish
11 shore crab
12 other Decapoda
13 Isopoda
14 Amphipoda
15 other Crustacea
16 lagomorph
17 rat
18 field vole
19 bank vole
20 shrew
21 wood mouse
22 sheep
23 squirrel
24 unidentified mammal
25 Charadriiforme
26 Galliforme
27 Passeriforme
28 Anseriforme
29 Columbiforme
30 unidentified bird
31 amphibian

Item	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
1 eel																														
2 3-spined stickleback	+																													
3 blenny	+	+																												
4 butterfish	+	+	+																											
5 rockling	+	+	+	+																										
6 seascorpion	+		+	+	+																									
7 seasnail	+				+	+																								
8 goby		+		−	+	−																								
9 15-spined stickleback	+	+	+	+	+	+	+																							
10 unidentified fish	−	−	−	−	−	−	−	−	+																					
11 shore crab	+	+	+	+	+	+	+		+																					
12 other Decapoda	+	+	+	+	+	+	+		+	+	−																			
13 Isopoda				−	−	+	+	+	+		+	+																		
14 Amphipoda					+	+					−	+																		
15 other Crustacea	+		+	−	+	+	+	+			−	−																		
16 lagomorph	−	+	−	−	−	−	−	−	−		−	−	−	−	−															
17 rat	−				−						−	−	−		+	−														
18 field vole	+	−		−	−	−	−		−		+	−	+	−	−	−	−													
19 bank vole	−		+	−		−			+		+	−	+	−	+	−	−	−												
20 shrew			−	−				+			+	+				−			+											
21 wood mouse	−	+		+		−		+			+	+	−			−				−										
22 sheep	+		+	+	+		−		+	+					−															
23 squirrel			+	−				+			+					−						+								
24 unidentified mammal							+				−					−														
25 Charadriiforme	−		−	−		−	−	−	−		−	−	−		+	−	−	−	−		+			−						
26 Galliforme	+		−			−	−			+	−					−	+	−												
27 Passeriforme	+		−	−	−		−	−	+		−	−				−	+	+	+	+		−								
28 Anseriforme	−		−	−					−		−	−	−			−	−	+	+	+		+								
29 Columbiforme	+	+	+							−	+					−	−				+	−								
30 unidentified bird	−	−	+	−		−	−	−	−		−	+	−		−	−	−	−	−		+	−		+	−	−	−	−	−	−
31 amphibian	+		+		+	+				−	−		+			−		+		+	+			−	−		+			−

Table 3.6 The degree of association of different prey items in mink scats

A matrix examining whether particular food items co-occur in scats more of less frequently than would be expected from the frequency of occurrence of all food items in all scats.

Figure 3.9 Niche overlap between the diets of male and female mink

Details of the calculation used to work out the index of overlap is given in the text.
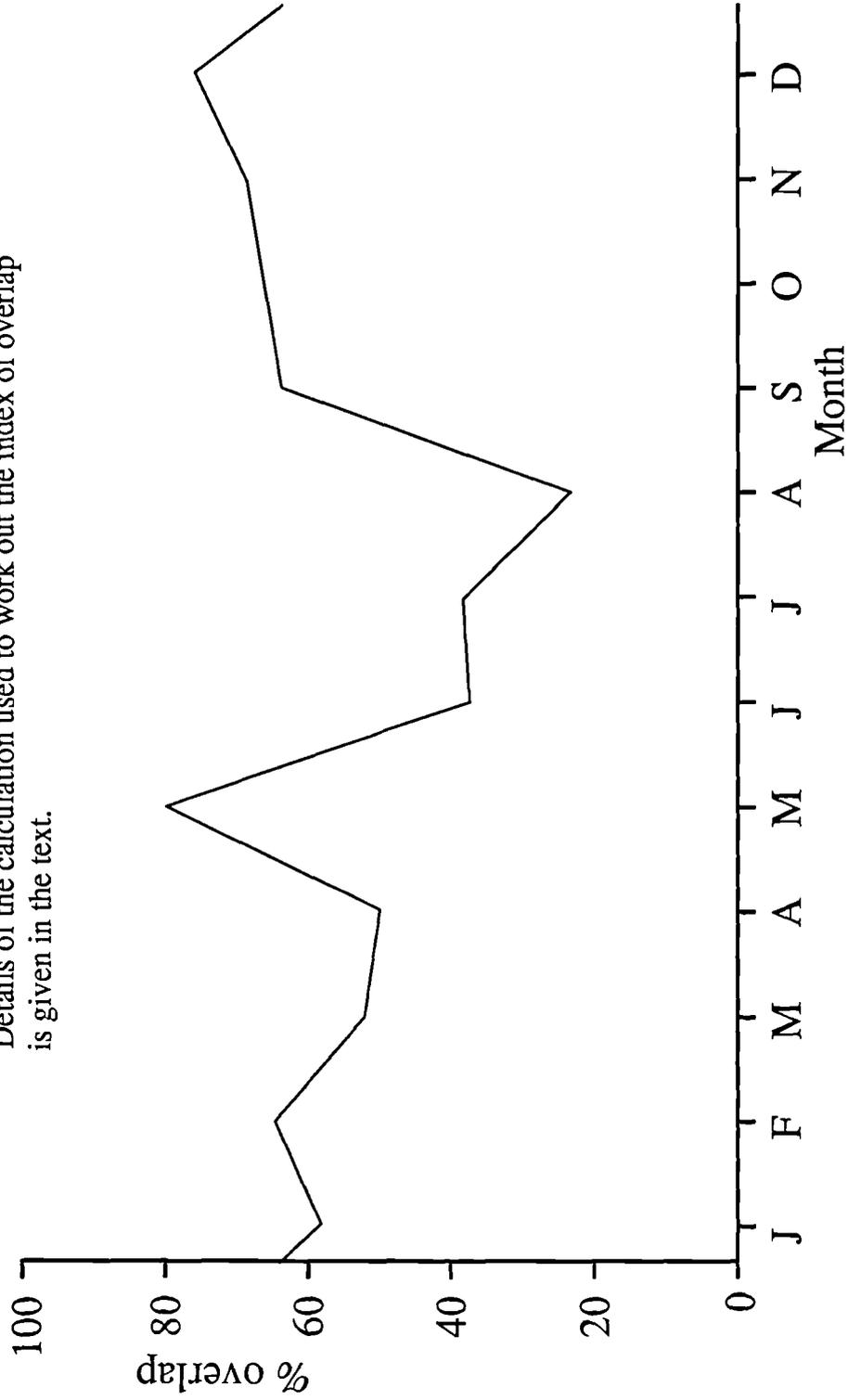
3.4 Discussion

3.4.1 Problems with interpretation

The use of faecal material is an indirect method of of assessing the diet of an individual or species. Errors range from biases in the collection procedure of the scats, through conversion of faecal remains to a measure of dietary intake, to assessing seasonal changes in the diet from relative measures of dietary composition. This has lead many workers to consider the errors so great that the techniques become worthless (Putnam, 1984). Yet, for a small nocturnal carnivore like the mink, it was the only way to obtain some idea of what they had been eating. A detailed discussion of the methods and associated biases is necessary before the results can be discussed realistically. Using a percentage bulk ("percentage weight of undigested material", Lockie, 1959), rather than a percentage occurrence method, reduces overestimation of the contribution of prey items which occur frequently, but as traces (Lockie, 1959; Englund, 1965; Erlinge, 1967; Day, 1968; Wise, 1978) and gives reasonable consistency for any prey species (Lockie, 1959; Wise, 1978). It has been criticized on the grounds that it uses a subjective estimate of relative bulk (Gerell, 1968), but Wise (1978) showed that, at least when bulk was estimated on a 1–10 scale, visual estimates were consistent between different workers.

Visual estimation of bulk could cause problems with polyspecific scats when skeletal remains from fish and crustaceans were being assessed against hair and feather remains from birds and mammals. However, most lagomorph and the majority of large bird remains were in monospecific scats (Figure 3.8), and fish and crustacean remains tended to be associated together in scats rather than with birds and mammals (Table 3.6). Trace constituents in a scat were allocated a tenth of its volume. This could have biased dietary composition slightly towards smaller items which occurred as traces, particularly crustaceans, but the problem caused would not be nearly so bad as when using frequency of occurrence to measure dietary composition.

No correction was made for the differing digestibility of different prey items. Correction factors have been calculated by a number of workers (Lockie, 1959; Akande, 1972; Moors, 1977; Wise, 1978). These vary for the same species between studies, but, in common to all studies, the larger the prey, the less remains were produced, both within and between different species. No correction factors were found for littoral fish or crabs in the literature, and birds could only be identified to order, not species, so prey size was not known. Also, it is likely that much of the predation of larger bird prey was

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directed against juvenile individuals. Because of these uncertainties, correction factors were not used and this probably biased estimates of consumption away from larger prey. As the major finding in the diet study was the male's preference for larger prey, levels of significance for sex differences probably should have been higher than reported.

Some biases were introduced with the collection procedure. Scats were collected from dens, and dens were found more easily amongst the rocks than in rabbit burrows, as scats were frequently deposited inside the burrow itself. In general, this probably biased the collection against scats containing lagomorph, and since males showed a preference for the latter types of den, against male lagomorph consumption. The effects of this bias are similar to those of ignoring correction factors (above).

Overmarking, the deposition of scats on or close to scats of other individuals (Robinson, 1987), presented another possible bias. which was more difficult to compensate for as its effect would depend on the sex of the individual which overmarked the scat. Its worst effect would be to reduce variance between individuals of the same sex in any one month, making sex and seasonal differences more significant. The large number of scats produced by an individual in its den would probably swamp any overmarking effect, and, as overmarking tended to be by depositing scats near, rather than on top of others scats (Robinson, 1987), care was taken to collect scats only from the main scat pile at a den, not individual ones near it. Still, it is another reason to be cautious about the significance attached to any result.

One limitation of the percentage bulk faecal analysis used here, is that the composition is simply an estimate of relative composition. No absolute figures are available as the amount of food consumed each month may vary depending on the demands on the mink at the time. By way of example, a mink may eat a constant amount of lagomorph each month, but if it requires extra energy, for example during the winter, it might make up the extra by preying on fish. Using faecal analysis, lagomorph consumption would show a yearly trend, decreasing during the winter despite there being no change in consumption.

Demands for food will probably increase during the moult, and for each sex differently during their reproductive cycles. Care has to be exercised, in not interpreting changes in relative consumption as absolute, but perhaps as changes in the relative ease with which the prey can be caught.

The data have been examined in the light of the potential biases discussed above. In many cases, particularly when between sex or between month comparisons have been

made, the bias is the same in both data sets and significant differences can be considered to be real.

3.4.2 Seasonal changes in prey consumption

Lagomorph consumption closely mirrored rabbit abundance as measured by the lagomorph counts, suggesting that , for both sexes, most consumption was of rabbits rather than of hares. The slight phase shift between abundance and relative dietary intake was probably an artefact caused by biases in the lagomorph count procedure. Rabbits are most active around dawn and dusk (Southern, 1940). Counts on the study area therefore commenced thirty minutes before dusk. The time of emergence is variable (Dunnet, 1957), and changes throughout the year (Rowley, 1957; Kolb, 1986), rabbits emerging after dusk from December through to mid-March (Kolb, 1986). This is presumably because the longer winter nights permit more grazing, rendering emergence during daylight unnecessary (Rowley, 1957). As counts were always made during daylight, the counts for the period December to March were probably lower than they should have been, and if this is taken into consideration, the form of the consumption and abundance curves will be even more similar.

Fish constituted a greater proportion of the diet of both sexes during the winter. This might have been because they were more available at this time, or because other prey items became more economical during the summer months. Details of seasonal changes in abundance of littoral fish were taken from the literature. Gibson (1967) found that there were large increases in the numbers of blenny and 5-bearded rockling in the littoral zone during the period July to September. Blennies, the major fish in the mink's diet, moved downshore during the winter making them less available. Thus it appears as if fish are consumed against a gradient of abundance.

Gerell (1968), studying mink in riparian habitats, showed a significant inverse correlation between water temperature and the proportion of fish in the diet. He suggested that fish become increasingly vulnerable to predation as the water temperature falls, and their swimming speed decreases. Thus, despite lower overall abundance, the actual availability of fish may be higher in winter. However, most of the fish in the diet inhabited the littoral zone, and as many were caught in rock pools, possibly in crevices and seaweed, swimming speed would be of less consequence. Gerell (1968) did not find marked seasonal fluctuations in his coastal study site either.

The secondary peak in the relative consumption of blennies by females was particularly interesting, occurring between June and August when female mink were raising kits, and when both lagomorph and fish density were high. A female mink's demand for food is likely to be very high at this time, and so the observed seasonal trend in relative consumption probably belies a very high absolute consumption of individual prey.

Data acquired during feeding trials with mink housed on farms showed that only 6% more food is required during gestation, but that a female might require almost twice her normal energy intake just prior to weaning the kits (N.Glem-Hansen, pers. comm.). The greatest demand on a female mink bringing up kits would probably occur some time in July, after weaning, but before her kits are able to forage for themselves. At this time she might have to find five times her normal food requirement, (depending on the number of kits she is rearing). Thus, in the wild, a female might actually be consuming more fish at this time than during the winter.

Qasim (1957) found that body condition in blennies (measured as a weight:length ratio), dropped to a low in July and August, after the blennies had spawned. Their condition remained low until September, after which it improved. They also displayed a drop in condition in late winter (February and March), probably due to lack of feeding. The results therefore indicate that there was an inverse relationship between the consumption of blennies and their condition, suggesting that blennies were preyed on by mink during periods of increased vulnerability.

If blennies were so available, why did a similar increase not occur in male diets? Restricted mobility of the female, caused by caring for the young could perhaps have led to local lagomorph depletion, and increased reliance on fish, as lagomorph predation usually involved staying with a kill rather than dragging it long distances to a den. Alternatively, the females might have changed diet in response to the needs of her kits. For example, optimal milk production in cows depends on the quantity of fat in the diet (Swift et al., 1948), and the amount of fat in the diet affects the digestibility of other rations in sheep (Swift et al., 1948). Many fish are rich in oils. In theory, as different prey comprise different proportions of protein and fat, changes in diet might be a means of optimizing milk quality for the kits. This is an unlikely explanation as fish consumption peaked in July-August, and weaning probably occurred at the end of June. Alternatively, as kits have demands different from adults, demands for tissue deposition and fur growth having to be met simultaneously, (Glem-Hansen, 1980a), different prey

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might be more suitable. Although the composition of many fish (Sidwell *et al.*, 1974), rabbits and birds (Gregory, 1987) are available, no information is available for rock pool fish. Values for fish vary so much between species that no further consideration of these factors was possible.

Predation on crustaceans showed no significant seasonal trend despite evidence from the literature that abundance of the main component, the shore crab, shows marked seasonal variation. Naylor (1962) found that a considerable offshore migration of large crabs occurs during the coldest months. The abundance of crabs in the littoral zone was highest in the summer and autumn, the mean carapace size increased to a maximum in autumn, and the greatest number of paired crabs were found in August and September. Some male mink may have responded to these changes in availability, whilst females continued to predate crabs at the same high level throughout the year. As with fish, seasonal changes in consumption by female mink may have been hidden by its measurement in relative terms. If this is considered, crab intake may also peak in the summer and the monthly changes may have been significant. Consumption may also have reflected crustacean abundance more closely.

Most of the bird remains found were Charadriiformes. The lack of significant seasonal trends of these birds in the diet was probably the result of their restricted and uneven distribution within the study area. Their prevalence in female scats in the autumn results from the inclusion of samples from female (F11) occupying an island with a limited breadth of prey species, at a time of the year when female scat samples were scarce. This points to the need for extreme caution during interpretation with such small samples.

That particular female mink's diet provided a good example of an individual taking advantage of abundant local food reserves. Harris (1964a) found that only 30% of the young herring gulls survived to the age at which they could fly. This suggests that a breeding colony would be a good source of carrion. In addition to this possible source of food, ringing returns in other areas suggest a high mortality of adult birds during the breeding season, between May and July (Harris, 1964b; Spaans, 1971). There certainly appeared to be carrion available in excess on Ross Island, comprising both adult and juvenile birds. In May and June, despite the availability of adult birds, most of F11's diet comprised unidentified, presumably unfledged birds. It is possible that F11 was still consuming carrion at this time, but nesting on the ground, young birds were particularly vulnerable and probably easy prey to mink. As mink were not radio-tracked at this time,

it was therefore uncertain whether predation was directed towards live young or carrion. In the years that the female was breeding on the island, the gull and cormorant colonies continued to expand (K.Bruce, pers. comm.), suggesting that the mink was not having any impact on it.

In summary, only the contribution of lagomorph to the diet had a strong, consistent relationship with its abundance within the study area, suggesting that it is a preferred prey type. However, using a relative measure of prey consumption may have hidden a closer relationship between a female mink's absolute consumption of aquatic prey and its availability throughout the year.

3.4.3 Sex-related dietary differences

The most significant sex difference concerned the contribution of lagomorphs to the diet. The rabbit is potentially a highly profitable prey item for mink, due primarily to its size. A fully-grown rabbit can sustain an adult male mink for two to three days (Linn and Birks, 1981). The rabbits' fossorial habits make them vulnerable to underground predation by mink because of the mink's size and shape, and because speed of pursuit is not vital (Birks and Dunstone, 1985). In general, larger prey, if readily available, make more sense on energetic grounds. Wise *et al.,* (1981) also found that rabbits were very important where available, and in North America, mink often prey heavily on muskrats, herbivorous, semi-aquatic fossorial rodents, similar in size to rabbits (Dearborn, 1932; Hamilton, 1959). Errington (1943) expressed his doubt that mink thrive in any areas in the North-Central states where muskrats do not thrive also. Other large prey, such as ground-nesting waterfowl are selectively predated where available in marsh and wetland areas (for example Gerell, 1968; Sargeant *et al.,* 1973; Wise *et al.,* 1981). Similarly, the female mink F11 ate almost exclusively large birds even when fish were probably abundant. Despite the advantages of larger prey, there were sex differences in the diet between large and small prey suggesting that the availability of some prey types differed between the sexes.

Availability is not simply a function of prey abundance. It is the prey utility which should really be considered. Utility is a function of the nutritional value of a prey item and its abundance, considered not in isolation, but set against the abundance of other available prey items. Gregory (1987) found that the differences in nutritional value reported by different workers, varied to a greater extent between studies than between

species. This being the case, the nutritional make-up of a prey item is probably of minor importance when assessing its value. The cost of search, pursuit and capture of the prey thus become important considerations. Understanding the costs involved in prey capture is necessary to understand the changes in the relative contribution of different prey in the diet.

The significant sex difference in the contribution of lagomorph to the diet, which was possibly underestimated by biases in the sampling and analysis (above), was very marked. Adult rabbits are large compared to mink, especially female mink. Observations of struggles between male mink and rabbits indicated that locating a rabbit did not guarantee a kill, and there were probably considerable costs in the pursuit and struggle, even without success. The much smaller female mink would probably be even less successful, both because of the inequality in size, and perhaps speed of pursuit. Alternative prey might thus be energetically more rewarding, and the result would be seen in sex differences in the diet, the female consuming more, smaller prey.

Lagomorph accounted for over 30% (perhaps an underestimate) of the female diet. There were suggestions that female mink may selectively prey on juvenile rabbits. One female was observed digging out a rabbit breeding stop (the sealed burrows where female rabbits raise their young) during the spring. Of nine rabbit carcasses found in a female mink's den during the summer of 1983, only one had a hind foot length that fell within the normal range of adult hindfoot sizes (Birks and Dunstone, 1983). This does not imply that female mink cannot kill adult rabbits. Stoats and weasels which are very much smaller than mink frequently kill rabbits (Day, 1968; Moors, 1974; Erlinge, 1975). It merely suggests that the high cost of killing rabbits (particularly during the winter because of their low abundance and large size) decreases the utility of rabbits to female mink to such an extent that other prey become equally or more profitable.

Both sexes showed increased relative consumption of smaller prey during the winter, when the abundance of most of the prey species was low. Whether this was primarily due to a decrease in the availability of preferred larger prey, or to an increase in availability of fish and invertebrates despite their lower abundance is open to question. The general shift to all types of small prey at this time suggests the that former explanation may be the more important. The increase of very small, not very profitable, crustaceans in the diet over winter might suggest food is becoming scarce, though on the other hand, it might be an incidental effect of an increase in littoral foraging.

Though little is known of the variation in absolute numbers of rabbits in the study area, the consumption of rabbits by mink of both sexes seemed to parallel apparent changes in their abundance. As the increase in rabbit numbers in the spring is due to the young of that year, the increase of lagomorph in the male diet, despite the probable increase in fish numbers, suggests that males are preying on juvenile individuals as well. Thus, difficulty in catching fully grown rabbits may give other prey higher utility, even to males, in the winter. Alternatively, a decrease in the contribution of lagomorph to the male diet might result from the inclusion of the scats from sub-adult males in the analysis. Sub-adults are still increasing in weight in February, and may not reach full size till their second year of life (Gerell, 1971). Juvenile males were first tracked, and their scats collected between October and December. If these smaller male mink prey on rabbits less frequently, the result would be an apparent winter decrease in male rabbit consumption. Unfortunately the sample size was not big enough to provide meaningful results when comparing adults with juveniles across months, but adult diets during the winter did contain appreciable aquatic prey.

The suggestion that males ate more rabbits because they were larger and more efficient rabbit predators was confounded by the lack of a significant covariant (weight) effect. It is possible that a relationship with size was hidden by variations in prey available to different mink in different ranges, and by the small sample sizes, but if not, it suggests that it is the sex which is important. Sexual dimorphism in head shape has been reported in many mustelids (Chapter 1), and its consequences are larger canine and carnassial teeth, and larger, more powerful jaw muscles. These adaptations would probably improve the chances of maintaining a hold on large prey, once captured, and may also contribute to the observed sex difference in the diet. A narrower head and snout, characteristic of female (and juvenile male) mink, might also help in the extraction of fish and invertebrates from crevices in the rocks where they typically take shelter. Therefore male mink may be inferior to female mink at aquatic foraging.

3.4.4 Intersexual competition

In many birds, there are differences in feeding apparatus as well as size which enable males and females to exploit different food resources (Selander, 1966). There is a consistent trend for female mustelids to consume smaller prey items than do males (Chapter 1), and in this study too, sex differences found in the diet would reduce the likelihood of both interference and exploitation competition. However, could the benefit

(intersexual coexistence) achieved by a reduction in competition have led to such extreme dimorphism?

Though sex differences exist, intersexual dietary overlap is still very high (King, 1977; Erlinge, 1979; Sealander, 1943; Gilbert and Nancekivell, 1982). Dietary overlap may be viewed as a maximum estimate of competition when preferred food resources become scarce or limiting (King and Moors, 1979). Food may become limiting either because of changes in availability or increases in demand. In the present study area, the diets of the sexes overlap to a large extent, overlap being highest during the winter and May, and lowest over the summer. The considerable overlap in May occurs at a time when both sexes prey heavily on rabbits, which are especially abundant at this time, and probably available in excess. Female demands for food are very high whilst rearing kits between June and August when niche overlap was at its lowest (though this result should be interpreted with caution as many of the scats collected at this time came from female F11, which was preying extensively on birds not available to other mink). Reduced niche overlap is not evidence of reduced competition however, as competition is perhaps forcing one or other sex to prey on less profitable items. However, the consistent difference between male and female lagomorph consumption throughout the year (Figure 3.1a) suggests that sex-related differences in consumption were simply due to the size difference between the sexes, and not due to any competitive interactions.

Mentioned previously, the proportionately larger jaw muscles and canine teeth of male mink (see Gregory, 1987) may result in males catching larger prey items more easily. It could then be interpreted as having evolved to promote the exploitation of different feeding resources. The dimorphism in skull shape in other mustelids lends support to this theory (Erlinge, 1979). However, there is a marked sexual dimorphism in the skull shape of otters and badgers as well (Wiig, 1986), and both of these species consume prey which are mostly smaller than themselves. In stoats, skull shape dimorphism increases with age, whereas it should occur early in life if it is associated with feeding (Erlinge, 1979). This suggests that some other factor was responsible for the dimorphism, possibly sexual selection. If that is the case, then sex differences in the diet may be incidental, either because of improved lagomorph capture or decreased littoral foraging efficiency.

The two schools of reasoning for sexual dimorphism are not necessarily mutually exclusive. Moors (1980) pointed out that the reduction in intersexual competition could be a valuable side-effect and could augment the main selective pressure for the trait.

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Similarly, if increased body size, and non-allometric growth of teeth and muscles led to advantages in competition with other males, advantages this accrued to males having to find more food, such as the more efficient capture of larger prey, could have lead to increased pressure for its selection.

4. ACTIVITY PATTERNS

4.1 Introduction

The energy demands of mink are unlikely to be constant throughout the year. Both sexes may require extra food during periods such as the moult and because of increased metabolic demands during cold weather. Females may suffer increased demands in the summer as they have to bring up their kits single-handed. Males probably have increased food demands during the rut when they compete for access to females. In addition, males need more food in absolute terms because of their larger size. Seasonal trends in activity were therefore examined to assess the effects of these changes in demand, and also to assess the extent of any energetic disadvantage caused by the sexual dimorphism in body size.

Mink diet varied with prey availability (Chapter 3). This led to seasonal changes in the consumption of different prey, and because prey availability and utility were probably affected by mink size, to a sex difference in the diet. Predators are known to synchronize their predatory activities with the activity periods of their primary prey (Curio, 1976), possibly because the detection of prey is easier when they are active (Bider, 1962; Kaufman, 1974). Concurrent activity patterns with prey have been shown for the pigmy owl *Glaucidium passerium* (Mikkola, 1970) and suspected for both mink (Gerell, 1969) and pine marten (Zeilinski *et. al.*, 1983).

The daily cycle of light and darkness is thought to be the most powerful 'zeitgeber', entraining the endogenous circadian rhythms of plants and animals (Daan and Aschoff, 1975), and Gerell (1969) has shown that it affects the activity of male mink. However, unlike riparian habitats, the coastline is also affected by the tidal cycle. With a period of approximately 12.4 hours, it is out of synchronization with the light/dark cycle, and as aquatic prey are important to mink, it may have a strong influence on their behaviour.

The activity budgets of male and female mink were therefore examined for correspondence with both cycles, and related to prey activity patterns to see if sex differences in the diet resulted in niche differences in the temporal plane.

4.2 Methods

The investigation of activity relies totally on data collected through radio-tracking (see chapter 2), though the results of dietary analysis (Chapter 3), and visual observations have been used to aid interpretation.

4.3 Results

A total of 22769 radio-fixes were collected (3795 hours), of which 10953 were obtained manually, the remainder by remote monitoring equipment. Fixes are broken down by sex and activity type in Table 4.1.

Table 4.1 A breakdown of all manually collected radio-fixes into each of the four categories of activity (see text), and also by sex.

Month	Male		Female	
	fixes	% activity	fixes	% activity
Inactive in den	3656	62.4	3399	66.7
Active in den	998	17.0	951	18.7
Foraging	790	13.5	585	11.5
Travelling	416	7.1	158	3.1
TOTAL	5860	100.0	5093	100.0

Twenty-five individuals, thirteen males and 12 females, were radio-tracked success-fully on 67 occasions. The distribution of these tracking episodes, throughout the year, is given in Table 4.2. These are the sample sizes on which the figures in Chapters 4–5 are based.

4.3.1 Overall levels of activity

In the analysis, the data collected from one individual in one month were used as one sample (termed an individual-month). The data collection technique led to biases in the number of fixes collected at certain times of the day. This was compensated for by calculating the mean activity in each of the 144 ten-minute intervals throughout the 24-hour cycle. These 144 intervals were then averaged as an estimate of the proportion of time spent active in 24 hours, for each sample. Sex-related and monthly differences were analysed using 2-way ANOVA, weighting each case by the number of fixes in each sample. Samples were only included in the analysis if data was available from at least

Table 4.2 A monthly breakdown of the number of manually collected radio-fixes and the sample of mink that were radio-tracked throughout the study. The total number of individuals actually refers to the number of monthly samples. Bracketed figures refer to the number of individuals for which more than 16 hours of data had been collected.

Month	Male		Female	
	Individuals	fixes	Individuals	fixes
January	5 (4)	1064	1 (1)	133
February	4 (4)	816	4 (4)	831
March	7 (3)	660	6 (6)	968
April	1 (1)	134	2 (2)	333
May	2 (2)	423	2 (2)	457
June	0 (0)	0	2 (2)	663
July	1 (1)	216	2 (2)	386
August	2 (2)	342	4 (4)	470
September	1 (1)	242	2 (2)	330
October	3 (3)	469	1 (1)	129
November	4 (3)	737	4 (2)	287
December	5 (5)	757	2 (1)	106
TOTAL	35 (29)	5860	32 (29)	5093

16 of the 24 hours throughout the cycle, reducing bias caused by activity estimates based on a limited part of the cycle.

Males were found to be more active than females. They spent an average of approximately 19% of their time (4.6±0.45 hours) out of their dens, compared with 14% (3.6±0.51 hours) for females. This sex-related difference was significant (F=4.88, df=(1,35), p<0.05), whereas there was no significant difference in the levels of activity between months (F=1.52, df=(11,35), N.S.).

For the purpose of analysis, the time spent out of the den was subdivided into time spent foraging and travelling. There was very little difference in the time each sex spent foraging per day. (F<0.01, df=(1,35), N.S.). Males spent 2.9±0.37 hours per day engaged in this activity, compared with the females' 2.8±0.42 hours. This amounted to 12% of the 24 hour cycle. When the monthly trend is plotted (using three-month running means) males and females are seen to behave similarly throughout the year, both sexes showing decreased foraging activity during late spring and early summer (Figure 4.1). The running means hide particularly low activity values for females in May. At that time the young had just been born and the female used predominantly one den, limiting the

extent of her movements (Chapters 5–6). The females spent 41±14.7 minutes per day foraging.

The seasonal monthly trends in time spent travelling per day differed between males and females (Figure 4.2). This was evidenced by a significant interaction in the two-way analysis of variance (F=2.74, df=(10,35), p<0.05). The data for each sex were therefore analysed separately using a one-way analysis of variance. Males were found to display significant monthly changes in travelling activity (F=2.57, df=(10,18), p<0.05). This occurred as two seasonal peaks, a major one in March and a subsidiary one in August and September. If the one data point for December is ignored, females showed increased, though not significant, amounts of travel, mainly during July and August (F=1.86, df=(11,17), N.S.). The sex-related difference in travelling was highly significant (F=8.43, df=(1,22), p<0.01). Males spent 2.1± 0.16 hours travelling whilst females only travelled for 0.8±0.19 hours a day. The majority of the sex difference was due to the males' behaviour between February and April (Figure 4.2).

4.3.2 Levels of activity within the 24-hour cycle

Figure 4.3 shows the proportions of time spent in each of the four different activity types, over the 24 hour period, based on manually-collected radio fixes. Both sexes spent the majority of their time in their dens, and during much of this time they were inactive. Out-of-den activity was at its lowest around midday, and was highest during the hours of darkness, especially for males.

One of the primary determinants of activity for mink is the day/night cycle (Gerell, 1969; Whitman, 1981). As the lengths of the dark and light periods show considerable variations throughout the year, the data were split into four 3-month periods to observe how activity was related to the light/dark and dark/light transitions. The four periods; February to April, May to July, August to October and November to January, were chosen as the main events in the minks' yearly cycle (i.e., the rut for males, the rearing of kits for females and the dispersal of juveniles), partitioned conveniently into the first three of these four 'seasons' respectively.

The day was divided into 24 one-hour samples and the mean activity level for each mink in each month for each one hour period was calculated. For each 3-month period, a two-way analysis of variance was carried out, to analyse the effects of sex and time (one hour sample) on activity levels. Samples were weighted depending on the number of

Figure 4.1   Monthly variations in the total time spent foraging per day
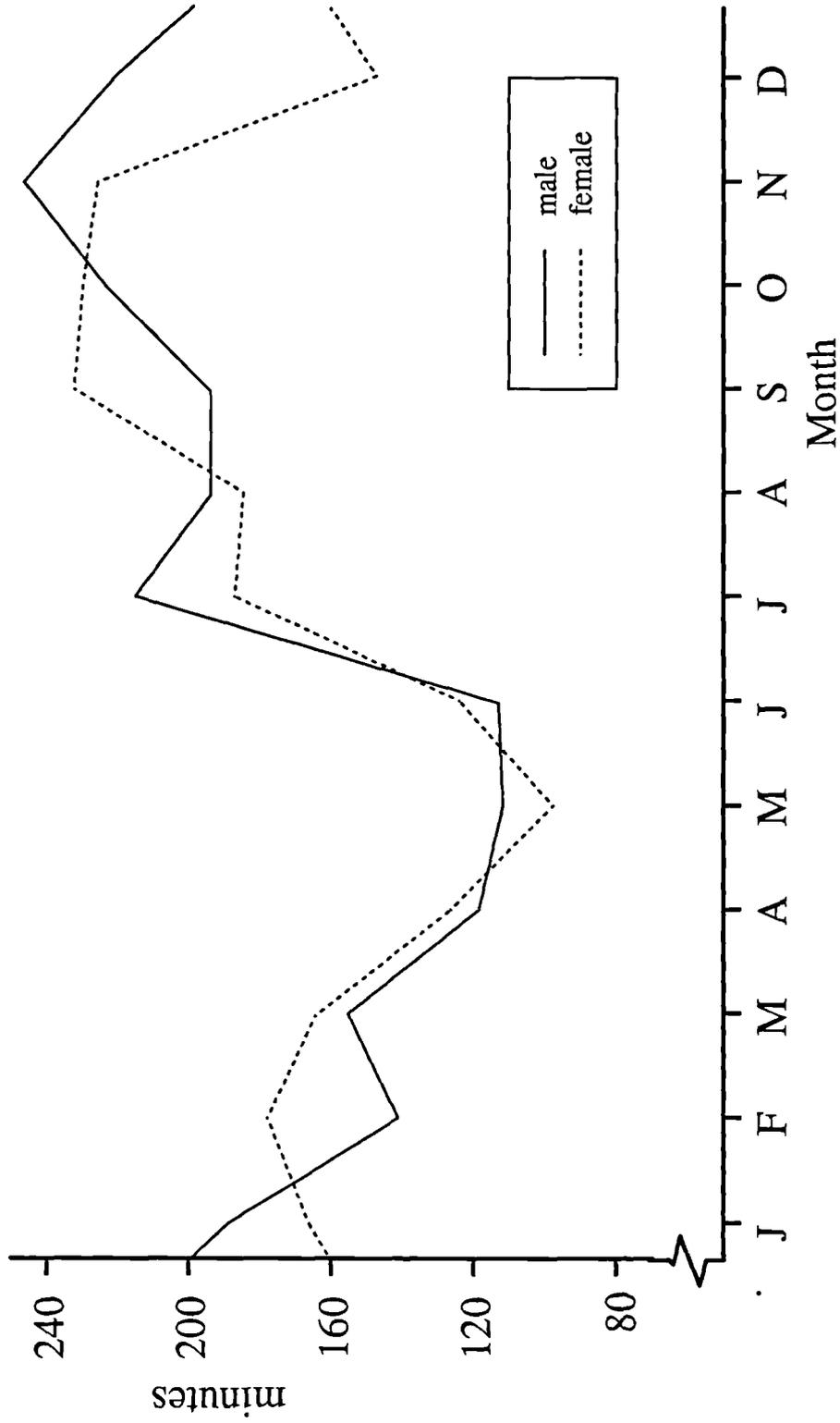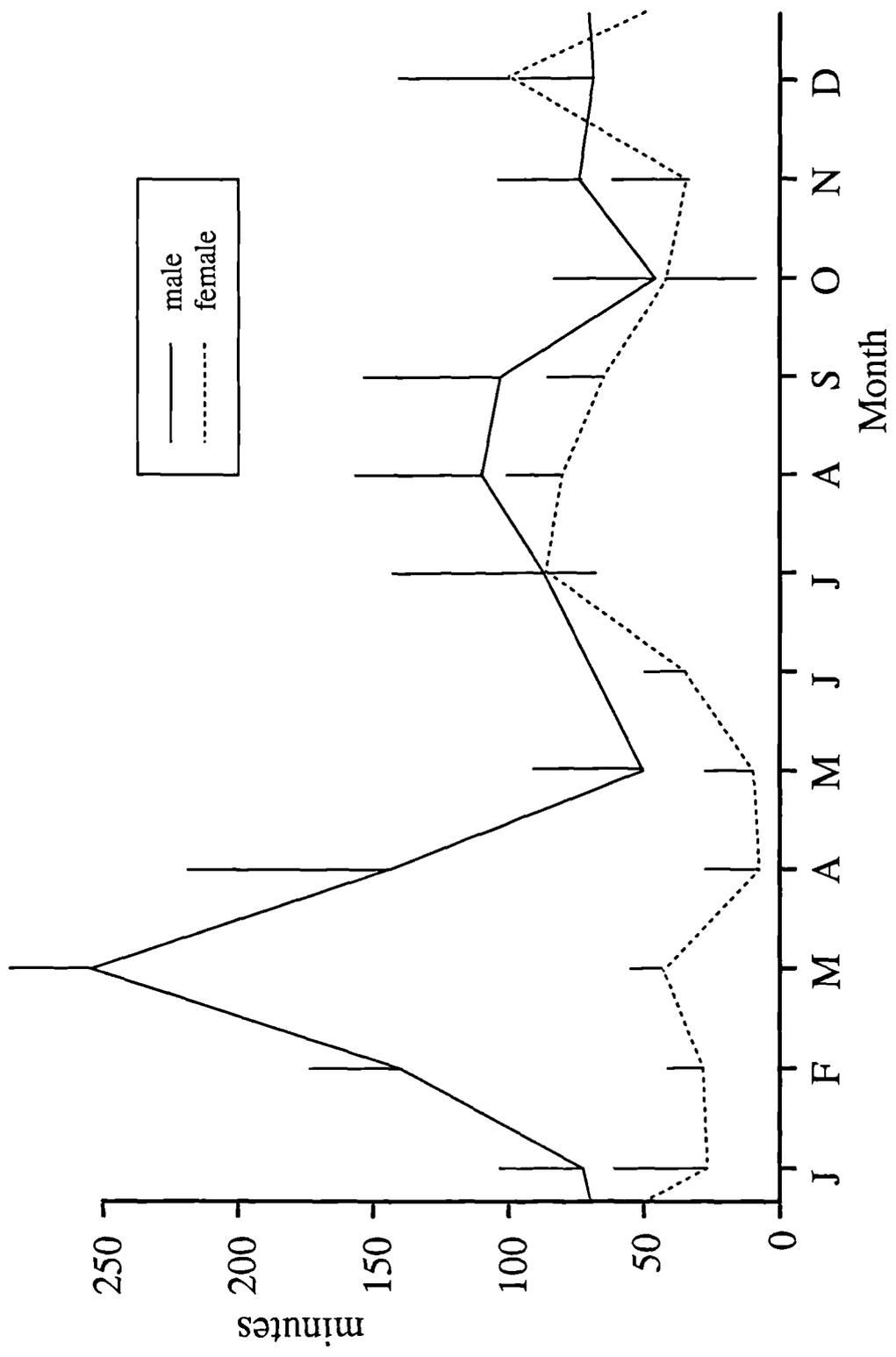(3-month running means)
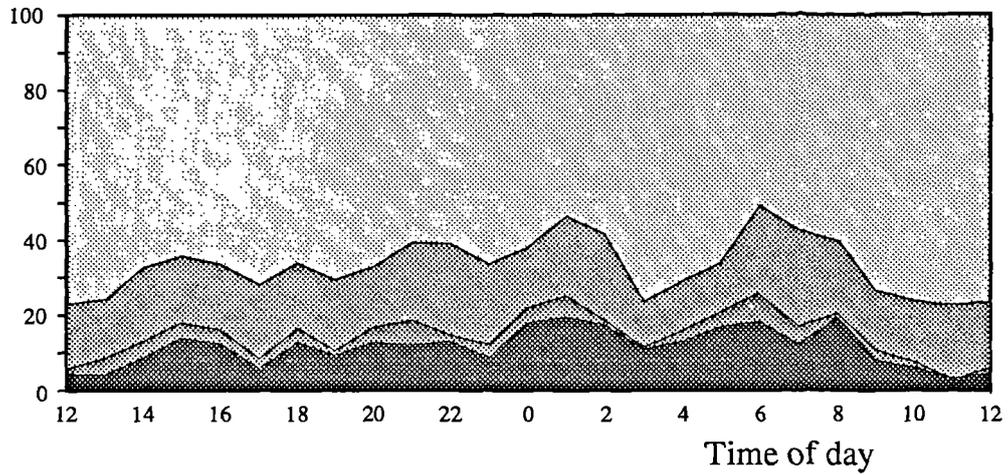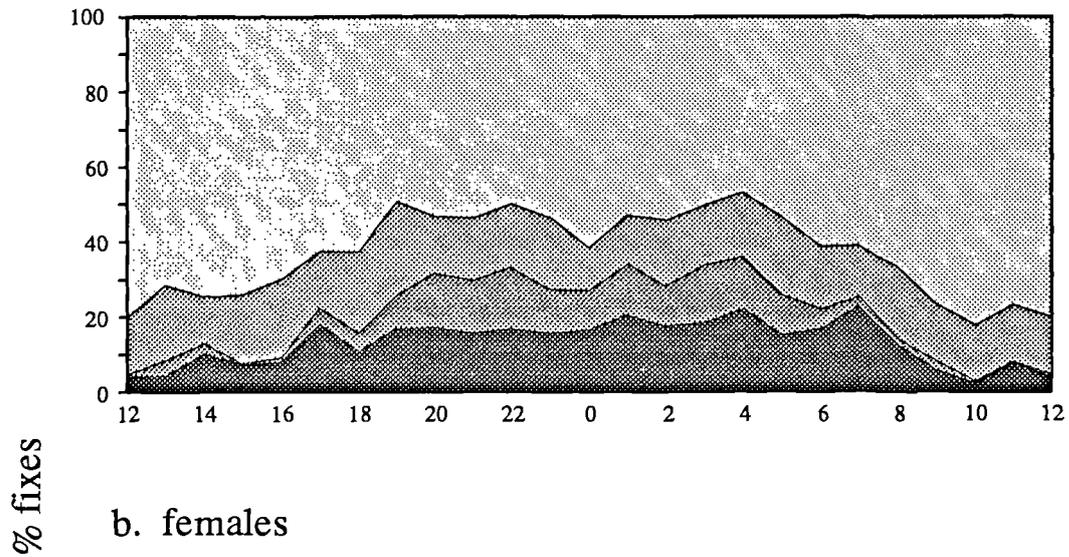
Figure 4.2   Monthly variations in the total time spent travelling per day

Figure 4.3 Patterns of activity throughout the 24-hour cycle

based on the activity types determined by the radio-signal summed for the whole year and divided into 1-hour samples throughout the day.

a. males

b. females

Time of day

inactive in den
active in den
travelling
foraging
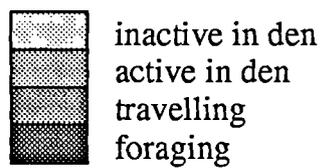
fixes used to calculate the activity in each one hour sample. Significant interaction effects were present during two of the 3-month periods (Table 4.3), therefore the effect of time on activity was analysed using a one-way analysis of variance for each sex separately (Table 4.4a). Sex effects were also analysed using a one-way ANOVA (Table 4.4b). The levels of activity throughout the 24-hour cycle are presented in Figure 4.4, a-d. Standard errors have been deliberately omitted to improve the clarity of the diagrams. The shaded bar above the graph depicts the light and dark periods, and the spread of times over which dusk and dawn (in this case civil twilight, the time when the sun is 6° below the horizon) occur, as this time changes over the three-month period.

a) February-April: A significant interaction between the two main factors, sex and time of day, was apparent. This suggested that both sexes were active at different times of the day. Two peaks in male activity were apparent during the night. Activity levels were high around dusk and dawn, with a lull in activity around midnight (Figure 4.4a). Male activity during the day was significantly lower than at night. There were no significant variations in female activity throughout the day. There was, however, a significant difference in the overall levels of activity between the sexes during February to April, males being active for 23% of the day compared with 14% for females (Table 4.4b).

b) May-July: A significant interaction effect indicated that both sexes were still active at different times. Males concentrated all their activity in the short time between dusk and dawn. Because of this, the chances of finding a male active at night were very high (Figure 4.4b). The levels of male activity varied significantly throughout the 24 hours. Females showed high levels of diurnality but also an increased level of activity at night, after midnight. Female activity also differed significantly over the 24 hours. Mean activity levels over the 24 hours were very similar for both sexes (males, 12.5%; females, 12.1%), but as Figure 4.4b shows, activity was temporally distributed quite differently for the two sexes.

c) August-October: Greater similarity between the behaviour of both sexes meant that there was no significant interaction between sex and time (Figure 4.4c). Male activity was again split into a dawn and a dusk peak, with low levels of diurnal activity. Differences in levels of activity throughout the day were significant for males, but not for females. Female activity was much higher than at other times of the year (Table 4.4b), there being very little difference in overall levels of activity between the sexes.

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Table 4.3 Two-way analysis of variance examining the effect of sex and time (one-hour periods throughout the 24-hour cycle) on levels of activity, during four three-month periods.

Period	error df	Sex (df=1)		Time (df=23)		Interaction (df=23)	
		F	sig	F	sig	F	sig
Feb–Apr	446	20.47	***	5.17	***	2.67	***
May–Jul	166	0.01	NS	4.61	***	2.21	**
Aug–Oct	239	0.28	NS	2.79	***	1.46	NS
Nov–Jan	367	3.71	NS	2.43	***	0.76	NS

The header spanning "Sex (df=1)", "Time (df=23)", "Interaction (df=23)" is under the group heading **Effect**.

Table 4.4 One-way analysis of variance examining the single effects of time (one-hour periods throughout the 24-hour cycle), and sex, on levels of activity, during four three-month periods.

a) time

Period	Male			Female		
	F	df	sig	F	df	sig
Feb–Apr	7.03	23,215	***	1.05	23,254	NS
May–Jul	6.51	23, 47	***	1.91	23,119	*
Aug–Oct	2.67	23,116	***	1.49	23,123	NS
Nov–Jan	2.21	23,294	**	1.20	23, 73	NS

b) sex

Period	ANOVA			Activity (hours)	
	F	df	sig	Male	Female
Feb–Apr	7.99	1,18	*	5.6±0.63	3.3±0.52
May–Jul	0.01	1, 7	NS	3.0±1.07	2.9±0.68
Aug–Oct	0.11	1,11	NS	4.6±0.60	4.8±0.64
Nov–Jan	0.60	1,14	NS	4.7±0.77	3.2±1.85

d) November-January: The levels of activity of males and females were quite similar with respect to the day/night cycle (Figure 4.4d), and therefore the interaction between sex and time was not significant. Average levels of activity throughout the night were lower compared with other 'seasons', the nights being of longer duration (Figure 4.4d). Males still became more active at dusk, and inactive near dawn, but this behaviour was also evident for females. In this period, females were less diurnal than the males. Only males exhibited a significant difference in activity throughout

Figure 4.4 Seasonal changes in the levels of activity throughout the day

based on individual mean levels of out-of-den activity.
(Standard errors not included)

The bar represents the light/dark cycle, intermediate shading (twilight)
representing the spread in the times of civil twilight throughout
the 3-month period.

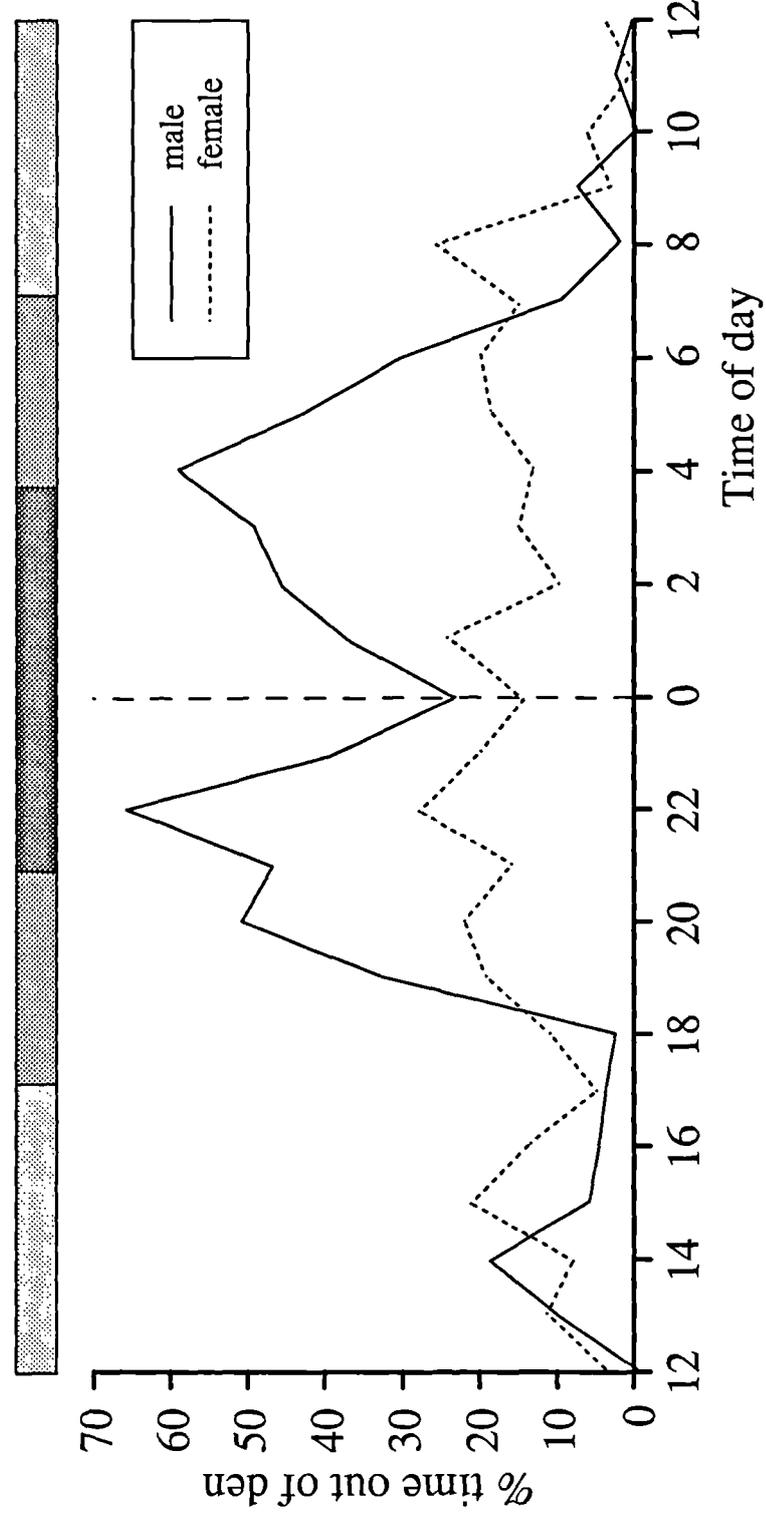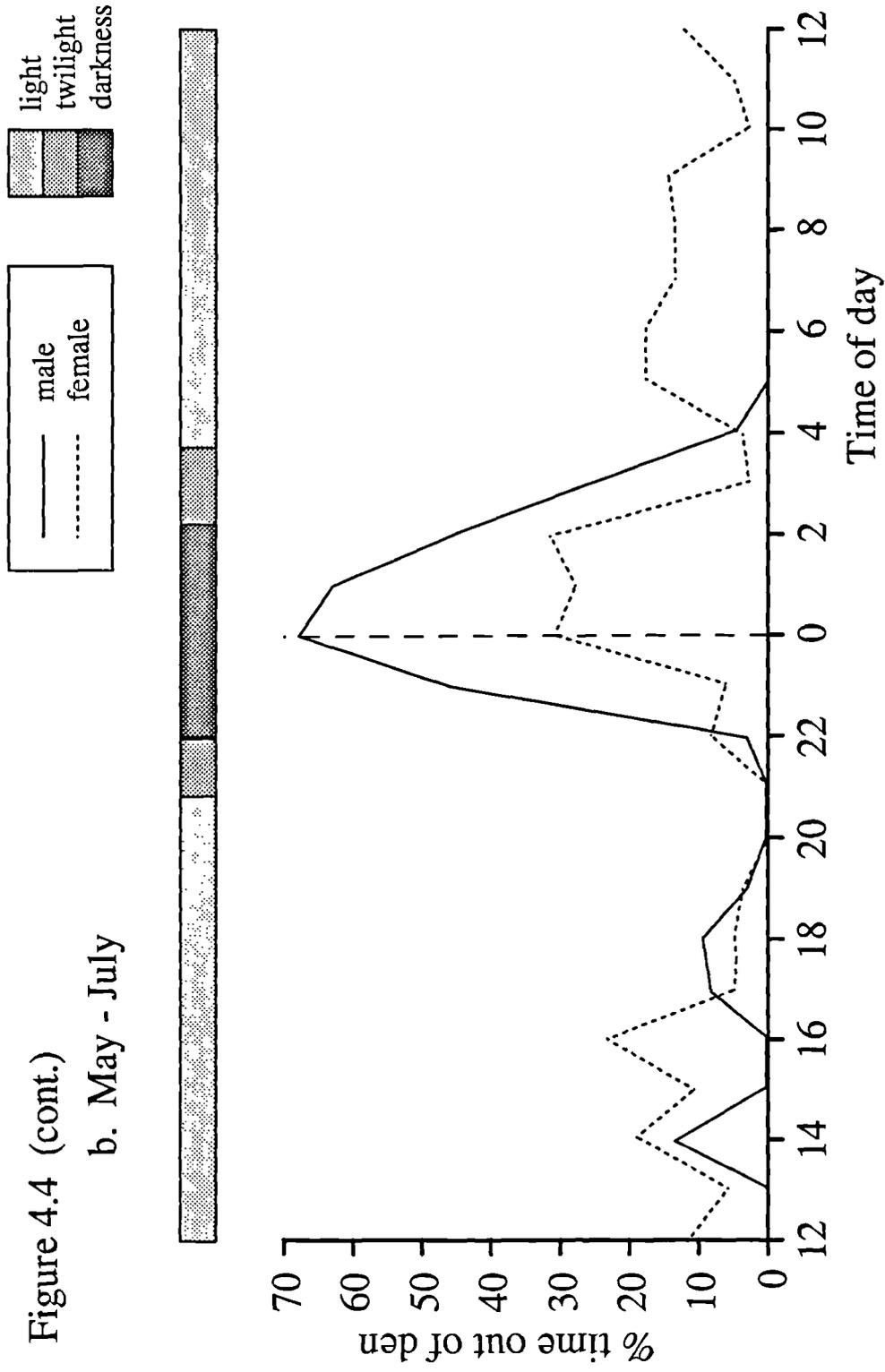## a. February - April

light
twilight
darkness
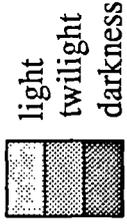
Figure 4.4 (cont.)
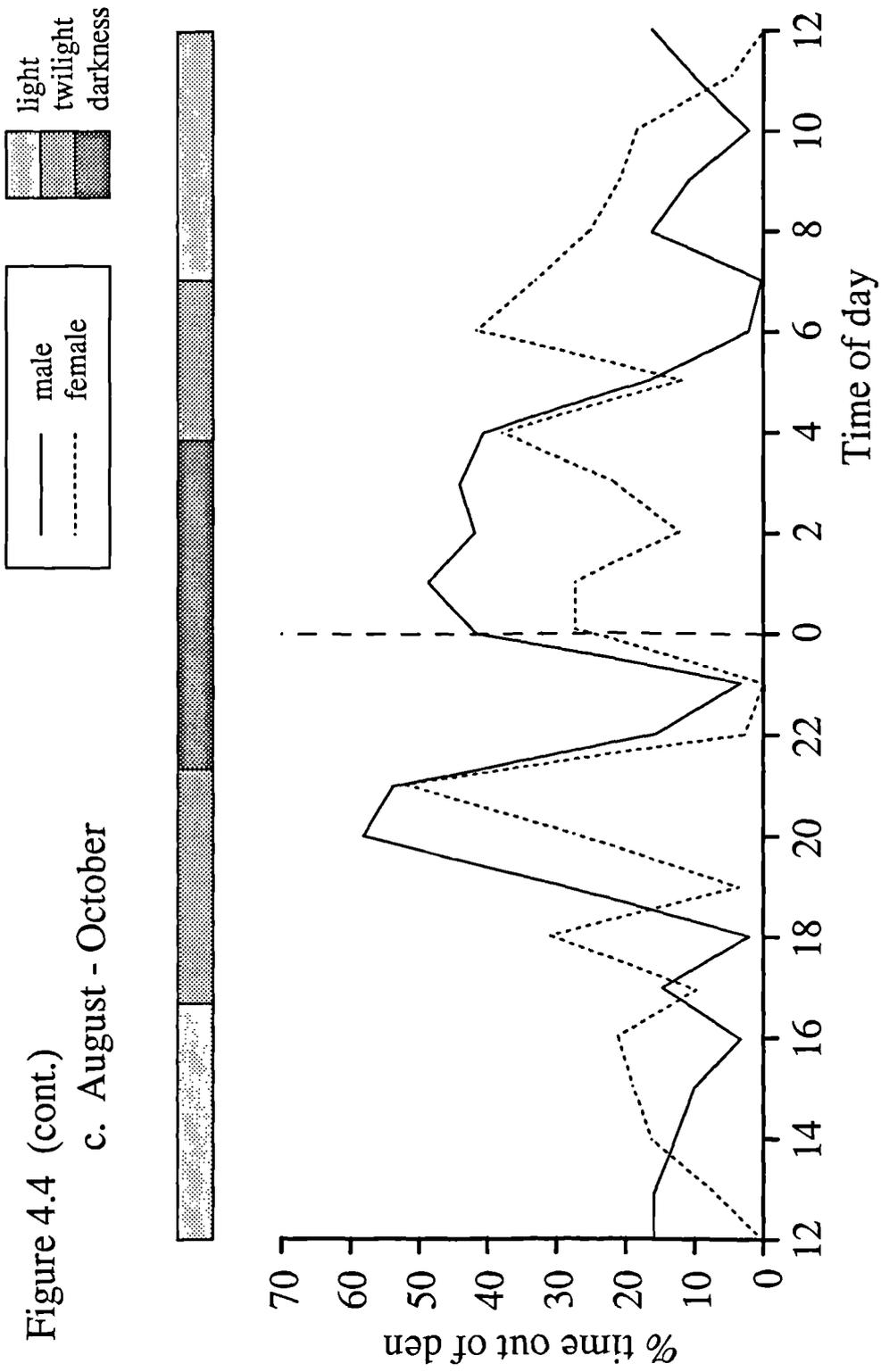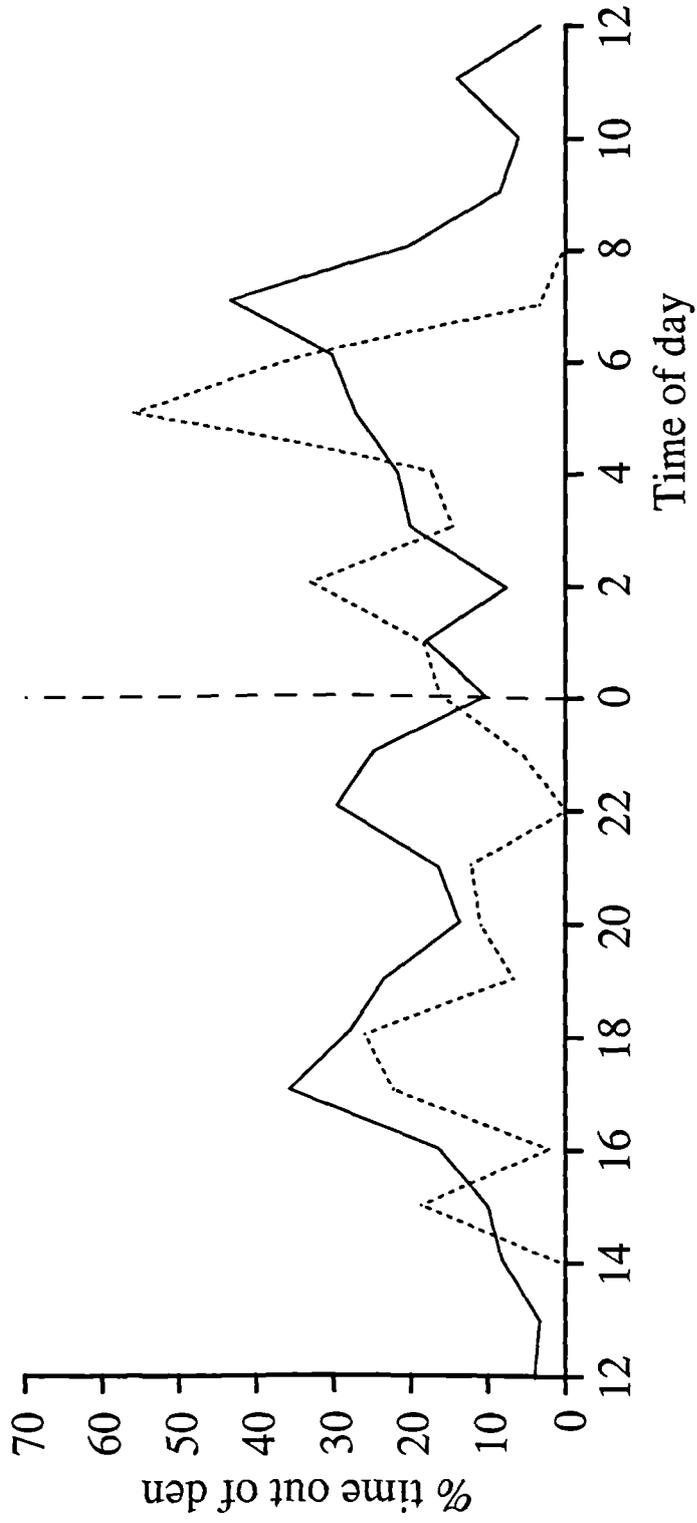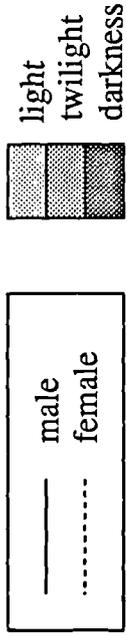b. May - July

Figure 4.4 (cont.)
c. August - October

Figure 4.4 (cont.)
d. November - January

the 24-hour period, and although males showed raised levels of activity with respect to females (18.6%:12.6%), the difference was not significant.

4.3.3 Levels of Nocturnal activity

Levels of nocturnal activity were calculated as the proportion of time a mink was out of its den during the dark period, in relation to the total amount of time it spent out of its den over the 24 hour cycle. This was calculated for each individual in each month, and analysed using a two-way analysis of variance.

84% of the male activity occurred during the hours of darkness compared with 64% of the females' $(F=11.77, df=(1,44), p<0.01)$. There was also a significant difference in the level of nocturnal activity between months $(F=2.62, df=11,44), p<0.05)$.

4.3.4 Crepuscular behaviour

This was investigated by considering activity in blocks of time relative to dawn and dusk. The duration of time between dawn and dusk varies considerably throughout the year, so activity relative to dusk has to be considered separately from that relative to dawn. Where the terms "dawn" and "dusk" are used, they refer to civil twilight rather than to sunset and sunrise *per se*. The mink's activity was split into two samples: that occurring closest to dawn, and that occurring closest to dusk. The cut-off times between the two periods were close to (but not exactly equal to) midday and midnight, Greenwich Mean Time. Mean levels of activity out-of-den were calculated for one-hour periods either side of dawn and dusk. These were analysed using a one-way analysis of variance, nesting multiple observations for the same individual within the one-hour periods. The analysis was weighted using the number of fixes used to make up each one-hour sample.

Significant interactions between the effects of sex and levels of activity were found both at dawn $(F=2.29, df=(16,688), p<0.01)$, and dusk $(F=2.09, df=(16,732), p<0.01)$. Each sex was therefore analysed separately. Highly significant differences in levels of activity with respect to dawn $(F=6.69, df=(17,366), p<0.001)$, and dusk $(F=5.94, df=(17,384), p<0.001)$ were exhibited by males. Figure 4.5a shows that the probability of activity was low during the day, but increased dramatically during the hour after dusk. There may have been a secondary peak later on during long nights. Activity was likely

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again 2-3 hours before dawn, remained high until an hour after dawn then returned to low levels.

The differences in activity either side of dawn and dusk were not so distinct for females (Figure 4.5b). However, activity was generally at a higher level at night. The levels of activity did not differ significantly either side of dusk ($F=1.47$, df=(16,348), N.S.), or dawn ($F=1.45$, df=(16,332), N.S.).

The diurnal component of activity was examined by grouping the radio-fixes (from all individuals within each sex), and then subdividing them into different activity classes or habitat-utilization classes (Figures 4.6–4.7). Travelling proved to be a predominantly nocturnal activity in males (Figure 4.6a), but did not account for much of the behaviour of females (Figure 4.6b). The distribution of shore-based activity of females (Figure 4.7b) was not different from the distribution of total activity in the females (Figure 4.5b), and the former still showed a major nocturnal, as well as a diurnal, component. Males were particularly active on the shore at dawn, and the chances of a male being active were still high an hour after dawn (Figure 4.7a). The plantations were the only habitat where diurnal activity was greater than nocturnal activity (Figure 4.7c-d); 58% of all foraging in plantations occurring during daylight hours. In all other habitats, the reverse was true (proportion of that time spent foraging which occurred during daylight hours: shore, 29%; scrub, 18%; rocks, 13%; pasture, 5%).

4.3.5 Activity with respect to the tide

The height of the tide for each radio-tracking fix was calculated using Admiralty Tide Tables. Harmonic constants necessary for the Admiralty method of tidal prediction (Admiralty, 1981) were not available for the Kirkcudbright Bay area, therefore a FORTRAN program was written to interpolate from the tidal curves for Liverpool. The known differences in tidal height and timing from Liverpool to the study area allowed tidal heights in the study area to be calculated to the nearest centimetre. This was obviously unrealistic due to inaccuracies in prediction, and because of meteorological effects so the height of the tide for each fix was rounded to the nearest metre.

For each mink, in each month, its activity (proportion of time spent active out of its den) was calculated for different tidal heights (based on one metre height intervals). The effect of sex and tidal height on activity level was then examined in a similar way to the 24-hour cycle analysis.

Figure 4.5 Levels of activity with respect to dawn and dusk
(means + standard errors)

dawn
dusk

a. males

% time out of den

Hours from twilight
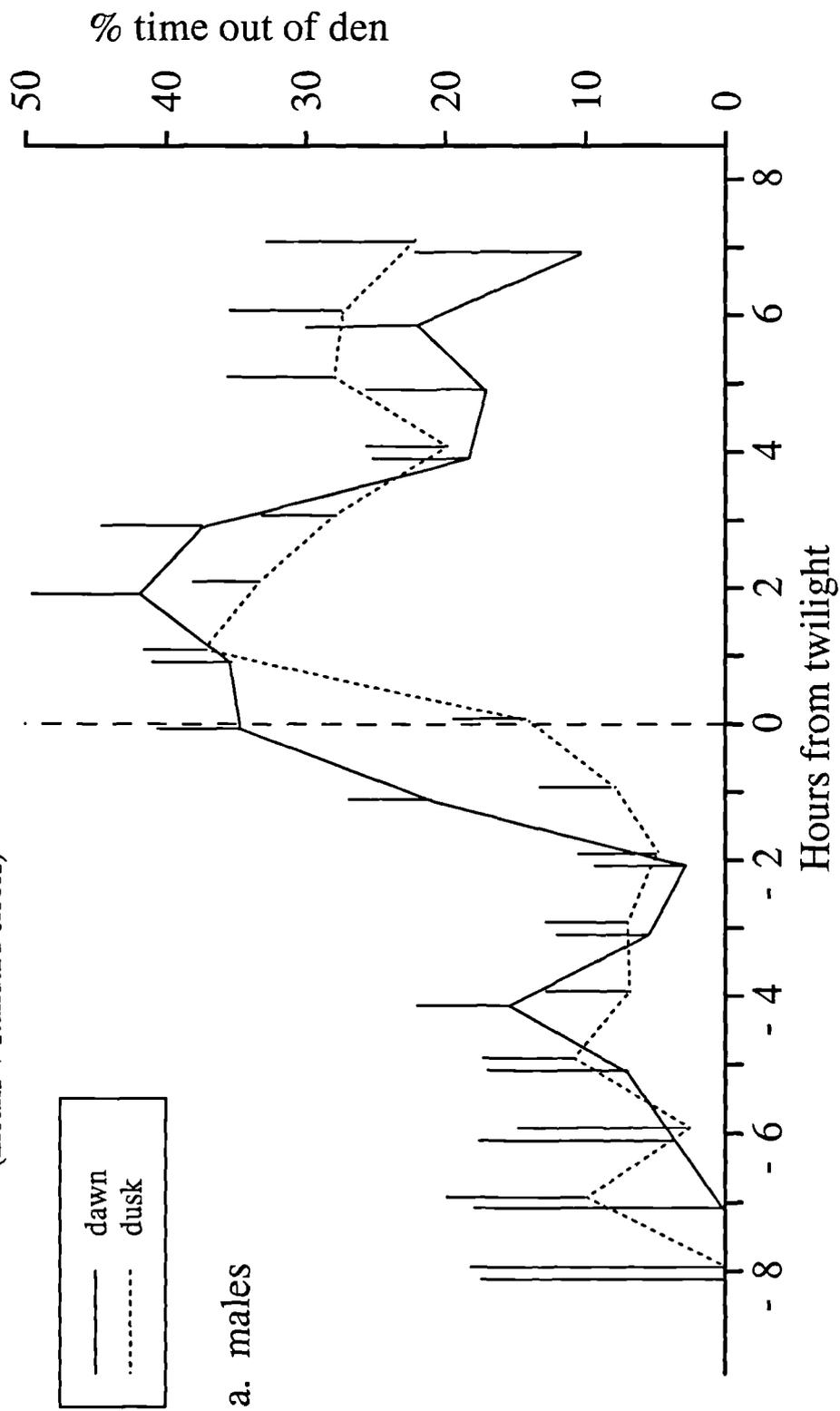
Figure 4.5 (cont.)
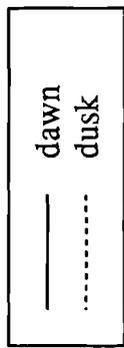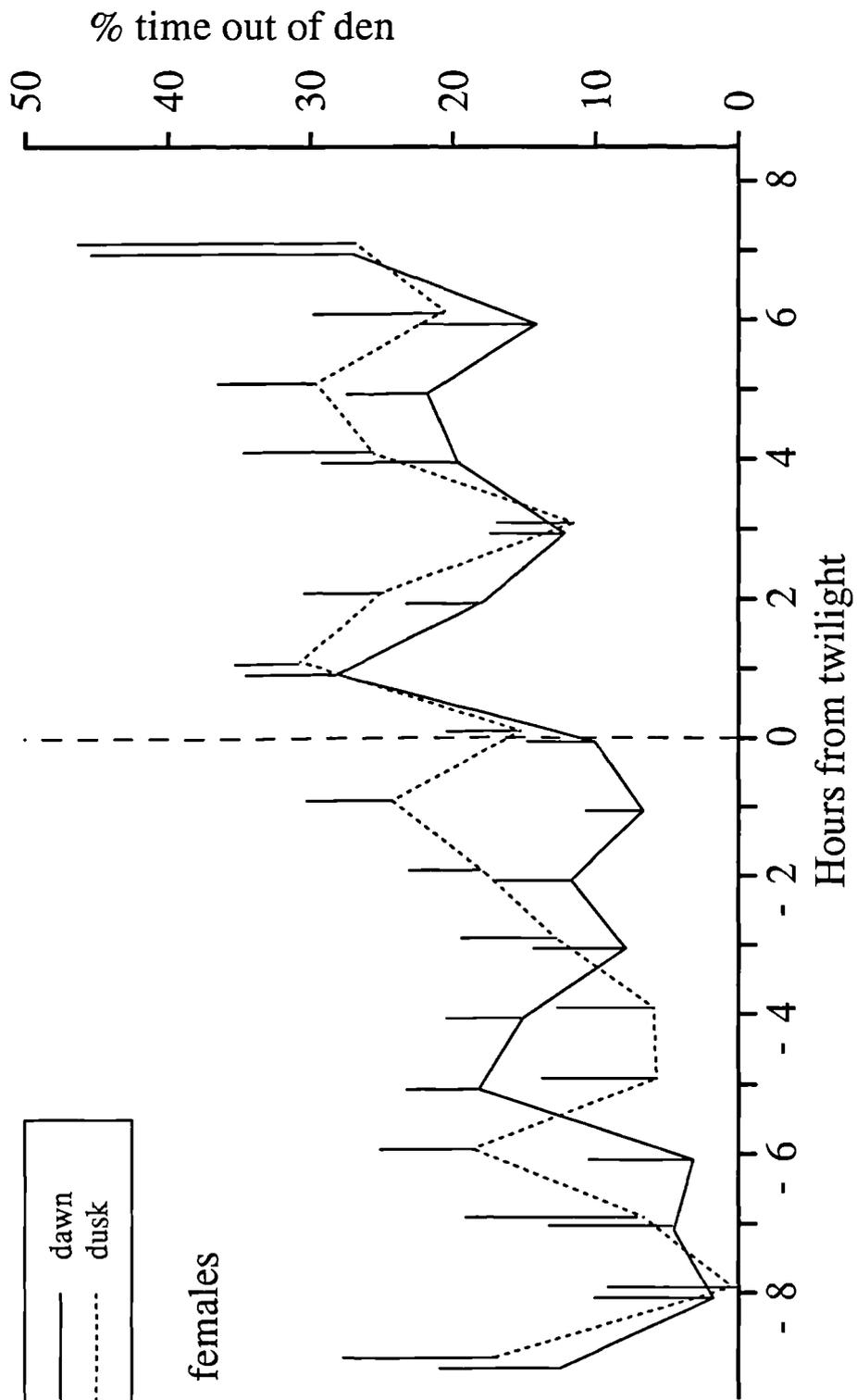
b. females

Figure 4.6   The proportion of time spent travelling with respect to dawn and dusk

based on the number of radio-fixes
categorized as travel as a percentage
of all fixes in one-hour samples
either side of civil twilight.

a. males
(5680 fixes)
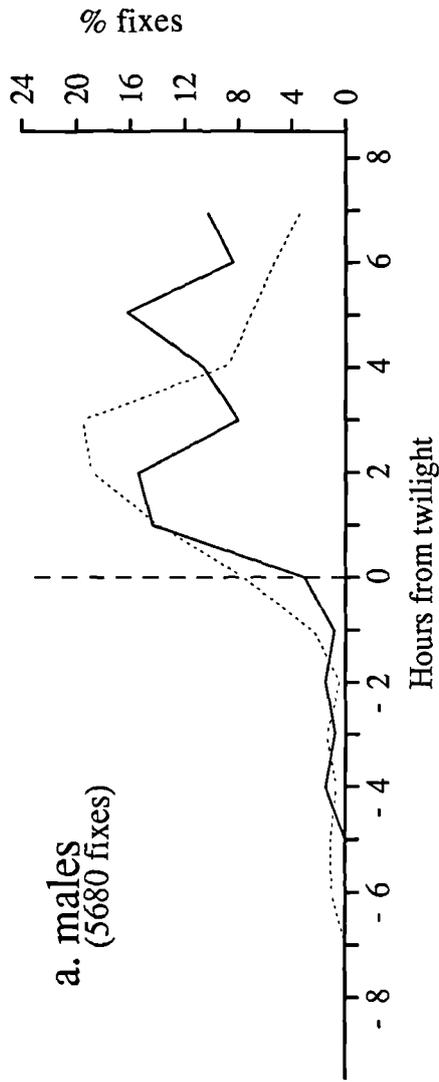
b. females
(5093 fixes)
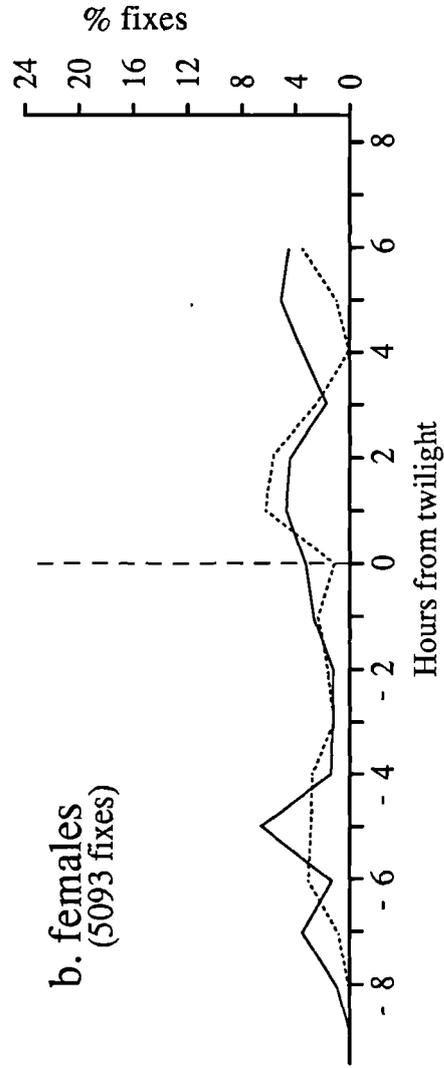
dawn
dusk

Figure 4.7 The pattern of activity with respect to dawn and dusk whilst in two different habitats

based on the number of out-of-den fixes recorded in two habitats as a percentage of all fixes recorded in one-hour samples either side of civil twilight.
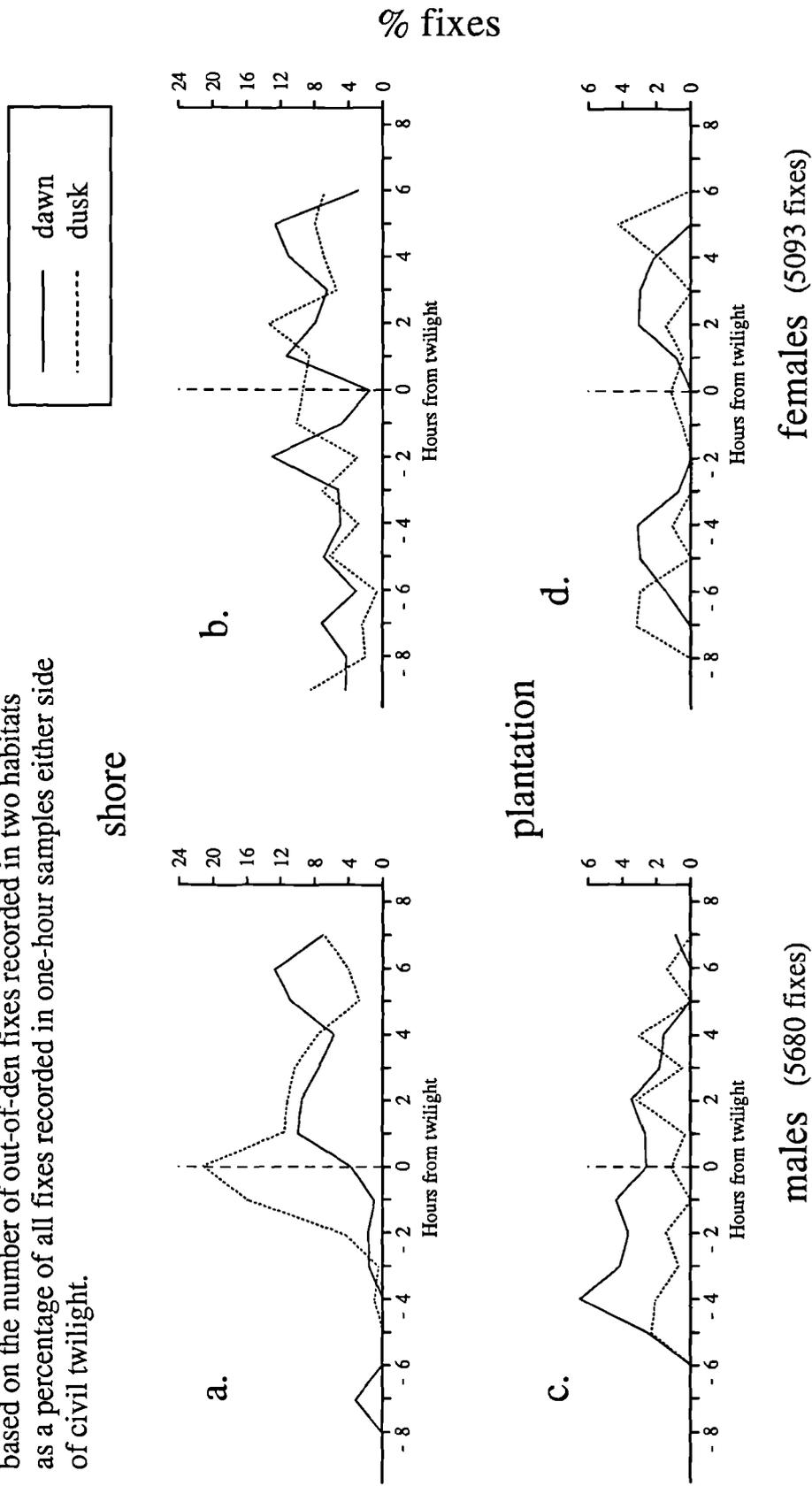
Figure 4.8a shows levels of activity related to tide level. Neither males nor females showed significant changes in levels of activity with respect to the tidal cycle (males, $F=0.55$, $df=(7,231)$, N.S; females, $F=1.32$, $df=(8,216)$, N.S). However, when mink were present on the shore (Fig 4.8b), the females exhibited a significant preference for activity whilst the tide was low ($F=2.98$, $df=(8,216)$, $p<0.01$), whereas males did not show this degree of selection ($F=0.84$, $df=(7,231)$, N.S). Whilst active on the shore, both sexes showed a slight preference for flood tides. 57% of the time males spent on the shore was during the period of the flood tide, compared with 56% for females.

4.3.6 Remote monitoring

Large quantities of data were collected by remote-monitoring six radio-tagged individuals that utilized particular dens for extended periods. These data are presented in Figure 4.9 as bars, representing periods when the individuals were absent from their dens. There was considerable variation from day to day in both the onset of activity bouts, and their duration. Much of the data collected was from females at various stages of breeding (pre and post-weaning) when they were restricted to one den. It was more difficult to monitor males remotely, as they rarely returned to the same den after a foraging bout.

Figures 4.9a and 4.9c clearly show the short foraging bouts and limited time spent out of den by females in May, shortly after parturition, when they have dependent kits. These bouts increase in duration somewhat during June (Figures 4.9b&d). Female F10 was often foraging between five o'clock and six o'clock in the mornings and evenings. These times did not correspond with dawn and dusk which occurred at approximately 2.30am and 16.30pm (all times in GMT). The female mink F11, who was raising probably weaned kits, had a completely different pattern of activity (Figure 4.9e). Most of her bouts of activity were centred around midnight. Whereas F10 was mostly foraging on the shore, F11 was feeding predominantly on bird carrion on Ross Island. Outside the mating season, it was difficult to get continuous information, even on females, as they were not restricted to one den by having kits. The activity bouts of F21 seemed well distributed throughout the 24-hour cycle. She was known to be foraging both on the shore, and on young rabbits in a plantation (Figure 4.9f).

Male M20 was consistent in the time he returned to his den from an activity bout in the mornings (Figure 4.9g). This was usually within an hour after dawn (Civil twilight 6:10am). The time at which he started foraging in the evening was also relatively uniform,

Figure 4.8 The effect of the tide on the levels
of activity of male and female mink.

Levels of activity are the mean values of all individuals of
each sex whilst the tide is at the specified hight above
Chart Datum, expressed as 3-point running means.

a. All out-of-den activity

b. Activity whilst on the shore
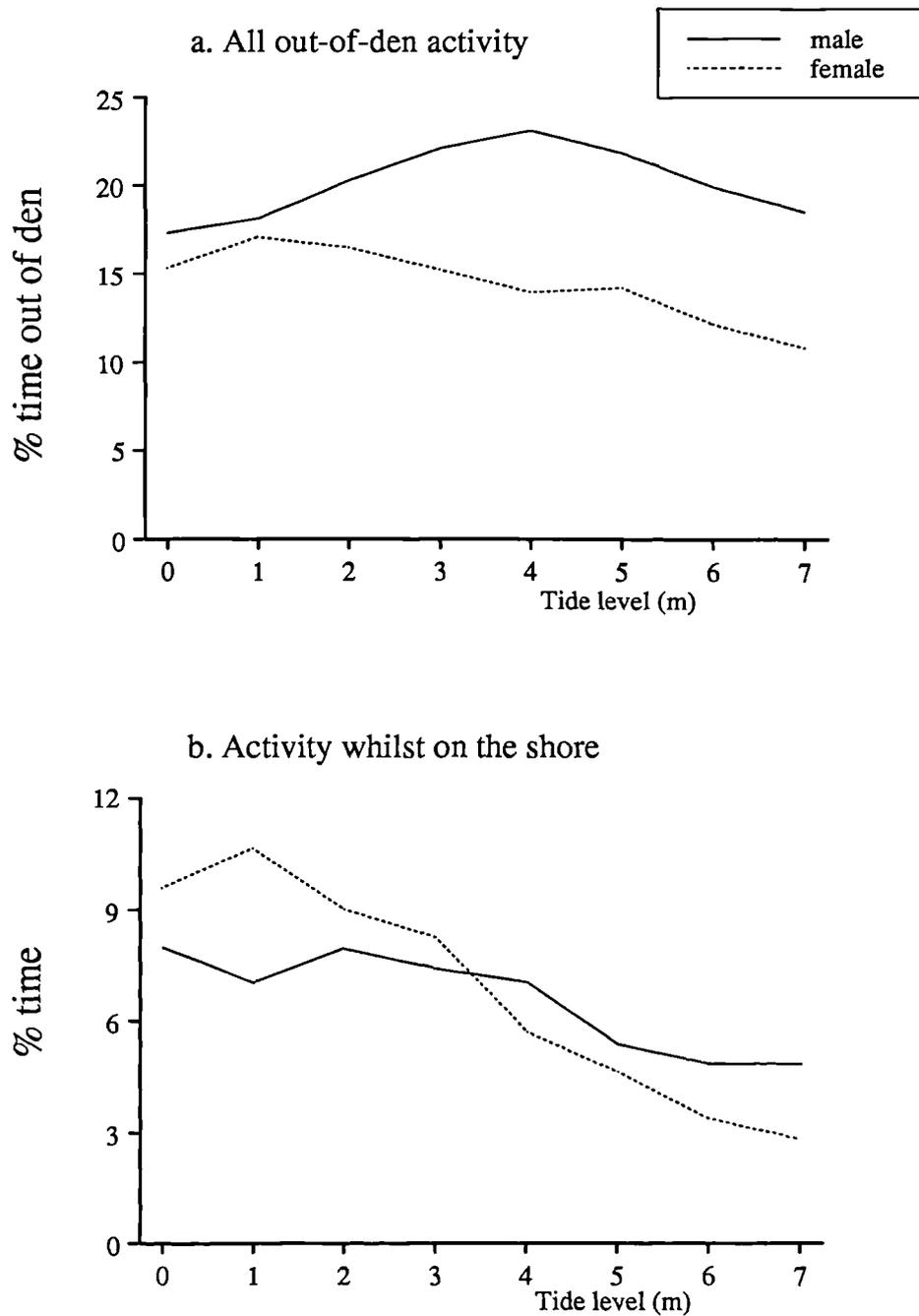
Figure 4.9 Activity diagrams

Data collected using remote monitoring apparatus.
Shaded bars represent periods when the absence
of a radio-signal indicated that the mink
was absent from its den.

a. F10 - May 1983

b. F10 - June 1983

Date
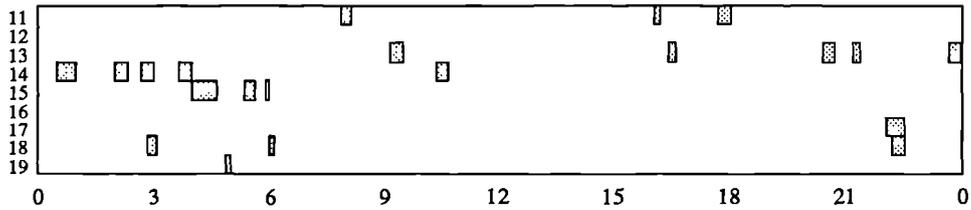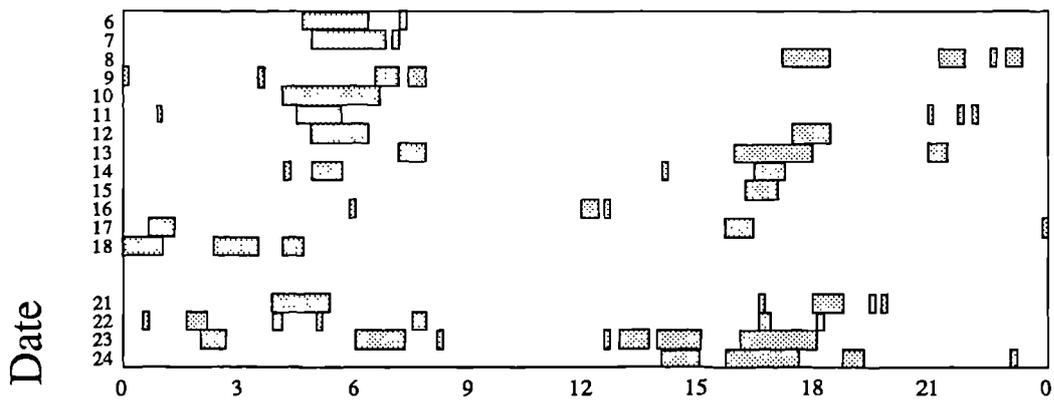
c. F19 - May 1984
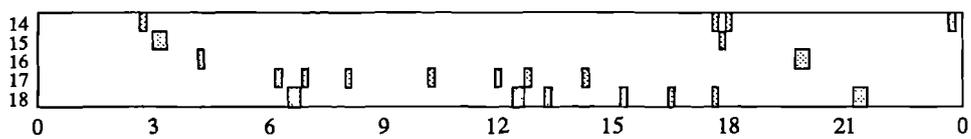
d. F19 - June 1984
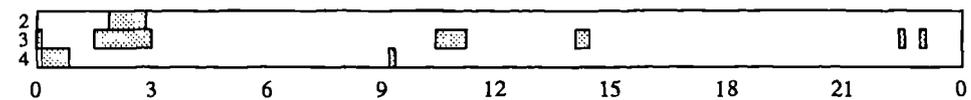
Time (24-hour clock)

Figure 4.9 (cont.)

e. F11 - July 1984
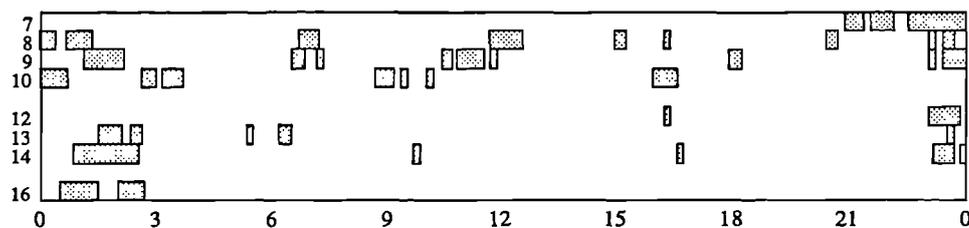
f. F21 - February 1985
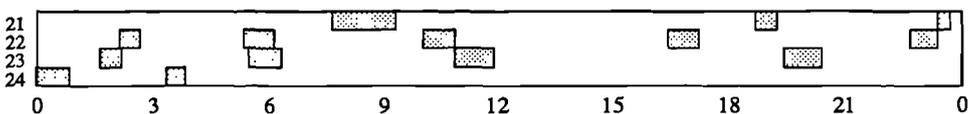
g. M20 - November 1983
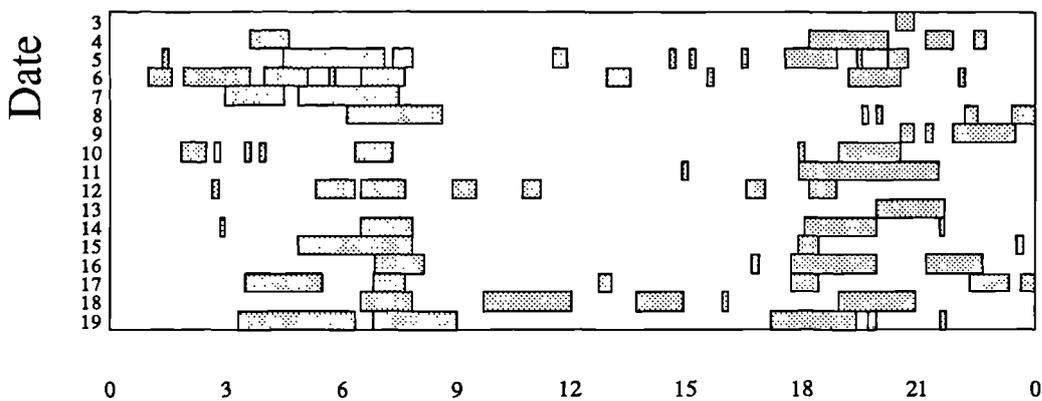
h. M29 - February 1985

Date

Time (24-hour clock)

roughly 90 minutes after dusk (civil twilight 16:50pm). A similar pattern was also shown by M29 in February (Figure 4.9f).

No pattern was evident with respect to the time of low tide. Any such pattern would be evidenced by activity bouts starting (or ending) successively 50 minutes later each day. What was evident from the diagrams was the lack of any strict patterns, and a high variability in the lengths of foraging bouts, and the time spent foraging each day.

The long time series recorded by remote monitoring equipment allowed the analysis of activity patterns using spectral analysis. Important periodicities in the data should, if present, show up as peaks in the spectral density (Y-axis). The higher and narrower the peak, the more rigid the periodicity at a particular frequency. The spectral density is normally plotted against frequency (cycles per time interval). The actual frequency is simply the reciprocal of number of cycles. This compresses all long periodicities at the far left hand side of any spectral density graph. The abscissa has therefore been transformed to show the spectral density relative to the time interval in hours.

Females did not leave the den for long periods in May. No clear-cut low frequency (large time interval) periodicities were apparent (Figure 4.10a). During this month, much activity occurred in the den, some probably associated with the care of her one kit, the rest perhaps eating cached food. These in-den active fixes were therefore included in the time series. As the Grant Squirrel chart recorder (Chapter 2) only recorded data on a presence/absence basis, only the data recorded on the Grant DB9–U could be used. Determining in-den activity from this the chart trace was not easy and probably prone to error, so the results were treated with some caution. Although use of these data did increase the spectral density of the estimate, periodicities were no more obvious (Figure 4.10a), though some periodicity in the region of three hours was apparent. The story was similar in the data from F19 in May. Small but consistent peaks were found close to two and three hours (Figure 4.10b).

In June, the short term periodicities had been replaced by one of longer term, with a frequency of approximately 12 hours and a subsidiary peak of about seven hours (Figure 4.10c). Weak periodicity on a 24-hour and 7-hour cycle was found for F11 in July (Figure 4.10d). A further 2.5 hour peak was also apparent. Outside the breeding season, F21 showed one main periodicity of six hours (Figure 4.10e).

The main periodicity in the behaviour of M20 was in the region of 10 hours (Figure 4.10f), whilst that of M29 was approximately 13 hours (Figure 4.10g). M4 was remotely

Figure 4.10 Periodograms of mink activity

Peaks in the graphs indicate periodicity in activity of the mink,
with a cycle length given by the peaks position along the ordinate.
See text for more details.

Figure 4.10 (cont.)

d) F11 July 1984

e) F21 February 1985

Figure 4.10 (cont.)

f) M20 November 1983 — activity out of den only

g) M29 February 1985 — activity out of den only

h) M4 December 1983 — activity in and out of den

periodicity (hours)

spectral density
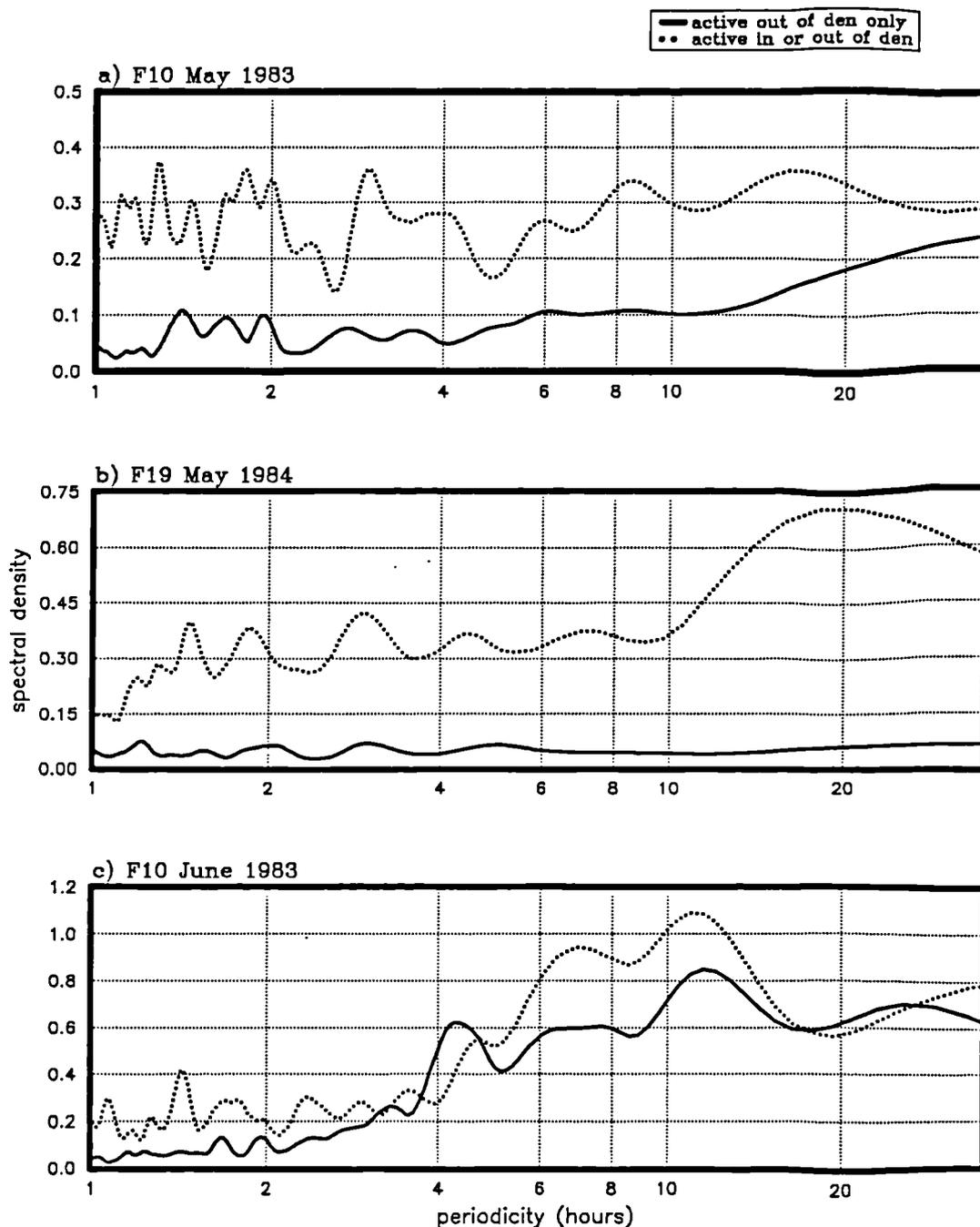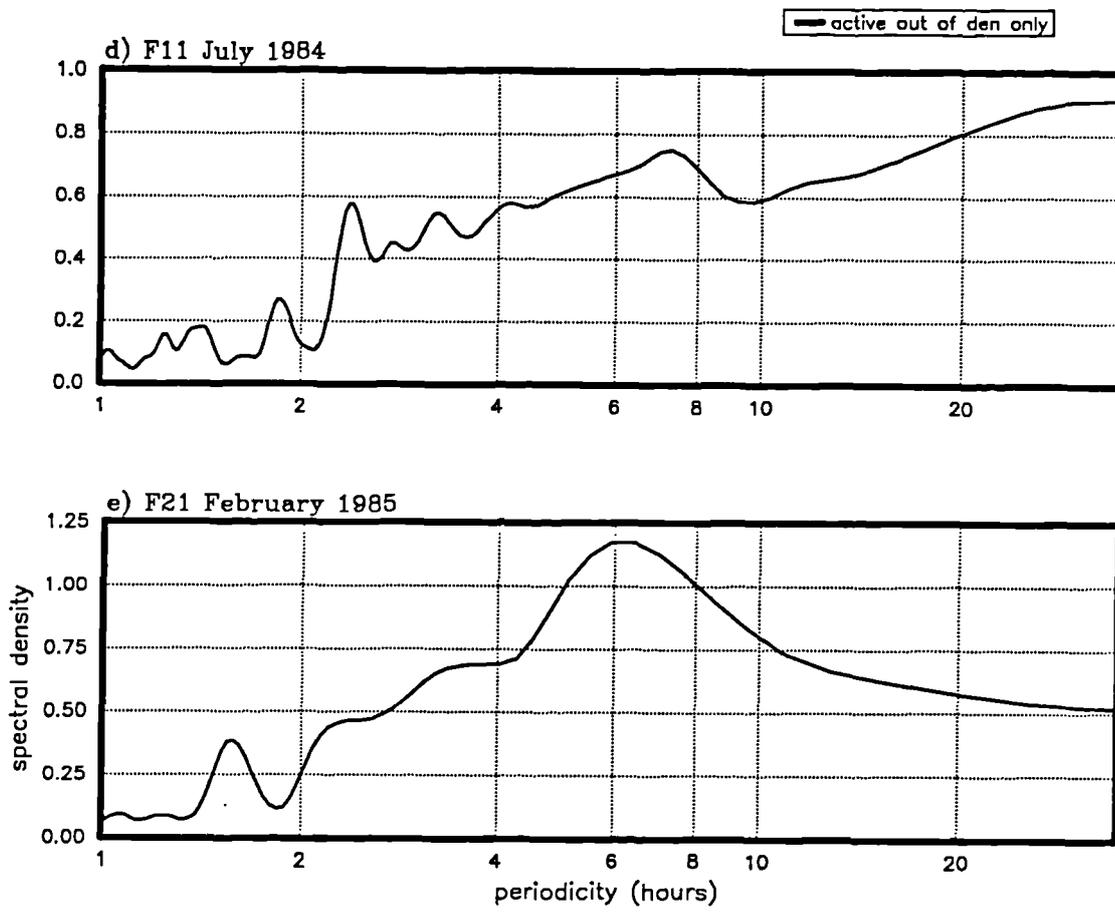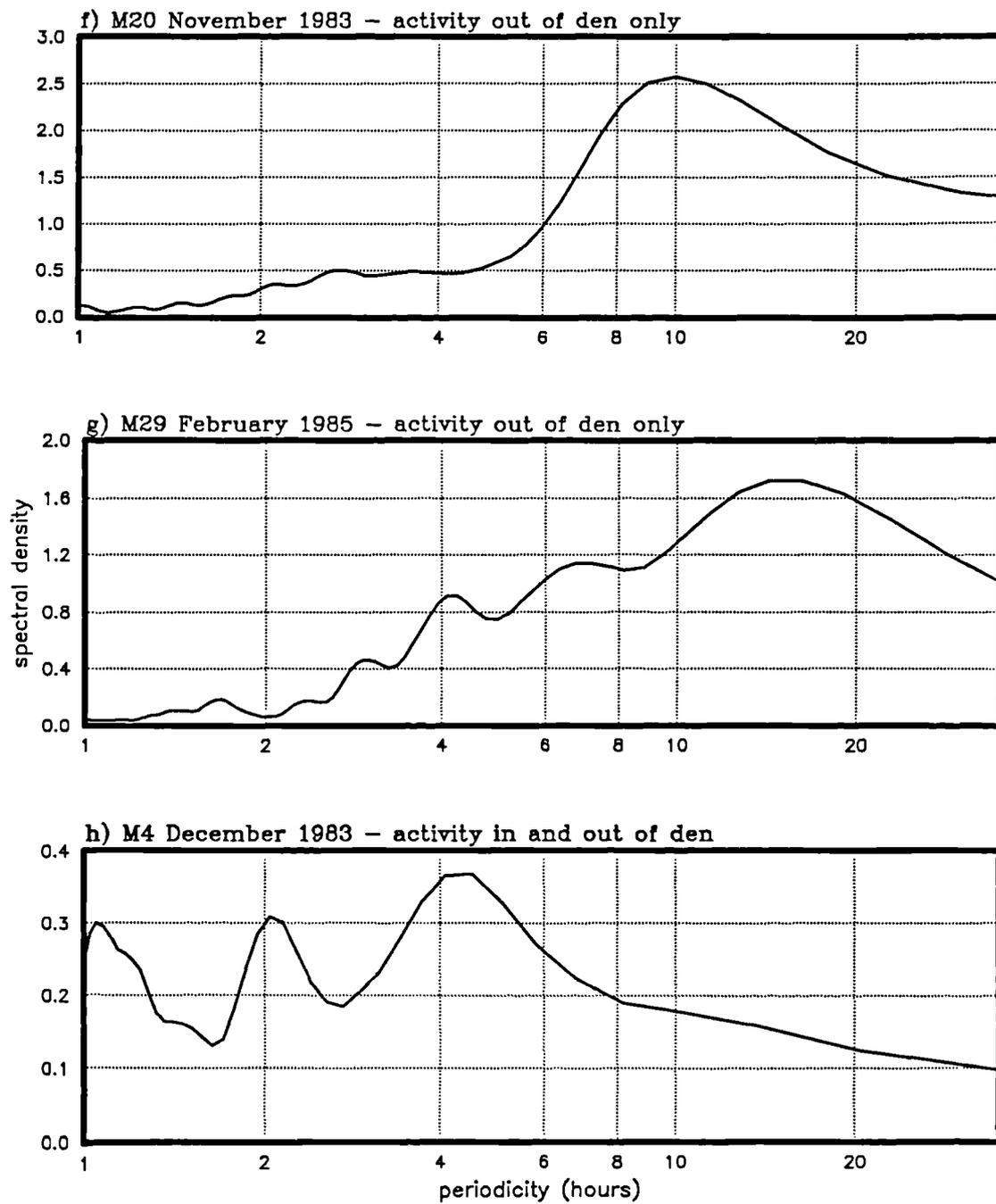
tracked for 40 hours whilst in a rabbit burrow near Third Forestry. He probably had a rabbit kill with him in his den and did not make the normal male nightly excursion. Marked periodicities occurred in his in-den behaviour at one-, two- and four-hour intervals (Figure 4.10h).

4.4 Discussion

4.4.1 Activity levels throughout the year

Whatever the reasons for the extreme dimorphism in mustelids, the immediate effect on a male is an increased energy requirement by virtue of its larger size. It was interesting to find therefore, that males spent similar amounts of time foraging, and that the trend for both sexes, was similar throughout the year. The maintenance requirements of mink are related to their body-weight to the power of 0.75 (Iverson, 1972). Thus, in this study area where the sexual dimorphism ratio was approximately 1.7 (Chapter 2), males require $1.7^{0.75}$ (i.e., approximately 1.5) times the energy just for maintenance. If all prey were the same size, assuming that both males and females foraged equally efficiently, (i.e., caught the same number of prey per unit time), male mink would have to forage for appreciably longer each day. The fact that they did not, suggested that they could be foraging more efficiently on the same prey, or that they foraged on a different prey with a higher utility. The diet study showed that males preferred lagomorphs. Thus increased size of the male appears to result in an increase in foraging efficiency by virtue of their increased success at catching larger prey.

The term foraging efficiency needs some clarification. As used above, it refers to the energy content of the food consumed, per unit of time taken to catch it. Thus, a male needs more food then a female, but only spends approximately the same amount of time out of its den looking for it. This does not take account of the energy required to find the food. For example, it might take far more energy to overcome a rabbit, than to catch a fish. Males may therefore expend the same or even more energy than females looking for food, per unit of energy obtained from the food. Data is not available to answer this question. Whether or not the finding has any relevance, depends on which is more important to a mink, minimizing time spent foraging, or minimizing energy utilized.

The accuracy of the results also rely on the fact that the distinction between foraging and travelling is correct. As mink were usually active at night, it was rarely possible to observe their behaviour, and the rather subjective distinction between foraging and

travelling, based on speed of movement, is prone to error. A mink could for example encounter prey or surprise prey by travelling quickly through its range. Obviously, some time is spent travelling between foraging sites, and these costs should also figure in the costs of prey capture. It is apparent from Figure 4.2 that a sex difference in travel is primarily due to markedly high levels by males between February and April. This corresponds with the mating season when males travel widely in search of mating opportunities (Chanin, 1976; Birks, 1981; Chapter 6). At other times of the year, levels of travel by both sexes are very similar. Increased levels of travel by both sexes between July and September, a time when the young of the year are dispersing and trying to find territories for themselves, are also suggestive of a social component to travel. The relationship between time spent travelling each month and changes in the social system suggest, indirectly, that the distinction between foraging and travelling in the data are reasonably accurate. The effects of any errors might lead to a slight increase in the time males spent foraging with respect to females, but this would not lead to anything like the factor of 1.5 suggested on energetic grounds.

Some of the changes in the amount of time spent foraging throughout the year were unforeseen. The very low value for females in May and June has already been associated with caring for her kits, but this occurs at a time when her demands, because of lactation, might be twice as high as normal (N. Glem-Hansen, pers. comm.). This observation, and the similar, though not significant decrease in the time spent foraging by males during May and June, suggests a possible superabundance of food. The fact that rabbits were especially abundant, and figured highly in the diets of both sexes at this time (Chapter 3), points to the high utility of rabbits, especially young ones.

A female's demands for food would probably be highest between late June and July, possibly early August, when she is required to find food for herself, and for her kits as well. Despite these demands, the time spent foraging by females was not very high (Figure 4.1). This could indicate that the greater abundance and availability of food at this time, more than compensated for increased demands. However, much of the data for June came from female F10 who only successfully raised one kit, and July's data came from F11 in two consecutive years, and though she raised three and four kits respectively, food in the form of sea bird carrion, was probably superabundant (Chapter 1). These conditions may or may not be typical.

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High levels of foraging over the whole autumn period, for both sexes, were also unexpected. This may have been related to the autumn moult which begins in August-September, the thick winter coat developing between September and November/December (Rust *et al.*, 1965; Glem-Hansen, 1980b). In an investigation based on a fur farm, Seier *et al.*, (1971) found that feed consumption increased by 97% during the furring process.

Only Whitman (1981) has looked into the way levels of activity change throughout the year. His method of determining activity probably did not separate in-den activity from that occurring outside, let alone discriminate foraging from other behaviours. However, Whitman's results were in broad agreement with the present study, there being little difference in activity between the sexes during autumn and winter. In the summer, females were slightly less active than males, which he too attributed to parental care, and males were far more active than females in the spring, presumably because of the rut.

Other studies of mink activity have included estimates of mean daily activity. These provide useful comparisons between different habitats. The mink on this coastal study area exhibited relatively lower levels of activity than those observed in riparian areas. The male mink in Gerell's study (1969) were active for 7.6 hours (31.8%) per day; whilst the one female mink he studied was active for 3.3 hours a day before parturition, and 7.3 hours per day six weeks later. Whitman's (1981) data suggested a mean activity of 11.2 hours a day (46.5%) for males, and 9.2 hours (38.5%) for females. Mentioned previously, this estimate probably included active in-den fixes. A rough comparison, taken from the data in Table 4.1, suggested figures for males of 37.6% and females 33.3% in the present study area.

In Hatler's study (1976), limited radio-tracking showed coastal mink to be active for approximately 6 hours a day (26%), although this may have included active fixes from within the den as well. Continuous tracking of one male revealed it to be out of its den for approximately 3 hours a day. These results are therefore similar in magnitude to the present study.

If levels of activity bear some relation to the food availability within a habitat, then these differences between the riparian and coastal study areas suggest that the coastal region is particularly rich in prey. It is unfortunate that more information is not available about activity levels of female mink in these other studies. In Hatler's coastal one, the main prey types were crabs. In Gerell's study area, the main prey were fish and small mammals, suggesting a shortage of larger prey. Comparisons between the sexes in these

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situations would clarify whether the presence of large prey really does help increase the foraging efficiency of male mink, or not.

4.4.2 Timing of activity

The main conclusion regarding the timing of activity, is that males are more nocturnal than females, their behaviour being more closely associated with dawn and dusk. Since significant differences were found between the diets of the sexes, can these be used to explain the observed differences in activity patterns? If not, it might suggest that other factors, such as anti-predator behaviour, or even interference competition might be involved.

The two main physical cycles with which activity may be synchronized in a coastal environment are the day/night cycle and the tidal cycle. The day/night cycle affects the activity of terrestrial prey. Lagomorphs (Southern, 1940) and small mammals (Brown, 1956; Miller, 1955) are predominantly active at night or crepuscularly, whilst the main bird orders predated are diurnal.

Mink have only a limited diving ability (Dunstone and O'Connor, 1979), and most aquatic prey were found on the middle and lower shore (J. Gregory, pers comm), the major fish in the diet, the blenny, being found predominantly below mean tide level (Qasim, 1957). As the tidal range was high (in the order of 8m), most prey would only be available to mink when the tide was out.

There was an appreciable diurnal component to the activity of females, and to a lesser extent, some males. As females preyed to a larger extent on aquatic prey (Table 3.4), littoral zone foraging seemed a likely explanation, as low tides could occur at any time throughout the day or night. A relationship was expected between tidal height and activity, especially for females. That none was evident attests to the mink's adaptability; with such a high non-aquatic dietary component, it is unreasonable to expect tide level to be the primary determinant of activity. However, female mink were more likely to be present on the shore when the tide was low. This was to be expected. It was not the case for males, suggesting that they may in fact be using the shore for other reasons. Certain males were known to forage along the top of the shore, possibly in search of carrion that was often washed up, especially during the winter. Aquatic prey was not important for males as a whole, but it did account for a high proportion of the diets of smaller juvenile/sub-adult males during the winter (Chapter 3). Two of these males were

monitored remotely (Figures 4.9g-h) whilst they were using a barn adjacent to the shore. Though activity appeared to be correlated with dawn and dusk (Figures 4.9g-h), M20 particularly was found to be more active when the tide was low.

Diurnal foraging for aquatic prey might arise if moderate amounts of light were necessary for catching prey. Mink visual acuity is reduced underwater in dim light (Dunstone and Sinclair, 1978) and movement may be a particularly important means of detecting prey, as a well-developed sense of smell is of little use underwater. Both males and females exhibited higher levels of activity on the shore at night than during the day (Figure 4.7a-b), negating this hypothesis. Aquatic foraging did account for the carry-over of male activity past dawn. The dawn peak was quite marked (Figure 4.7a) and its cause obscure. In California, the rock blenny *Labrisomus xanti*, an intertidal fish, tends to be more active during the day, being seen most often within an hour of sunrise or during mid-afternoon (Hobson, 1968). If this behaviour is common to all blennies, and was responsible for the dawn peak in the activity of male mink, it is surprising that it was not also shown by female mink, whose consumption of blennies was much higher.

It should be noted that littoral foraging did not account for all the diurnal activity of males or females. The question arises then, should the predominantly nocturnal patterns of prey activity make mink forage nocturnally as a matter of course? Although interactions between rabbits and mink have been observed on the surface, it was mentioned in Chapter 3 that rabbits were probably hunted down their burrows. Since a high proportion of the rabbit population feeds at night, it would make more sense to hunt for rabbits in their burrows during daylight hours. Rabbits emerge from their burrow at different times throughout the year; well before dusk in the summer, and after dusk in the winter (Kolb, 1987). Male mink typically become active shortly after dusk (Figure 4.5) at all times of the year (Figures 4.4a-d). This might be explained if rabbits were hunted on the surface and darkness was important for hiding the mink while it was approaching its prey? Mink are of a very dark brown colour, which aids camouflage at night. The utility of darkness whilst hunting underground is less obvious.

Figures 4.7c-d show that, whilst in plantations, presumably foraging for rabbits, daytime foraging was at least as as important as night-time. This was predicted if foraging for rabbits occurred underground, though the same effect was not evident in other habitats where rabbits were found. Plantations provide a lot of shelter and hence the reasons for the nocturnality of male mink might be related to anti-predator defence?

This idea is supported to some extent by observations of the extreme caution and great speed exhibited by mink when trying to cross exposed stretches of ground. Travelling was one behaviour that necessitated moving over open ground, and male mink travelled almost exclusively by night (Figure 4.6a). If the reason for nocturnal activity is anti-predator defence, rather than foraging, then the question remains as to why females are more diurnal, even when not on the shore. A possible adavantage in finding shelter, by virtue of their smaller size and greater agility was thought unlikely to have accounted for such pronounced behavioural differences.

Mink diurnality might however be due to their short gut transit time, which is of the order of 1–3 hours (Sibbald, 1957; Waller, 1962; Gregory 1987). A mink can only eat until its stomach is full. It must then wait 1–3 hours before it can eat again. If a mink eats a rabbit, it has no need to forage again for a while as it can stay in the burrow with its prey and eat when required. Foraging on small aquatic or terrestrial prey requires that a mink leave a suitable den-site to find food. After satiation, the caching of small aquatic or terrestrial prey is not economical as only one item may be taken back to the den at a time. It would probably be more efficient to have another foraging bout (after the gut had emptied) rather than make a succession of journeys to and from the den to bring back small prey. Smaller items are also less valuable in terms of digestible content. Individuals feeding on smaller items will therefore have to leave the den more often. This seems to happen in females, which tend to have short-duration bouts of foraging on the shore; whereas males tend to engage in long bouts at night, often finishing the bout in a rabbit burrow. This was seen in 3–6 hour peaks in the spectral analysis of females compared with the longer ones shown by males. When all the activity periods of M4 were examined whilst he was in a rabbit burrow, the short-duration periodicity could be interpreted as feeding bouts within a den, presumably eating a rabbit.

Thus, if the daily food requirements of a female cannot be met by nocturnal foraging, she must leave the den in search of food and exhibit some diurnality. A male, though perhaps needing food during the day, may not need to leave the den if he has recently caught a rabbit. The result would be more nocturnal behaviour. If Figures 4.4a-d are examined, they show that between May and July, (when lagomorph predation was at its greatest), and even though the light period was longest, there was very little male diurnal activity. During the winter however, when lagomorph consumption was lowest, and fish consumption was highest (Figures 3.3&3.1), male diurnality was at its highest. Thus the

degree of diurnality in males seemed to be related to prey size, and the ability to eat prey in a den.

If nocturnal foraging is advantageous to mink, then diurnal activity would be expected only when the daily requirements for food cannot be found, eaten and digested during the night. This is most likely to occur when demands are highest. For a female, this would be during lactation, in May and early June, and perhaps during July when she is not only finding food for herself, but for her kits as well. Much of the activity during this period is diurnal (Figure 4.4b), despite males fulfilling their needs during the short night period. The female peak after midnight was mostly due to F11 who was feeding on large prey.

These arguments still do not explain why males and females did not time their foraging bouts on the shore similarly. Those males which did spend long periods on the shore, also had a reasonable amount (26%, M20–November) of lagomorph in their diet, however, and hare and rabbit remains were often found in their dens. The same trend of diurnality related to prey size was not apparent in females. Their degree of diurnality was highest between August and October, and lowest from November to January, and bore no relation to the degree of consumption of lagomorph.

The results of the present study were similar to other studies of mink in riparian habitats. Males were also found to be mostly nocturnal, and females less so (Gerell, 1969; Whitman 1981). The crepuscular patterns, activity just after dusk, but carrying on after dawn has also been reported (Gerell, 1969; Melquist et al, 1981). The strong correlation between foraging activity and tidal level, found by Hatler (1976), based on daytime observations only, was absent. The diets of both sexes in that study consisted, almost exclusively, of aquatic prey.

There were large differences between Hatler's (1976) coastal study and the present one. In the present study, there were obvious differences between individuals eating different prey (Figures 4.9b&e). In one individual, differences in both timing and duration of activity were evident from day to day (Figure 4.9). These different types of variation suggest considerable plasticity in activity patterns rather than a strong synchronization with either of the main cycles, and an ability to respond easily, as in their diet, to the prevailing conditions.

Many of the sex differences in activity patterns can be explained in terms of diet and demands. Thus, through diet, competition between the sexes has been reduced in

a temporal plane. Competition does not need to be invoked to explain the differences. However, the data presented in the analysis were an agglomeration of many individuals from different parts of the study area. The present study was lacking, in that it was rare to track two individuals in the same area, especially simultaneously. This type of information is necessary to assess the effect one sex is having on the behaviour of another. Erlinge (1977b) for example found that male stoats dominated female stoats, and that females became inactive if a male was active in its vicinity (Erlinge 1979). Differences in the timing of activity are only of importance when assessing competitive interactions, if home ranges of the different sexes overlap, and if they are using the same habitat. These are the subjects of the next two chapters.

5. HABITAT UTILIZATION

5.1 Introduction

Many studies describe the habitat types used by mink (Chapter 1), and on this basis, Allen (1983) developed a model which attempted to define a habitat's suitability for mink. No studies have examined, quantitatively, the way in which mink use particular habitat types within their range. This study attempts to do just that.

It was shown that mink diet varied both between the sexes and between months (Chapter 3), therefore, quantitative measures of habitat use were examined to see how accurately they reflected trends in the diet, and to assess the relative importance to mink of the different coastal habitat types. Mink do not, however, spend all their activity bouts looking for food. Travelling accounts for a significant proportion of a mink's activity budget. Though obviously integral to finding food, travelling was also thought to have significance socially (Chapter 4), so utilization was examined to find which habitats were important in the social context. Den-use patterns were also investigated, because of their importance in the suitability of a habitat to a mink (Birks and Linn, 1982; Allen 1983), and because, without resorting to long periods of radio-tracking, they could be used as an indicator of range use.

Finally, sex differences in all aspects of habitat utilization were examined for relevance to the hypotheses regarding sexual dimorphism (Chapter 1), as differences might reduce the chances of interference competition between the sexes.

5.2 Methods

The study area is described in Chapter 2. Habitats were categorized into five main types, i.e., shore, rocks, scrub, plantation, and pasture. Radio-tracking techniques were used to gather habitat usage information (Chapter 2) by recording the location of the mink at 10-minute intervals. Whilst radio-tracking a mink at night, the habitat boundaries were not very evident. For this reason good local knowledge, and a beta-light mounted on the radio-collar, were essential for accurate determination of the habitat type being used by the mink.

Radio-fixes could not be considered independently of each other when analysing habitat utilization, since the habitat used in one 10-minute interval would affect the likelihood of the mink being in a particular habitat during the next interval. Therefore,

the habitat utilization was calculated for each individual during any one month for which there was radio-tracking information available for it.

The activity of the mink was sampled more or less evenly throughout the 24-hour cycle. An estimate of total daily activity in each month was therefore possible (Chapter 4), and this permitted the analysis of habitat utilization on both relative and absolute scales. Relative habitat utilization for each mink (during each month) was calculated from the time spent in each habitat expressed as a proportion of the total time spent out of den in any one month. Absolute habitat utilization was calculated by multiplying these proportions by the amount of time the mink spent active per 24 hours in that month, and was an estimate of the number of minutes per day that a mink spent in each habitat.

The effects of sex and month on habitat utilization were analysed using a two-way analysis of variance, unless interaction effects were significant, in which case a one-way nested analysis was used.

5.3 Results

5.3.1 Sex differences

Table 5.1 gives the F values and levels of significance for the analysis of variance used to determine the sex and monthly differences in proportional measures of habitat use. Whilst out of the den, females spent a significantly greater proportion of their time on the shore than did males ($F=6.06$, $df=(1,44)$, $p<0.05$). The only significant difference between months involved the use of the rocky zone ($F=2.47$, $df=(11,44)$, $p<0.05$).

Figure 5.1 presents the use, by each sex, of the various habitats available in the study area. Females spent most time on the shore (49%), and partitioned the majority of the remainder between the rocks (22%) and the scrub (18%). Males spread their time more evenly between these same three habitats but still used the shore the most. Use of forestry plantations by both sexes was infrequent, as was their use of pasture.

Table 5.2 shows, for each sex, the relative proportion of the time spent in each habitat, broken down by the type of activity. The habitat utilization varied between the activity types. The shore was even more important to the females when foraging behaviour was considered in isolation, and the significance of the sex-difference increased correspondingly. There were no significant sex differences evident in foraging behaviour whilst utilizing terrestrial habitats. However, areas of scrub and plantation were similar

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Table 5.1 Two-way analysis of variance examining the effect of sex and month on the proportion of time spent in each habitat type.

a) All out-of-den activity

Effect	df	Habitat									
		Shore		Rocks		Scrub		Plantation		Pasture	
		F	sig	F	sig	F	sig	F	sig	F	sig
Sex	1,44	0.32	NS	16.24	***	1.84	NS	0.28	NS	0.65	NS
Month	11,44	1.56	NS	2.03	NS	0.59	NS	1.15	NS	0.43	NS
Interaction	10,44	0.67	NS	1.80	NS	0.85	NS	0.94	NS	0.23	NS

b) Foraging only

Effect	df	Habitat									
		Shore		Rocks		Scrub		Plantation		Pasture	
		F	sig	F	sig	F	sig	F	sig	F	sig
Sex	1,44	2.51	NS	3.41	NS	1.25	NS	0.10	NS	0.02	NS
Month	11,44	2.16	*	1.41	NS	0.60	NS	1.15	NS	0.38	NS
Interaction	10,44	0.90	NS	1.58	NS	0.76	NS	0.90	NS	0.32	NS

c) Travelling only

Effect	df	Habitat									
		Shore		Rocks		Scrub		Plantation		Pasture	
		F	sig	F	sig	F	sig	F	sig	F	sig
Sex	1,44	17.72	***	17.21	***	1.56	NS	1.14	NS	3.11	NS
Month	11,44	1.18	NS	1.64	NS	0.79	NS	0.62	NS	0.39	NS
Interaction	10,44	1.20	NS	1.78	NS	0.88	NS	0.77	NS	0.27	NS

Figure 5.1 Habitat utilization

The proportion of total out-of-den activity
spent in each of the five main habitat types
based on the mean activity of all individuals
throughout the year (plus standard errors).
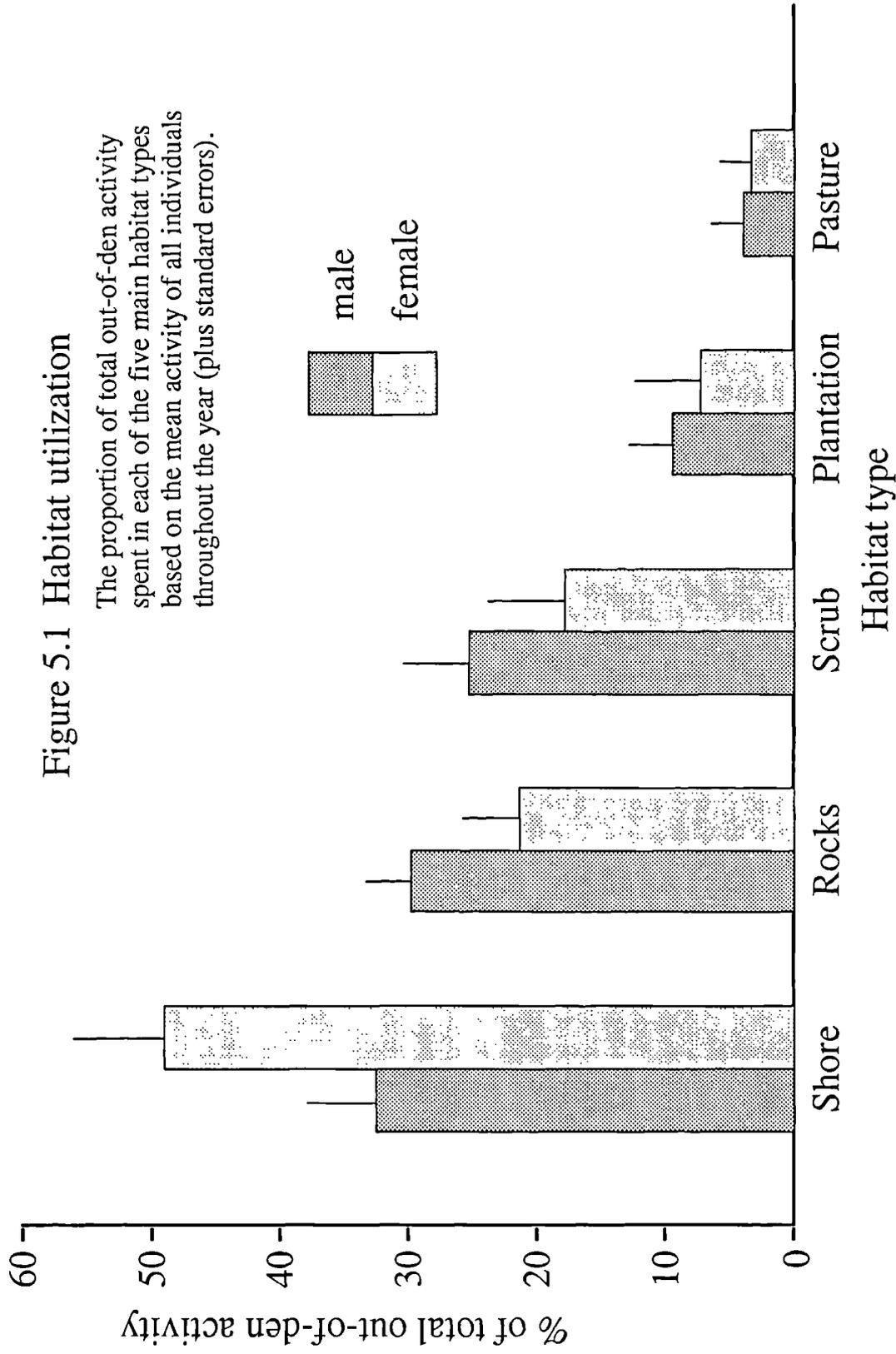
in that they both provided dense cover. Therefore, when combined as one habitat type, re-analysis revealed that males used them significantly more often than females ($F=4.42$, $df=(1,44)$, $p<0.05$).

Table 5.2 Sex differences in the usage of different habitat types (expressed as the time spent in one habitat in relation to all habitats), broken down for each activity category.

a) All out-of-den activity

Habitat type	Habitat usage (%)			
	Male		Female	
	Mean	SE	Mean	SE
Shore	33	5.3	49	7.2
Rocks	29	3.1	22	4.1
Scrub	25	5.1	18	6.8
Plantation	9	3.6	8	4.9
Pasture	4	2.0	3	2.7

c) Foraging only

Habitat type	Habitat usage (%)			
	Male		Female	
	Mean	SE	Mean	SE
Shore	32	6.8	58	8.2
Rocks	24	3.5	15	4.2
Scrub	30	6.2	16	7.4
Plantation	12	5.0	9	6.0
Pasture	2	2.0	2	2.4

c) Travelling only

Habitat type	Habitat usage (%)			
	Male		Female	
	Mean	SE	Mean	SE
Shore	27	3.8	18	6.5
Rocks	43	4.5	41	7.6
Scrub	20	5.4	30	9.2
Plantation	1	1.8	4	3.0
Pasture	9	3.1	7	5.2

The habitat the mink moved through when travelling was particularly interesting. Most travel occurred in the rocky zone by both sexes (Table 5.2c). Very little time was

spent travelling in the plantations, whereas much more time was spent travelling across pasture.

5.3.2 Seasonal effects

Figures 5.2a-e show the monthly differences in the use of different habitats for active male and female mink. The results are expressed as 3-month running means to reduce the effects of individual variation, as the sample in each month was small. Males used the rocks increasingly from December through to May. This change was observed whilst mink were foraging as well as travelling. Shore use was relatively consistent throughout the year. Although there was a significant sex difference in utilization, males did use the shore almost as much as females during the autumn and early winter. Pasture was used less during the summer, as were the plantations, in the case of males. The use of plantations peaked in the autumn.

5.3.3 Habitat use adjusted for habitat availability

An attempt was made to compensate for the differing amounts of each type of habitat within the study area, when calculating habitat usage. In Table 5.3, the mean proportion of time spent in each habitat has been transformed, dividing it by the area of each habitat. This was estimated within a zone 500m from the high water mark. The value of 500m was used because that was the furthest distance inland that a mink was ever radio-tracked. The index was recalculated so that activity in all habitats added up to 100%. An alternative adjustment factor was also used. The area of the two large sandy bays was subtracted from the total area of shore used in the correction. This was because mink only travelled across the bays occasionally, but they accounted for a disproportionately large amount of the area between high and low tide. This allowed a more realistic comparison between the usage of the shore and the scrub. The indices finally calculated, gave an indication of the relative importance of the different habitats. The weighting was the same for males as it was for females, so it did not affect the sex differences.

The corrections reduced, even further, the minor contribution of pasture as a habitat in which mink were active. It increased the apparent importance of the plantations to roughly the same as scrub. Finally, it shows how important the rocky zone is to mink. The indices may still underestimate the importance of the shore, as the most important area of it, i.e., the lower shore (Chapter 3), is only available to the mink when the tide is out, and this has not been taken into account with the corrections.

Figure 5.2   Monthly changes in habitat utilization

based on a mean estimate
for individuals each month
smoothed using 3-month running means.

————	male
------------	female

a. shore

b. rocks

Figure 5.2 (cont.)

————	male
··········	female

c. scrub

Month

d. plantation

Month

e. pasture

Month

% time out of den
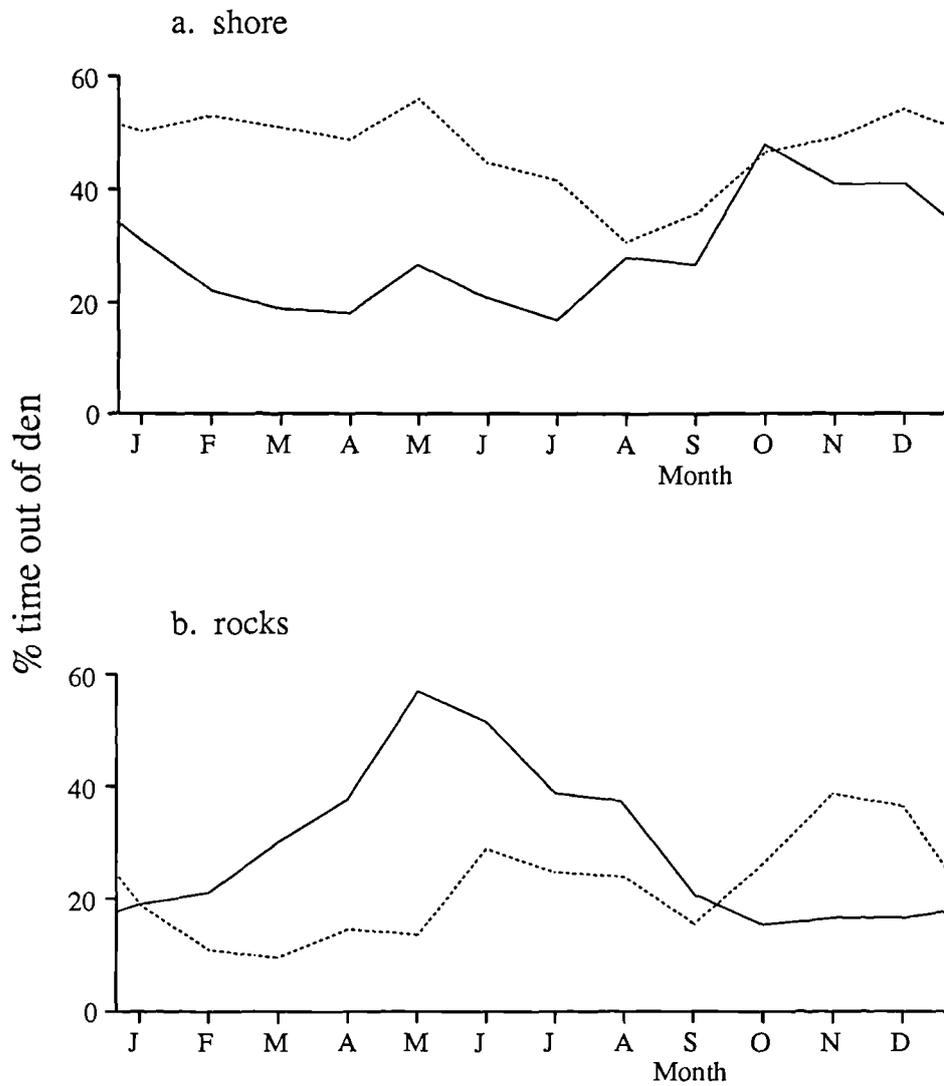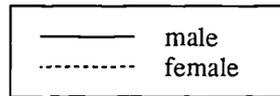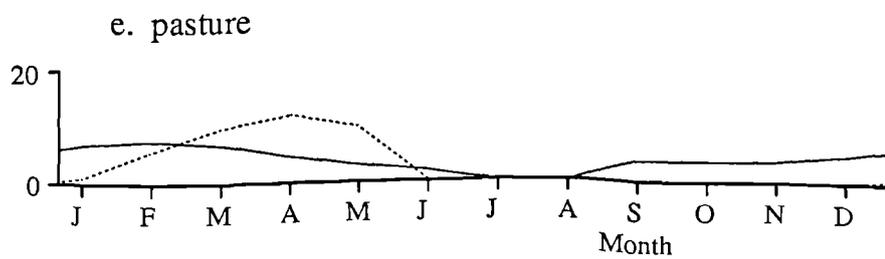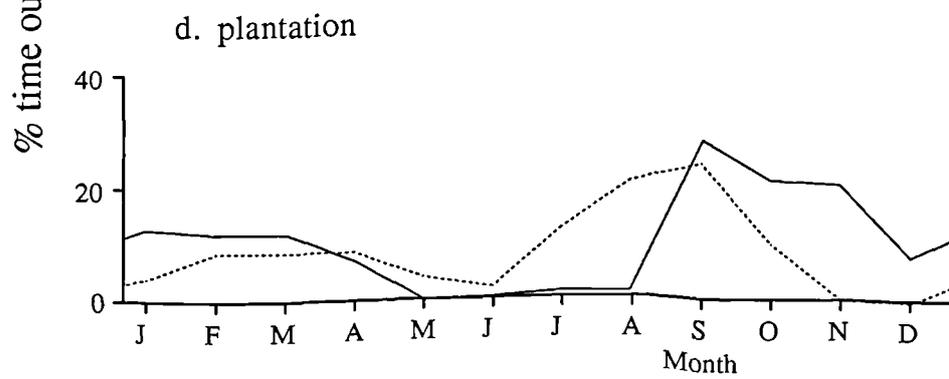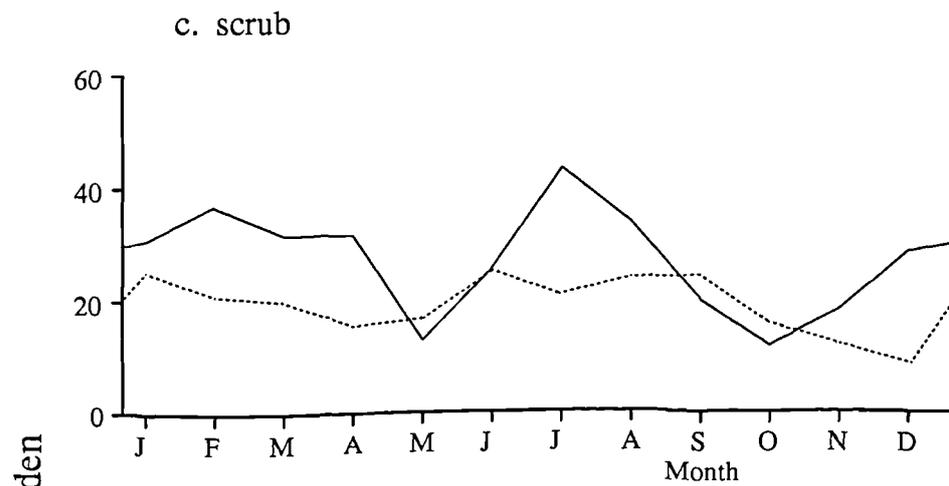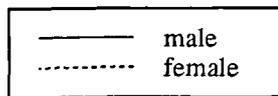
Table 5.3 Indices of habitat usage by male and female mink, calculated by correcting the measured usage (Table 5.2) for the availability of different habitats up to 500m inland.

a) Adjusted for available area of all habitats in study area

| Habitat type | Area (ha) | Percentage habitat usage | | | |
| | | Male | | Female | |
		Real	Index	Real	Index
Shore	134.54	33	12	49	20
Rocks	28.57	29	48	22	42
Scrub	58.93	25	20	18	17
Plantation	22.27	9	19	8	20
Pasture	280.55	4	1	3	1

b) Adjustment with area of sandy bays excluded.

| Habitat type | Area (ha) | Percentage habitat usage | | | |
| | | Male | | Female | |
		Real	Index	Real	Index
Shore	59.33	33	23	49	36
Rocks	28.57	29	42	22	34
Scrub	58.93	25	17	18	13
Plantation	22.27	9	17	8	16
Pasture	280.55	4	1	3	1

5.3.4 Absolute measures of habitat usage

Table 5.4 gives the F values and levels of significance of the 2-way analysis of variance used to determine the sex and monthly differences in the time spent each day in each habitat, and Table 5.5 gives a breakdown of the mean time spent each day in each habitat, for each sex. Whereas there was a significant sex difference in the mink's use of the shore relative to other habitats, in absolute terms the difference between the sexes was less marked and not statistically significant. Males were found to travel for longer than females when on the shore (F=17.72, df=(1,35), p<0.001) and amongst the rocks (F=17.21, df=(1,35), p<0.001). Of the time spent on the shore, females spent virtually all of it foraging (Table 5.4), whereas the time spent in the rocks and scrub was more evenly balanced between the foraging and foraging. Males divided their time amongst the rocks equally between these two activities, whereas the shore, the scrub, and the plantations were predominantly used for foraging.

Table 5.4 Two-way analysis of variance examining the effect of sex and month on the total amount of time spent in each habitat type.

a) All out-of-den activity

| Effect | df | Habitat | | | | | | | | | |
| | | Shore | | Rocks | | Scrub | | Plantation | | Pasture | |
		F	sig	F	sig	F	sig	F	sig	F	sig
Sex	1,35	6.06	*	5.80	*	0.73	NS	0.01	NS	0.22	NS
Month	11,35	1.45	NS	2.47	*	0.65	NS	1.41	NS	0.74	NS
Interaction	10,35	0.93	NS	2.11	NS	0.82	NS	1.59	NS	0.53	NS

b) Foraging only

| Effect | df | Habitat | | | | | | | | | |
| | | Shore | | Rocks | | Scrub | | Plantation | | Pasture | |
		F	sig	F	sig	F	sig	F	sig	F	sig
Sex	1,35	9.05	**	2.48	NS	3.44	NS	0.53	NS	0.00	NS
Month	11,35	1.73	NS	2.12	*	0.79	NS	1.61	NS	1.00	NS
Interaction	10,35	0.87	NS	1.82	NS	1.11	NS	1.93	NS	0.38	NS

c) Travelling only

| Effect | df | Habitat | | | | | | | | | |
| | | Shore | | Rocks | | Scrub | | Plantation | | Pasture | |
		F	sig	F	sig	F	sig	F	sig	F	sig
Sex	1,35	2.71	NS	0.16	NS	3.19	NS	0.09	NS	0.45	NS
Month	11,35	0.93	NS	1.98	NS	0.85	NS	0.60	NS	0.86	NS
Interaction	10,35	1.15	NS	1.19	NS	0.66	NS	0.65	NS	0.89	NS

Table 5.5 Sex differences in the mean time per day (in minutes) spent in each habitat, broken down for each activity type.

a) All out-of-den activity

Habitat type	Minutes per day			
	Male		Female	
	Mean	SE	Mean	SE
Shore	94	19.3	107	21.7
Rocks	85	9.9	47	11.2
Scrub	67	15.0	41	17.0
Plantation	21	10.2	16	11.5
Pasture	9	6.0	4	6.8

c) Foraging only

Habitat type	Minutes per day			
	Male		Female	
	Mean	SE	Mean	SE
Shore	66	17.0	100	19.2
Rocks	41	7.4	25	8.4
Scrub	46	10.9	26	12.4
Plantation	18	9.9	15	11.2
Pasture	3	4.4	3	4.9

c) Travelling only

Habitat type	Minutes per day			
	Male		Female	
	Mean	SE	Mean	SE
Shore	28	3.8	7	4.4
Rocks	44	6.2	22	7.0
Scrub	21	6.1	15	7.0
Plantation	3	2.1	1	2.3
Pasture	6	3.1	1	3.5

Figures 5.3–5.4 show the monthly variations in the amount of time spent per day, in each activity, in each major habitat type. The peak in time spent foraging on the shore during the late autumn and early winter is particularly noticeable for both males and females (Figure 5.4a). For males, this was mainly due to the behaviour of two juvenile/sub-adult males, tracked between October and December. Both started increased

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their usage of plantations as they got heavier. M20, weighing 830g in November, fed almost exclusively on the shore, but had to forage for over six hours a day. In December, his weight had increased to 900g, and he had started to utilize plantations and cliffs. By this time his daily activity budget had decreased to approximately three hours a day. M29, another juvenile male (weighing 960g), foraged mainly on the shore in November, but started making extensive use of the plantations in December and January, having increased in weight by 70g. Conversely, there were also females who spent very little time on the shore, particularly between February and April. In these cases, most time was spent in plantations and in the scrub.

It can be seen from Figure 5.3 that the time males spent travelling peaked twice during the year, firstly in the spring and also in late summer or early autumn, and this peak occurred in all the major habitats. Only one such peak was obvious for the females, and this was during late summer and early autumn. These peaks corresponded with changes in the social system. Peaks associated with changes in foraging behaviour (Figure 5.4a-b), appeared more related to changes in prey availability. This suggesting that the two activity types were distinct, and that the radio-tracking data had not been misinterpreted.

5.3.5 Diet and habitat usage

The correlation between the diet of a mink, and its relative usage of each habitat, was calculated using Spearman's rank correlation coefficients. Significant correlations were found between lagomorph consumption and the use of scrub (τ_b=0.375, n=43), pasture (τ_b=0.345, n=43) and plantations (τ_b=0.265, n=43). There was no significant correlation between the consumption of two aquatic prey groups (fish and crustaceans) and the use of the shore. Some of these correlations resulted from major sex differences in the diet, as when the sexes were analysed separately there were no significant correlations at all for males. Females in isolation still showed significant correlations between lagomorph and scrub (τ_b=0.538, n=22) and plantations (τ_b=0.437, n=22), and better, though not significant, correlations between the shore and fish (τ_b=0.340, n=22) and crustaceans (τ_b=0.303, n=22). In addition there was a significant correlation between the females' use of the rocky zone and consumption of large birds (τ_b=0.375, n=22).

Figure 5.3 Monthly changes in the amount of time spent travelling in the three major habitat types

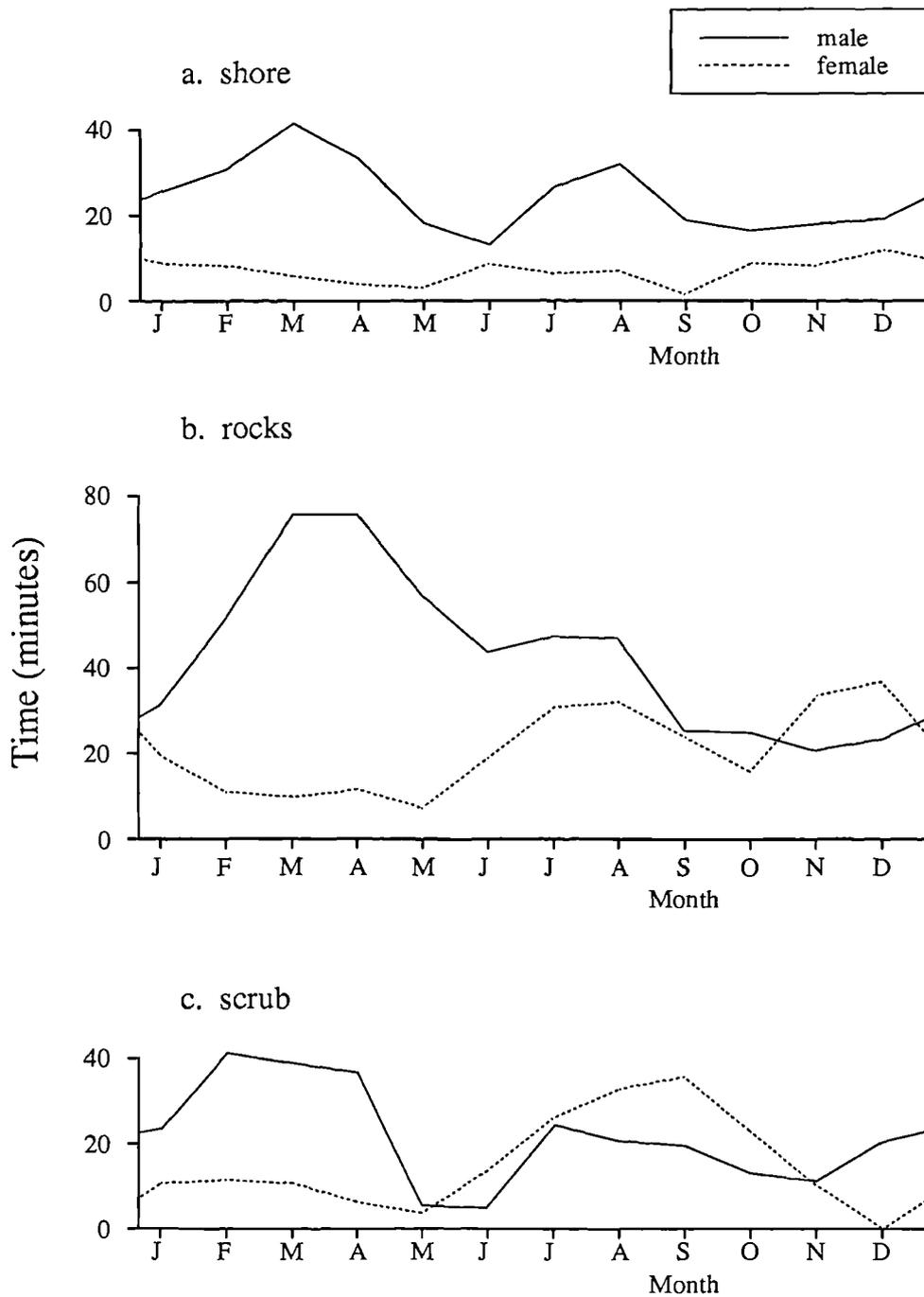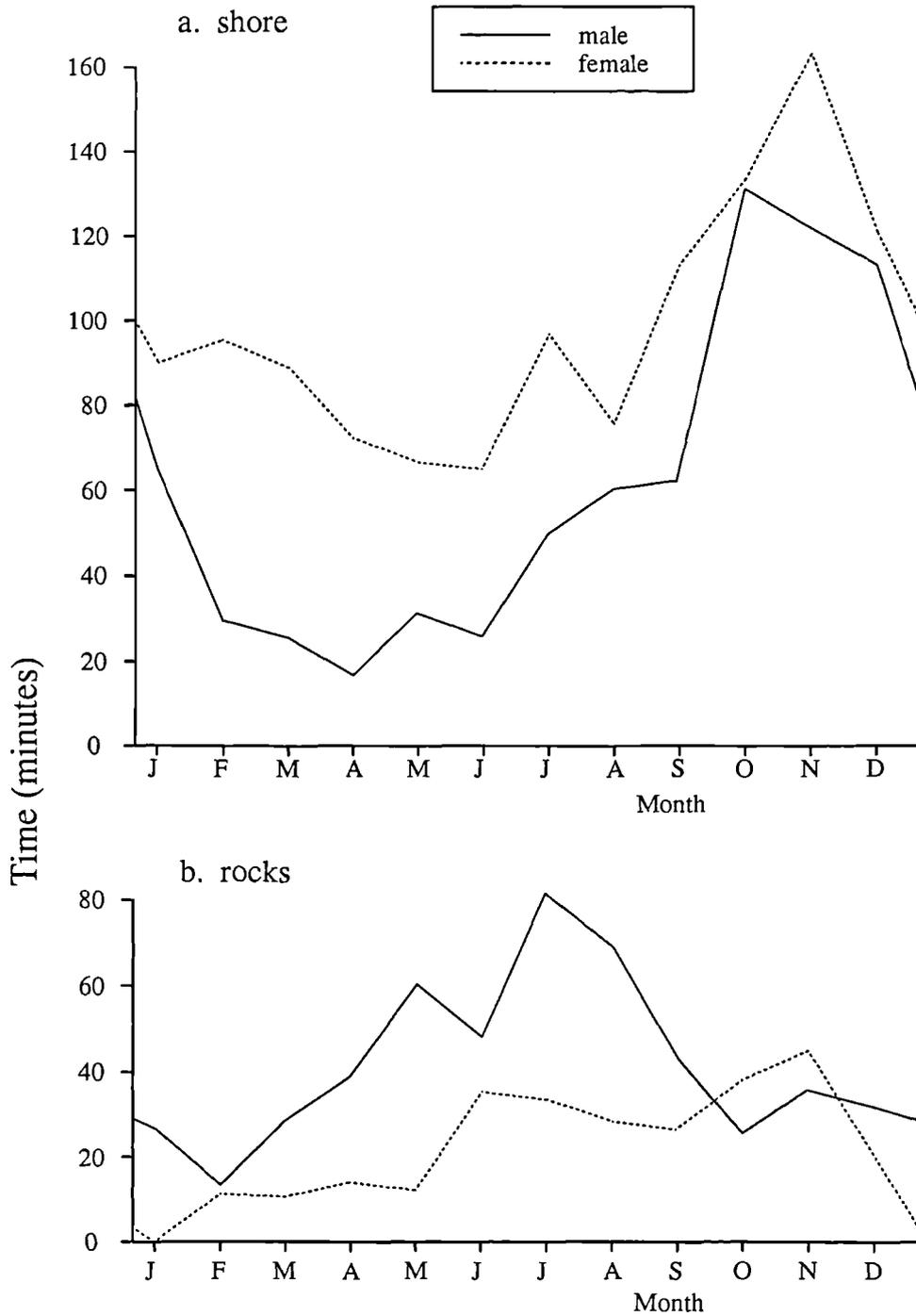based on mean individual estimates
plotted as 3-month running means.

Figure 5.4 Monthly changes in the amount of time spent foraging in the two major habitat types
based on mean individual estimates plotted as 3-month running means.

Table 5.6 A breakdown of dens by type, and by sex of user.

Type of den	Male		Female	
	Frequency	%	Frequency	%
Rocky	26	21.0	37	35.6
Scrub	11	8.9	15	14.4
Burrow	80	64.5	45	43.3
Man-made	4	3.2	5	4.8
Barn	3	2.4	2	1.9

5.3.6 Den use

278 dens were used by telemetered mink over the course of the study. Many others were detected by locating the pile of scats frequently left at den entrances, but these were excluded from the analyses as the user(s) of the den was unknown.

The characteristics of 233 dens were known. The remainder were inaccessible, being located on cliffs or within very dense scrub. In all, 57% of the dens were rabbit burrows. Almost 11% were in open scrub, but some of these might have been concealed rabbit burrows. The majority of the rest were cavities under rocks. Only 5% of the dens were located in or associated with human artifacts. Two of these were in stonework, namely a bridge abutment and a jetty. Others included refuges under sheets of corrugated iron, an old water tank, a wooden plank along the shoreline and some in rubbish tips. The three barns, though frequently disturbed by farm hands, were very important as dens when they were full of hay or straw, and provided a very secure wind proof den and possible rodent prey. Ten of the 22 mink tracked used a barn at some time. Some dens were used by more than one mink; one den was used by two individuals (although never at the same time), when their home ranges overlapped; six dens were shared by a male and a female mink during the mating season; but multiple use of one den usually occurred when an individual took over a den site once the original owner had vacated the range.

Virtually all dens were used opportunistically, unmodified by the mink, though occasionally they were known to extend natural cavities. One heavily-used den had three further entrances excavated during the course of the study.

Table 5.6 categorizes the dens by type for each sex. The majority of both male and female dens were in rabbit burrows, though these accounted for a greater proportion of male dens (χ^2=5.30, df=1, p<0.05). Females on the other hand, had relatively more dens in the rocks (χ^2=3.84, df=1, p=0.05).

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Table 5.7 categorizes the dens by habitat type. Occasionally, individuals had dens on the shore, and these were typically temporary, used only once, between two foraging bouts, though one female lived in a den below the high water mark with her well-grown male kit for four days. This den was occupied on neap tides, but vacated nearer spring tides when the water approached the den. The majority of dens for both sexes were in the scrub, with rocks forming the next largest proportion. There were no significant sex differences in the habitats in which dens were located.

Table 5.7 A breakdown of den locations by habitat type and sex of user.

Habitat	Male		Female	
	Frequency	%	Frequency	%
Shore	3	2.1	2	1.7
Rocks	21	14.4	31	26.5
Cliffs	16	11.0	6	5.1
Scrub	77	52.7	52	44.4
Plantation	19	13.0	23	19.7
Pasture	7	4.8	1	0.9
Barn	3	2.1	2	1.7

Previous studies have shown that mink make oscillatory movements throughout the length of their ranges, and that these movements have a territorial significance (Gerell, 1970; Birks, 1986). The rates at which mink changed den were therefore examined. Most telemetered mink were located at least once a day, so an index was formulated, based on whether or not a mink had changed its den on any two consecutive days. The index varied from one to one hundred, and was the proportion of pairs of consecutive days in which the mink changed its daytime den. Differences in these indices between the sexes and between months were analysed using a two-way analysis of variance. Due to the wide variations in tracking effort, the index for each animal was weighted by the number of pairs of consecutive days an individual was tracked. In this way, more emphasis was placed on those individuals which had been radio-tracked for the longest period.

There was no significant sex difference in the index ($F=0.39, df=(1,44)$, N.S.), males changing den overnight 59.9% of the time, females 60.4%. In other words, both sexes were just as likely to have moved den between successive days. However, the standard deviation for females (32%) was greater than that for males (26%), suggesting a greater variability in female behaviour. This is evidenced in Figure 5.5. Monthly changes were

significant (F=3.22, df=(11,44), p<0.01). Males moved den most often in March, during the rut, and least often during the winter (Figure 5.5). If the values for December and January are ignored (due to the small sample size during these months), females changed dens most during the spring and autumn, changing between dens very infrequently between May and June, when they had dependent kits.

Dens suitable for long term use were not available on the shore. However, the geology of the area was such that the rock slabs were common in the rocky zone near the shore, and cavities under these slabs provided shelter for mink. Including the burrows from the the extensive rabbit population, suitable den-sites were probably superabundant in most areas, thus enabling mink to den close to suitable foraging areas, or features such as home range boundaries. This, in turn, allowed dens to be used as a medium for investigating home range utilization.

The distribution of dens throughout a mink's range was examined using a nearest neighbour analysis (Hammond and McCullough, 1978). The mean distance between dens was compared with that of a random distribution of the same number of dens within a known area. Inherent within these methods is the problem of defining the area in which to calculate the random distribution. If this area was defined as the mink's home range as calculated using a grid-cell analysis (Chapter 6), the nearest neighbour index that resulted suggested a completely regular distribution. Using a subjective judgement of habitat suitable for both finding dens and for foraging (all habitats minus the shore and pasture), the resulting index for the same data suggested a dispersed (regular) distribution, whereas if the area was defined by a minimum convex polygon formed around the dens, the index suggested random den spacing. Because of these problems, a linear nearest neighbour index was used. At least ten den locations were necessary for this analysis to be reliable (Hammond and McCullough, 1978), and the five individuals for which ten dens were recorded, had negligible inland components to their range. (Further justification for the linear approximation can be found in Chapter 6).

That part of the high tide line closest to each den was marked on a map. Nearest neighbour distances were calculated in terms of length of shoreline between these points, and their mean was compared with the mean of a random distribution of dens along the length of coast defined by the linear component of the mink's home range (Chapter 6). Observed/expected values yielded an index below one if dens were more clumped than expected, and above one if there was evidence of regularity. Levels of significance were

Figure 5.5   Monthly changes in the rate at which mink changed dens
Based on the probability of a mink changing dens in two consecutive days
Data are means of all individuals during each month
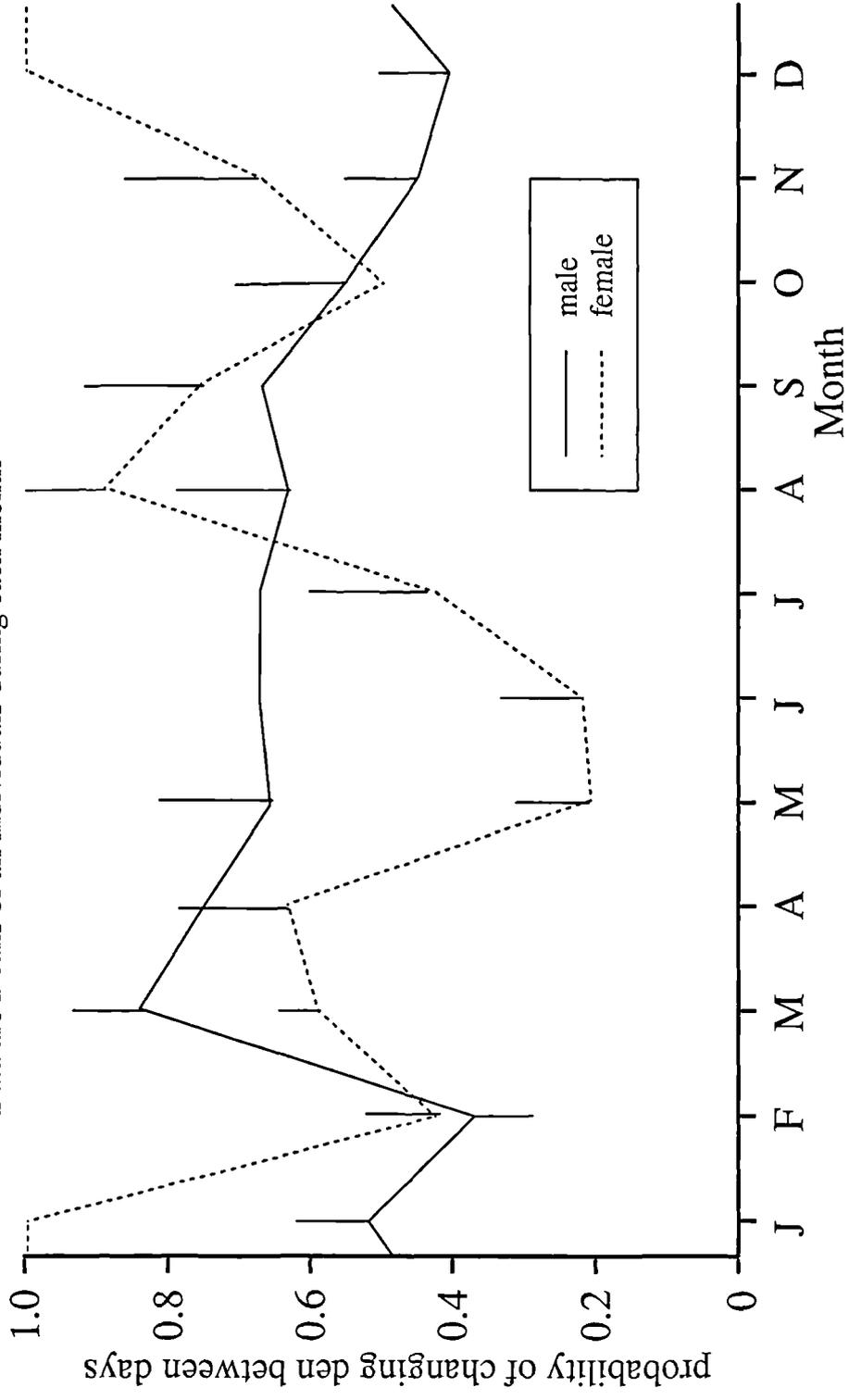
drawn from a graph based on the standard errors of 100 computer generated random distributions (Hammond and McCullogh, 1978). Of three males tested, none had den distributions significantly different from a random distribution (M32, March 1985, index=0.95, n=10, N.S.: M18, September 1984, index=1.20, n=10, N.S.: M29, November 1984, index=1.04, n=10, N.S.). However, the distribution of female dens within their ranges showed a significant element of regularity (F19, March 1985, index=1.67, n=16, p<0.05: F21, February–March 1985, index=1.43, n=15, p=0.05). The distribution of dens for the three males and the female F21 are shown in Chapter 6.

The knowledge of den locations was also used to investigate how closely mink associated with the shoreline. Two-way analysis of variance was used to examine the monthly and sex differences in the distances the mink dens were located from the shore. The analysis compensated for the differing levels of usage of different dens by counting each time a mink was located in a den, in any one day, as a data point. A significant interaction effect was present between the two main factors ($F=4.22$, $df=(11,707)$, $p<0.001$) so they were analysed separately. Both sex ($F=14.75$, $df=(1,707)$, $p<0.001$) and month (males: $F=9.25$, $df=(11,312)$, $p<0.001$) (females: $F=7.15$, $df=(11,352)$, $p<0.001$) were found significantly to affect the mean distance of the dens from the shore. Males spent the winter in dens well away from the shore, but most of the summer was spent in dens very close to it (Figure 5.6). Females spent the winter close to the shore, moved further away from it in the early spring but returned to it in the summer. As summer progressed they again moved away, returning in late autumn.

5.4 Discussion

5.4.1 Habitat usage and diet

Both sex-related and seasonal differences in habitat utilization were expected, because of the statistically significant dietary differences described in Chapter 3. The lack of many significant sex or monthly differences in habitat usage was therefore somewhat of a surprise, especially since there was no overlap in the spatial distribution of the two major prey groups i.e., lagomorphs and fish. Dietary studies have however, shown mink to be opportunistic foragers (Chapter 3) and in order to forage efficiently when the relative abundances of different prey are fluctuating seasonally, an individual must spend some time monitoring the alternative prey populations. This type of behaviour has been demonstrated for great tits *Parus major*, who spent most time in profitable patches

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Figure 5.6   Monthly changes in the mean distance of dens from the shore
Data expressed as 3-month running means.
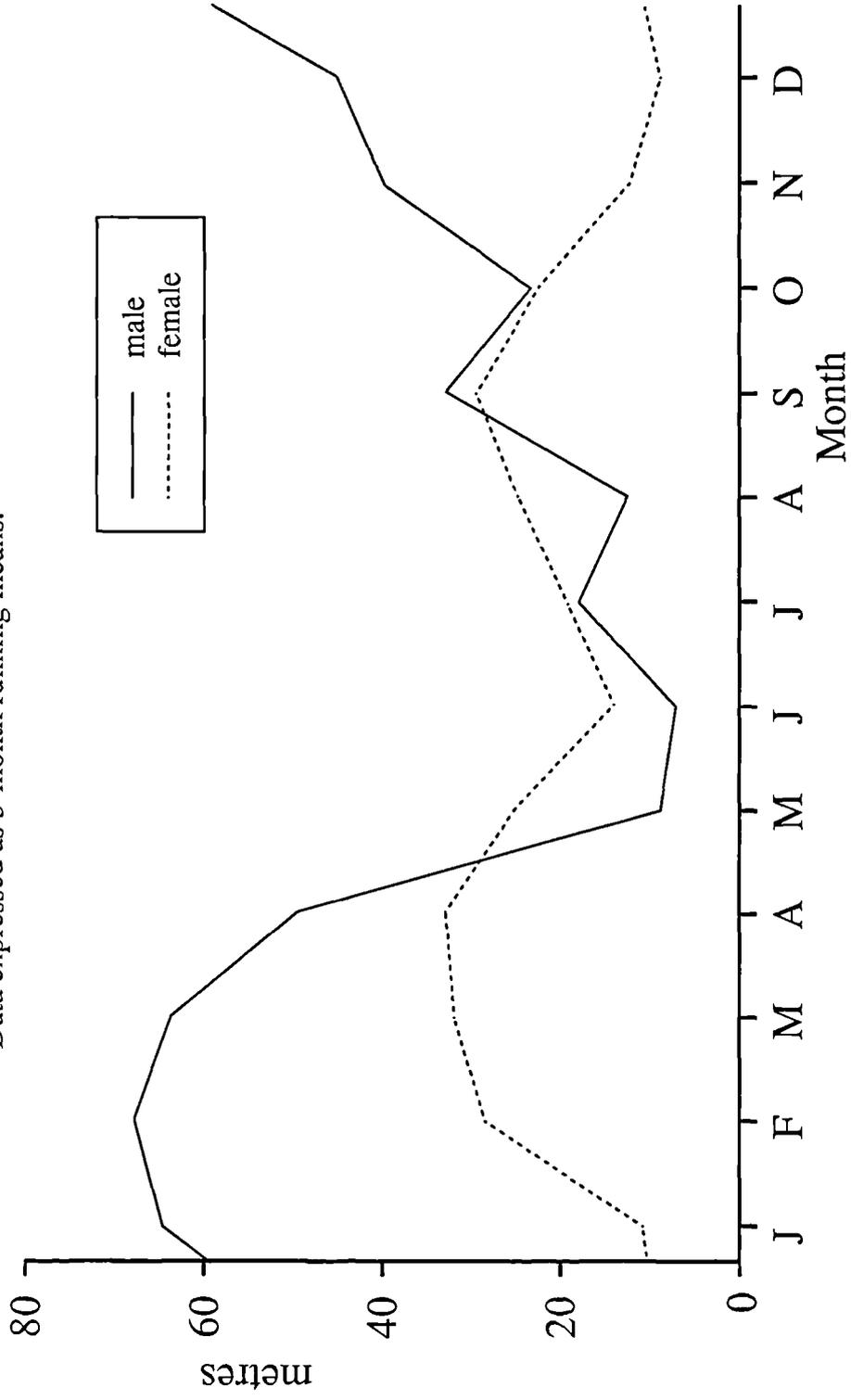
but spent more time than predicted in less profitable ones (Krebs and Cowie, 1976). This probably enabled them to switch directly to the next most profitable patch when the best one was reduced in quality (Smith and Sweatman, 1974). Similar behaviour in mink would result in the less clearly defined monthly differences in habitat utilization. Furthermore, the habitat in the study area was quite heterogeneous. Some individuals had access to plantations or cliffs whilst others did not. This could have resulted in individual variations in the usage of different terrestrial habitats, reducing the chances of significant results.

The greater use of shore by females and of the scrub by males, whilst foraging, was expected. This reflected the sex differences apparent in the diet, and indicated the importance of food availability in determining overall habitat preferences. The lack of other significant habitat differences could be explained with respect to classification of the different habitats used in the analysis. Rabbits, although particularly abundant in plantations on the hillsides, were present in most other habitats including pasture, scrub and cliffs. When estimates for habitat usage were corrected for available area (Table 5.3), plantations were shown to be similar in importance to scrub. Thus, when the times spent in the scrub and in plantations were combined, a sex difference did result. The best distinction would have been between terrestrial and aquatic habitats, but there was little point in this comparison as habitat was measured as a proportion of all habitats used, and the usage of terrestrial habitats would therefore be perfectly negatively correlated with aquatic habitat use.

The only significant changes in habitat use throughout the year occurred in the rocky zone, and were mainly due to changes in foraging behaviour (Table 5.1). The rocky zone, principally the cliffs, supported large numbers of breeding sea birds with rabbits on the less steep and more vegetated areas. Many rabbit burrows were also found in sparsely vegetated coastal slope, an area also included in the rocky zone classification. The monthly change in usage of this zone was most apparent for the males (Figure 5.2b). This was not thought to be due to exploitation of the birds as they occurred, in the males' diet, mainly during the winter. The peak in the males' usage of the rocky zone corresponded with the consumption of lagomorphs.

The divergence between the sexes in the distances of dens to the shore was particularly informative. The male mink used dens far from the shore during winter. These dens were in rabbit burrows, often in the hillside plantations where they presumably foraged

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for rabbits. However, lagomorph formed the largest proportion of the diet between May and June, a time when males used dens close to the shore. Figure 5.2b showed that, at this time, males were using the rocks, in this case the cliffs or coastal slope where rabbits were also reasonably abundant. This suggested that habitats close to the shore were preferred, as even denser juvenile rabbit populations in the plantations were not utilized at this time. It also suggested that lagomorphs were superabundant in the summer, and perhaps, that this prey was becoming scarce during the winter. It is interesting to note the behaviour of the juvenile males over the winter period. Concurrent with an increase in size in December, they started to use inland plantations, despite the low rabbit abundance at this time, and simultaneously decreased their foraging effort. This could be taken as an argument for both the energetic gain when feeding on rabbits and also the greater ease with which large mink catch rabbits. Neither explanation is necessarily correct. There is an almost a 100% increase in feed consumption during the furring process in ranch mink (Seier *et al.*, 1971). The development of a new pelt in the mink should have been complete by December and so the extra dietary requirement should have finished, and this could have accounted for the decrease in the activity budget. Despite the bias against rabbits in counts over the winter period (Chapter 3), rabbit numbers will probably be near a seasonal low in December, as breeding does not start until January (Corbet and Southern, 1977). The switch from shore-based activity might well indicate that larger mink size is making rabbit predation easier. However other possibilities, such as greater rabbit vulnerability due to a winter decrease in condition, should not be ruled out.

5.4.2 Habitat usage and social behaviour

The temporal distribution of mink activity within the various habitats was different for travel compared to foraging, suggesting that the two activities had different functions. The amount of time spent travelling increased around March for males and around August for both sexes (Chapter 4), suggesting that travel was associated with the mating season, and with the the establishment and maintenance of home ranges or territories (Chapter 6). A habitat use index, based on proportions, was satisfactory for comparing foraging habitats because it overcame the effects of the slight, though not significant, differences in the foraging activity of the sexes. It also compensated for any changes in foraging effort that might have occurred throughout the year, due to the changing energetic demands of the mink, or changing availability of prey. It was also useful when comparing diet with habitat utilization, since diet was also measured on a relative scale, rather than in terms of absolute consumption.

Absolute measures of habitat utilization were considered to be more relevant when investigating monthly changes in the amount of travel, because of the significant interaction between sex and month which was apparent when travel was examined in isolation (Chapter 4).

There could have been many reasons for both male and female mink travelling predominantly in the rocky zone. The rocks extended the whole length of each individual's home range, and provided abundant shelter in case of threat. The rocky zone was also situated between the two main foraging habitats, i.e., the shore and the scrub. Dense scrub would be more difficult to travel through; and the shore as a route for travel is dependent on the tide, and provides a much less even terrain. The pasture, although easy terrain to cross, is exposed, and, as mentioned above, mink tend to avoid exposed locations.

The rocky zone of the coastal strip also seemed to have some social significance, though this could simply be because it was the zone most mink travelled through, and in which the chances of social interaction were therefore maximized. Almost all the frequently used scatting sites in the open occurred in the rocky zone, usually on grassy patches, or where rocky masses jutted out into the sea (Robinson, 1987). It should be pointed out however, that scatting sites in the scrub would have been difficult to find. No scats were found away from the coastal strip or along the routes, such as walls, that mink followed when visiting plantations (Robinson, 1987), but they were occasionally found at den entrances inland. Scent marks, either in the form of scats, urine or anal sac secretions, should be left where individuals will encounter them (Gosling, 1982). It is impossible to tell whether mink travel through the rocks because that is where clues to ownership of a range or intrusion are found, or whether the clues are left there because that is the most likely route an intruder would follow.

The rocky zone was not the only habitat important in the context of the social system. Figure 5.3 showed that during the spring, males spent more time travelling on the shore and in the scrub, not just in the rocks. Unlike the rest of the year when contact between individuals was uncommon, and communication was probably via an indirect and long-lasting medium (scent marks), the mating season was a time when direct and immediate action against intruding males or with oestrus females was intended. Under these conditions, scent communication would probably be insufficient to deter intruders. The female would also have to be actively sought, a male following the shortest route,

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rather than a route along the coast through the rocks. This could have been the reason for the peak in travel during March occurring in all habitats. Similarly, the summer peak in travel occurred in rock and scrub habitats for both sexes, as well as on the shore for males. This peak was not as great as that recorded in the mating season for males, and because of low sample sizes at this time it could have been an artifact. Otherwise, its occurrence across different habitat types suggested that territorial maintenance at this time involved the active removal of intruding individuals (kits), rather than the more passive maintenance of an already established territorial boundary, which could possibly be accomplished using scent marks in the rocks only.

Dens, although serving a number of functions such as concealment, shelter, and resting place, may have other functions as well. The association of den location with suitable foraging sites has already been mentioned, but Gerell (1970) found that mink made patrolling movements throughout their range over a number of days, a behaviour which he interpreted as evidence of territoriality. This type of movement might be reflected in the rate at which mink changed dens. If this were so, then the lack of a significant difference between the sexes might mean that the pressures acting on females to maintain a territory, were the same as those on a male. This could also have been inferred from the similar percentage of time each sex spent travelling in the rocks.

However, if the rates at which mink changed dens was affected by territorial pressures, one might expect peaks occurring in the autumn, as juvenile mink are attempting to establish territories for themselves. Peaks would be expected for both sexes, but they only occurred in the denning behaviour for females at this time. Peaks did occur in the spring for both sexes. For males, this was probably the result of increased levels of travel in search of females. For females, the peak was probably a result of a change in behaviour as they starting to prey on small rabbits. A succession of rabbit burrows were used for durations of one or two days, perhaps because the rabbits were young or because breeding stops were utilized (Chapter 3). The numbers of dens used by females between May and June were also low, due to the mothers restricting their activities whilst looking after the young. The number of dens used increased as the kits grew, possibly due to the accumulation of waste material (Shladweiler and Storm, 1969) or to the increasing size of the kits. Territorial defence therefore seems an unlikely cause of seasonal changes in the rate at which mink changed den.

Scats are thought to be important in territory demarcation (Robinson, 1987). As the majority of scats are probably deposited in or just outside dens, dens themselves could

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serve as territorial markers. Mink scats are deposited in a clumped fashion near prominent features along the coastal linear component of an individual mink's range (Robinson, 1987). Boundary marking of a home range or territory, exhibited by mammals such as the badger (Kruuk and Hewson, 1978) and the spotted hyena *Crocuta crocuta* in Ngorongoro (Kruuk, 1972), may not be suitable for mink, as an intruder could enter a resident's range from the sea. If dens served a territorial marking function, they should be sited so as to maximize the chances of an intruder finding one. This might occur if dens were evenly spaced throughout a range. However, male dens were distributed in a random fashion throughout the range. Female dens were distributed more regularly, but if dens were located with regard to foraging areas, which their distribution within different habitats seems to suggest, this might simply indicate a sensible resource utilization strategy. This does not imply that dens serve no function as indicators of range ownership, just that other factors are more important in their siting. Of more import in discussions of territoriality is the distribution of a mink's dens with respect to its neighbour's dens. Too little data was available from mink in abutting ranges for any clear conclusions to be made.

5.4.3 Comparisons with other studies

A quantitative assessment of habitat use has not been previously reported for mink or for other small mustelids. However, there is sufficient literature about den-sites to allow comparisons with other studies. The present study was similar to others (e.g., Birks, 1981) in that den use was found to be opportunistic, the mink making use of any available refuges rather than excavating their own. The availability of dens is thought to affect the suitability of a habitat for mink (Gerell, 1970; Northcott *et al.*, 1974; Birks and Linn, 1982; Allen, 1983). The geology of the study area was such that refuges in the rocks near the shore were superabundant, and numerous rabbit burrows provided extra den sites in the coastal slope, most areas of scrub, the hillsides, cliffs and plantations. Despite the numbers of dens available, particular den sites were used by consecutive occupiers of a home range for reasons which were not immediately obvious.

Hatler (1976) did not record the types of den occupied in his study, other than to report feeding middens under rocks. Dens in coastal habitat were obviously different to those reported in riparian habitats. The most commonly used den site in the present study was the rabbit burrow. The use of burrows had been reported by Birks (1981), but they only accounted for about 20% of the dens used in that study. These were used predominantly when aquatic prey were scarce and the mink foraged away from the water

(Linn and Birks, 1981). The bankside tree root system, reported to be the most important den site in riparian habitats (Gerell, 1970; Birks, 1981), was absent on the coast, and the dens nearest the water were in cavities under rocks. In North America, abandoned or seldom-used muskrat burrows were found to be very important dens (Sargeant *et al.*, 1973; Eberhardt and Sargeant, 1975). These had the dual advantage of providing a safe burrow system close to the water, with underwater exits. The thick grass used by mink on Ross Island had an equivalent in Louisiana, where dense stands of sawgrass *Cladium jamaicense* were reported to provide excellent cover, elevation above the water level, and prey for mink in the marshes (Allen, 1983).

Birks (1981), Linn and Birks (1981), Melquist *et al.* (1981) and Birks and Linn (1982) suggested that mink select dens that are close to preferred foraging areas, or concentrations of prey items. The superabundance of suitable den sites through most of the study area meant such selection was easy. Sex-related differences in den use in this study area, reflected sex differences in the diet, thus backing up these conclusions.

Other factors were thought to be important for den site selection. Barns were often used by mink, even when available dens in the rocks or scrub were closer to foraging areas, indicating that the quality of the den was also important. Many dens were close to a supply of fresh water, either in the form of pools in the rocks above high tide level, streams, springs or outflows from boggy or undrained areas. In riparian, lacustrine and marsh habitats, abundant fresh water is always available. In coastal regions, sources of fresh water may take on a special importance not seen in other prime mink habitats. Activity bouts of short duration were recorded as mink left their dens to drink. One male living in a plantation, had to travel for 10 minutes in order to drink at a spring, after which he returned to his den. Also, on release from a trap the first thing mink do is find a suitable pool to drink from (Hatler, 1976; pers. obs.). Fresh water would probably be most difficult to find in the summer when many of the strand-line rock pools dry out. However, none of the dens of breeding females, those mink most restricted in movement, was adjacent to any known stream or spring, suggesting other factors were more important in den site selection, at least for females with kits.

In previous studies, mink have generally been found in association with bushy, or wooded cover, adjacent to aquatic habitats. (Marshall, 1936; Gerell, 1970; Allen, 1983). This association was used by Allen (1983) to develop a habitat suitability index model for mink. One of the main factors influencing suitable habitat was the percentage of

tree and/or shrub canopy closure within 100m of the water's edge. Activity calculations (Chapter 4) and the length of coast used by female mink (see Chapter 6), suggest that the coastal habitat is richer for mink than many riparian habitats. This is despite generally low levels of vegetative cover close to the shore over the main section of the study area. Allen's logic was that cover provided an adequate prey base, as well as potential den sites, escape and foraging cover. Most ranges in the present study did provide some vegetative cover close to the shore, and this was used where available. The rocky uneven terrain, both on land and on the shore, though not providing cover from above, did provide a good measure of foraging cover (especially with regard to the size of the mink), and many possibilities for concealment under rocks. Rabbit predation, presumably underground (Chapter 3) would also be less dependent on cover.

The importance of cover, possibly for protection, was commented on in Chapter 4, as male mink were often active in dense forestry plantations by day. This was emphasized by the large bias against use of open habitat (Table 5.2–3). This avoidance of open areas, also noted be Gerell (1970), Burgess (1978) and Birks (1981), could have been due to the availability of prey, or because the mink 'preferred' to be close to shelter for protective reasons. The majority of the pasture was well grazed, and the main prey available here were hares, rabbits and roosting or feeding birds, such as lapwings and oystercatchers. Rabbits were very abundant in pasture near plantations, or dense scrub, but the lack of cover would have reduced the ability of a mink to approach its prey without detection. Although some foraging did occur on the pasture at night, mink were rarely seen on open pasture except when travelling between other habitat types. When foraging inland necessitated travelling through pasture, the mink travelled along, or next to, dry stone walls. Mink showed particular caution when moving from an area of cover into an exposed area. On one occasion, when a mink chased a rabbit across open pasture, its great burst of speed was matched on its return journey as it ran back across the field to the more sheltered cliffs. These observations do suggest the latter explanation for reduced use of the pasture. The coniferous plantations showed a high usage in relation to their small area, but they did have high rabbit densities and, where tree cover was not too great, a dense understory harbouring a high population of small mammals (Chapter 2).

5.4.4 Sexual dimorphism and habitat usage

Moors (1980) pointed out that in addition to dietary niche differences, coexistence of the sexes in competitive equilibrium can be maintained by different foraging strategies or differences in habitat utilization. Erlinge (1979), working on stoats, found that sex-related dietary differences lead to differences in habitat utilization, although these differences were not quantified. Similar findings were also reported for weasels (Erlinge, 1975). In the present study, dietary differences, evolving for whatever reason, have lead to some differences in habitat utilization and these would decrease the chances of interference competition arising by reducing the time each sex spent foraging in the same habitat. However, both sexes travel mainly in the rocky zone, increasing the chances of contact, and suggesting that differences in habitat utilization are not driven by the need to reduce the chances of contact and conflict. A divergence in habitat utilization was also observed in the winter when, based on denning behaviour, males moved away from the shore whilst females remained close to it. Occurring as it did, when prey was probably least available, this could have suggested competition, and the exclusion of the smaller females from the best foraging areas. However, as most rabbits are large during the winter, and as large predator size is probably advantageous when catching rabbits, the restriction of female mink to the shore is not surprising and provides a simpler explanation. Habitat divergence between the sexes is in any case, only of relevance when attempting to understand sexual dimorphism if both sexes share the same length of coastline. This has yet to be shown, and is the subject of the next chapter.

6. THE SOCIAL SYSTEM

6.1 Introduction

Social organization is influenced by the availability and dispersion of resources within a habitat and over time. Resources usually, but not always, constitute food. Possession of a territory is seen as an adaptation to defend a limiting resource (Davies and Houston, 1984), and is presumed to occur when benefits, such as increased foraging efficiency, exceed costs such as territorial defence (Brown and Orions, 1970). Territory size, in solitary females at least, is thought to be determined by the food requirements of the females during times of scarcity (for example Kruuk and Macdonald, 1985).

Food availability changes throughout the year (Chapter 3), and as prey types change, so does food dispersion. Food resources will also be different between the better studied riparian habitats and the coast. During the mating season, in addition to food, females become a limiting resource to males (Erlinge and Sandell, 1986). Thus, other workers have found the rut to be a time of great social instability, male mink leaving their home ranges at this time in search of females (Chanin, 1976; Birks, 1981). The present study suggested this picture to be an oversimplification.

The social system was not studied specifically, although the tracking and trapping data provided many clues to its organization. The first part of this chapter defines the mink social system in terms of inter/intrasexual relationships and dispersion, and assesses its stability over time. The second part attempts an interpretation of the mating system by trying to fit the observations within a framework based on female availability. In this way, it was hoped to find evidence on which to base an assessment of the pressure for sexual selection, the probable cause for the development of extreme sexual dimorphism.

6.2 Methods

Attempts were made to locate telemetered mink at least once a day. The pattern of radio-tracking observations, designed primarily to cover the 24-hour cycle for time budget analysis, (Chapter 4), reduced the utility of the tracking information for range determination as 83% of the fixes were obtained from mink while they were in dens. For this reason, two methods of measuring the extent of the home range were investigated. These were linear measures based on length of water-course over which the mink travelled (Gerell, 1970; Chanin, 1976; Birks, 1981; Whitman 1981; Dunstone and Birks,

1983), and a grid-cell analysis (Voigt and Tinline, 1980; Kenward, 1987). Probablistic methods (for example Dixon and Chapman, 1980; Anderson, 1982) were not employed as most of the locations were non-independent (i.e., consecutive 10-minute radio-fixes) and there were only an average of 27 (standard deviation 21.9) active fixes for any individual. Techniques which attempt to define those fixes which can be considered spatially independent (Swihart and Slade, 1985), cause data redundancy which was considered unacceptable for this number of fixes. In the analysis, radio-tracking evidence with and without trapping data was examined.

Whenever possible, traps were set outside the known range of telemetered mink both to monitor the other mink present in the area, and also in the hope of catching an individual if it made an excursion outside its known range whilst not being radio-tracked.

The majority of the data about the mating system came from radio-telemetry, and direct observation of telemetered mink. In the final two years of the study, radio-collars were attached to as many resident individuals as was possible (limited by the number of collars available), to investigate interactions between the individuals. Radio-tracking of male mink during March was particularly difficult owing to their wide-ranging movements, and the short range of the transmitters. Most males visited Ross Island, and when a mink appeared absent from the study area, it was uncertain whether a mink was visiting females outside the study area, or whether it was on the island. Radio signals were only received from the mainland facing side of the island, and then only occasionally, because of its distance. During the winter the island was usually unreachable by boat. Only one male who was absent from the study area was ever located by radio-tracking when searches were carried out up to 4km north and west of the study area extremes. Another possibility was that collars might have malfunctioned (four of eight collars fitted to males during March stopped transmitting in less than seven days). Collars were not fitted to transient individuals since it would have been very difficult to retrieve collars once mink had left the study area.

For these reasons, the status of other residents, and the large apparently transient population, was monitored by a continuous trapping program throughout the whole of the winter period (November until early April) in the final two years of the study. Interpretation of the mating system would have been impossible without the biometric data collected during trapping. This allowed determination of reproductive condition and weight, and a thorough examination of the neck and facial area for scabs which resulted from injuries inflicted during copulation and fighting.

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6.3 Results

6.3.1 Residency

Figure 6.1 shows the residential status of mink captured within the study area, assessed using a combination of trapping, radio-tracking and incidental observation. It can be seen that some individuals of both sexes were present within the study area in one month only, whilst others were resident for periods in excess of one year. One female (F11) was present for 31 months of the main study, though she was also present in August 1985 bringing her residency on the study area to almost 3 years. Males tended to disperse in late winter, so they tended to be resident for shorter lengths of time. One male, which remained in his normal range after the rut, was resident for 25 months.

There appeared to be two main periods of immigration into the study area. These are demonstrated in Figure 6.2 which shows the number of captures of new individuals throughout the year, excluding those mink present at the start of the study. Many new mink were caught in July and August, typically the young of the year. Fewer new individuals were caught towards winter, but in March, many new males, both adults and juveniles were captured. The sex difference was highly significant (Binomial test: $p < 0.001$), and coincided with the rut.

6.3.2 Home range size

Trapping is the easiest way to gather large amounts of information on mink home ranges. In the present study however, traps were laid mostly in a linear manner along the coast with the aim of capturing individuals for tracking rather than determining the size of their home range. It is common for mink researchers to measure the size of a home range in terms of length of watercourse. This is despite references to mink utilizing habitats well away from the water (Birks and Linn, 1982; Allen, 1983; Chapter 5). For this reason, range size was calculated as an area calculated from a grid-square analysis (Voigt and Tinline, 1980) as well as by linear measurement of the length of watercourse along which a mink moved.

The movements of individual mink were plotted on a 1:2500 map, and a line was drawn between any two consecutive fixes. The map was divided into 25m squares since the accuracy of radio-fixes (in the absence of direct observation or beta-light sightings) in homogeneous habitat was probably of this order. Any 25m square touched by this line was included in the range of the mink. If the delineated range then consisted of more

Figure 6.1 Residency of mink

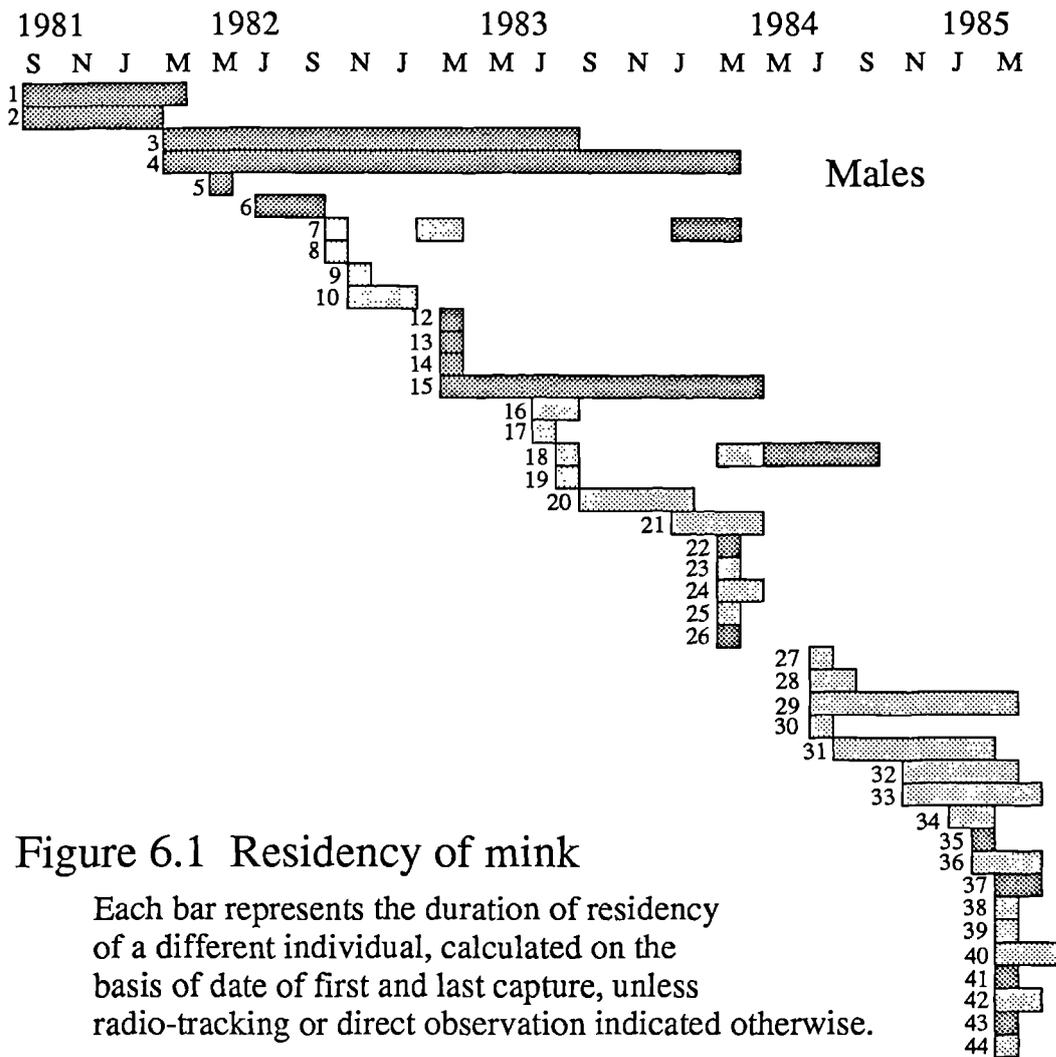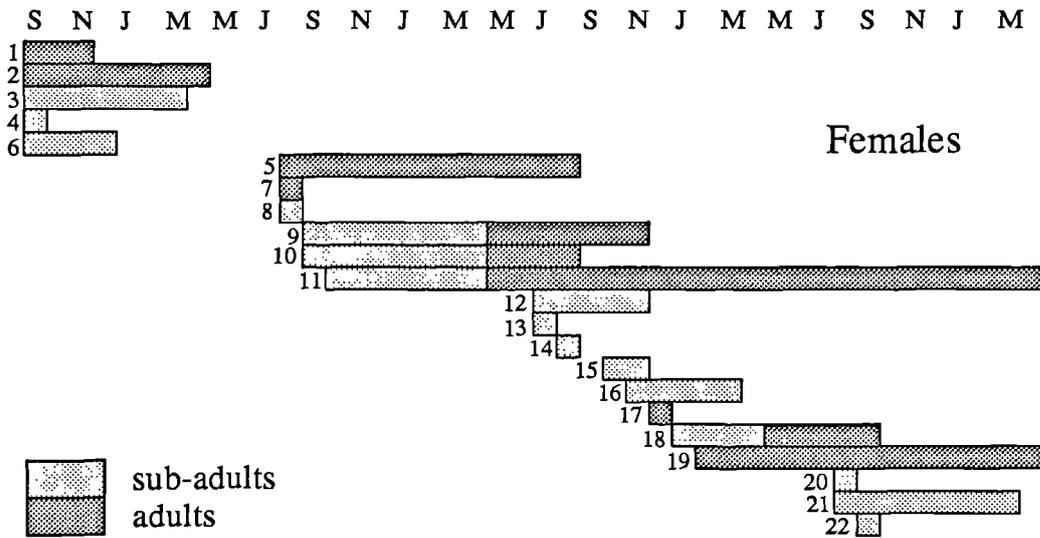Each bar represents the duration of residency
of a different individual, calculated on the
basis of date of first and last capture, unless
radio-tracking or direct observation indicated otherwise.

Figure 6.2   Captures of new individuals
in the study area

Based on all captures from October 1981 to April 1985
but excluding resident mink present at the beginning
of the study.

sub-adults

adults
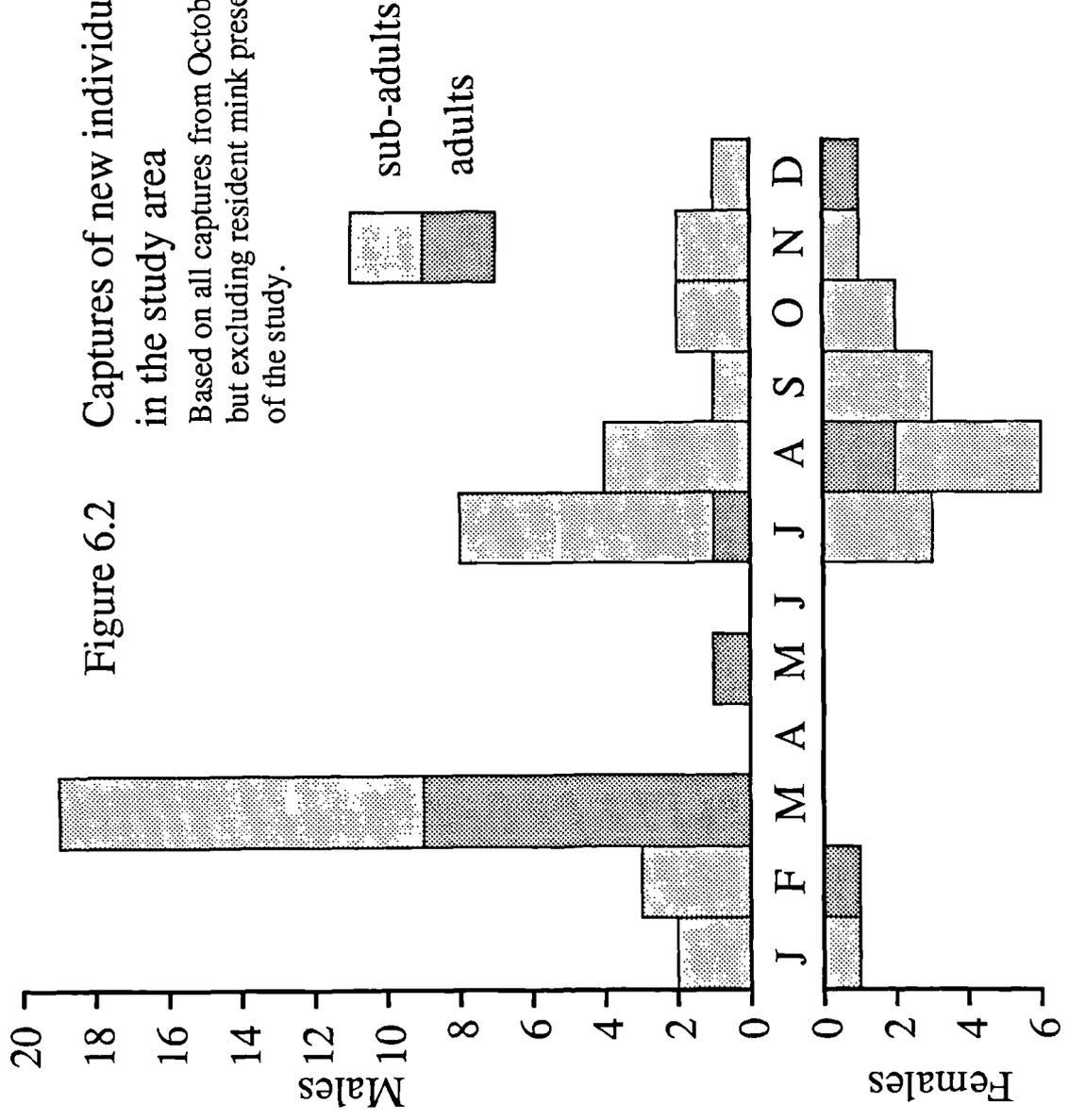
than one discrete area, disjoint areas were joined by a line following the shortest route on the basis that the mink had moved between the two areas. Any squares touched by these lines were considered to be part of the mink's range. Disjoint areas resulted from three situations: when the tracking period did not encompass a movement between two foraging areas; when once daily fixes on an individual revealed another den; and when trapping information revealed a range component outside the area delineated by radio-tracking. The 'linked cell' method of adding unfilled cells between pairs of fixes (Voigt and Tinline, 1980), could lead to errors if a mink followed an indirect route between two points. This was particularly likely when two disjoint areas were joined. However, it was considered better to include a minimum estimate of the intervening range than to make too many assumptions about the route a mink might have taken.

The length of watercourse method involved measuring the shortest distance of water body which connected all known locations of the mink along that water body (in this case coast). Where the mink was in a location away from the coast, it was considered to inhabit that section of coast closest to its position. If a mink used two lengths of coast which were widely separated and tracking indicated a possible overland route between the two areas, (for example M29 in December 1984, see Section 6.3.3), the length of the home range was calculated as the sum of the two disjoint lengths, possibly underestimating the real home length. The length of coast was calculated by joining all intersections of MHWS (mean high water springs) line with the 25m grid used in the grid-cell analysis. This removed small scale topographic features which could bias range length measurements in areas where the coastline was particularly convoluted.

The amount of time it took for a mink to reveal the full extent of its home range was assessed for one female and one male mink for which there were the largest quantities of data. Figure 6.3a shows the extent of the range of F10 during June 1983, as measured by the linked cell grid square technique. She was recorded out of her den during 101 10-minute fixes, during which time her home range was estimated as 7.6 hectares. Figure 6.4a shows how the range size increased with the number of active fixes. It should be noted that only 65% of her estimated home range was revealed after 27 fixes, the average number collected on one individual in one monthly sample. Within the extreme limits of her movements along the coast during June, there was also some unused habitat. The area of useful foraging habitat (shore, rocks and scrub, but excluding the pasture) within these limits was approximately 12.9 hectares, of which she was observed to utilize only 7.6ha, i.e., 58% in the 16.8 hours she was observed outside her dens.

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Figure 6.3   Home range extent of, and utilization by sub-adult female and male mink.

Density of shading represents the number of times a mink was recorded to have passed through a particular 25m square.

○ Den

>20
11-20
6-10
3-5
1-2

not used by mink but probably suitable foraging habitat

〜〜〜 MHWS
‥‥ MLWS

b. M20 November 1983
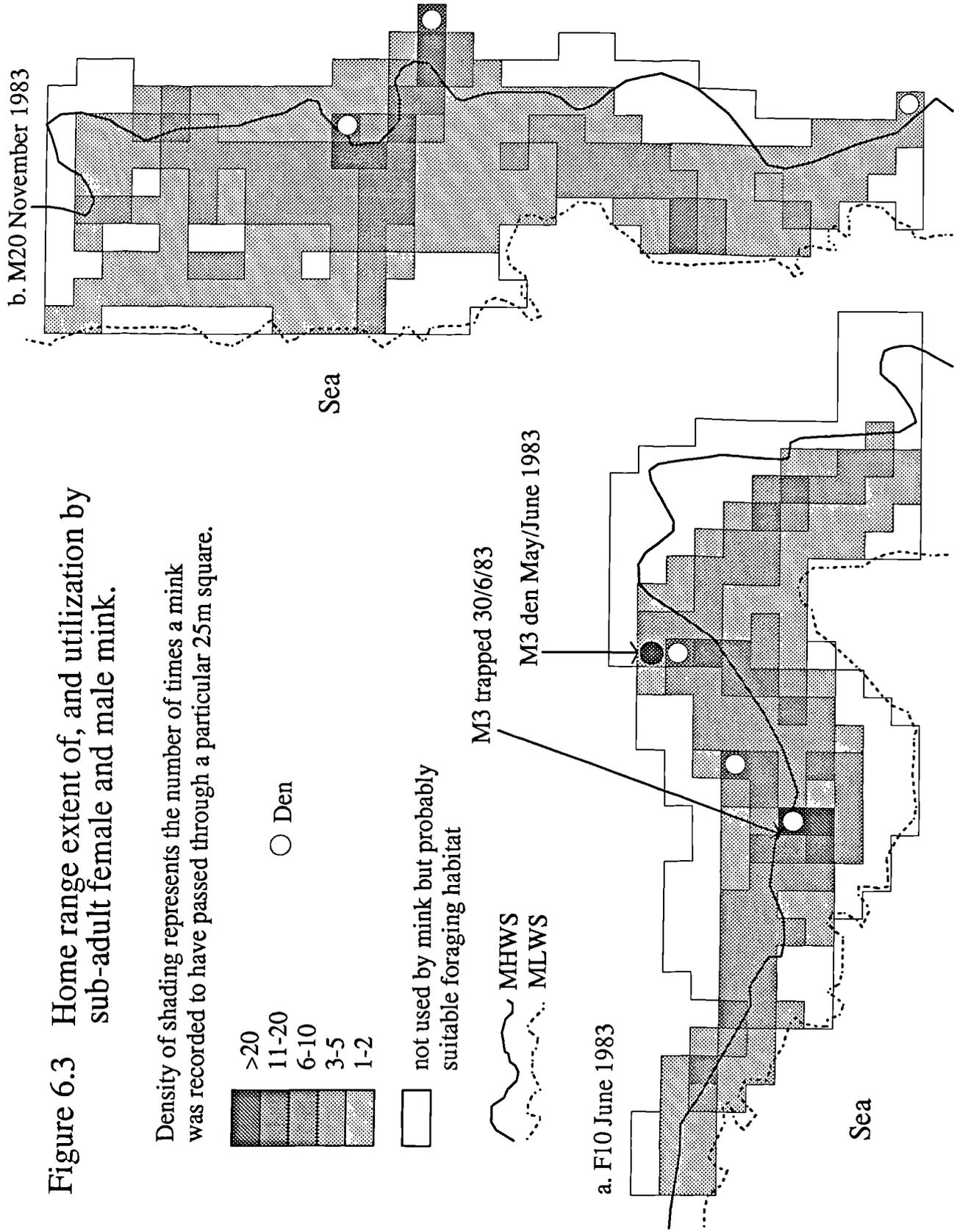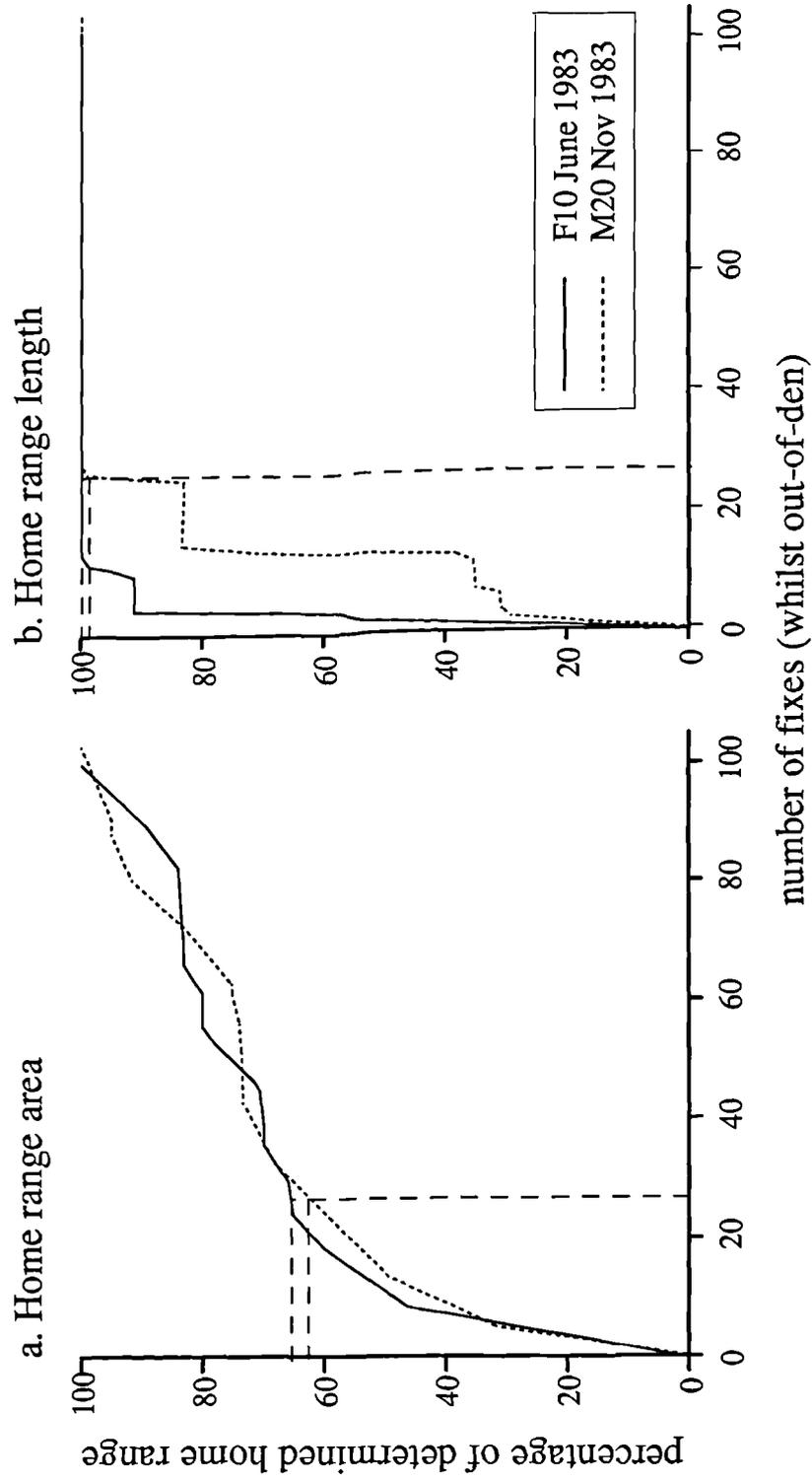
Sea

a. F10 June 1983

M3 den May/June 1983

M3 trapped 30/6/83

Sea

Figure 6.4　The percentage of final home range size revealed as
　　　　　　a function of the number of radio-fixes collected.

a. Home range area

b. Home range length

number of fixes (whilst out-of-den)

percentage of determined home range

F10 June 1983
M20 Nov 1983

The situation was similar for male M20. Figure 6.3b shows the range occupied during November 1983, and Figure 6.6a the way range size increased with the number of fixes recorded out of den. Like F10, his range still appeared to be increasing appreciably, even after 104 out-of-den fixes (17.3 hours) had been collected. Only 62% of his final range had been revealed after 27 radio-fixes had been obtained (Figure 6.4a). The potential area of useful foraging habitat within his known movements along the coastline was 14.8ha, of which he used 11.1 (75%). There was also a further 3.1ha of scrub and plantation well back from the coast which he did not use in November, but started using in December.

Obviously, the mean number of active fixes collected on the mink (i.e., 27) did not permit an adequate measure of range size and habitat usage to be made. However, the extent of a home range in length of coastline was revealed far more quickly. Figure 6.4b shows how much of the linear extent of the ranges of F10 and M20 were revealed in terms of number of radio-fixes collected. It can be seen that 100% of F10's linear range was revealed after only 13 active fixes. Most (90%) of M20's linear range had been revealed after 15 fixes, and 98% was revealed after 27 fixes. Thus, although the length of coastline did not provide information of actual habitat use, it was very valuable in defining the limits of the home range. The small number of fixes required to define the coastal-linear component of the range also suggested that the continuing increase in home range area, determined by the grid-cell analysis, was not due to a progressive change of the home range.

Figure 6.5 shows how out-of-den radio-fixes are distributed with respect to distance from the MHWS for a number of individuals. It can be seen that the majority of fixes occur very close to the high tide line, for both males (Figure 6.5a-f) and females (Figure 6.5g-j), emphasizing the importance of this zone. The number of fixes tails off with distance inland. If the mink were defending two-dimensional territories, one might expect more fixes inland. Small subsidiary peaks of activity were evident inland for M3 and M29 in February. These corresponded with use of inland rabbit burrows on a hillside (M3) and Third Forestry (M29), and could be interpreted as defence of an inland range boundary. However, inland use of plantations was essentially a winter phenomenon, a probable result of a shortage of lagomorph prey near the coast (Chapter 5). During August and September, a time when territorial defence is likely to be strongest as juveniles are trying to set up territories of their own, activity is largely limited to the coast (Figure. 6.5a&c).

Figure 6.5 The distribution of radio-fixes with respect to the high water mark.

a. M4 August 1983

b. M7 March 1984

c. M18 September 1984

number of radio-fixes

Distance (m) above mean high water spring tide

Figure 6.5 (cont.)

d. M3 February 1983

e. M29 November 1984

f. M29 February 1985

number of radio-fixes

Distance (m) above mean high water spring tide
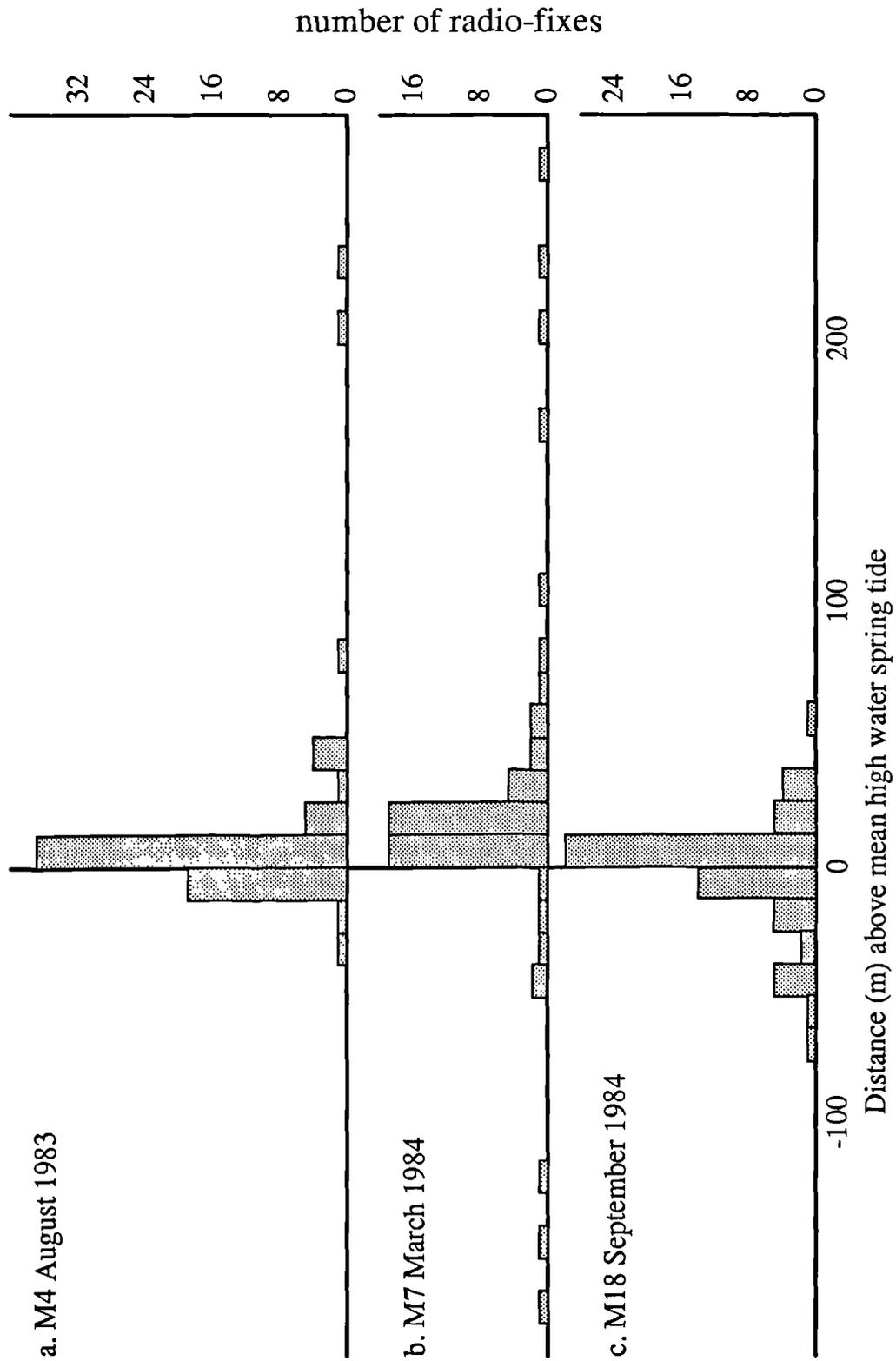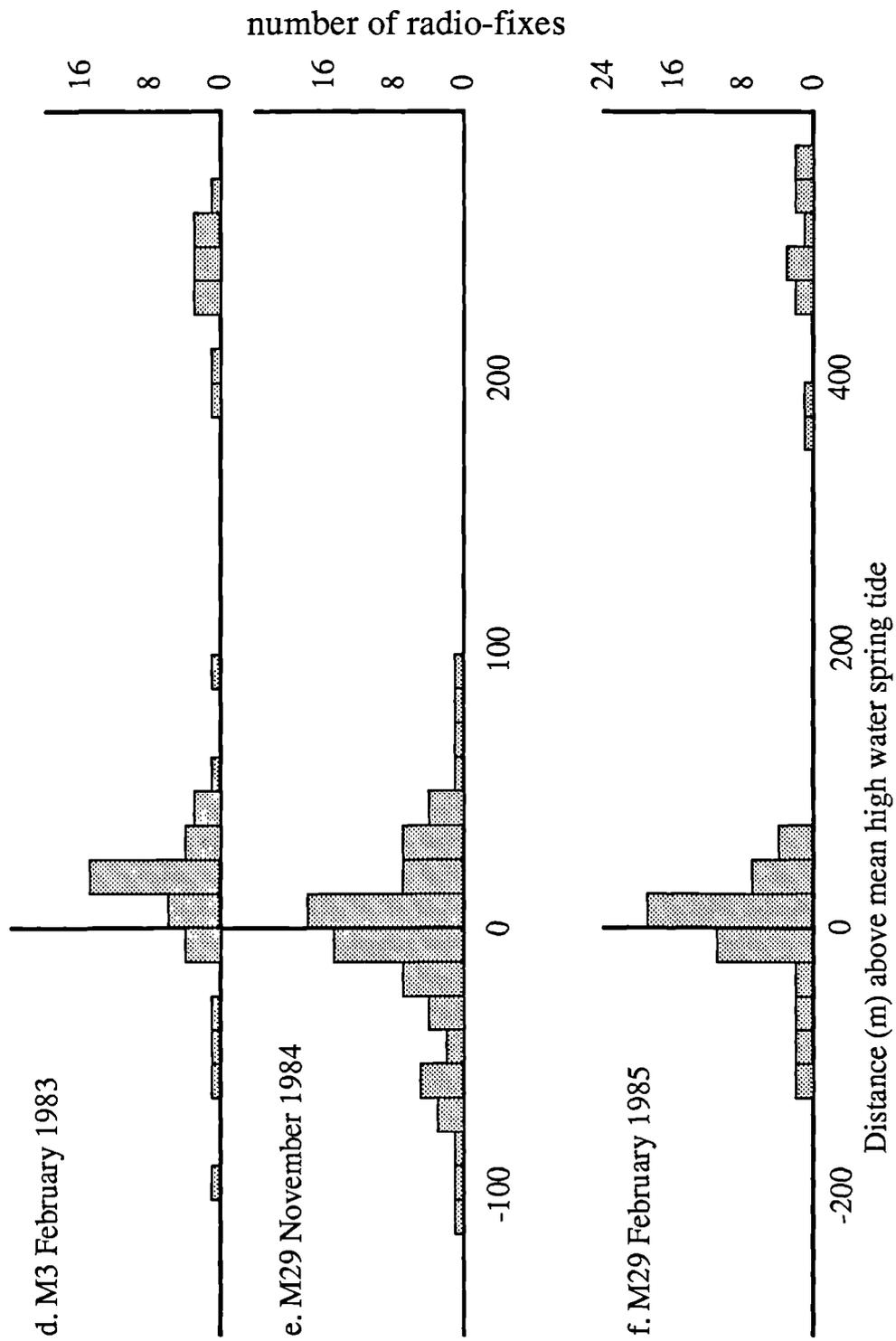
Figure 6.5 (cont.)

g. F9 February 1983

h. F16 February 1984

i. F19 March 1985

j. F10 June 1983

number of radio-fixes

Distance (m) above mean high water spring tide
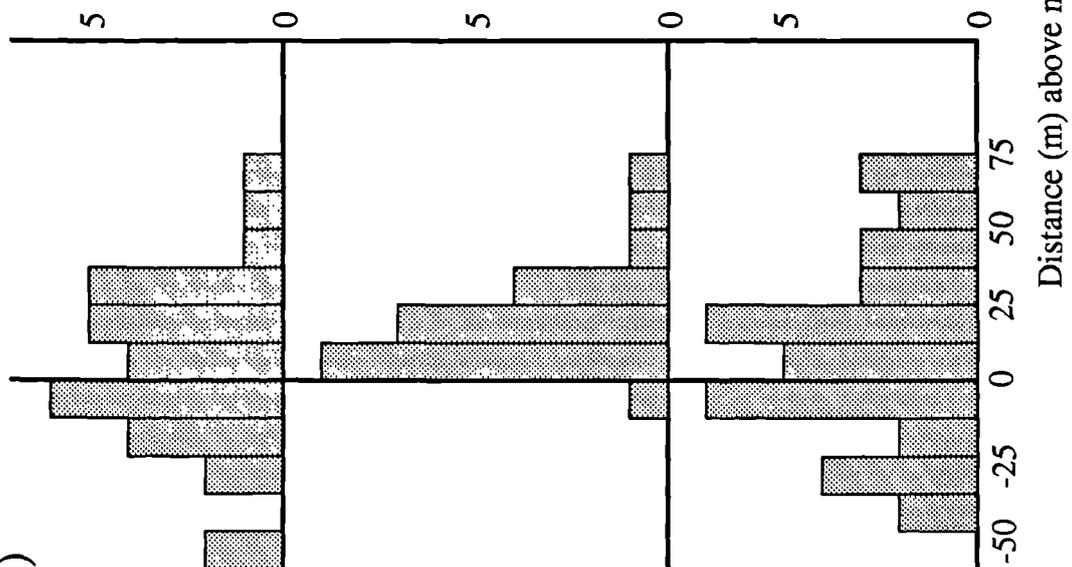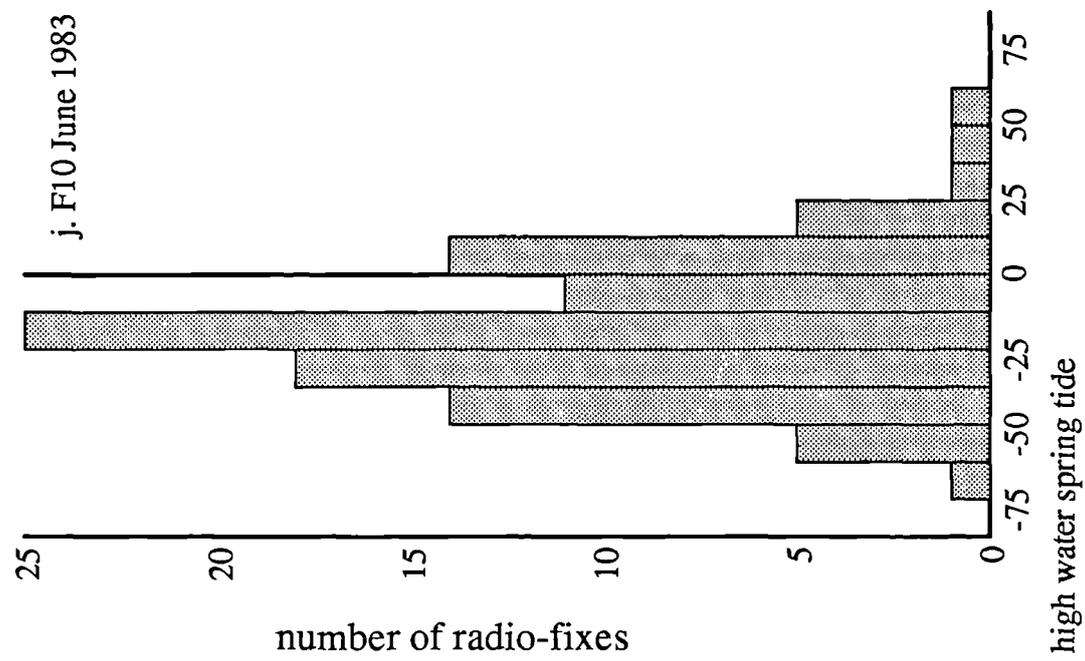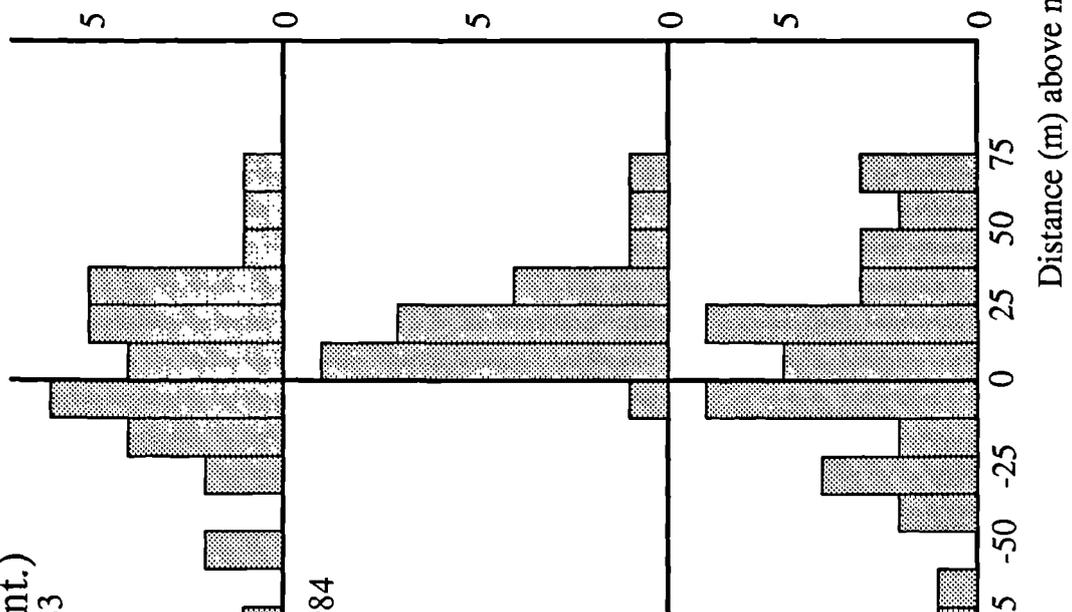
Linear range lengths were calculated on the basis of radio-tracking alone, and when trapping information was included in addition to the radio-tracking data. The latter resulted in an increase of 8.7% over the former for male ranges, and a 13.6% increase for female ranges. As traps were laid along the coast, it was considered valid to include trapping data in a linear range length estimate if the extra length was a simple extension of the known range. As tracking was discontinuous, den movements occurred between tracking episodes. Thus, even in the absence of any out-of-den radio fixes, the linear extent of a range could be delimited by these dens if fixes were collected on a sufficient number of days for the mink to have used dens throughout the whole of its range. Limited radio-tracking meant that the limits of a home range were frequently determined by a den location. This was despite the finding that not all individuals had dens at the extremes of their ranges (the distribution of dens throughout a range can be found in several figures later in this chapter). This fact would account for the extra component of the home range revealed by trapping.
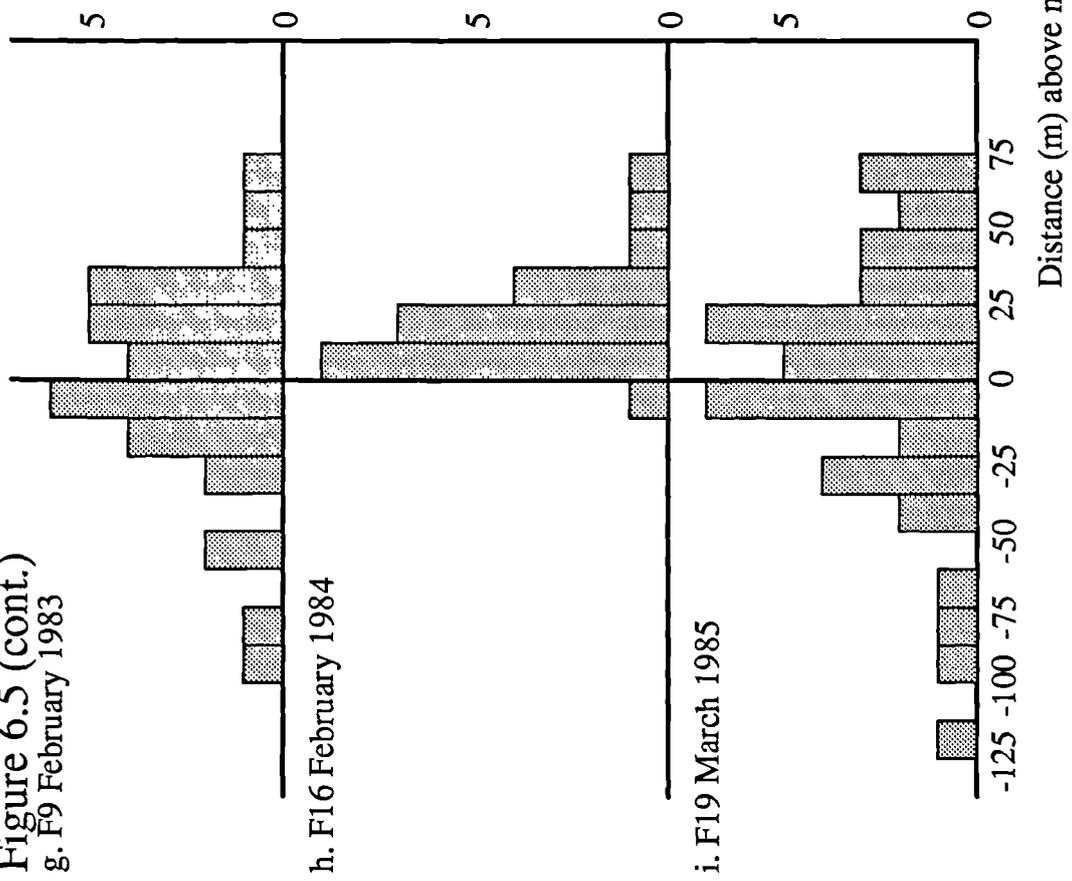
Figure 6.6 shows how a linear measure of home range increased with the number of days' information collected. It can be seen that there was little increase in apparent range length after seven days of monitoring. Many ranges did not increase in length after three or four days. The situation was not so clear cut with females, but most range lengths had levelled off by seven days. Therefore, in the analysis of sex and monthly differences in extent of linear range, cases were downweighted linearly by a factor of one seventh for each day less than seven for which information was available on a mink in that month.

Despite the problems inherent in both methods of range assessment, each revealed significant differences between the sexes. Males occupied a significantly greater length of coastline (males, 2650 ± 254m: females, 1240 ± 273: $F=25.06$, $df=(1,46)$, $p<0.001$) and area of land (males, 12.3 ± 1.1ha: females, 4.9 ± 1.0ha: $F=32.15$, $df=(1,39)$, $p<0.001$). Interestingly, male range length was 2.1 times that of a female, whilst their home range area was 2.5 times as large. These figures reflect the high linear component of a range, as a 2.1 fold increase in one range dimension should indicate a greater than four fold increase in area. There were significant changes throughout the year in the linear extent of a mink's range along the coast ($F=2.22$, $df=(11,46)$, $p<0.05$). When analysed separately for each sex, this difference was only significant for males ($F=2.74$, $df=(11,25)$, $p<0.05$), probably due to a large increase during the rut, especially in March (Figure 6.7). There was no significant difference for females ($F=1.12$, $df=(11,21)$, N.S.), though if the period May to June was compared to the rest of the year, females moved over a significantly

Figure 6.6   An illustration of the way in which the size of the linear
component of a mink's home range was revealed over time.

a. males

Figure 6.6 (cont.)

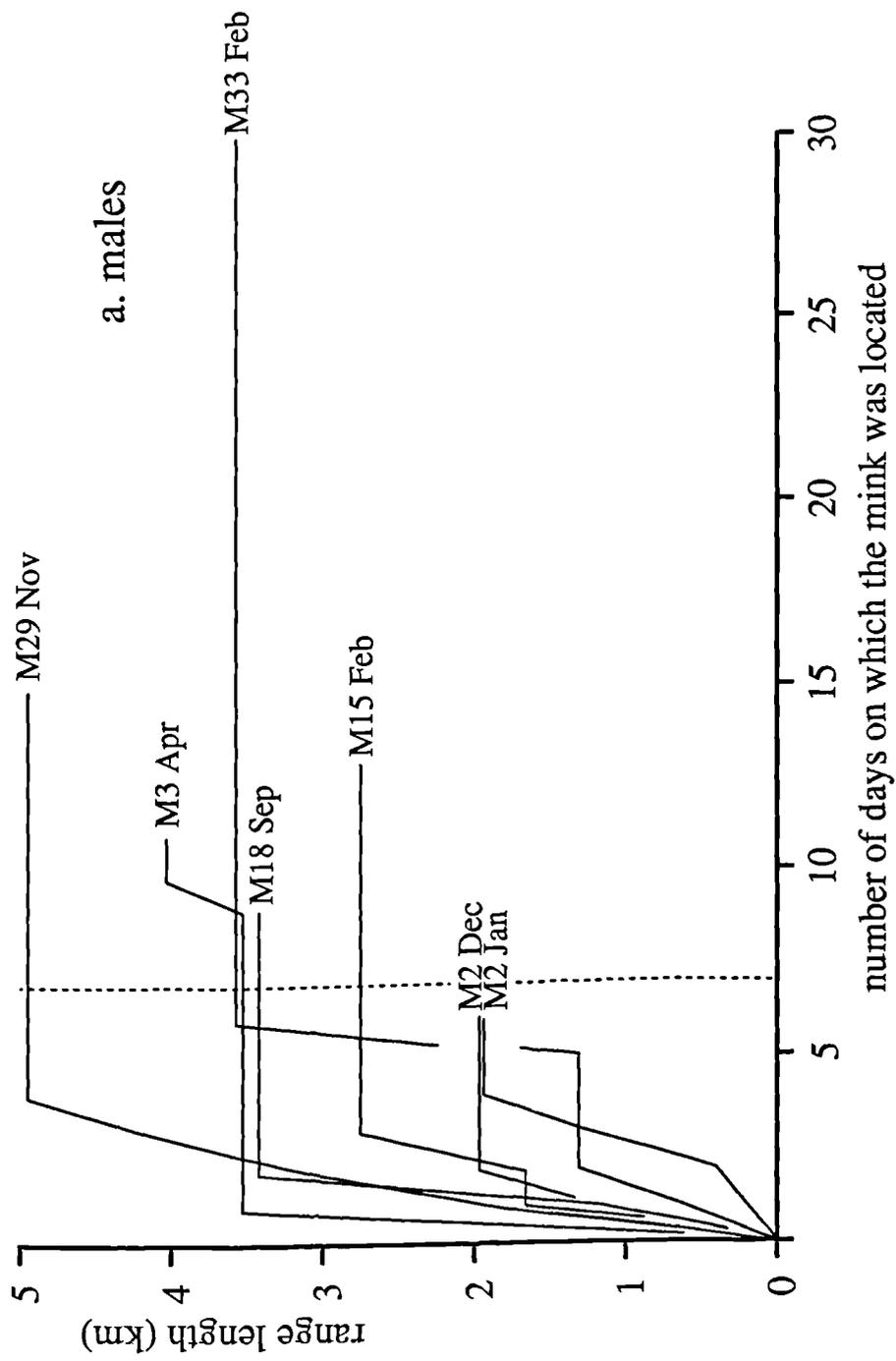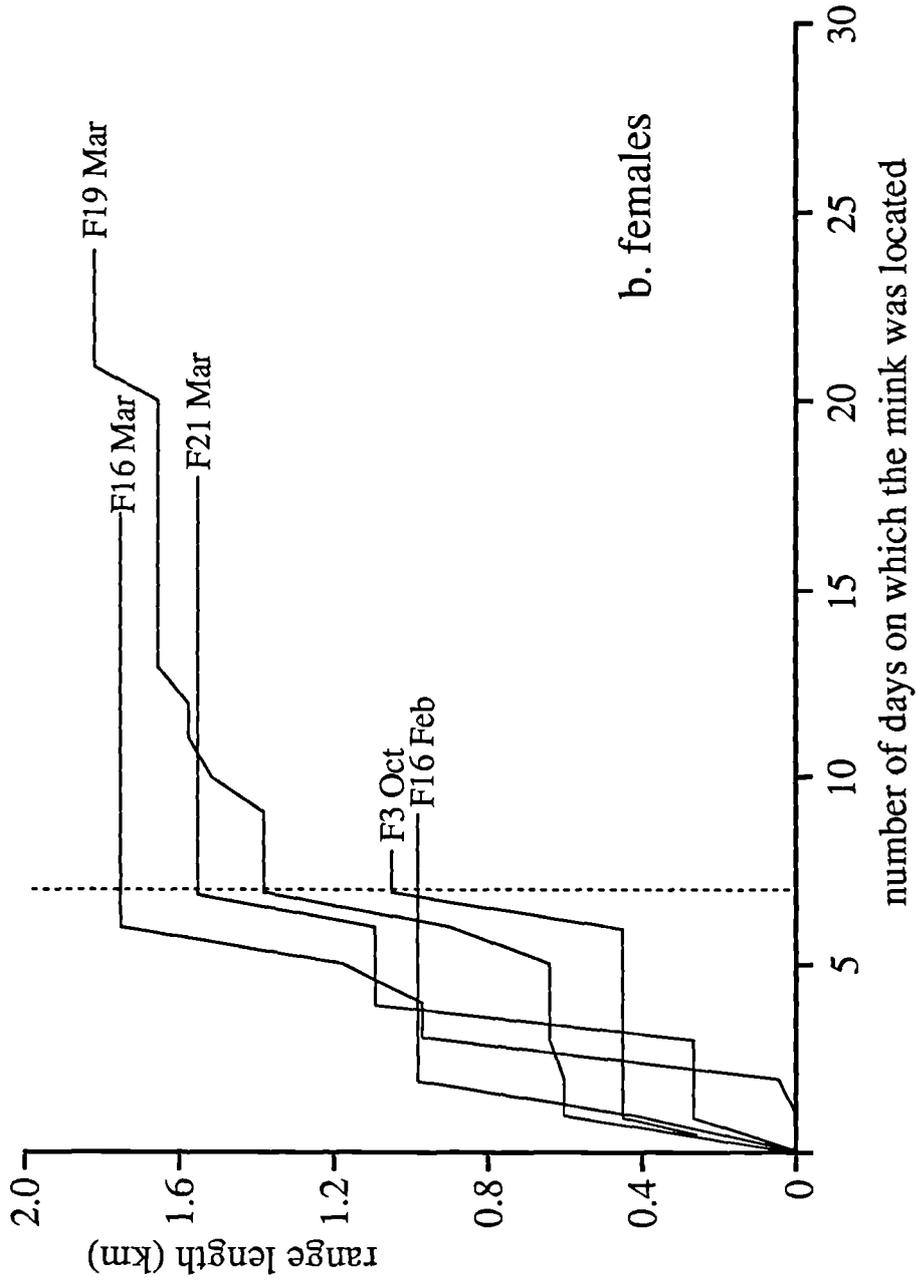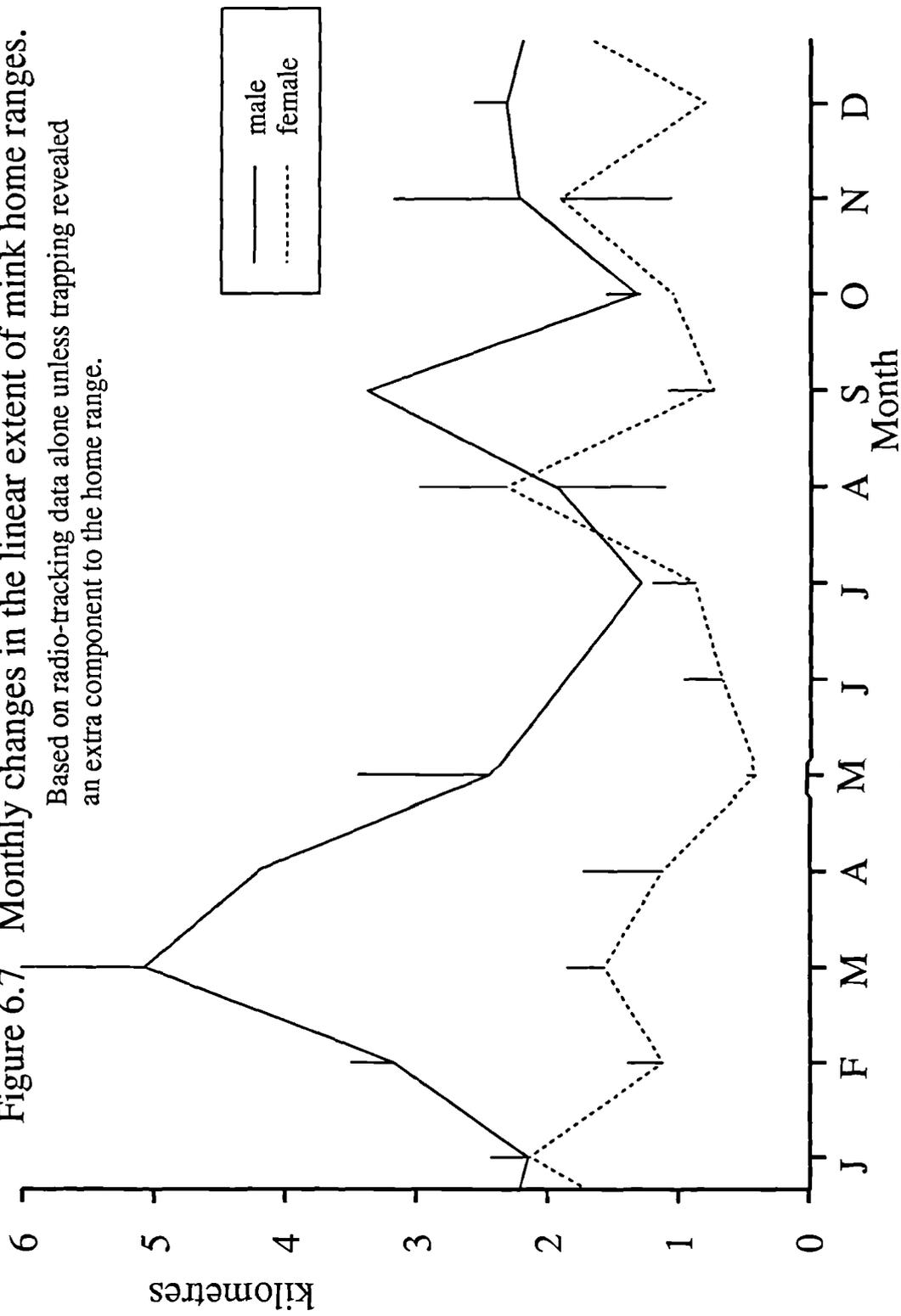

b. females

Figure 6.7   Monthly changes in the linear extent of mink home ranges.
Based on radio-tracking data alone unless trapping revealed
an extra component to the home range.

smaller length of coast ($F=6.93$, $df=(1,19)$, $p<0.05$). May to June was the period when females were bringing up dependent kits and so could only make limited movements from their dens (Figure 6.8, Chapter 4). It can be seen from Figure 6.7 that differences between the sexes were most marked during the period from February to June. Outside the mating and breeding seasons, sex differences were negligible in most months.

This similarity in range lengths outside reproductively important periods appears to be reflected in the sex ratio of resident individuals within the study area. Trapping results were biased towards males (Chapter 2), but by using the information in Figure 6.1 to pick out those individuals considered to be resident (i.e., mink that were present for three months or longer), it was possible to look at the way the sex ratio changed throughout the year. Combining data for all three years because of the small sample sizes, the sex ratio is seen to vary little from 1:1 (Figure 6.9).

Measurements of home range size allow comparisons between different sites and may indicate seasonal changes in mink behaviour or resource quality, but provide no information about intra- and intersexual relationships. These were therefore examined on an individual basis using ranges mainly determined by the grid cell analysis.

6.3.3 Intrasexual overlap

Intrasexual overlap was demonstrated from trapping results, rarely from radio-tracking, because simultaneous tracking of males in contiguous ranges was rarely accomplished. Spatial range overlap was demonstrated as some traps captured more than one individual in one month. A simple index, based on the number of traps, which having captured one mink, went on to capture a different mink of the same sex during the same month, was used to examine sex-related and monthly changes in the occurrence of range overlap. It should be restated that the index examines only the occurrence of overlap, not the extent of any overlap in spatial terms. Two-way analysis of variance revealed a significant interaction between sex and month suggesting that the sexes behaved differently throughout the year ($F=4.64$, $df=(9,58)$, $p<0.001$). These differences are evident in Figure 6.10. Levels of overlap between males (as determined by the index) were low for most of the year (usually less than 10%) but were very high (55%) during the rut in March, suggesting a change in the social organization. This resulted in significant differences between months for males ($F=5.16$, $df=(11,32)$, $p<0.001$). The differences between months were not significant for females, the only months when trapping overlap

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Figure 6.8   The change in the size of the home range of F10 during the breeding season

16-19/7/83 (with kit).

3,5/8/83

2/8/83

1/8/83

MLWS

MHWS

Trapped 30/7/83 (kit present)

6/7/83
7/8/83

7/8/83

6/8/83

After occupying well defined areas in May and June,
F10 was observed, radio-tracked and captured
throughout most of the study area during July
and August. Usually, it could not be ascertained
whether or not her kit was present with her.

May 1983
June 1983

Dens

1km
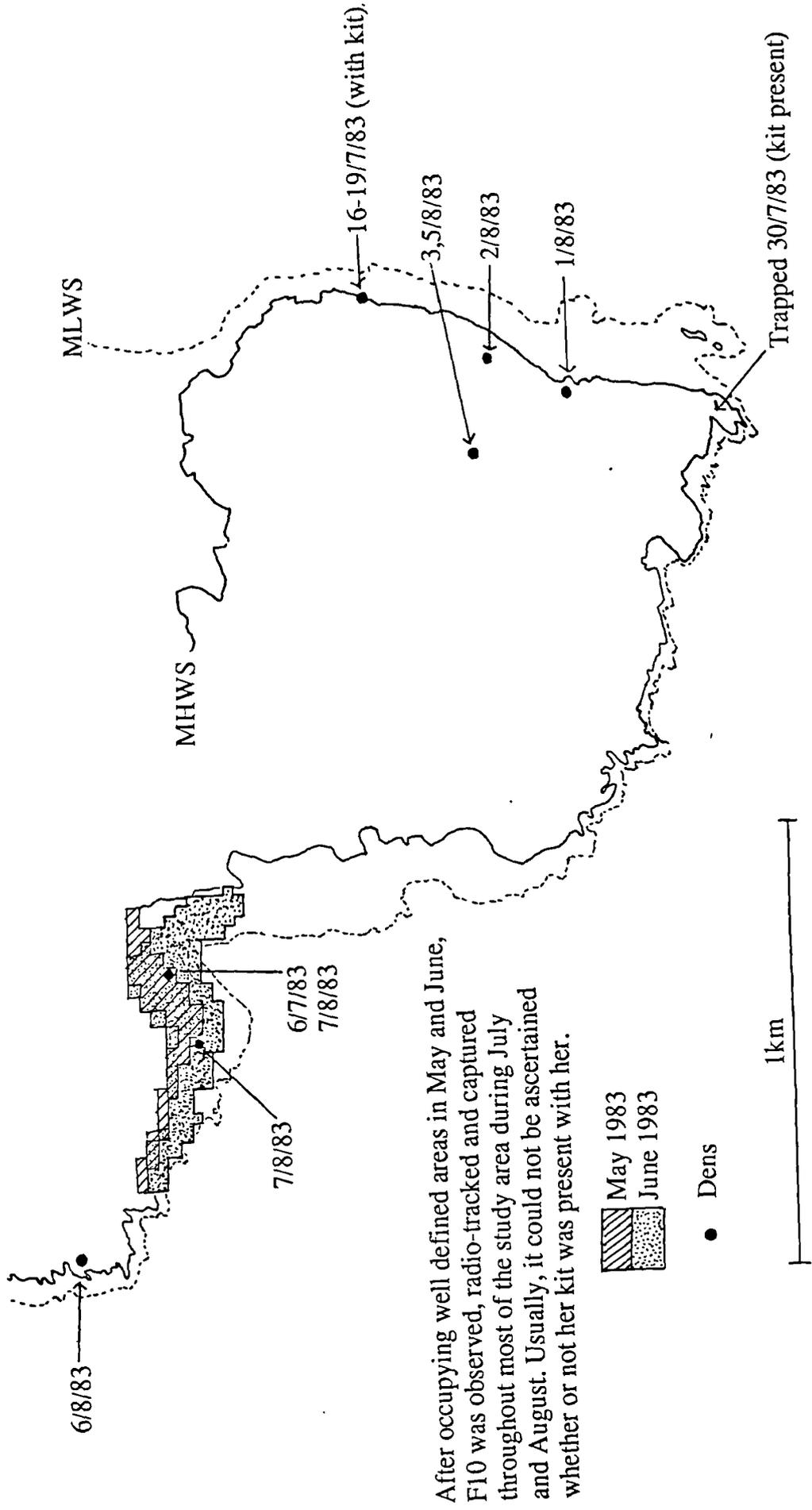
Figure 6.9   The sex ratio of resident mink.
Based on the number of resident mink present in each month.
Data for each month combined for the whole study period.
Mink were only included in the ratio if they were present for
at least three consecutive months, based on a combination of
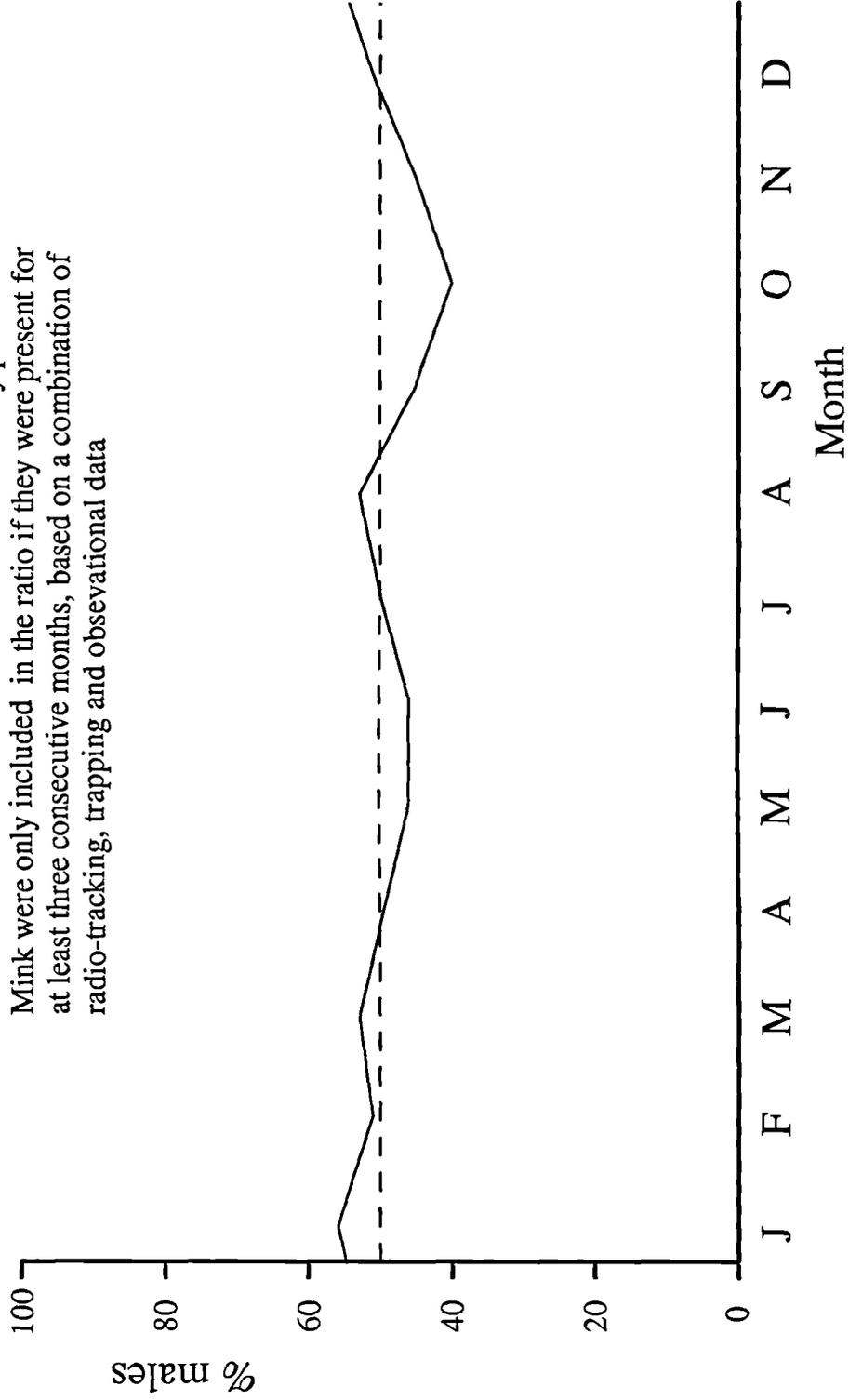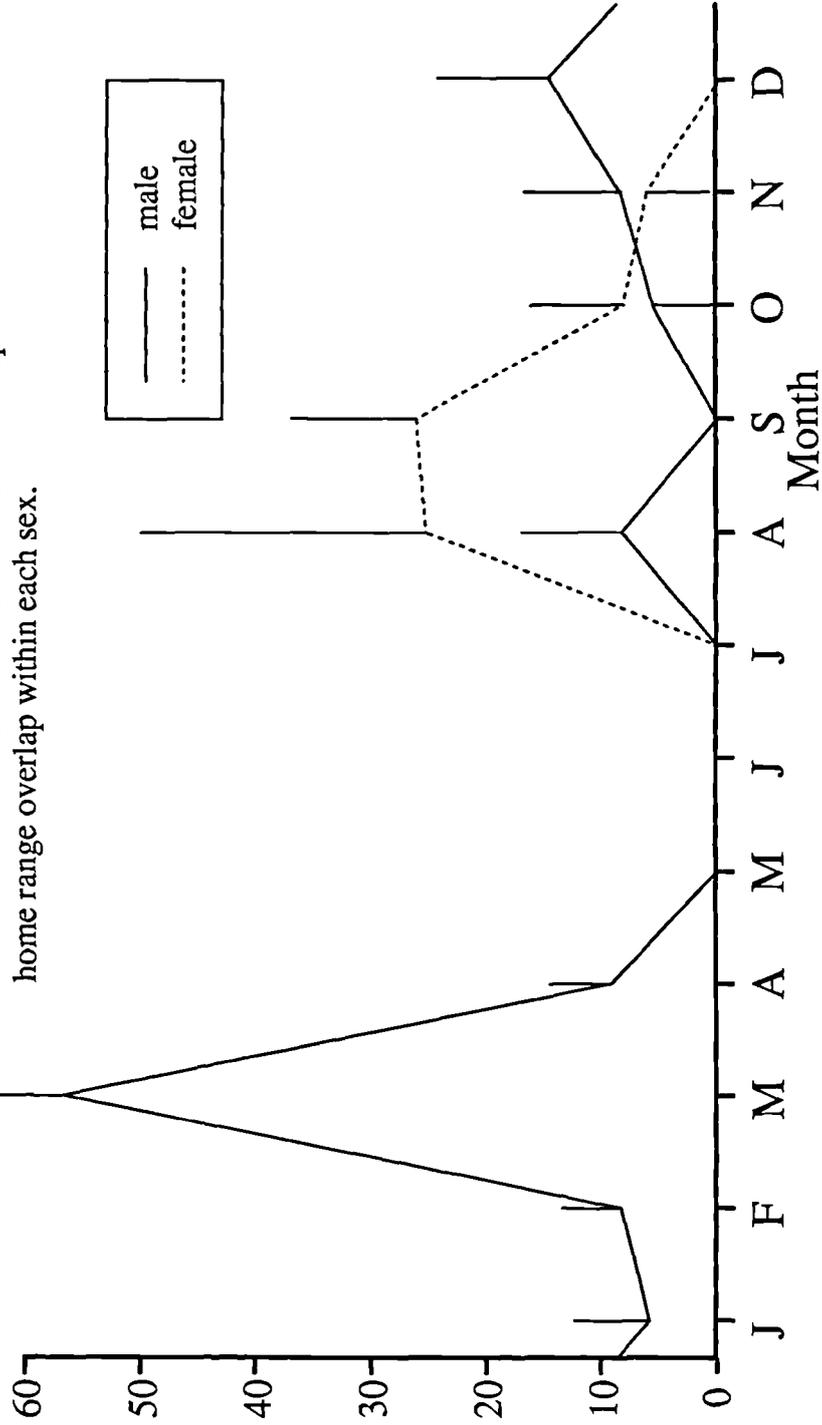radio-tracking, trapping and obsevational data

Figure 6.10   Captures of more than one individual at the same location.

The proportion of traps which, having captured one mink, capture another of the same sex during the same month. This could be considered a crude measure of spatial home range overlap within each sex.

occurred at all being August to November, when the kits were trying to establish ranges for themselves.

Radio-tracking revealed some interesting relationships between individuals. One good example of interactions between males came from a mixture of trapping and tracking of M29 and M33 between November 1984 and February 1985 (Figure 6.11). M29 was one of the four kits of F11, raised on Ross Island. In September, M29 was trapped four times between First Forestry and Fox Craig, suggesting that he was taking up residency, in a contiguous range to an adult male, M18, whose range extended over most of the study area at this time (Figure 6.11a). This adult died, of unknown causes, in October. By November, M29 (weight 960g), had expanded his range to cover most of M18's. Trapping suggested that the rest of M18's range had been taken over by a smaller sub-adult male, M32 (weight 910g), and indicated that M32 made an incursion of 400m into M29's range in November. A larger male, M33 (weight 1140g) was also caught at Fox Craig in November. Tracking in later months suggested he was living primarily on Ross island (Figure 6.11b).

In December, the situation had changed slightly. M29 (now weighing 1030g), was utilizing First and Third Forestry. He was also trapped three times on the east side of the peninsula, though his route there was uncertain as he was not tracked whilst moving between the areas. M33 (1140g), appeared from trapping data to have expanded his range on the east side of the peninsula (Figure 6.11c).

In January, equipment failure prevented effective tracking. However, trapping and limited tracking showed that M33 (now 1110g) was using the whole of the east side of the peninsula, as well as Slack Heugh and the southern edge of Second Forestry. M29 (1100g) was not trapped or tracked on the east coast, but made an overland trip from Third Forestry to the eastern edge of Second Forestry. He was also trapped in Brighouse Bay, overlapping the presumed range of M32 (see also Figure 6.23).

At the beginning of February, M29 (now 1140g) was located for the last time in Second Forestry. His range now extended along the west and south sides of the peninsula, and as far as Slack Heugh in the east (Figure 6.11d). On one foraging trip, M29 entered Slack Heugh whilst M33 was present and inactive in a den in the cliffs. M33 became active in his den, which M29 did not approach, returning to his own den in Third Forestry shortly afterwards. M33 (1140g) was radio-tracked and shown to be making extensive use of dens in Slack Heugh, Second Forestry, and on Ross Island (Figure 6.11d). He also

Figure 6.11   Changes in the spatial organisation of male mink home ranges
between September 1984 and February 1985.

(see text for detailed explanation)

MLWS

MHWS

M29 (trapped)

M29 (trapped)

1km

■ M18 dens September 1984

a. September 1984
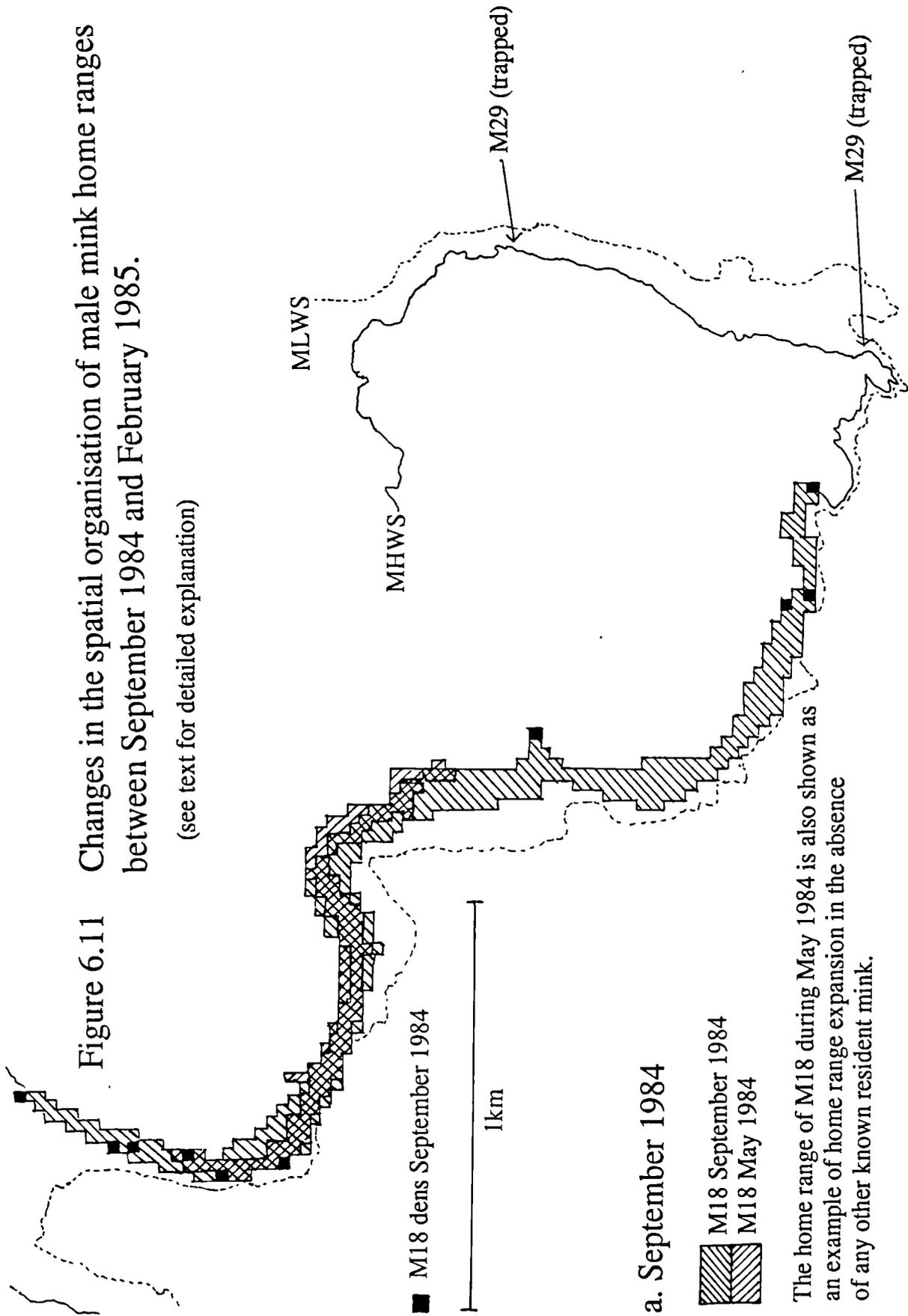
M18 September 1984
M18 May 1984

The home range of M18 during May 1984 is also shown as
an example of home range expansion in the absence
of any other known resident mink.

M29 (trapped)

M32 (trapped)

M32 (trapped)

M33 (trapped)

M29 (radio-tracking)
M29 (trapping)

■ Den

—— MHWS
········ MLWS

500m
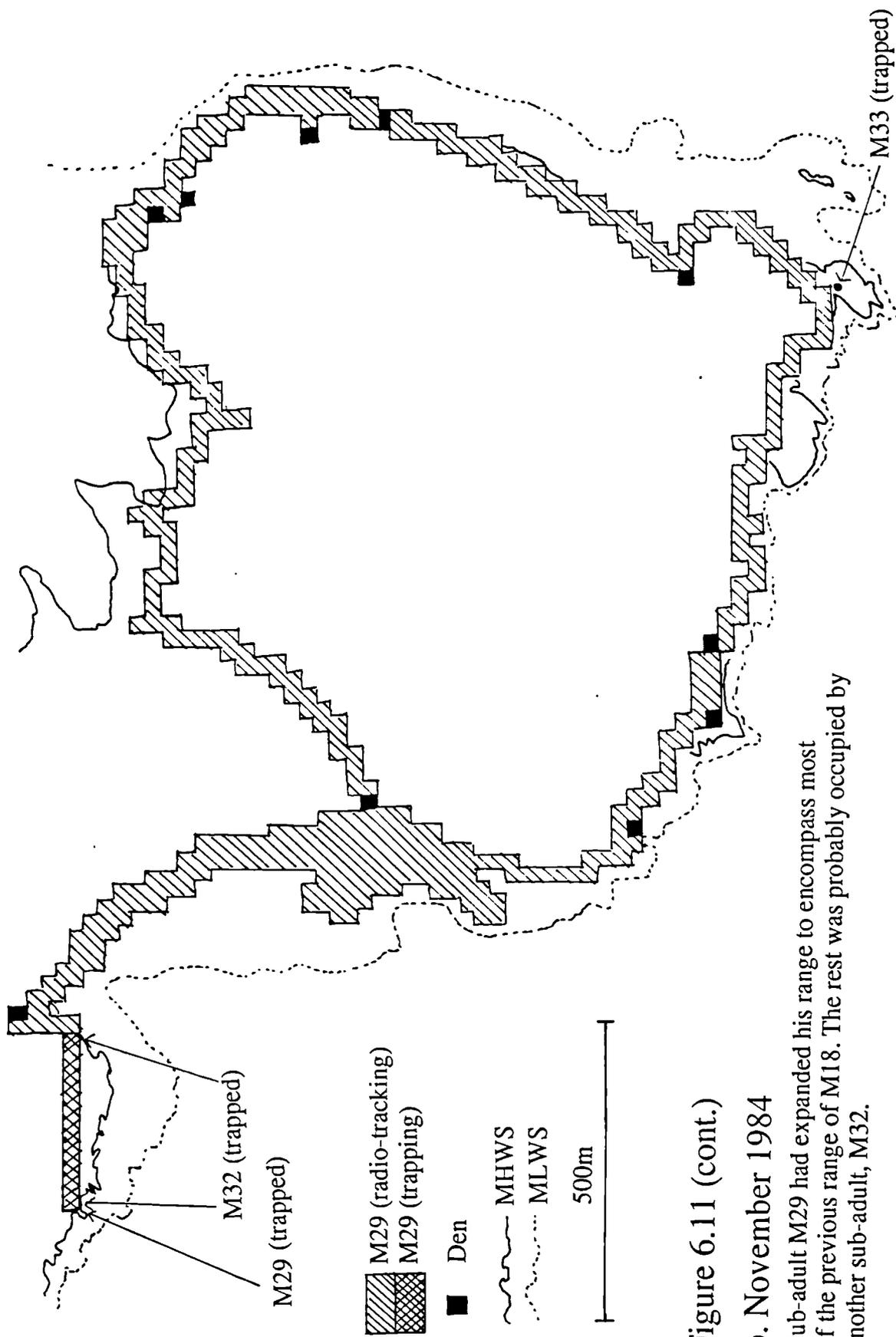
Figure 6.11 (cont.)

b. November 1984

Sub-adult M29 had expanded his range to encompass most
of the previous range of M18. The rest was probably occupied by
another sub-adult, M32.
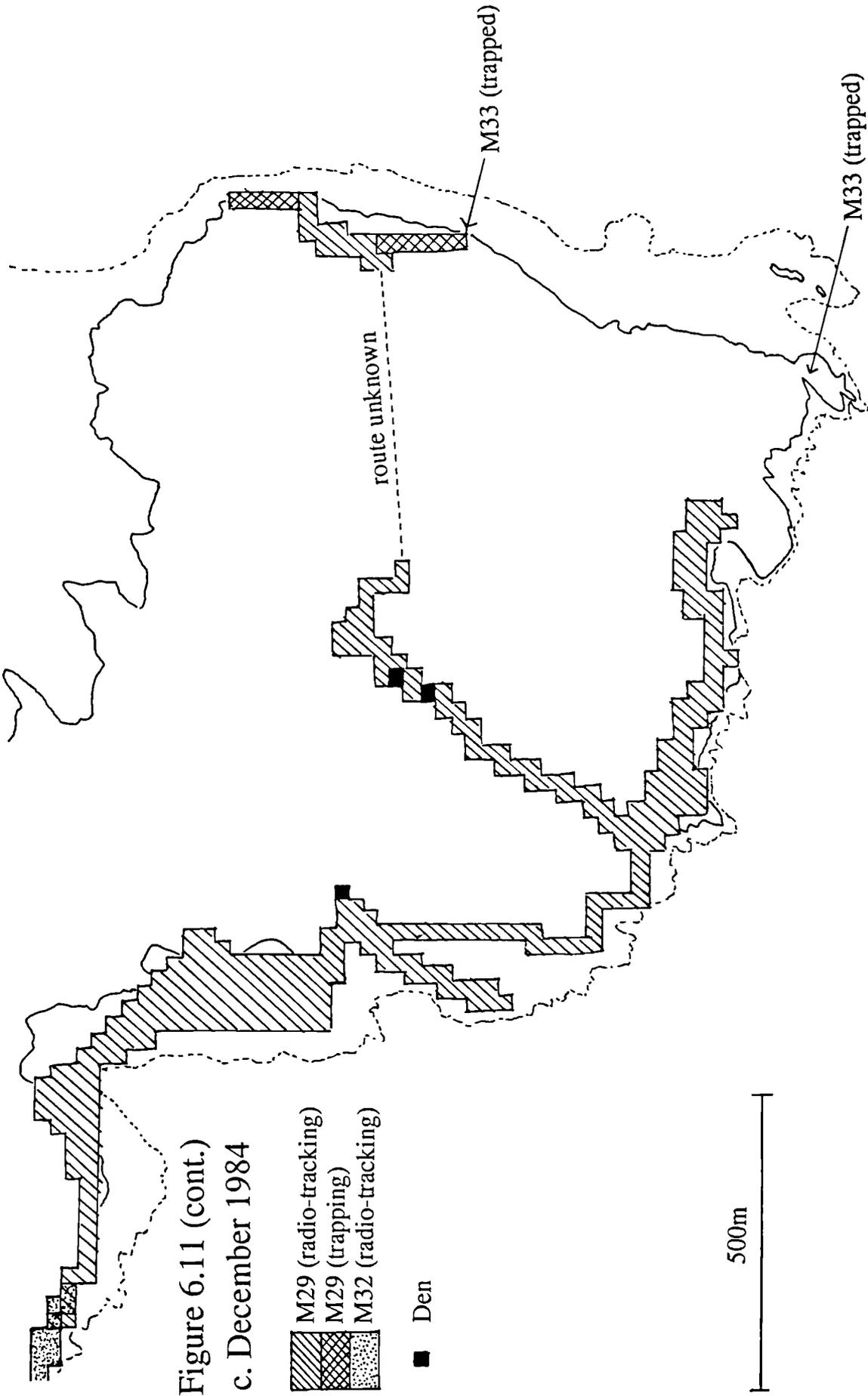
Figure 6.11 (cont.)
c. December 1984

M29 (radio-tracking)
M29 (trapping)
M32 (radio-tracking)

■ Den

route unknown

M33 (trapped)

M33 (trapped)

500m

Figure 6.11 (cont.)   d. February 1985

Tracking revealed that the home range of M33 extended to the north of Ross Bay. Other than on the first day of February, M29 was no longer located along the east side of the peninsula.

M29 den 1/2/85

M33 den

M29
M33
Den

1km
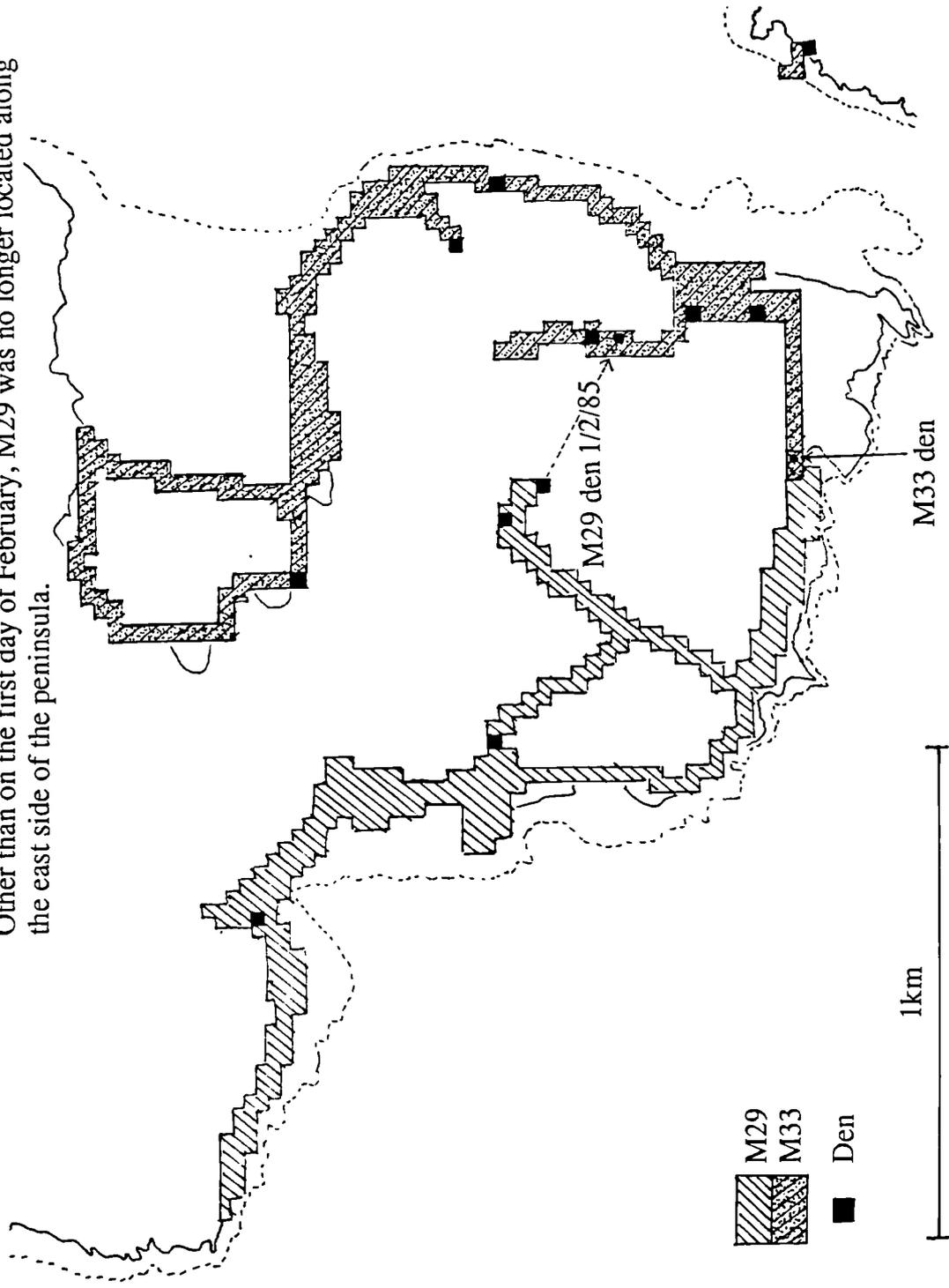
made a night-time trip round Ross Bay, returning before morning. On the 23rd February, M33 started occupying different types of rocky den, subjectively described as female den types. This will be expanded upon later.

At the beginning of March, M29 was trapped on the West side of Brighouse Bay. Since signs of collar abrasion were appearing, his collar was removed. He was never trapped again. Normally extremely easy to catch, it was assumed he had left the study area completely. He had also put on a lot of weight, and at 1370g was the heaviest mink recorded on the peninsula that year. M33 continued to expand his range North, out of the normal study area. Whilst to the North side of Ross Bay, he visited one and used another of the dens of F21, but his furthest movements North were even beyond the extremes of her range (see also Figure 6.14b). At the beginning of the month he weighed 1200g, but lost weight through the month, weighing 1140g on the 27th.

Thus it appears that, despite changing home range boundaries, the ranges of both males were distinct, with perhaps a small degree of overlap at the extreme boundaries. Data are more limited for females but one example suggests the same pattern.

In February 1984, a sub-adult female (F16, weight 600g), first trapped on the east of the peninsula the previous November, was radio-tracked. Scabs on the back of her neck suggested that she had recently been mated. She was tracked intermittantly for 9 days, and appeared to have a stable range, based mainly in a barn, but extending to Ross Bay (Figure 6.12). The only other female in the area was thought to be adult F11 (weight 800g), occupying Ross Island, and making occasional trips to the mainland where she was trapped at Fox Craig.

At the beginning of March, F16 (630g) was tracked mainly at the entrance to Ross Bay, in rabbit burrow dens. She made one trip back to the barn, on the 5th March, but then made a move along the stone walls to Third Forestry. At this time, F11 (750g) was captured three times within F16's February range, near First Forestry. F16 spent much of her time in a variety of rabbit burrows in Third Forestry, and also on the shore of the Fauldbog (Figure 6.12), a range M20 had probably vacated at the end of January (below). Apart from one trip back to First Forestry on the 20th March, her range had shifted completely. F11 continued to be trapped on the peninsula until the end of March. These observations suggest that female ranges are probably intrasexually distinct as well, but as F11 was not radio-tracked successfully, a degree of uncertainty remains. The cause of the range shift by F16 was not known. Female F11 was an adult, and also heavier,

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Figure 6.12   The relationship between sub-adult female F16 and adult female F11

This figure shows the expansion/shift in the range of F16, possibly in response to an expansion in the range of F11 (normally resident on Ross Island). See text for detailed explanation.

F16 February 1984
F16 March 1984

Den F16

F11 trapped 10/3/84

F11 trapped 9,27/3/84

F11 trapped 7,14/2/84 23/3/84

F16 den 20/3/84

F16 den 5/3/84

MHWS

MLWS

500m
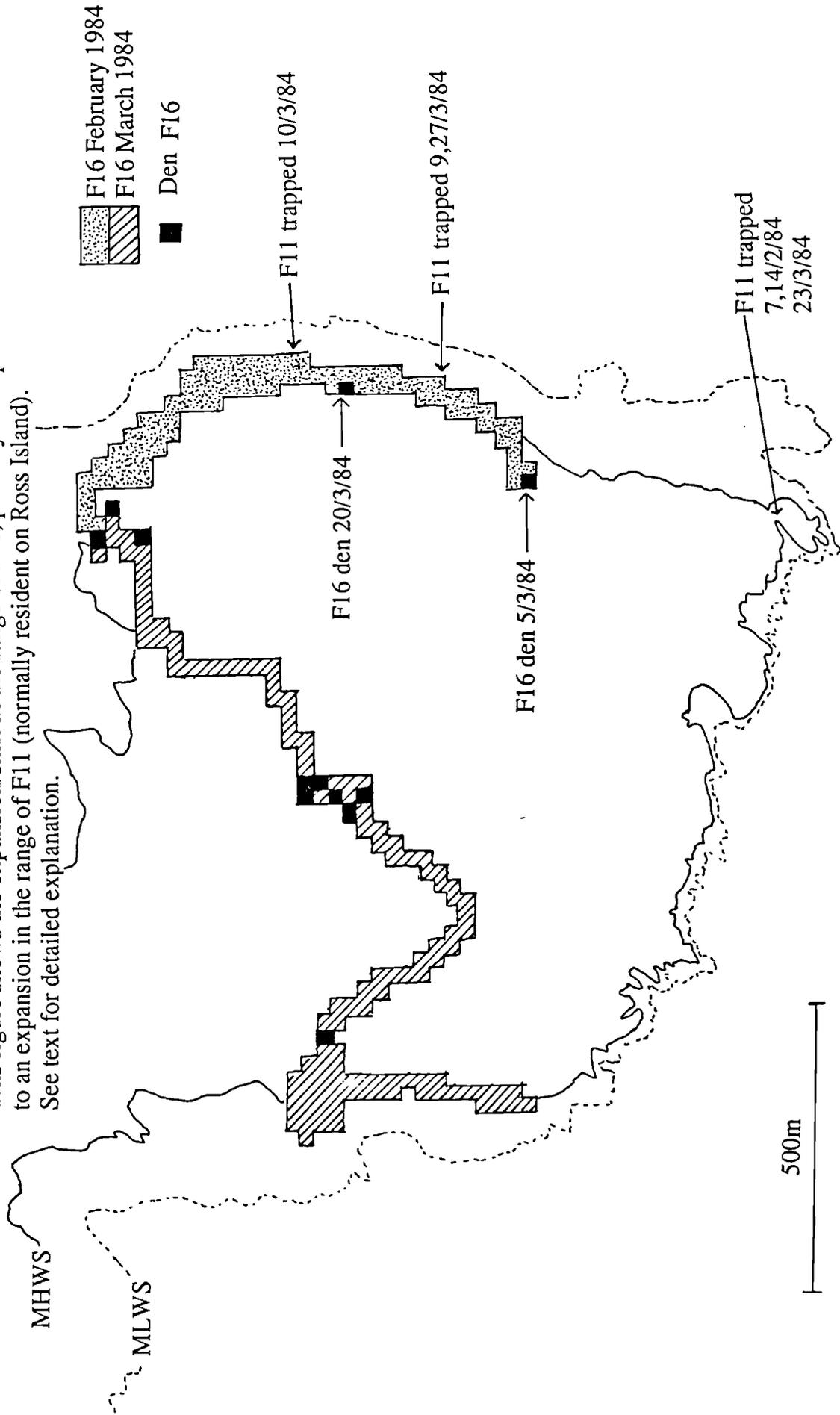
so she presumably could have been displacing F16 from her range. F11, living on Ross Island, did not have rabbit prey available and so this could have been the reason for her move to First Forestry on the mainland. Alternatively, F16 moved to Third Forestry and the Fauldbog, the best areas for rabbit prey and foraging on the shore respectively. F11's use of the mainland could have simply been a response to F16's move to a preferable, and probably unoccupied habitat.

The large length of coastline utilized by males during March, in conjunction with the large number of males trapped at that time (Chapter 2), suggested that intrasexual range overlap must have been occurring. As this period coincided with the rut, it will be discussed in a later section.

6.3.4 Intersexual Overlap

Assuming a mink's range includes all the habitat between its extreme movements along the coast, there is some evidence of intersexual range overlap for 29 of the 43 months of the study (67%). Unlike females, whose range is probably determined by food availability alone (Erlinge and Sandell, 1986), male ranges are probably influenced by the distribution of females, at least at certain times of the year. Thus, for those months between the descent of the testes and the end of the rut (December to April), apparent range overlap occurred in 19 of 20 months (95%). It occurred in only 10 of the 23 remaining months (43%).

The fact that a male and a female are present on the same stretch of coastline during one month does not necessarily indicate overlap as they may be using slightly different habitats along the coast or may be separated temporally. In order to assess intersexual overlap accurately, simultaneous tracking of both sexes in an area of overlap is essential. This was only rarely achieved, usually during the mating season. This fact by itself suggested that overlap was rare.

Intersexual range overlap was known to occur. In June, F10 passed within 1m of a den occupied by M3 (Figure 6.3a), though he was inactive at that time and no interaction was observed. He was also captured in a trap 7m from one of her breeding dens. However at that time, her radio-collar had stopped functioning so her true position was unknown. In July, M3 was observed stealing prey (a small mammal), from a breeding female (F9), on the Mull of Ross (see Figure 6.15), this time showing that both range overlap and interaction were occurring.

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In October 1981, when collars were simultaneously fitted on a male (M2) and female (F3), they occupied almost contiguous ranges (Figure 6.13a). In December however, when he was tracked in isolation, his range had expanded to include her October range as well, though she was resident within it, evidenced by trapping (Figure 6.13b). Trapping did indicate that F1 was found within M2's range in October, and both had been caught in the same trap (separated by two days) in September.

One interesting point emerged from the tracking of F9, a juvenile female, originally tracked around the cliffs and the Bents in September (Section 6.3.5). She disappeared from the trapping records in November when F10 had taken over her range. A new sub-adult male, M10, took up residence on the peninsula in December, and he was tracked in January. He apparently left the study area in February, and his range was taken over by F9. Similarly, as already discussed, F16 started using M20's range after he had (presumably) left the study area. This might suggest that females only occupy ranges not used by males. Alternatively, if F9 had been present whilst M10 was resident, it might suggest that the presence of a dominant male causes avoidance reactions by the female, reducing her chances of being trapped.

6.3.5 Stability of Home Ranges

Some of these ranges revealed by the grid-cell analysis appeared quite stable with time. Figure 6.14 shows the ranges of one male (M6) and one female mink (F21) in two consecutive months. During this time, ranges hardly differed in extent. Those differences present in 6.14b were probably an effect of limited tracking information as many radio-fixes are required to delimit that component of the range perpendicular to the coast. This factor will be expanded upon later. Another example of range stability was demonstrated by female F11, whose range was centred on Ross island for three years, where she raising three litters. Though centred on the island, trapping revealed that she made excursions to the mainland, especially during winter and autumn. Whenever a radio-collar was fitted to her, she always returned to the island by the following day.

Many ranges however appeared more dynamic in nature. The range shift of F16 has already been described (Figure 6.12). Figure 6.15 shows the range of female F9 in September 1981 and March 1982. During this time, her range had changed completely and she appears to have exchanged ranges to some extent with F10. The reasons for these changes were unknown. However, there were two occasions where mink died, and this caused a consequential increase in the range size of adjacent mink, or at least

Figure 6.13   The changing relationship between the home ranges of adult male M2
and sub-adult female F3, October 1981 - January 1982

Intersexual range overlap is indicated by captures of adult female F1 within the range of M2 in October
and from one den and two captures of F3 within M2's range between December and January.
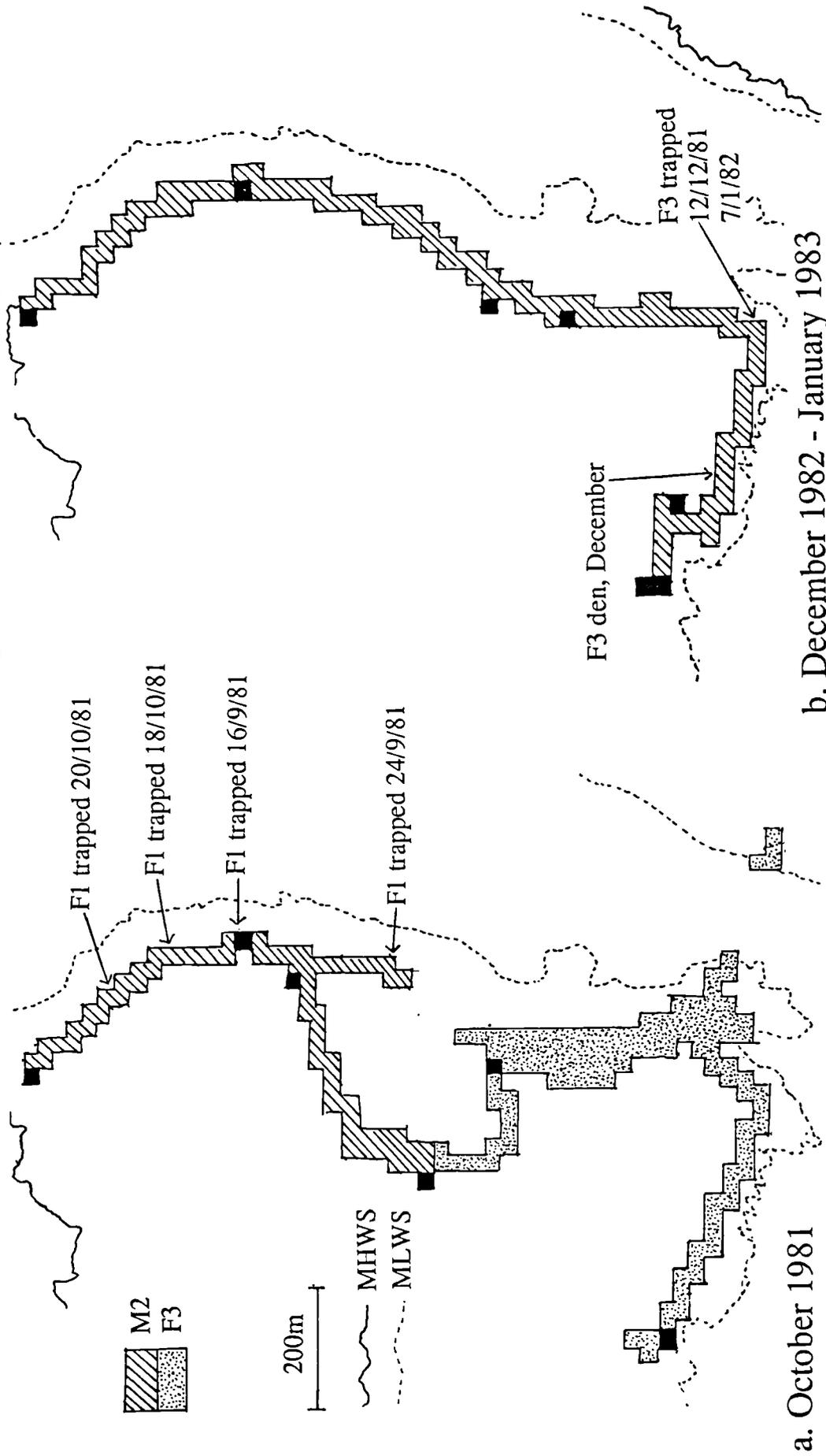
a. October 1981

b. December 1982 - January 1983

Figure 6.14   The home ranges of M6 and M21 in two consecutive
months, demonstrating stability in range extent with
with time

a. adult male M6 July-August 1982

July
August

• Dens

MHWS

MLWS

500m
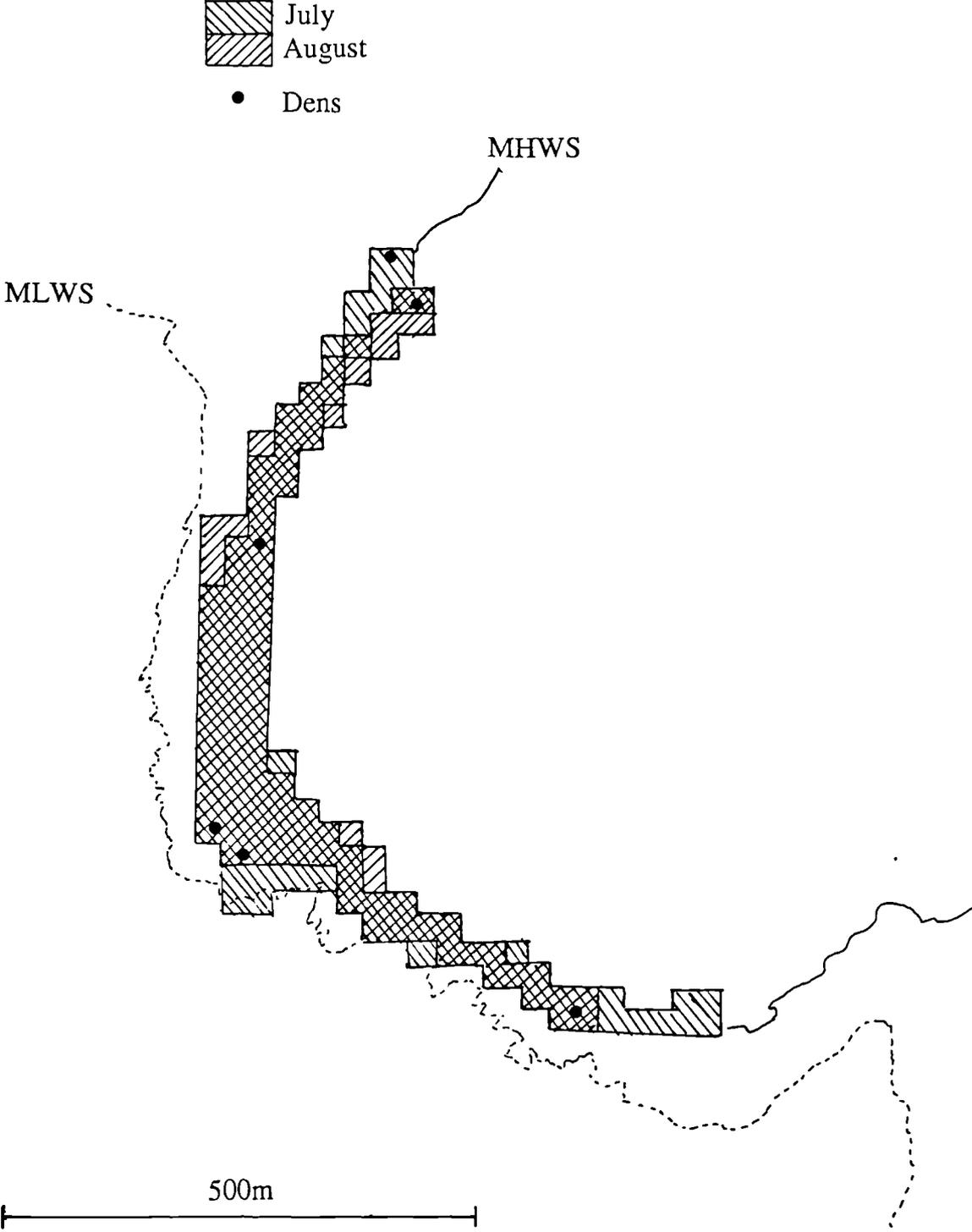
Figure 6.14 (cont.) b. Sub-adult female F21, February-March 1985

M33 den 26/3/85

In addition, this figure shows the locations where M33 was trapped and radio-tracked in March 1985.
These locations form an extension to his range revealed by radio-tracking in February 1985.

February
March

● Dens

200m

M33 trapped 16,27/3/85

M33's collar shed in m21's den 22/3/85

M33 trapped 26/3/85

Den used by M33 adjacent to that of M21 18/3/85

MHWS

MLWS
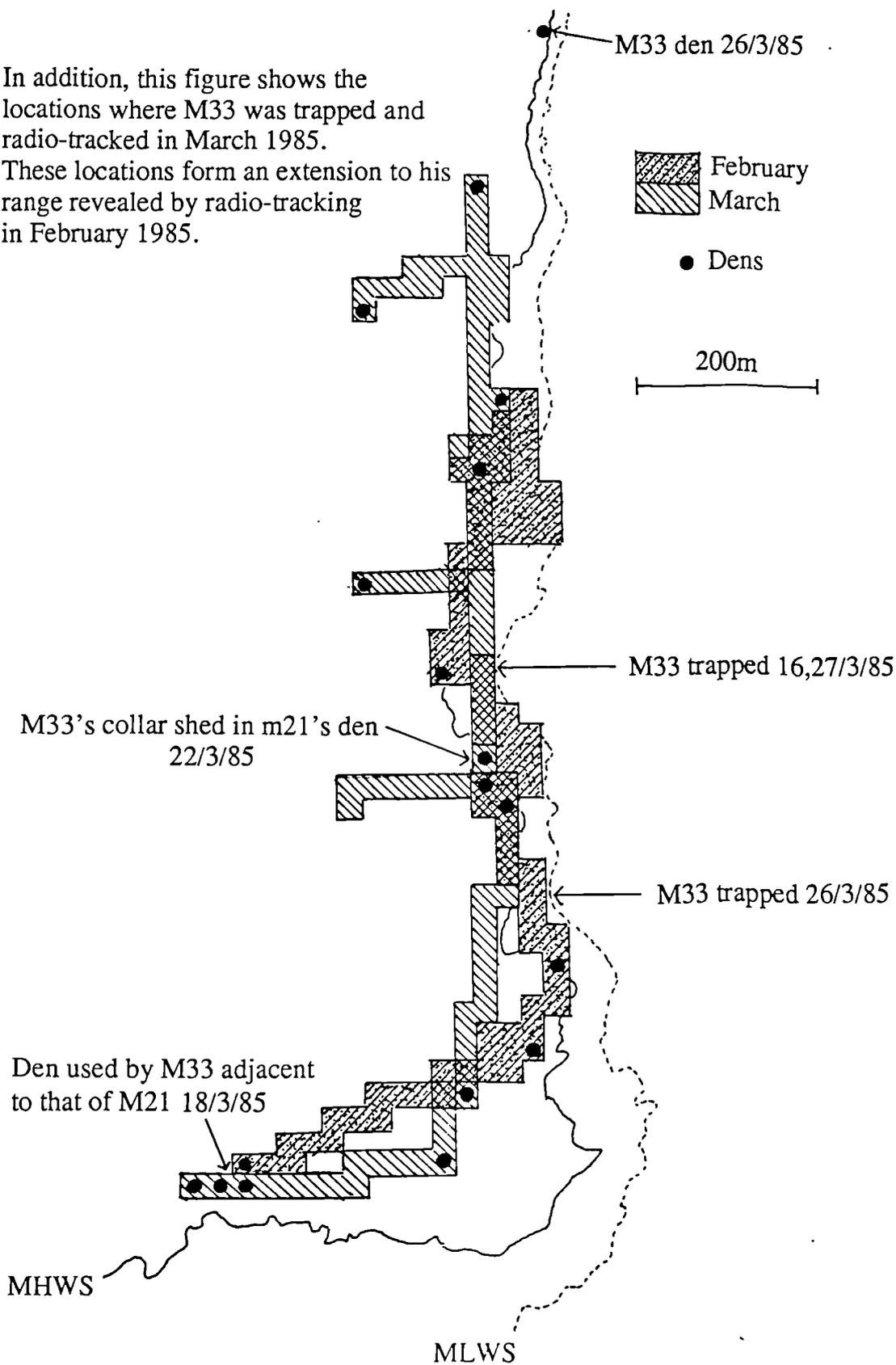
Figure 6.15   An example of home range translocation exhibited by a sub-adult female F9

Between September 1982 and July 1983, she appears to have moved range completely, twice.
It appeared that F9 swapped parts of her range with another sub-adult female, F10, between September and March.

F9 September 1982
F9 March 1983

Den

MHWS
MLWS

F10 trapped   15/9/82
10/10/82
5/11/82
+den January 83

Adult male M3 observed
stealing prey from F9
July 1983

Linear extent of home range
of F10, March 1983

1km
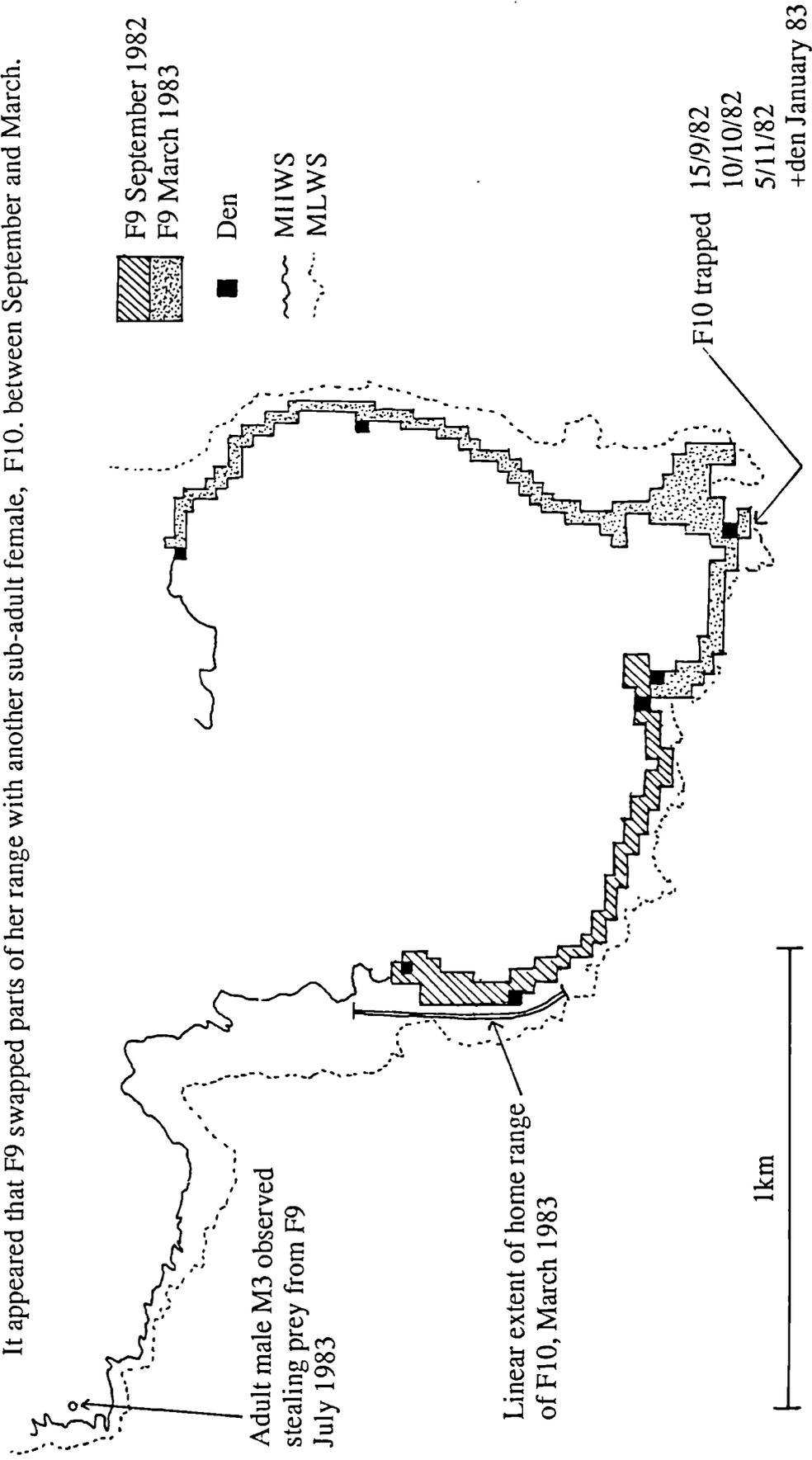
in the likelihood of their being trapped. The effects of the death of M18 have already been discussed (see Figure 6.11a-b). The effects of the death of M3 were less clear cut, because the previous status of his successor, M4, was unknown. The adult male M4 was thought to be living on Ross Island, because, like F11, he was usually trapped on Fox Craig. Also, when collared on a previous occasion, he swam back to the island the same day. M3 had occupied a range covering most of the peninsula and part of the Mull of Ross in April and May (Figure 6.16a). He was trapped within this range in June and August. After the death of M3 in early August (weight 1110g), M4 (weight 950g) was captured in all the traps on the east side of the peninsula. He was tracked in August within a range encompassing most of M3's up to The Bents (Figure 6.16b). Trapping indicated that a juvenile male (M20: weight 870g) had taken over much of the rest of M3's range in September, and this was confirmed by radio-tracking between October and January.

The system of home ranges of sub-adult females appeared to be in a state of flux between September and February each year. The switch in the ranges of F9 and F10 has already been mentioned. In September 1982, F10 was trapped at Fox Craig and in October, F11 was captured in the same trap and a collar fitted. On her release however, F10 was seen swimming from the island. She then ran up to the trap, and fought F11, who screaming submissively, swam over to the island. The following month, F10 was resident between The Fauldbog and Fox Craig, F11 was captured on the east side of the peninsula, and F9 was not trapped again until February (see Figure 6.15).

A similarly inexplicable situation arose the following year in November 1983. One female (F12), one of the kits of F6 from the north side of Ross Bay, was caught in a trap placed 400m north of Ross Bay and also at Fox Craig. Subsequent tracking showed she occupied a range in north of Ross Bay. Another juvenile female, (F15) was captured on the same night as F12 in another trap on Fox Craig, (five metres away). When fitted with a collar, she was found to occupy a range extending north from Fox Craig. A third female (F16) was captured between these two ranges. In December, neither F12 or F15 could be located. Adult F11 was trapped twice at Fox Craig, and another adult female was located round Ross Bay (F17). F17's place was taken over by sub-adult F18 in January and February, F18 eventually raising three kits to the North of Ross Bay. F16 remained resident on the peninsula at least until March (see Figure 6.12).

Male home range patterns or behaviour also changed throughout the year. Changes were noticed in December, for example, M2 showed a large expansion in range (Figure

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Figure 6.16 The change in social organization resulting from the death of a resident male

a. adult male M3, April 1983

Radio-tracking revealed a similar home range in May, and trapping results suggested that the range was maintained throughout the summer.

MHWS

MLWS

M3 died on 12/8/83

■ Den

500m
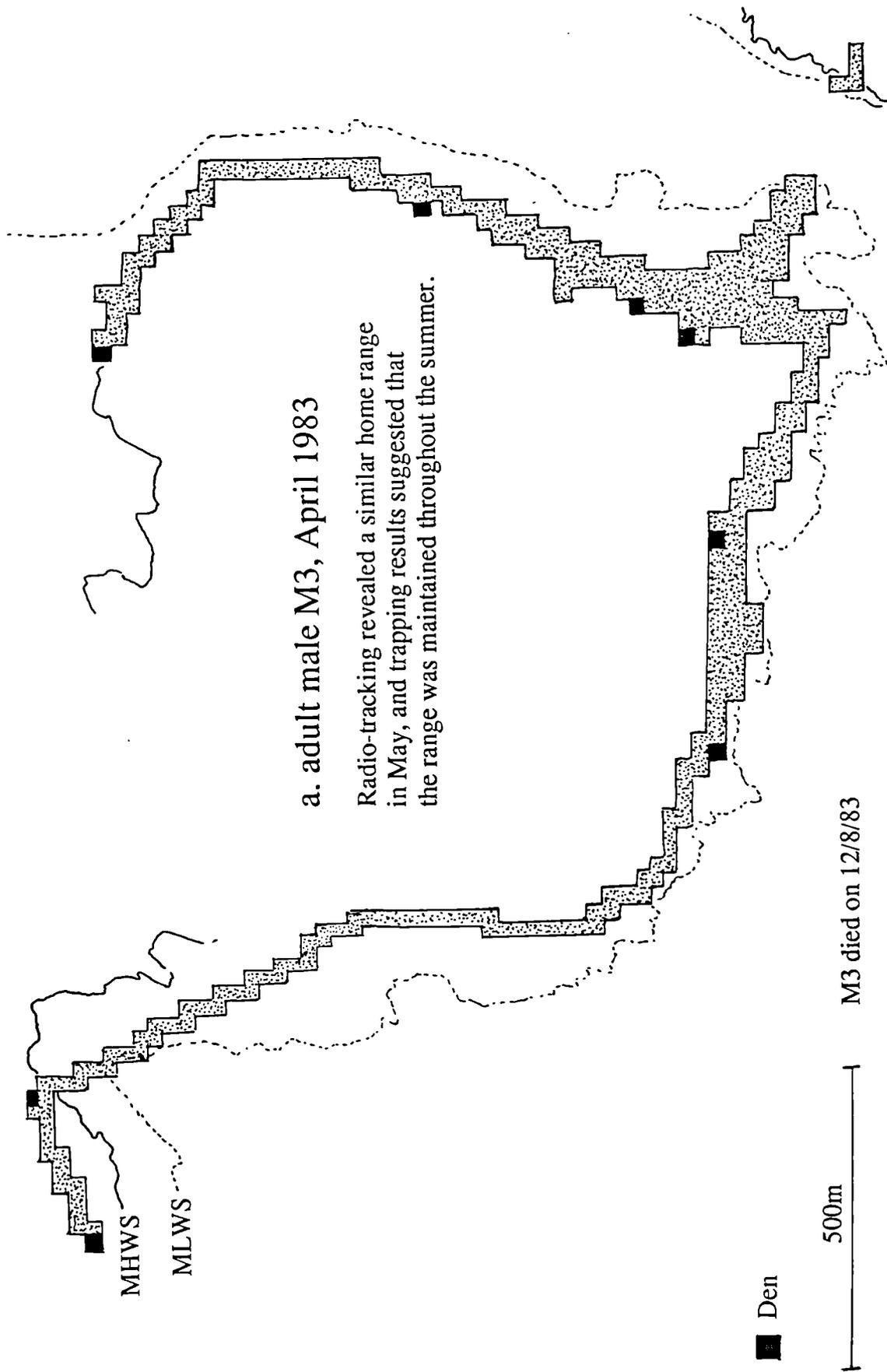
Figure 6.16 (cont.)
b. August 1983   (After the death of M3)

MHWS
MLWS

M4 August 1983
M20 November 1983

Den

500m

M4's range prior to August was unknown, but most likely Ross Island.

Juvenile male M20 was first captured in September and took up residence immediately. (see text for details)
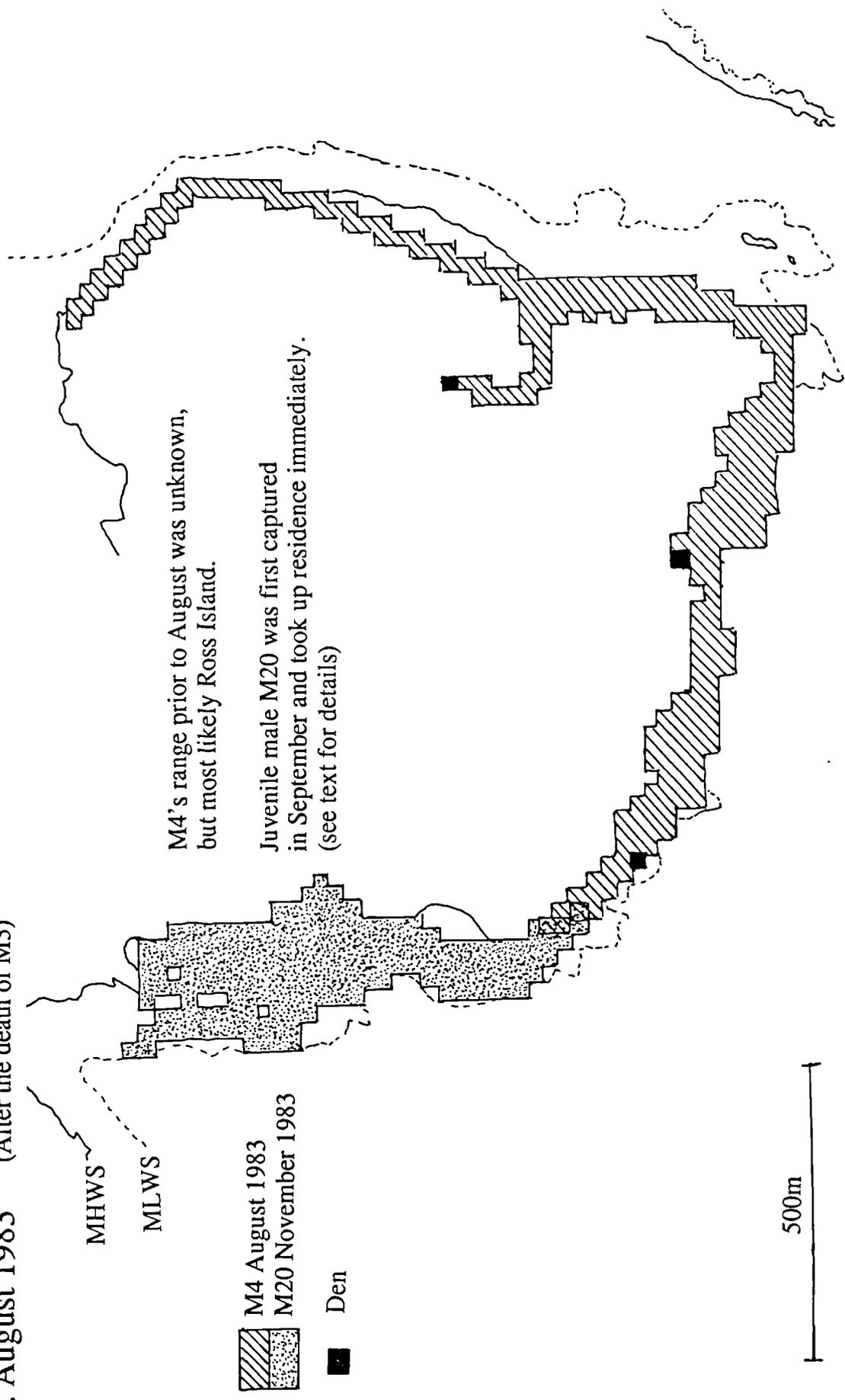
6.13), M4, presumed resident on the island (above), started to be trapped on the peninsula (last previous capture in May), similarly M33 (Figure 6.11c). M31 was captured twice within the range of M32 (see Figure 6.23) These changes corresponded temporally with the descent of the testes. The earliest record of palpable descended testes was on 6th December. Over all years, 70% of males had detectable testes by 20th December, and all males had by January. Testes continued to increase in size to a maximum by late February/early March (Figure 6.17). They became flaccid by the end of March, or in early April, and then regressed markedly during April.

Apparent range incursions in December did not usually lead to the displacement of resident individuals. In late January however, the resident male population started to change. In both 1983 and 1984, the only sub-adult resident male present within the study area, left. In 1983, trapping revealed that an adult male (M4: weight 1170g), started to encroach on the range of the then resident sub-adult (M10: 970g), who subsequently left. The following winter, the relationship between the adults and one sub-adult was not as straightforward. Between October and November, the sub-adult male M20 (weight 830g), lived within a well defined range on the Fauldbog, using the barn as its main den. The same was true until December (M20: 880g), when he was trapped well outside his normal range on the east side of the peninsula (Figure 6.18). This was within the range of adult male M4 (M4: 1030g). In January, a large adult male (M7: 1250g) was trapped within M20's range, and M20 expanded his range along the cliffs into that of M4, made extensive use of inlang rabbit burrows, and spent five days in a rabbit burrow well outside his old range, again visiting the range of M4. After a short return to the Fauldbog, he left the study area completely on the 29th, and was never located again. By early February, two adult males (M4: 1130g, and M15: 1250g), were trapped within M20's range (Figure 6.18).

Between the end of January and in early February from 1983 and 1985, four new sub-adult males were captured in the study area, adding further evidence for sub-adults leaving their ranges at this time. Two adults not normally resident within the study area were also captured in January and February 1984 (M7 and M15 respectively). These had been captured previously, and were believed to be normally resident outside the main study area and had presumably expanded their ranges.

In 1982, there were no sub-adult males resident in the study area. In 1985 the study area was dominated by three resident sub-adult males, none of which left the study area in January or February, though home range expansion did occur (e.g., Figure 6.11c-d).
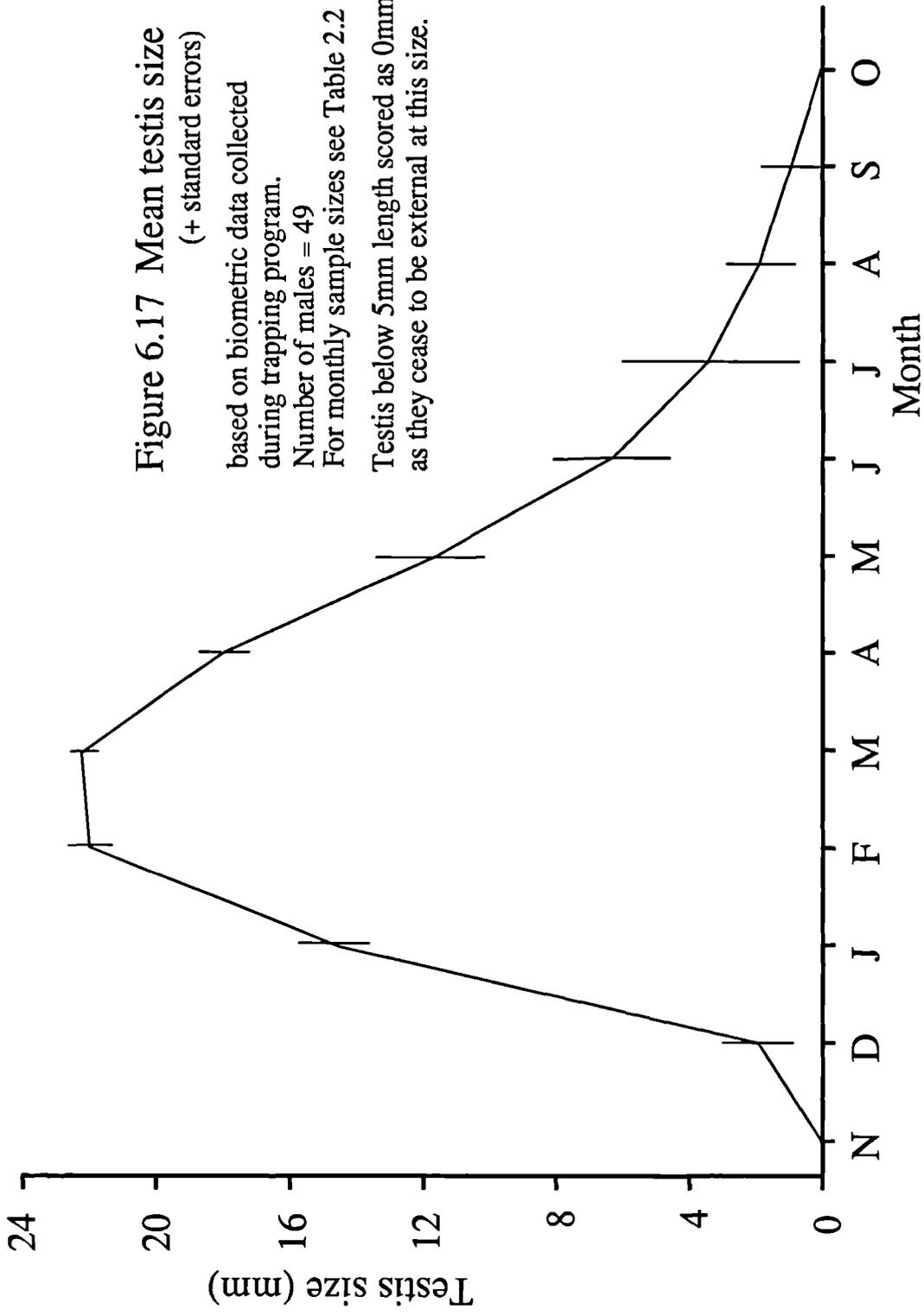
Figure 6.17 Mean testis size
(+ standard errors)

based on biometric data collected
during trapping program.
Number of males = 49
For monthly sample sizes see Table 2.2

Testis below 5mm length scored as 0mm
as they cease to be external at this size.

Figure 6.18 The changes in home range preceding the departure of M20

Adult male M7 was trapped within M20's range.
M20 expanded his range relative to November.
He was located twice within the presumed range of M4.
M4's range was probably similar to that shown in Figure 6.16b.

M20 trapped 19/12/83

M20's Betalight recovered from barn

M20 den 22–25/1/84

M4 trapped 16/2/84

M7 trapped 6/1/84
M15 trapped 7/2/84

M4 trapped 15/2/84

MHWS
MLWS

M20 November 1982
M20 January 1983
M20 dens January

500m

6.3.6 Reproductive behaviour

Although testes descended in December, it was not until mid-February that mating, usually determined by the presence of a mating scar on a female's neck, was first observed (Table 6.1).

Table 6.1 The date at which first mating was shown or suspected based on different types of evidence. The data are from all the years of the study.

February	Year	Indiv	Evidence
8th	1982	F2	Fresh mating scar. Vulva everted
9th	1982	F3	Fresh mating scar. Vulva everted
11th	1984	F19	M15 attempts mating. Success uncertain
14th	1983	F9	Male noises (chuckling) coming from inside female den. Female also present
14th	1984	F11	Fresh mating scar
14th	1984	F16	Fresh mating scar

At about this time, some males started to occupy rocky dens above the shore that were more typical of females dens. Radio-tracking in March showed that those occupied by M15 in February, were in the range of, or used by, F19. At the beginning of March, she had a well developed mating wound suggesting that she had been mated a number of times. No female was trapped near the dens occupied by M33 in late February, but as many males were captured in three adjacent traps along the same stretch of coast in March and April, it suggested that there was a female present in the vicinity.

It was not until March that trapping records (Figures 2.3, 6.2) and activity budgets (Figure 4.2) suggested that major changes to the social system were occurring. Success in the trapping of males peaked in March (Chapter 2), there being a steady increase in success from mid-February until the last week of March, and a rapid decline thereafter (Figure 6.19). A simple measure of range overlap, based on the number of different males caught in a single trap within one month also peaked in March (Figure 6.10). Trapping records showed that many new males, both adult and sub-adult, were captured in March (Figure 6.2). During the two years in which trapping was continued for the whole of March, six new males were caught in 1984 on a 5 km trap-line, and eight on an 11 km trap-line in 1985. These males were caught from one to a maximum of nine times, and some were still being captured in the study area a month later. If the length of time an

Figure 6.19 Trapping success throughout the rut
data combined for all years of the study.
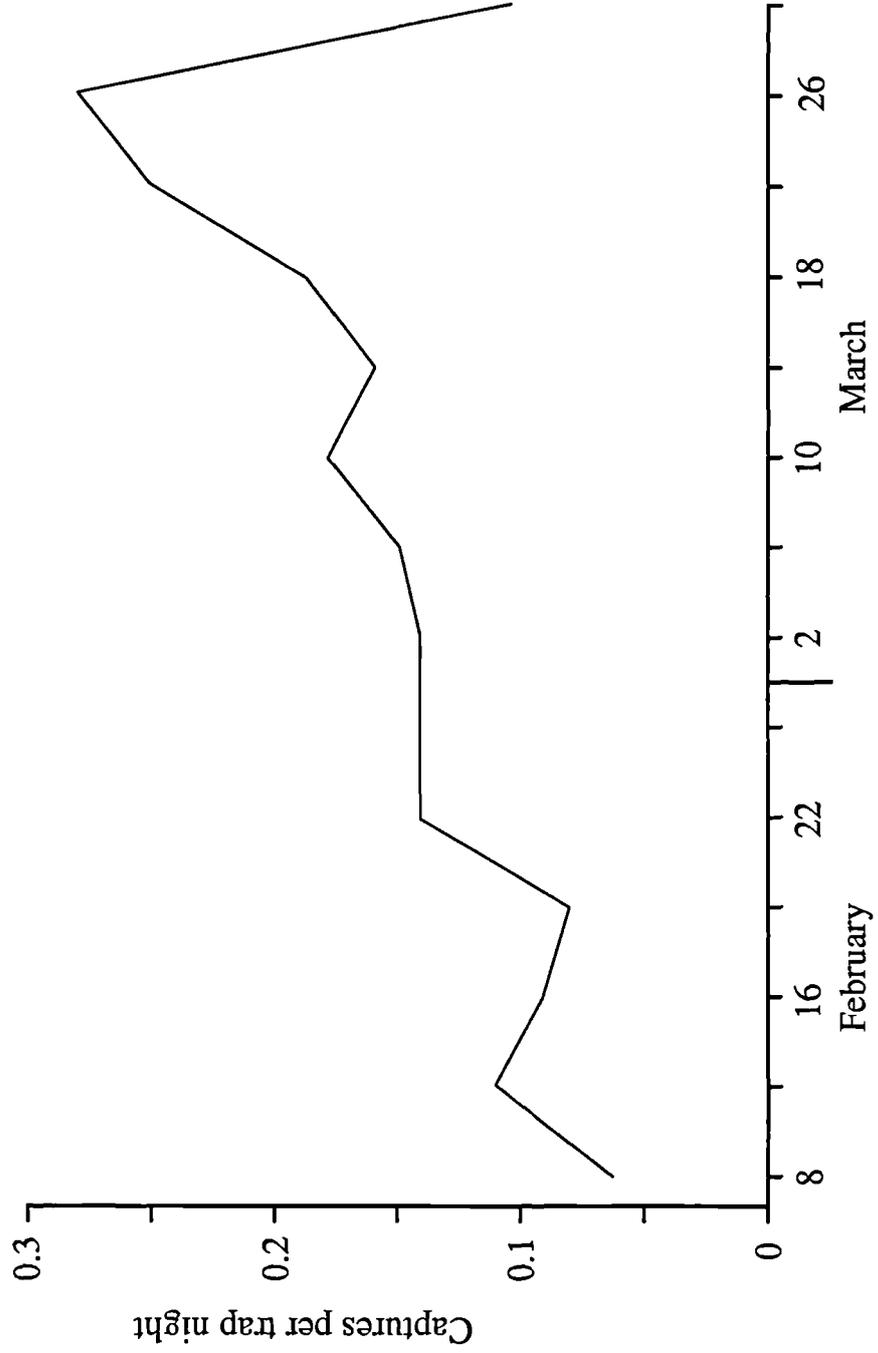
individual is associated with an area is determined from the time between first and last capture, then there was a peak in the number of individuals present on the study area at the end of March in both 1984 and 1985 (Figure 6.20).

Resident male mink did not leave the study area at the same time as the transient males arrived. Figure 6.21 represents the residency of a number of resident males over the winter period. Many of these males remained associated with their home area for the majority of the rut. Of eight males resident within, or adjacent to the study area at the beginning of March, two disappeared in the first week of March. The rest were associated with the study area until the end of March after which two remained resident, two were never recaptured, and two were still present when the study finished in April 1985.

Resident adult males usually traversed greater lengths of coastline (eg, M4, Figure 6.22). Sub-adult males were only resident in the absence of resident adult males (March 1985). Of these M33, a large sub-adult male, expanded his range considerably, encompassing the ranges of at least two and possibly four females (Figure 6.11&6.14b). One day he stayed in a den immediately adjacent to F21's den, possibly in the same rabbit warren, and later the same week, shed his collar in another of her dens. In contrast, M32, a small sub-adult male, expanded his range along the coast only slightly (Figure 6.23). He was also thought to have mated with F19 at the extreme edge of his range. M29, a large sub-adult, left his range at the beginning of March, but no females were trapped throughout his range at that time.

Trapping indicated that many other males were present or passing through the same stretch of coast during March. One complete night of tracking showed that an adult male (M7) travelled 8.6km in 8.7 hours, though he was only active for five of these (Figure 6.24). On his travels, submissive screaming was heard from two traps which contained juvenile males. He passed through 3 female ranges in this time but did not achieve a mating. He approached one female's den, but a fight ensued with another male which must have been in or close to the den. He left the den immediately, but approached it twice more that night, once withdrawing immediately, and later passing near it without stopping. This final time was after dawn when two other sub-adult males were seen in the vicinity of the den, M21 and M25.

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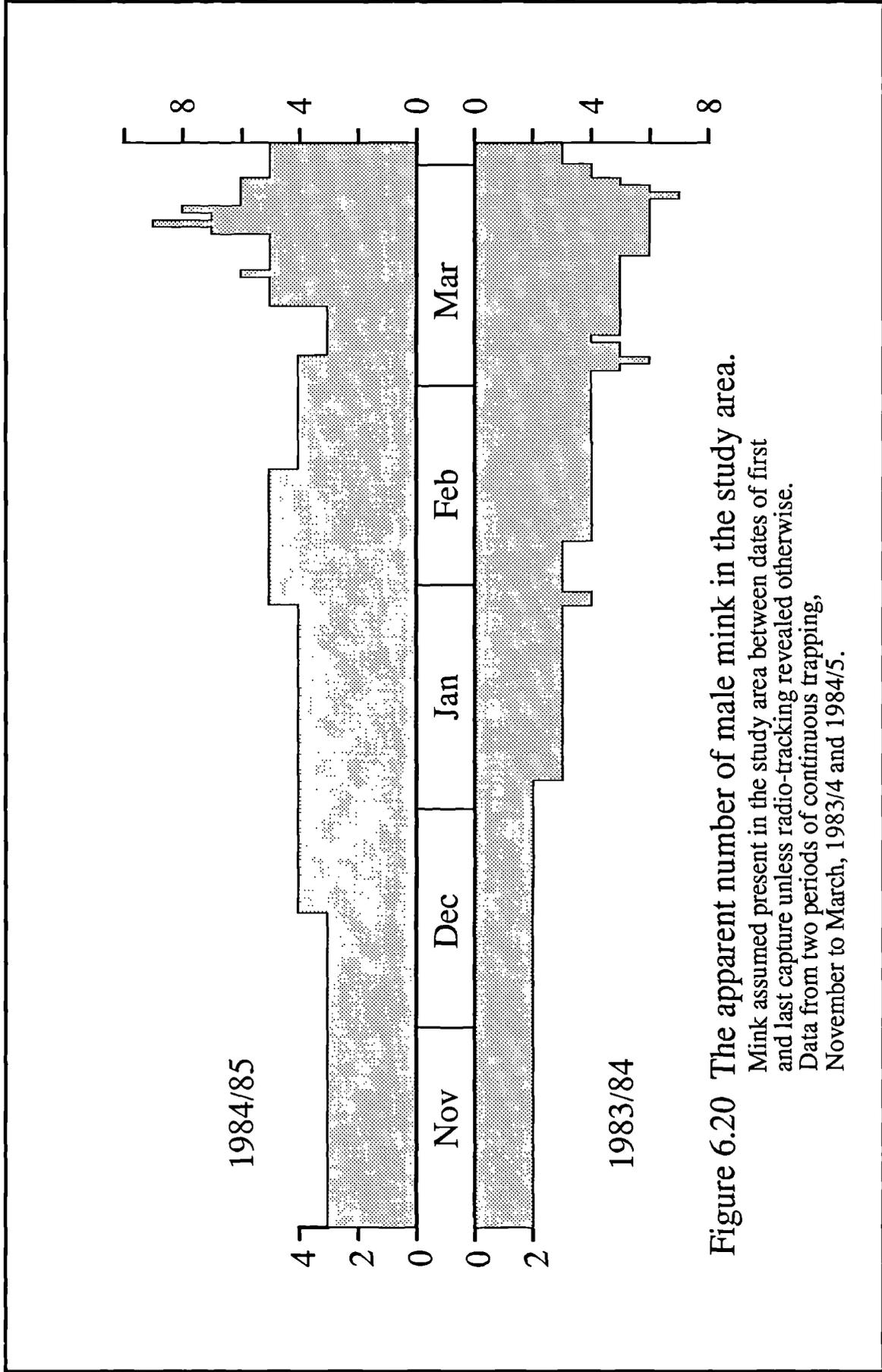
Figure 6.20 The apparent number of male mink in the study area.

Mink assumed present in the study area between dates of first
and last capture unless radio-tracking revealed otherwise.
Data from two periods of continuous trapping,
November to March, 1983/4 and 1984/5.

Figure 6.21   A graphic illustration of the duration of residency and dates of departure of adult and sub-adult male mink from the study area

Based on trapping and radio-tracking data.
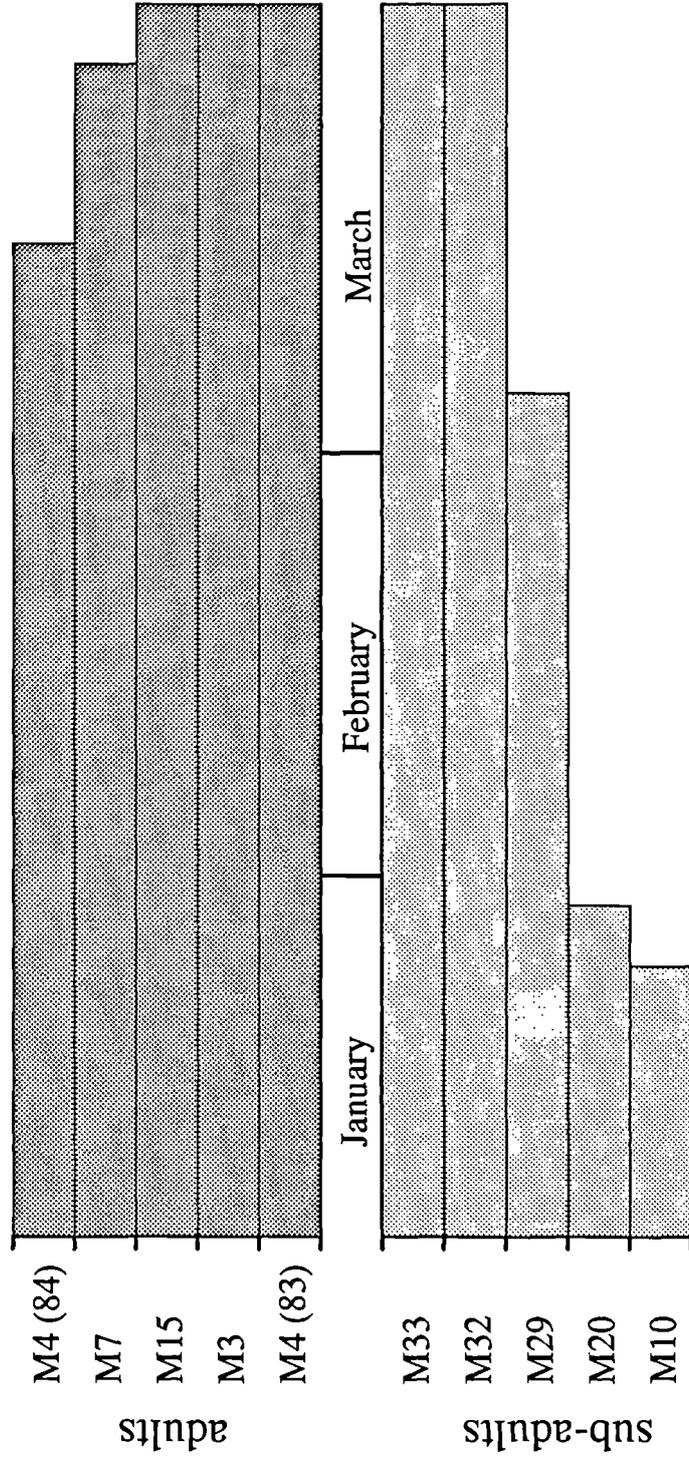
Figure 6.22 The expansion in the home range of adult M4
during the rut, but before he left the study area
completely

(compared to his range in August 1983)

M4 August 1983

Den August 1983

|—————————————————|
1km

MHWS
MLWS

den 8/3/84

den 7/3/84

trapped 16/2/84

trapped 6/3/84

trapped 15/2/84

7/3/84 pm

trapped 4,14/3/84

den 4/3/84
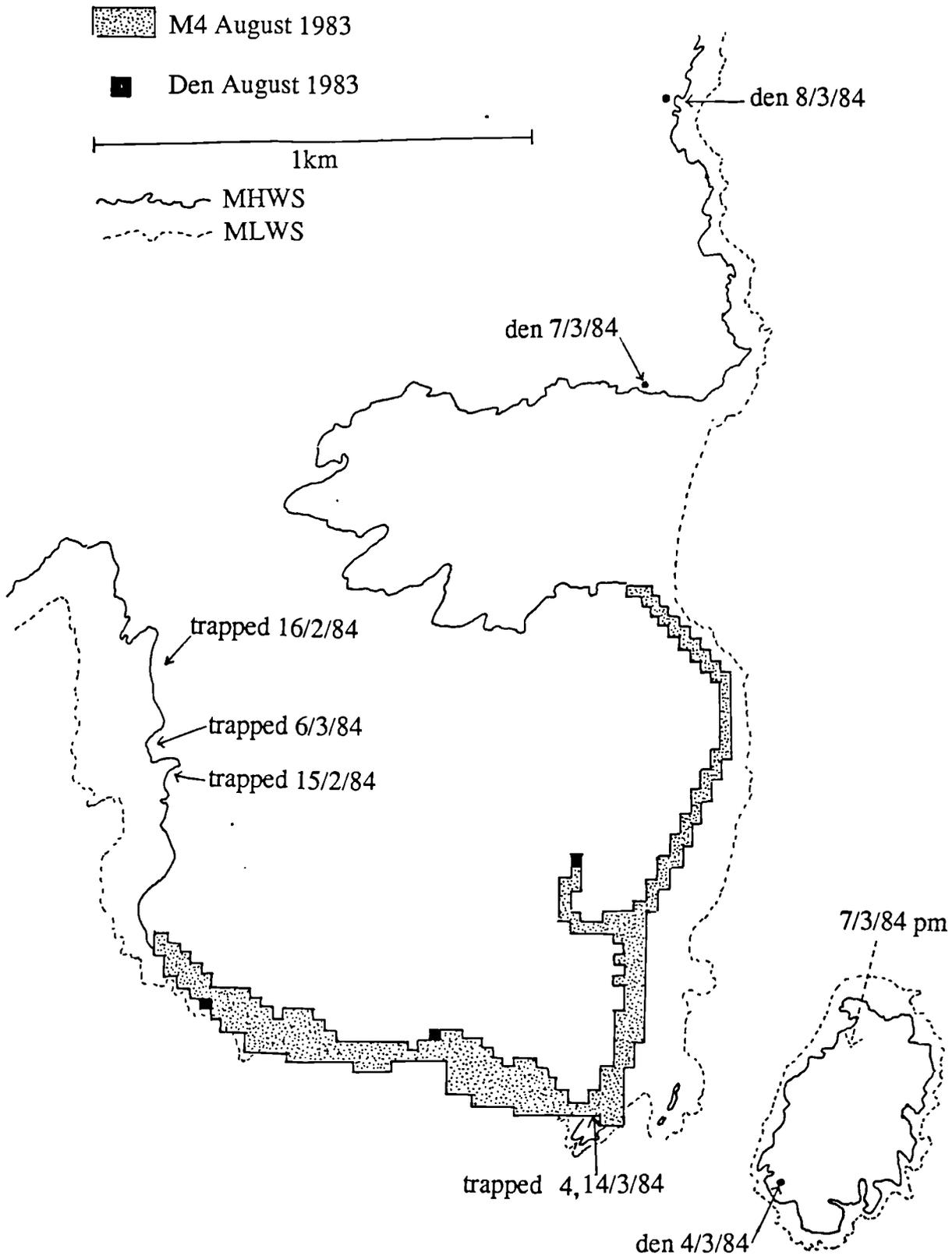
Figure 6.23 The small increase in the home range size of M32 between December 1984 and March 1985

M32 December 1984
M32 March 1985
F19 March 1985

M32. Dens, March 1985

MHWS
MLWS

M31 trapped, 18/12/84
M29 trapped, 25/1/85

M29 trapped 3/3/85

M32 mated with
F19 17/3/85

M31 trapped, 5,11/2/85

M31 trapped, 16/12/84

500m

MHWS
MLWS
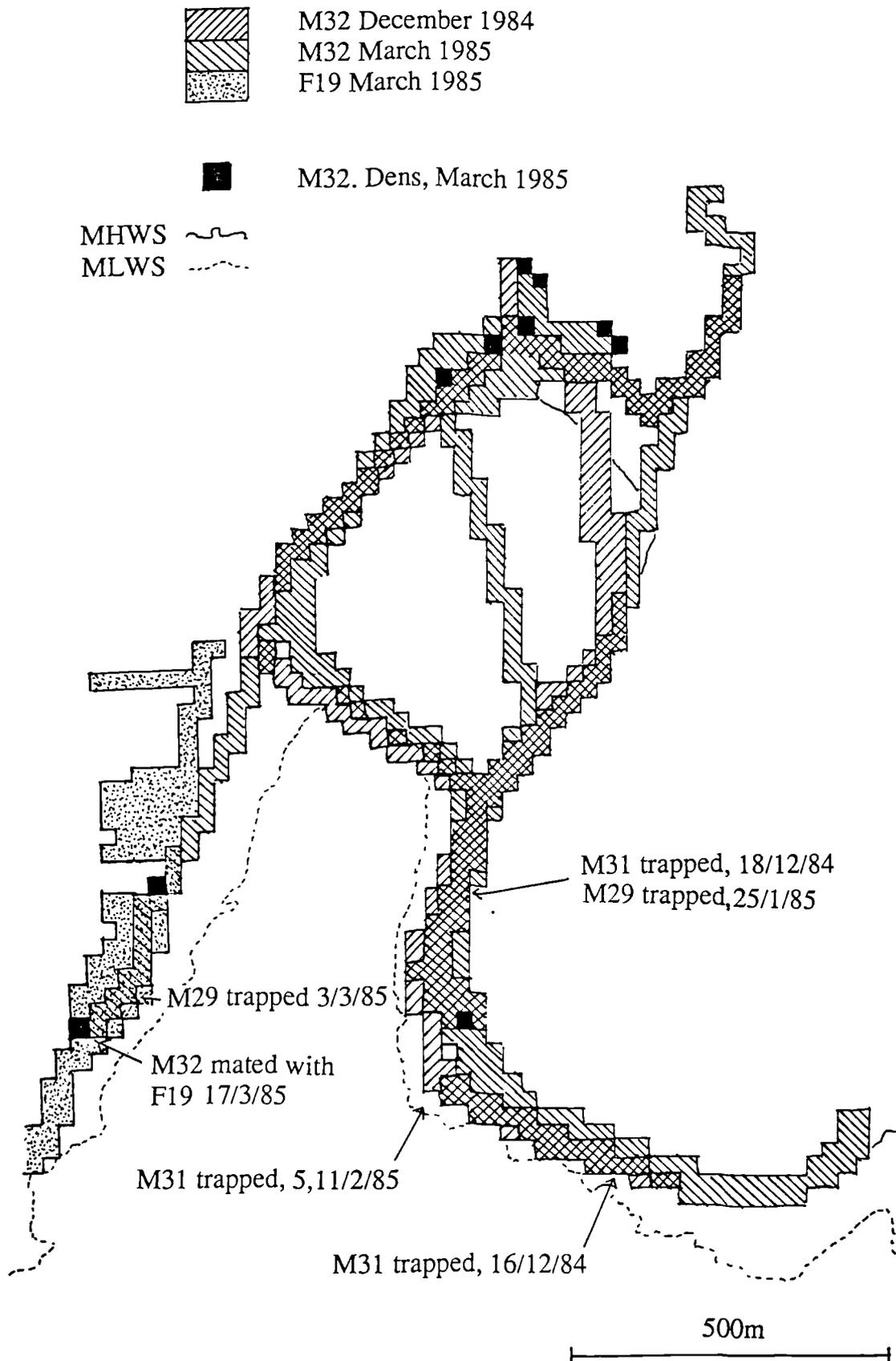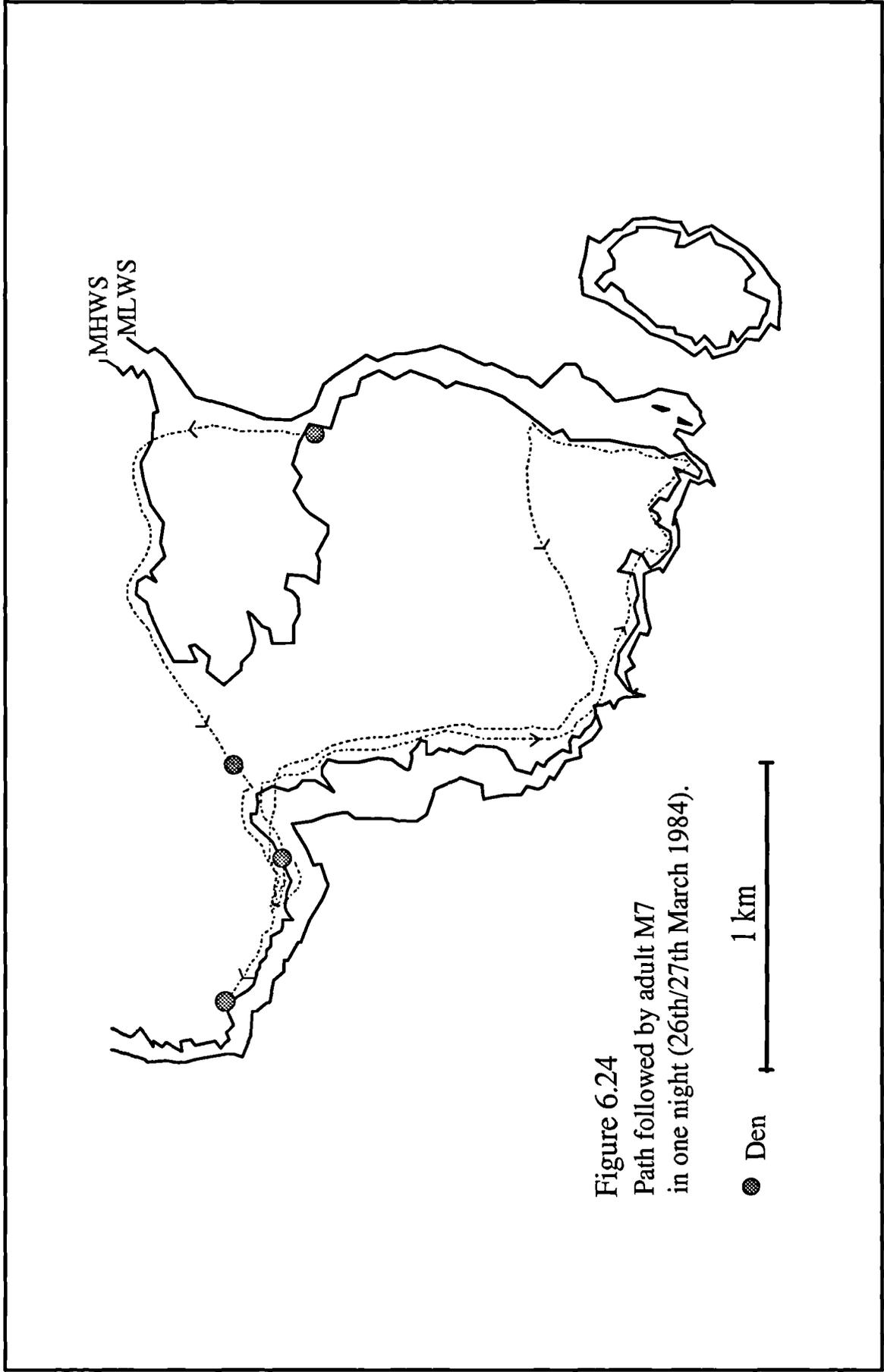
Figure 6.24
Path followed by adult M7
in one night (26th/27th March 1984).

● Den

1 km

6.3.7 Agonistic behaviour

Fighting between males, though not observed very often, was probably a common occurrence. After mating with F19 in March 1985, M32 (a sub-adult), left the mating den with her and was involved in four short fights with two sub-adult males, one of which kept returning to the vicinity. In the last of these fights, F19 was not present, having moved to a den further along the shore. Later that evening, whilst occupying a den close to the females post-mating den (F19 was foraging in woodland elsewhere), M32 was involved in another fight and was presumably beaten as he moved off at high speed back to his normal range, and was never trapped in F19's range again. Other males, trapped during the rut, often had scabs under the fur around the cheeks and nape of the neck. These were presumably the result of aggressive encounters with other males, and were first noticed between the 10th and the 16th March. They were common on most males by the end of March, and observed in greater numbers on larger adult males.

6.3.8 Changes in condition over the rut

Body weight data from early March and the end of March were available for seven male mink. All except one had lost weight during this period. The mean weight loss was 50.3 ± 17.94g (Paired $t=-3.03$, $df=6$, $p<0.05$), suggesting that male mink may have been operating at a negative energy balance at this time.

6.3.9 Male/female associations, mating and mate guarding

A female in heat attracted a number of males to her vicinity. Two examples of this have already been described. Further evidence comes from trapping. Traps located in the vicinity of a female den during March were always very successful. Four traps near a female den caught six mink a total of 10 times in 10 trap-nights in March 1983. These individuals included all four transient adults and the one transient sub-adult which were caught in the study area that March. In 1984, two traps near a female den caught five of the six transient males trapped in March. Traps in which females were caught in March were occasionally completely excavated by males trying to get them. On one occasion, a male tried to drag a trap containing a female back into her den which he was also using. Females did not always have males in attendance during the rut, perhaps suggesting that there were cycles in female receptivity.

Examples of males using female dens in February have already been described. This may have been guarding, simply waiting for the female to leave or return in order to

achieve matings, or resting after copulation. M7 shared one den with F19 in March 1984. He would emerge from the den at any sign of disturbance. When a trap containing another male was brought into the vicinity, (though not into sight of the den) M7 left the den completely, but on release, the other male ran away, no interaction occurred and M7 returned to the den. He was not present at the den the following day.

On another occasion, M7 met F16 whilst she was travelling through the rocks of the Fauldbog. A struggle ensued lasting 5 minutes, after which he ran off towards F19's range. He returned 40 minutes later just as she re-entered her den in the barn. Copulation ensued next to the barn for 13 minutes before he dragged her into the barn. Both remained in the barn, F16 returning to Third Forestry 11 hours later.

After mating, M32 and F19 left the den together, but the two separated, M32 fighting briefly with two other males. That evening however, both were tracked briefly out-of-den in the same vicinity, M32 settling in a den adjacent to the den she had used immediately after mating.

None of these associations lasted more than a day so making 'mate guarding' an unlikely cause. However, the den of F19 from which M7 had been repelled by another male, had 2 separate scat piles in it. This suggested that if M25 or another male had been sharing the den, it had been for some time (at least two days). Also, in March 1983, F10 was released from a trap near her den in which M3 was also found to be present. Whilst trying to capture him and remove his non-functioning collar, both F10 and a subadult male (M7) were trapped. M3 disturbed both traps, trying to drag F10's back into the den. When eventually caught, on release he tried to mate her in the open. M3 was present in F10's den for at least 2 days, though the situation was unnatural because of trapping activities.

6.3.10 The behaviour of transient males

Other studies have reported the capture of many new males in March. These males have been termed transients (Birks, 1981) as they pass through the area during the one month only. Resident males have also been reported as leaving the study area (Chanin, 1976; Birks, 1981) thus assuming transient status. Because of the absence of tracking data on transients, their behaviour can only be speculated on, based on trapping records. In 1984 and 1985 extensive trapping was carried out from the beginning to the end of

Table 6.2 The duration of stay of adult and sub-adult mink that entered the study area in March of 1984 and 1985, based on the dates of first and last capture. Values represent the number of each age group in the specified duration class, longer durations not being inclusive of smaller ones.

Residency (days)	adults	sub-adults
1	3	3
≤ 7	1	0
≤ 14	0	1
> 14	1	5

the rut. Table 6.2 shows the presumed length of stay of new adult and sub-adult males throughout these two mating seasons.

Adult males tended to be caught only once. The exception (M37) was always recaptured in one of four adjacent traps, in an area where a trap-shy female was thought to be resident. Almost half the sub-adult males captured remained in the study area until the end of the rut, and were captured a mean of 6.0 ± 1.12 times. The sub-adult male (M25) present for just over one week was particularly large (1500g), and thought to be sharing a den with an oestrus female. Transient adults and sub-adults were observed to associate with, or remain in the vicinity of oestrus females, and may have achieved matings.

Certain individuals were captured throughout the whole study area. M36, a small (990g) sub-adult, was usually trapped round the West side of Brighouse Bay, where he settled after the rut and was still resident 17 months later. He probably had sub-dominant status as he was defeated by M32 in a fight near an oestrus female. Though trapping revealed his range extended east as far as the Bents, this could have been an artefact caused by one trip outside his normal range during which he was caught at most intervening traps. On the other hand, another transient sub-adult male, M24, was captured in traps throughout the whole study area in no particular pattern during three weeks in March, suggesting that he was temporarily resident in the area.

The full extent of the movements of transients is unknown, but if the males had come from outside the study area, the numbers involved suggest that they could have come from the coast 6–8km either side of the study area. This is within one evening's travel by a male mink. Thus, the mink may not have been resident between first and last capture, but simply making short trips into the study area only to be trapped and not able to return.

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The fate of those residents that left the present study area was uncertain. Attempts were made to locate them using radio-tracking, but these were rarely successful. On three occasions, where collared mink had 'disappeared' during March, the mink returned, on two occasions with functioning radio-collars. Both these mink were one-time residents of Ross Island, and so it was uncertain whether they had left the study area or were present all along.

6.3.11 Observations during gestation, parturition, lactation and weaning

A dramatic fall in success at trapping male mink indicated that the rut usually ended at the beginning of April, although in 1985 there were still males roaming in mid-April. The wounds on the neck of F19 were healing on 4th April, 1984 and in the following season her large mating wound had healed over by the 12th April. There was no evidence of a previously bad mating wound on the neck of F10 by the 20th April, 1983. By this time she had increased in weight, and foetuses could be felt in her uterus. No females were trapped between 22nd April and 13th July in any year of the study. All the following details of female and kit behaviour were derived from radio-tracking and direct observation of three females (F10, May-August 1983; F11, July-August 1983 and 1984; F19, May-June 1984).

A change in den, and a very distinct change in activity levels, marked the probable date of parturition for one female as 3rd May. One other female was also thought to have given birth in early May. This corresponds closely with dates of birth of kits on mink farms at this latitude. Changes in the foraging activity and den use following parturition have already been reported in Chapters 4–5.

The first time a kit was observed out of its den alone, was on 23rd June. The majority of observations of kit behaviour were carried out on the young of F11 which brought up litters in three consecutive years on Ross Island. These kits were making short trips to the shore with their mother in early July. On July 8th, the mother was observed to drag a herring gull carcass to where they were sheltering under a rock, before moving off to another carcass to feed herself. This suggested that they were weaned at this time. Four or five gull carcasses were found in two of the breeding dens, often unconsumed. On the same day, the kits were seen playing, without their mother, in the rocks and scrub not far from the den. Mother and kits were still denning together, but the mother made solitary foraging trips around the island at night. By the 26th July, the kits were observed out alone (or in pairs) on the shore, swimming in open water and making short duration

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dives, usually lasting 2–3 seconds (5 seconds maximum). At this time, although mother and kits were occupying the same area of scrub, it appeared that they were using slightly different areas. One kit was ejected violently when it visited the female's resting place, after which the female moved to a different part of the island, suggesting that intolerance was developing. The female still appeared to be foraging alone at night, though one diurnal trip was observed where the female escorted the kits across the island.

In August the kits seemed to become completely independent of their mother. The heaviest of the kits from the 1984 Ross Island litter, M28, was caught on the mainland on 10th August (weight 1010g). A radio-collar was attached and the kit left the study area on the 15th/16th. One of the other kits from that litter, (M29), remained on the island during August, eventually taking up residence on the mainland in September (Figure 6.11a-b). None of the kits was denning with the female from the 10th August onwards. A similar pattern had been observed the previous year. Kits were present in the mother's range but she was denning alone. By the 8th August, the female was acting very aggressively towards her kits. One female kit was seen loosely in attendance whereupon she was viciously attacked for three minutes by her mother despite submissive screaming. This behaviour was only observed once, but there were two other occasions on the 10th and 11th August when aggressive interactions were heard near the den of an adult female (F6) on the mainland.

There seems to be a high level of variability, between different families of mink, in the timing of the various events in the behavioural development of the kits. Large variations in the age of dispersal of kits within a litter were apparent (above), and large variations in the weights of males and females caught in August (males, 690–1150g; females, 410–685g), suggest that appreciable variation was present between the litters of different females.

The number of kits in a litter was only known with a reasonable degree of certainty for 3 litters. Observations suggested that F11 had 3 kits in 1983. She also had three enlarged nipples. In 1984, 4 kits were observed and trapped, although she still had only three enlarged nipples. All her kits were well developed at this time. In April 1983, palpation of the abdomen of F10 revealed at least four foetuses. In May, at least two, probably three kits were heard screaming when F10 returned to the breeding den with food. By June however, only one kit was in evidence at her den, hence some post-natal mortality must have occurred. At the beginning of August, she had one large nipple, and

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two very small, regressed ones. This small amount of data suggest that nipple counts are at least a reasonable measure of the number of kits surviving to independence. When trapping had been extensive near a breeding den, litters of 4 (5 nipples on mother), and 2 (2 nipples) were recorded. The mean number of kits raised to independence, suggested by nipple counts for all females captured in August, was 2.9 ± 0.14 (range 2–5).

6.4 Discussion

6.4.1 Home range organization

Detailed simultaneous radio-tracking of contiguous individuals is a prerequisite to establish the existence of territories (Gerell, 1969), and this level of telemetering was not achieved. However, telemetric data on males in adjacent ranges, and a mixture of telemetry and trapping of females did suggest that a series of intrasexually distinct ranges did exist. The general exclusivity of these ranges, and the speed with which the coastal-linear component of a range was delineated, suggested that the range was patrolled and defended as a territory.

Although some minks' ranges appeared quite stable over time, the organization of home ranges was generally unstable, range translocations, expansions and contractions occurring throughout the year. In addition, the population appeared quite unstable, resulting in apparent range overlap, particularly in the autumn for females and March for males. However, population change and range overlap were generally apparent from trapping data, and misinterpretation sof such data could lead to many false conclusions.

The biological characteristics of a population prevent random sampling in live-trapping studies (Kikkawa, 1964). Differential trappability has been demonstrated mainly for small mammals. Baiting is known to affect trapping success on shrews *Sorex* spp. (Crowcroft, 1957), and this can cause seasonal effects in trapping success, individuals being more likely to enter traps when food is scarce (Tanton, 1965). Individual effects include trap-proneness and trap-shyness. A correlation has been demonstrated between these effects and social dominance, both disappearing from female trapping records if males are not present (Crowcroft and Jeffers, 1961; Kikkawa, 1964). In mink, Gerell (1971) found seasonal differences in trapping success, and that juveniles were more likely to be recaptured than adults.

In the present study, trapping success varied both with the sex and month (Chapter 2), but these factors could be explained with reference to mink activity levels and life

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cycle. Major problems were more likely to be caused by instinctive and learned trap shyness, and temporal, spatial or dominance related variation in trap avoidance. If, for example, an individual only entered traps in its own territory, not when moving through another mink's defended area, range overlap, measured by trapping, would be underestimated. Similarly, a female mink's sub-dominant status in a male range might reduce the likelihood of her being trapped, decreasing apparent overlap, and range size. For this reason, only radio-tracked mink were included in the sample used for the home range size analysis. Trapping information was used to supplement tracking information because of the generally low amounts of data collected for each mink. The inclusion of trapping data did not appreciably affect sex differences or seasonal trends.

If a mink became trap-shy over time, it would probably lead to the mistaken conclusion that an individual had left the study area or had died. Instinctive trap shyness would result in apparent gaps in the system of ranges, and would bias sex and age ratio estimates if female and juvenile individuals were more prone to it, as was suggested by small mammal studies (Crowcroft and Jeffers, 1961). Baiting traps may have caused individuals to make unusual movements, however bait was rarely eaten in traps. Trapping also suffers from the fact that it simply indicated that an individual was present at the trap-site during some period, and therefore it cannot be used to work out temporo-spatial interactions between individuals. However this was not too important, as radio-tracking effort was also insufficient to look at this type of behavioural interaction. The uncertainties involved in the interpretation of trapping results meant that where possible, only radio-tracking evidence is used, and if conclusions do rely on trapping data, the effects of interpretational errors have been discussed.

Seasonal changes in range size probably had simple explanations. Raising kits limited the movements of a breeding female, as she could not easily move the kits throughout the whole length of her range. Her short foraging bouts limited the distance she could move from her den, and thus her apparent range size. A female's range expanded as the kits grew and became more mobile, or alternatively as she had to travel progressively further in search of food as demands increased. The increase in male range size during the rut was expected. Males were polygynous and as females were widely dispersed along the coast, the only way to increase their mating success would be to range further afield.

The appearance of new males in the study area during February and March, the disapearance of some residents and the extensive overlap evidenced by trapping, suggested

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that the territorial system had broken down. There were, however, many examples of resident males with expanded ranges, consorting with resident females throughout the rut. If the residents in the study area expanded their ranges, some leaving, this was probably duplicated in adjacent areas, and one would expect an influx of new individuals. This suggested that the influx of new males was real, and not due to, for example, previously untrappable resident mink changing their behaviour and being caught in the traps. They were obviously attempting to mate, and at least one may even have succeeded, but in general, all matings observed or suspected, were by known adult, or resident sub-adult male mink. It must be admitted, however, that only three matings were actually observed to justify this conclusion.

There were no significant seasonal changes in range size other than those associated with reproductive events, suggesting that range size did not change with food availability. However, female F11, normally based on Ross Island, was frequently trapped on the mainland in July-August and late winter, the times of highest demand and and lowest prey availability respectively, which might suggest otherwise. However, if sea bird carrion on the island did provide sufficient food for mother and young, another reason must be sought for her use of the mainland during the summer. Increased male home range size following the death of a neighbour suggests that male range is socially determined to some extent. This of course assumes that the males who expanded their ranges, were not originally using/sharing the expanded range and not being trapped within it, as the males were not telemetered until after they had become the major resident. Males certainly seem to have ranges larger than strictly necessary for food requirements alone. Male M29 continued to increase in weight despite a decrease in his range size due to the incursion of M33. However, data from activity budgets gave no indication that food was ever particularly scarce in the study area.

Data were not available to suggest that females occupied larger ranges than strictly necessary, although occasionally a female was radio-tracked along an exceptionally long stretch of coast (for example F10, 3790m in August 1983). As maintenance of a larger range or territory than necessary presumably entails some cost, there must also be some compensatory benefit. A larger range may benefit a male by overlapping with more females, but this argues against a mating system in which a male vacates his normal range in search of mating opportunities (Chanin, 1976; Birks, 1981), unless those females within the range have been mated before the male left, or if familiarity with the

females, their dens and habits led to a mating advantage during the rut. However, radio-tracking evidence of extensive range overlap was lacking, (although the wider coverage of the study area as a whole attained by trapping suggested both sexes sometimes used the same lengths of coast). Apart from February and March, when mating obviously requires overlap, whether by lack of foresight, or real effect, no female was radio-tracked within the range of a collared male, though overlap at range boundaries was occasionally recorded. Information about intersexual overlap is very important, as niche difference theories suggested that it was the reduction in competition for food, between the sexes, in overlapping home ranges, that provided the main selective pressure leading to the development of dimorphism (Chapter 1).

Virtually all the details about the social system in this chapter are in accord with other tracking and trapping studies of mink in riparian habitats. Intrasexually distinct ranges have been reported by Gerell (1971), Chanin (1976), and Birks (1981). Despite movements inland when food is scarce (Linn and Birks, 1981), mink have been shown to move along the waterway regularly, presumably scent-marking for territorial defence (Gerell, 1971; Birks, 1986). Gerell (1971) found intersexual territory overlap, but by simultaneous tracking of both sexes, showed that the female was, temporarily at least, able to defend a boundary against a male. Birks (1981) found extensive intersexual territory overlap to be uncommon in lacustrine and riparian habitats. Gerell (1971) and Birks (1981) found that many females leave their ranges in the autumn, and most workers have commented on the promiscuous nature of the mating system (Marshall, 1936; Enders, 1952; Mech, 1965; Hatler, 1971).

The length of waterway used by individual male mink was similar to that used in riparian habitats, but females occupied shorter lengths of coast than they did rivers (Gerell, 1969; Chanin, 1976; Birks, 1981; Whitman, 1981). Errors may have been introduced by measuring a two-dimensional range in a linear way, but the linear form of many of the ranges, especially those of females, may mean the comparison is still valid, especially as other workers also ignored the two-dimensional nature of the ranges. As food availability probably affects female range size more directly than that of males, this suggests that the coastal habitat may be richer than riparian habitats, a fact also supported by less overall mink activity in coastal habitats (Chapter 4). This was also found by Hatler (1971). In his coastal study area in Canada, he found one male mink per 0.74km of coastline, and one female every 0.41km, based on visual observations in productive habitat. These

findings are similar to those of Kruuk and Hewson (1978), who found that coast-living otters had smaller ranges than their riparian counterparts. They suggested that the coast, rather than inland water, might be the optimal habitat for otters. The same might also be true for mink.

Kruuk and Hewson (1978) also found a much higher degree of overlap in ranges on the coast, than Erlinge (1968) found on rivers. They suggested that this might be due to different patterns of food availability. Limited observations on the present study area suggested that intersexual range overlap was small except during the rut, though Hatler (1976) found higher degrees of range overlap in populations of a much higher density. This suggests that a degree of plasticity in social behaviour occurs in mink, as well as in otters.

Brown and Lasiewski (1972) speculated that sexual dimorphism may have evolved in mustelids to promote niche differences and reduce intersexual competition. In order for it to be an advantage, the sexes must overlap spatially. The results of the present study and that of Birks (1981) study suggested that intersexual overlap was not particularly extensive. Powell (1979b) characterized mink social system as exhibiting intrasexual territoriality and intersexual overlap. This was largely based on the radio-tracking results of Gerell (1970) who found that in December, a male mink's range completely encompassed that of a female. However, that particular adult female had probably defended her range against an adult male in September. In the present study, it was suggested from trapping data that males started to expand their ranges in December, and as this was coincident with testis descent, expansion might have had an exploratory explanation. Gerell's results were therefore not inconsistent with the picture of limited range overlap during part of the year. Even when intersexual overlap was extensive, Gerell's male did not have a foraging core area within the female's range, suggesting that the male was not utilizing the zone of overlap for his own feeding requirements.

Once a female's range was encompassed by that of a male, she restricted the extent of her own movements, and reduced her range size (Gerell, 1970), suggesting subdominant status. Similarly, Erlinge (1977a) showed that females retreated and became inactive in the presence of males. Birks (1981), using arena based diadic interaction trials, showed that females were almost always dominated by male mink, often showing voluntary subdominance to reduce the likelihood of attack. The one exception to this pattern occurred when a female was close to parturition. Considering this subdominance, the

lack of intersexual overlap is surprising, as males would surely occupy female ranges, unless females occupied sub-optimal habitats.

The co-occupation of a male range by a female, despite her subdominant status, might be advantageous. Since intrasexual territoriality exists, a female would not have to defend her range against other males, as this would be done for her. However, a dominant male would have to allow the female to reside within his territory, and the resultant exploitation competition for food and consequent increase in minimum required range size would suggest a considerable cost to the male. As the sexes behave independently for most of the year, the obvious advantage to the male would be increased mating success during the rut.

The finding that mammal group size often depends on the richness of food patches, and territory size on the dispersion of feeding patches (Bradbury and Vehrencamp 1976; Macdonald, 1981; Kruuk and Parish, 1982) led to the advancement of the resource dispersion hypothesis (Macdonald, 1983). A refinement to the model, in which a single owner maintains a territory containing sufficient food to meet or exceed its requirements for a proportion of feeding periods, allows one or more individuals to use the range, albeit at a lower level of food security (Carr and Macdonald, 1986). There need be no functional advantage from dual occupancy for either occupier, and the primary owner is only rarely disadvantaged. Using this model, a female could exist within a male's range, with limited intersexual competition unless food was extremely scarce. If this were the case, the male could in theory exclude the female. Lockie (1966) found that at times of food shortage, male weasels become more aggressive, tending to treat females like males, leading to higher female mortality. Erlinge (1974) also found that food shortages affected female weasels more than they did males, though this could have been due to males utilizing a wider range of prey. Either way, niche differences by virtue of diet, activity or habitat usage are likely to reduce the threshold at which a male will become intolerant of a female. In addition, despite the breakdown of the male mink social system during the rut reported in other studies (Chanin, 1976; Birks, 1981), the present study indicates that resident mink do achieve matings, and male tolerance of female overlap might be increased consequently.

Although trapping data can present a distorted view of a territorial system, all trapping studies to date suggest the existence of intersexual overlap. More telemetry-based studies are required to simultaneously track adjacent or overlapping individuals of both sexes,

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in order to clarify whether intersexual range overlap really exists and the mechanisms behind its maintenance, or whether it is a consequence of the misinterpretation of trapping data.

6.4.2 Reproductive strategy

A thorough understanding of the mating system is important if the contribution of sexual selection to body-size dimorphism is to be assessed. Fortunately, as the mink is a commercially reared animal, there is a wealth of research available into its reproductive physiology. (for example Hansson, 1947; Enders, 1952; Venge, 1971; Chapter 1).

Females are a limited resource for which males must compete. Female mink are widely dispersed because of intrasexual territoriality and the linear nature of the habitat. It would be difficult for a male to defend, effectively, more than one female at a time. As mating is seasonal, Erlinge and Sandell (1986) put forward this change in the males' "decisive resource", (i.e., from food to females), to explain the breakdown of the territorial system in stoats during the mating season. The primary reproductive strategy was called 'roaming', whereby a male left its normal range, and roamed in search of females with which to mate, staying with each successive female for two to seven days (Sandell, 1986).

Trapping data acquired in the first year of the study, as well other accounts of territorial breakdown (Chanin, 1976; Birks, 1981), and the wide-ranging movements of male mink during the rut (Gerell, 1969), suggested that a similar mating system occurred in mink. However, certain inconsistencies demanded caution in this interpretation. For example, in stoats, territorial breakdown occurred concurrently with female oestrus (Erlinge and Sandell, 1986). In mink, first matings probably took place in mid-February, whilst the major disruptions in the social system appeared (from trapping data) to have occurred in March, especially late March. Secondly, roaming stoats were without exception adults. However, large adult, presumably dominant male mink tended to be present throughout the whole of the rut. If any section of the population became mobile first, it was the sub-adults, possibly being displaced by the adults in late January or early February.

The late departure of most adult males, and high trapping success of males at the end of March, could be explained physiologically. As mink can ovulate a number of times during the rut, and matings during the last ovulation result in the most kits (Chapter 1), then presuming that this is still the case in the wild, mating effort at the end of the season will be more rewarding. In possible support of this hypothesis is the fact that males

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spend successively longer copulating as the rut progresses (Hansson, 1947). Arguing against this explanation is the fact that although some females may ovulate as many as four times during the season, many have fewer ovulations (Venge, 1971).

If this is not the explanation, then why do resident adult males remain associated with, or keep returning to their normal ranges? This too might have a physiological explanation. As female mink are induced ovulators (Hansson, 1947; Enders, 1952) the time lapse between copulation and ovulation promotes the possibility of superfecundity (Section 1.2.8). Once a male has mated with a female which has just come into oestrus, he needs to prevent other males from copulating with her for 48–72 hours to guarantee it is his sperm that fertilizes the eggs. Similarly, because of superfoetation (Section 1.2.8), the same male would have to return some days later and monopolize the same female again, and perhaps even later in the season as well, in order to guarantee paternity of the litter.

Tracking and trapping data did suggest that an occasional male left the study area for five days to a week, but tracking results were not complete enough to show definite patterns of this type. If males did keep returning to females, then it could explain their presence within the study area throughout the rut. The high levels of investment in a particular female would also put limits on the time available to mate other females. Having to monitor females for signs of oestrus would limit time even further. Thus, the reproductive physiology of a female mink could in theory limit the effectiveness of a roaming strategy in mink, even though it appears optimal in stoats.

Why should the apparent influx of males occur at the end of March? Instead of representing peak mating activity, it could indicate that the rut was coming to an end. If the first females come into oestrus in mid-February, then even those females that have four waves of ovulation will be coming to the end of oestrus in mid-March. By the end of March, fewer and fewer receptive females will be available, and competition for these females will be extremely high. Males will be forced to move further and further away from their normal ranges in search of such females. This increased mobility would result in the increased trapping success, and greater throughput of males in the study area.

This explanation would be consistent with dominant males remaining within their own ranges during the mating season, as it would be sub-adult or subdominant individuals that are forced to look elsewhere for females. As the season continues, fewer and fewer females remain available, and those left will be even more fiercely guarded during their

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final ovulations. Most of the wounds on the necks and cheeks of males were evident at the end of March, though this could have been a cumulative effect. The effect of the reduction in female availability might well be the main cause of the turnover in the male population during the rut, rather than a particularly promiscuous mating strategy!

6.4.3 Alternative strategies

On theoretical grounds, alternative mating strategies (Partridge and Halliday, 1984) may be predicted. A roaming strategy requires that any female can be monopolized, or taken over in the face of competition. As juveniles stoats are sub-dominant to adults (Erlinge, 1977a), this would not be possible in that species. Sandell (1986) found that all juvenile male stoats exhibited one of two subsidiary strategies: 'stayers', juveniles who remained in their own expanded ranges, presumably waiting for a mating if a female was in heat, and no other adult was around; and 'transients', whose movements bore little relation to the whereabouts of females.

In female mink, the proportion of time in oestrus compared to that between successive ovulations, suggests that perhaps only a third to a quarter of females are in oestrus at any one time during the rut. Trapping data indicated that the sex ratio in an established territorial system was approximately 1:1. If this presents a reasonable estimate of the real ratio (i.e., the non-trappable population is negligible, or it has a 1:1 sex ratio as well), then three or four males will be competing to mate with each female. This incidentally compares quite well with the three males observed on two occasions in the vicinity of an oestrus female.

Little is known about the factors affecting intrasexual dominance relationships in wild mink. Birks (1981) found that, in enclosure experiments, adult male mink domi-nated juveniles (as in stoats), that males familiar with the surroundings dominated naive individuals, and that confrontations were more likely to escalate into fights during the mating season. In polecats however, dominance appears to develop on the basis of size and experience (Poole, 1972, 1974). Of the male mink captured during the rut, approxi-mately 50% were adults. Again, trapping could introduce distortions through behavioural differences between the classes. It follows from the male to oestrus female ratio above, that this would indicate about two adult males are present for every oestrus female. On this basis, sub-adult mink would stand little chance of a mating, hence strategies similar to those of juvenile stoats might develop.

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In the present study, different sub-adult males exhibited markedly different be-haviours. One resident sub-adult mink (M32) did adopt a strategy of remaining in a home range only slightly larger than his normal one throughout the rut (Figure 6.23), and also achieved a mating on the 17th March 1985, displaying dominance over two non-resident sub-adults. His association with the female was short-lived as he was later defeated in a fight (Section 6.3.7). Another resident sub-adult (M33) displayed more adult-like behaviour, with a vastly expanded range and possible association with resident females (Figures 6.11b-d, 6.14b). Both these examples occurred in the absence of resi-dent adult males. In other years, when adults were resident in the study area, sub-adult males left before the date of first mating, suggesting a normally transient behaviour. However, unlike stoat transient behaviour, transient male mink movements were related to the location of females, often being caught and seen in the vicinity of female dens. One (M25) may even have shared a den with a female and fought off a smaller (though normally resident) adult male.

No account has been taken of the effect of female choice on male reproductive behaviour. Enders (1952) reported that if a male mink could get a firm grip of a female's neck, then copulation would result, despite unwillingness on the part of the female. By using dens where males cannot gain access, a female could in theory, only make herself available to particular males. Hatler (1976) reported two incidents which seemed to suggest mating with one male in preference to another. Preference on the part of a female could, for example, reduce the time a male spends in defence of the female, freeing it to mate with more females and reduce the effectiveness of the physiological restriction mentioned above.

Even in the absence of choice, a female's reproductive physiology has evolved to maximize her chances of becoming pregnant. As a male has to adjust his behaviour with respect to a female's cycles, the evolution of a particular physiology may exert an indirect form of choice. It is evident from the big mating wounds on a female's neck at the end of the rut, that they are mated many times. By how many different males is unknown. Observations did not support Hatler's (1976) statement that "males simply took turns". However, Sundquist and Gustafsson (1983) and Tung et. al., (1984) reported that there was a constant population of between 10–20% of infertile male mink on ranches. The possibility of male infertility in the wild would mean that females should mate with more than one male in order to prevent the loss of a litter. Superfoetation and superfecundity allow for this possibility, and allow the possibility of mating with different males to

ensure pregnancy, but also conceivably allow an element of choice in which male fathers the litter by allowing him to mate at the best time. Obviously then, extremely detailed observation of females as well as males is required for a fuller understanding of the mating process.

Fertility problems, examined in fur farms, if occurring in the wild, might also affect mating behaviour in other ways. Sundqvist et. al.(1987) found that male fertility increases with age to a maximum at two and three years, decreasing thereafter. The mating system has developed such that sub-adult males probably get few opportunities to mate, and that one male would find it difficult to monopolize a female throughout the whole rut, both of these factors increasing the chances of a successful fertilization for the female. Similar factors affect male choice. Female fertility increases from the first to the second litter, and decreases thereafter (Tauson and Alden, 1985), and many instances of non-breeding females have been recorded in the wild (Gerell, 1971; Chanin, 1976). Thus males should invest more effort in adult females, if present, and also tend towards promiscuity to increase the chances of output into the next generation.

In summary, mating strategies still appear to be different from those of the stoat. Female mink are distributed along an essentially one-dimensional habitat. As this would not prevent a roaming strategy, some other factors must be responsible for the differences. The combination of physiological constraints and competition on potential reproductive output of the male, may limit the utility of wide-ranging movements by a male. The consequences of superfoetation would probably not limit male movements directly, as concentrating investment on a few individuals within a limited area would result in approximately the same reproductive output as would random matings with many females, though a tendency towards some level of promiscuity by both sexes might be favoured by infertility in the wild population. Otherwise, the benefits to a male who remains on or near familiar habitat, where he knows the dispersion of food resources and the den sites of the females, might outweigh the benefits of possible matings with more females. This does not mean that the system is not promiscuous, indeed "overlap promiscuity" (Wittenberger, 1979, 1981) is probably a good description of the system observed. However, the scope for a promiscuous strategy in mink, even for a dominant male, is limited in extent. The consequences of this interpretation of the mating system to the sexual dimorphism argument will be examined in the next chapter.

7. GENERAL DISCUSSION

Shubin and Shubin (1975), when discussing the behaviour of different mustelid species in the USSR stated,

> "But ecological differences between the females and males are so great in these animals, particularly as regards their methods of obtaining food, their behaviour, and their activity, that they are as different from each other as absolutely different species."

In the case of mink in the present study, "different species" may be considered an overstatement, as there were high degrees of overlap in habitat utilization and diet between the sexes. However, despite this overlap, significant sex-related differences were found in the diet, temporal distribution of activity, habitat utilization, den usage, and social behaviour.

The reasons underlying these differences were considered to have two separate causes, neither being directly related to the other. The primary cause was the different reproductive roles of the sexes. Males attempted to increase their input into the next generation by adopting a primarily polygynous or promiscuous mating strategy. Attempts to mate with more than one female led to wide ranging movements during the rut. This resulted in a significant increase in activity compared to that of females and also to a significantly greater size of home range. Similarly, the role of the females in raising kits led to significantly lower levels of activity during the early stages of lactation, and a combination of short activity bouts and restriction to the use of one den for long periods, led to a decrease in the size of range used by females at this time. Outside these critical periods in the life-cycle, levels of activity were similar for both sexes.

The other sex-related differences were considered to be an effect of the extreme level of sexual dimorphism in body size, males being heavier than females by a factor of 1.75. Thus, the increased level of consumption of lagomorph by male mink compared to females was attributed to the male minks' greater size, leading to a relative decrease in the energetic costs of catching large prey. Female consumption of larger prey was thought to have comprised not the adults, but the young, (juvenile rabbits and unfledged birds), or carrion, such as hares and adult gulls (Chapter 3).

Sex-related differences in other aspects of mink ecology were thought to have resulted from these dietary differences. Female mink spent proportionately more time on the shore,

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a reflection of the greater aquatic component in their diet. Similarly, males spent more time in the scrub and plantations, in association with their predominantly terrestrial diet. Den-use was also linked to feeding areas and habitat utilization, males using more rabbit burrows and females more dens in the rocks near the shore.

Differences in the temporal distribution of activity throughout the 24-hour and tidal cycles were more difficult to relate to diet. Sex-related differences in the distribution of activity over one daily cycle, and in the levels of activity with respect to dawn and dusk reflected the greater nocturnality of males. Male mink could have been more nocturnal as a result of the activity/availability of their terrestrial prey; however, they were generally nocturnal whilst foraging on the shore as well. Females, in contrast, were more diurnal, foraging in any habitat during the day or night. Since rabbits provide sufficient food for more than one meal, males may have been able to avoid foraging during the day by remaining in a burrow with prey which could conceivably last for a number of days. Alternatively, the different activity patterns exhibited by the sexes could have resulted from temporal avoidance. Unfortunately, the absence of simultaneous radio-tracking data from both sexes in the same vicinity precluded examination of this possibility.

It was stated previously, that the majority of the sex-related differences in behaviour were due to two separate or distinct factors, namely reproductive roles and sexual dimorphism. These factors may however be directly related. The arguments for the extreme levels of sexual dimorphism in mink fall into two categories: those suggesting that it was a means of reducing intersexual competition between the sexes (for example Brown and Lasiewski, 1972; Shubin and Shubin, 1975), and those that suggest it is a function of the demands or constraints imposed on the individuals by their differing reproductive roles (Erlinge, 1979; Moors, 1980; Powell and Leonard, 1983; Ralls and Harvey, 1985).

In support of the the first hypothesis, the observed divergence in many aspects of mink behaviour would lead to a decrease in competition between the sexes, both interference competition via differential habitat utilization and temporal differences in activity patterns, and exploitation competition through the utilization of different prey. Theoretical considerations (Chapter 1) suggest that it was not the avoidance of competition which led to the evolution of body-size dimorphism, as competition would be most intense when prey were scarce, and the smaller member of a dimorphic pair could then be at a disadvantage (Erlinge, 1974). This may be particularly so for mink, as males can and do take all the prey species available to females, and are probably dominant over females in direct competition (Birks, 1981).

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However, the smaller size and the lower status of a female compared to a male does not always lead to a disadvantage. In cervids for example, males often occupy poorer quality habitats (Geist and Petocz, 1977; Clutton-Brock et al., 1982; Staines et al., 1982). This is probably because female cervids graze the best habitats so heavily that males are unable to get sufficient digestible material from the same swards, as males' energetic requirements increase with increased weight to the power of 0.75 whereas their bite size only increases to the cube root of their increased weight (Clutton-Brock et al., 1987; Illius and Gordon, 1987). Although a similar allometric effect will occur in mink, it is unlikely to be so important in mink or other mustelids as, unlike grazers, the time spent and energy consumed in finding and capturing prey is likely to be high compared to that needed to consume it.

A reduction in competition, if not the cause of sexual dimorphism, could still be of advantage in a series of intersexually overlapping ranges. Within a heterogeneous environment, a sub-dominant individual could exist in an overlapping range with a dominant individual at a slightly lower level of food security, but with very little, if any, competition (Carr and Macdonald, 1986). If female mink live within male ranges on this subdominant basis, then the reduction in competition caused by the dimorphism in body size might reduce the threshold at which, in times of prey scarcity, intersexual competition became a significant factor. Apart from Gerell (1971), no-one has simultaneously tracked males and females in overlapping ranges. This information is necessary to assess the potential for competition, not in the usual dietary terms, but with respect to habitat use and temporal patterns of activity, between the sexes.

The second hypothesis for the evolution of sexual dimorphism suggests that it occurs because of sexual selection for large size in males and/or selection for small size in females. The present study suggested that competition for females was intense during the rut. Though not quantified, most males bore scars on their cheeks and necks at the end of the rut indicating that fighting had taken place. Three fights were observed where the weights of the individuals were known and it was always the heavier male that emerged the victor. Traps set in the vicinity of female dens during the rut were particularly successful, and direct observations revealed that more than one male was often present near the den of an oestrus female. There was no indication that males simply "took turns" to mate with a female as was suggested by Hatler (1971). Thus the element of competition for females which is a prerequisite for sexual selection was present in the population. However, as Moors (1980) pointed out, this type of observation

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provides only circumstantial evidence that large male body size is actually an advantage in reproductive terms.

However, there may be other reproductive advantages to large body size in male mink. Female mink are widely dispersed (Chapter 6), and mating success may depend on the ability to move large distances into contact with more females, or more likely, in an ability to move quickly between neighbouring females. The importance of travelling to males during the mating season has already been shown in Chapter 4. Larger animals (using the same mode of locomotion) are able to travel faster than smaller ones (Peters, 1983). Furthermore, though transport costs are higher in absolute terms for larger animals, relative to the increase in weight, energy costs are lower (Peters, 1983). Thus sexual selection may have acted to increase male body size not solely because large males could overcome smaller ones, but because large males could travel from one female to another more easily. Again however, there is no evidence for this. A detailed knowledge of the relationship between lifetime reproductive output and male body size would be required to investigate the pressure for the selection of large male size.

Both Erlinge (1979) and Moors (1980), considered that the strength of sexual selection was not sufficient to account for the degree of dimorphism exhibited by small mustelids. In the present study, dominant males often remained in a localized area during the rut. Considering the wide dispersal of females therefore, the potential for polygyny or the maximum reproductive output of males was unlikely to have been as great as that for other similarly dimorphic mammals, for example the red deer *Cervus elaphus* (Clutton-Brock et al., 1982). This also suggested that some factor, other than sexual selection, contributed to the degree of dimorphism in mink and other mustelids.

The alternative factor, in the case of mustelids, may be selection for the small size of females. In raptors such as the sparrowhawk *Accipiter nisus*, the female is large, accumulating large body reserves in preparation for breeding (Newton, 1986). As the male supplies all the food prior to laying until the young are half grown, it is small, presumably because small size leads to greater flying ability (Andersson and Norberg, 1981) and a greater facility in prey capture. In mustelids however, the female brings up the young unaided by the male, and a small size may enable her to channel more energy into reproduction by minimizing her resource energy requirements (Moors, 1974, 1980; Erlinge, 1979; Powell and Leonard, 1983). Small size would only be of advantage whilst raising kits if finding sufficient food was in fact difficult, and the reduction in size

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reduced the amount of time necessary to find food (Powell and Leonard, 1983). These workers found that a female fisher would have had difficultly raising the same number of young if she had had to find the extra 300-500KJ/day needed to sustain a male-size body. In the present study, females radio-tracked during June and July (the time when the kits were still mainly dependent on the female for food) were no more active than at other times of the year. This suggested that the greater availability of food during the summer more than compensated for a female's increased energetic demands at this time. This would then imply that selection for smaller females may not be advantageous, as the time available in which to find prey was not limiting. However, these data were collected from a female with only one surviving kit (F10), and another female (F11), which lived on Ross Island where seabird carrion was probably superabundant. These circumstances are unlikely to be typical.

Models which presume that a smaller female can invest a greater proportion of her energy into reproduction, typically assume that foraging efficiency is independent of body size. The results of the present study suggested that foraging efficiency increases with body size i.e., an increase in body weight does not lead to a similar increase in the time spent foraging. Thus males, although having approximately 1.5 times the resting metabolic requirements of females, only needed to forage for a similar length of time per day. This they probably achieved by increasing the proportion of larger prey items in their diet. If an increase in size did lead to a similar increase in foraging efficiency, then this would remove any constraint on female size, since being smaller, though reducing absolute food requirements, would make catching prey proportionately more difficult. However, the categorization of activity into foraging and travelling used in the present study was somewhat subjective (Chapter 4), and it is unlikely that catching larger prey compensated totally, in terms of time, for a male's increased food demands. It is also the activity budget between May and August, and not the annual figure which is likely to be important, as this is the time when a female's demands will be greatest. During May, just after parturition, both male and female mink were preying predominantly on lagomorph. At this time, females were foraging for 42 minutes per day, compared to 108 minutes for males. Thus, when prey is abundant and diets are similar for both sexes, a smaller body size could still confer an energetic advantage.

It may be that the advantage of small size to female mink or mustelids does not lie in the ability to channel more energy into reproduction, but in a reduction of the time a female needs to leave her kits unattended. Selection will favour female behaviour which

maximizes the chances of pregnancy, but once pregnant, there will be strong selection to improve the survival of her kits. Kits are completely dependent on their mother for the first few weeks of life, being born naked and blind. Stoats, less than 5–7 weeks old, are unable to maintain their body temperature when left in the nest alone (King, 1989), entering a reversible cold rigour when the nest temperature drops below 10–12°C. Full homiothermy at temperatures down to 0°C is only achieved when the fur is fully grown after two months. Thus the survival and rapid growth of kits will be dependent on the presence of the mother.

Selection may act to limit female size if this reduces her energetic needs and consequently reduces the time she needs to leave the den and find food. This appeared to be the situation in May and June when the kits were most vulnerable. The present study showed that the absolute amount of time spent foraging by female mink was very low in May, and also that foraging bouts were very short and dispersed throughout the day (Chapter 4). While the exact susceptibility of mink kits to cold is unknown, a further advantage to mother and kits of her continued presence in the den, would be in a reduction of the susceptibility of the kits to predation.

Ralls and Harvey (1985) were sceptical of hypotheses which suggested that females were constrained in size. Little was known of the relative foraging efficiencies of the different sexes, and they suggested that a more profitable way of viewing size differences would be to seek the selective pressures which had operated to make males large and energetically inefficient. However, the results of the present study suggest that males may not be energetically inefficient. If sexual selection does promote larger male size, and if the size attainable by males is limited by the energetic costs of being larger, then the removal or reduction of the energetic constraint should lead to an increase in the optimal size. In the case of male mink in the present study, the energetic costs of maintaining a larger body size, measured in terms of time spent foraging, were negligible or at least significantly reduced, as males were more efficient at foraging on larger, energetically more economical prey. Similarly, the males of many other small mustelid species also consume larger prey (for example Day, 1968; Brugge, 1977; Erlinge, 1979) but no information is available as to whether the males of these other species are similarly more efficient foragers. Can the availability of larger prey to larger individuals, and the consequent removal of an energetic constraint on large size, be used to explain the extreme levels of sexual dimorphism in mustelids?

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Ralls and Harvey (1985) suggested that the degree of sexual dimorphism was related to prey availability, but for the hypothesis (above) to work, a direct link must be established between the availability of **large** prey and large male size. Somewhat paradoxically, the size a male attains (the main determinant of the level of sexual dimorphism), is primarily dependent on the food available to the female during the period of rapid growth of young males (Sinclair *et al.,* (1962); Gregory, 1987). It has been established that females feed on **small** prey items (Chapter 3). During the period of kit growth, these included a high proportion of young rabbits and birds. Since the availability of these young is directly related to the abundance of the adult population, an indirect link is established between male size and the availability of large prey.

However, the size a male attains is not wholly dependent on the mother. Nutritional factors have the greatest effect on adult body size during the first five months after-weaning, when growth rates and metabolic requirements are highest (Tauson and Alden, 1985). The plane of nutrition will therefore be important to male mink even after their dispersal. In the wild, the growth of the male kits continues at least until December (Whitman, 1981; pers. obs.) and possibly through the second year of life (Gerell, 1971). The extent to which male size continues to increase, and therefore the degree of sexual dimorphism, may therefore depend on the availability of the larger, energetically more economical prey items. The larger the males are at independence, the quicker they will be able to take advantage of such prey.

The indirect nature of the link described demands caution when applying the energetic arguments for extreme sexual dimorphism in a wider context. The reduction of an energetic constraint on large body size by virtue of the availability of large prey could however be used to explain the inverse relationship between sexual dimorphism ratio and body size described in mustelids by Moors (1980). The smallest of the carnivores, the sub-family Mustelinae, differ from the most other members of the order in their ability to catch and kill, single-handed, prey much larger than themselves (King, 1984). Thus the diet of weasels *Mustela nivalis* often contains appreciable amounts of rabbit, and male mink have been observed to attack and kill adult hares which weigh three times as much as themselves. However, both the density of prey (Elton, 1927; Dalmuth, 1981), and the number of species of animal (Peters, 1983), are inversely related to their size. Thus, the larger the predator, the the lower the abundance of, and number of species of, larger prey that potentially become available to it. The much heavier otters and badgers prey almost exclusively on items substantially smaller than themselves. Though larger terrestrial prey

are available, they are not fossorial. The advantage of typical mustelid morphology, i.e., a long thin body and short legs, is reduced, this body shape being a disadvantage in pursuit of prey in the open. Since many members of the family Mustelidae have similar social structures, i.e., intrasexual territoriality (Powell, 1979b), their potential for polygyny should also be similar (the badger being an obvious exception). Thus, sexual dimorphism would be expected to decrease as its members increased in size because the larger prey required to reduce the energetic cost of maintaining a large body size would be less available.

Although the availability of large prey may permit the development of extreme dimorphism, it does not imply that prey availability lead to its evolution. The relationship between body size and social dominance in mustelids is not straightforward. Though increased body size is generally considered an advantage in competition, nothing is known of how body size influences lifetime reproductive success. Other mammals have similarly high or even higher sexual dimorphism ratios, for example the red deer (Clutton-Brock *et al.*, 1982) and the elephant seal *Mirounga angustirostris* (LeBoeuf, 1974). The red deer on Rhum have a sexual dimorphism ratio in the region of 1.7 and this occurs against a distinct energetic disadvantage as males do not meet the greater energetic demands by switching to more economical foods. As female red deer form herds, a harem-holding male is able to defend and gain almost exclusive mating rights with many females. The high rewards to a successful male therefore presumably offset the high energetic cost and mortality risk of being larger. Less polygynous species of deer have lesser degrees of sexual dimorphism (Clutton-Brock et al., 1982). Male mustelids have a reduced facility for polygyny by virtue of the dispersal of their females (Chapter 6), and so the degree of sexual dimorphism should be smaller.

The maximum number of matings a male can achieve in one mating season can not be used as a measure of the strength of sexual selection, since it does not take into account the longevity of an individual. The energy and/or time expended in mating will be a compromise between the benefits accruing during that mating season and the effect on his condition during future mating seasons. The cost of mating success is often high, for example successful male elephant seals die within a year or two of their reproductive peak (Le Boeuf, 1974). It is life-time reproductive success that should be maximized. Red deer often live to the age of 10 years and although their mating success in one rut might be high, they cannot achieve this success every year. (Clutton-Brock *et al.*, 1982). In contrast, small mustelids are usually short lived. Although mink can live for more than ten

years (Enders, 1952), both Mitchell (1961) and Gerell (1971) found an almost complete population turnover every three years in the wild, suggesting a mean mortality of about 60% per annum. In general agreement with these figures, age ratios based on trapping results in the present study suggest that the life expectancy for mink is approximately 1.4 years from independence (although this represents an underestimate if sub-adults are more easily captured than adults). A similar estimate of 1.4 years was calculated for male stoats by Erlinge (1983). Thus for mink (and possibly other small mustelids) the low probability of surviving to a future mating season could mean that they are prepared to invest relatively heavily in adaptations (i.e., increased body size) designed to increase mating success, despite the low potential for many matings. A positive relationship exists between body size and longevity in mammals (Eisenberg, 1981). Both badgers (Kruuk and Parish, 1987) and otters (Chanin, 1985) seem to have much lower mortalities (approximately 25% per annum) than the smaller mustelids. Larger (presumably longer-lived) mustelids would be less likely to take the energetic risks of a larger body size as the emphasis shifts from immediate to long-term reproductive success. This could result in the observed inverse relationship between sexual dimorphism ratio and body size.

Whichever is the main reason for the extreme sexual dimorphism exhibited by small mustelids, its extent does seem to be linked to the availability of prey. It is possible that the presence of larger prey simply helps to sustain a dimorphism resulting from other factors. Alternatively, the observed geographical variation in dimorphism may just be a result of increased mortality of individuals larger than the optimum for a particular habitat. Whether or not the availability of larger prey is indeed linked to the evolution of the trait is open to speculation, but questions such as these can only serve to emphasise how important a detailed knowledge of energetics is to the interpretation and understanding of life history strategies.

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SUMMARY

1. A study was conducted to look both at the ecology and behaviour of mink in a coastal habitat and, in particular, at the effects of sexual dimorphism in body size on the behaviour of the sexes. The sexual dimorphism ratio, calculated from the weights of 49 male and 33 female mink was 1.75:1.

Diet

2. The dietary study involved the collection of 3007 mink scats. Of these, 1957 scats were collected from the dens of known individuals and this permitted examination of dietary differences between individuals and between the sexes.

3. Lagomorphs, both rabbits and hares were the major constituent of the diet, comprising 41% of the bulk. Fish were the next most important component (30%), comprising most of the available rock-pool fish, but predominantly *Lipophrys pholis*. Birds, primarily Charadriiformes but with appreciable amounts of Passeriformes, comprised (17.4%). Unidentified birds were important but these were thought to be the young of other identifiable species. Crustacea accounted for 11% and comprised almost entirely *Carcinus maenas* with very small amounts of Isopoda, Amphipoda and other Decapoda. Small mammals were relatively unimportant (4.3%). Carrion was thought to have been important, but its contribution to the diet was impossible to assess.

4. Significant sex-related differences were found in the consumption of three major dietary constituents, males consuming more lagomorphs, females more fish and crustaceans.

5. Significant seasonal changes were found in the consumption of lagomorphs and fish. Both male and female mink consumed lagomorph, mainly rabbit, in relation to its abundance as determined by counts. Fish were however mostly consumed by both sexes during the winter, apparently against a gradient of abundance, and perhaps availability.

6. A subsidiary peak in the consumption of *Lipophrys pholis* during the summer was attributed to their poor condition after spawning.

7. The consumption of birds may have been as carrion. The diet of one female who reared kits adjacent to a herring gull colony consisted almost exclusively of Charadriiforme. It is suggested that she was predating young birds early in the season.

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Carrion, in the form of unfledged and fledged juveniles and adult birds was super-abundant, but predation on live young could not be ruled out.

8. Sex-differences in the diet were attributed to the male's ability to capture large (more energetically efficient) prey more easily, primarily due to the male mink's greater size. However, within each sex, consumption of lagomorphs was not affected by mink size.

Activity patterns

9. Examination of activity patterns and habitat utilization was accomplished using radio-telemetry. 22769 radio-fixes were obtained from 25 individual mink, 13 males and 12 females. 10953 of these were collected manually allowing determination of activity type and habitat usage. 11816 were collected remotely by chart recorders which monitored the presence or absence of a mink in its den.

10. Mink were found to be less active than in all other freshwater habitats reported in the literature. This was attributed to greater food availability in this coastal area.

11. The majority of a mink's time was spent in its den. Males spent significantly more time out of their den than females (4.6:3.6 hours/day).

12. Males and females spent very similar amounts of time foraging, (2.9:2.8 hours per day). Foraging activity was higher than expected during the autumn, and this could have been due to high food requirements during the moult.

13. Males spent significantly more time travelling than females (1.7:0.8 hours/day). This difference was primarily due to the large distances travelled by males during the rut.

14. Males were more nocturnal than females. Commencement and cessation of male activity was generally associated with dawn and dusk. The reasons for greater male nocturnality were obscure.

15. Neither males or females exhibited activity patterns correlated with the tidal cycle. However females, but not males, tended to forage on the shore primarily when the tide was low.

Habitat utilization

16. The habitats used by mink reflected to some extent their diet, females foraging primarily on the shore, males in the scrub and plantations. The absence of many seasonal and intersexual differences was tentatively attributed to the mink's opportunistic behaviour and their need to monitor the abundance of different prey resources.

17. Both sexes travelled primarily through the rocky zone. Many scats were found in this zone suggesting it may have been important in a social context.

18. Dens were used opportunistically. Most mink dens were in rabbit burrows. The next most important den-site was in cavities under rocks. Male mink had proportionally more dens in burrows, whereas females had more dens in the rocks, the latter in close association with the shore.

19. The distance of mink dens from the shore suggested that males moved away from the shore in the winter. Females however moved away from the shore in the early spring. These movements correlated with changes in the availability of rabbits to each sex.

Social system

20. Two different methods of measuring home range size were assessed. Insufficient radio-fixes were collected on most individuals to allow an accurate determination of the land area used by mink. However, the linear component of a mink's range along the water-body (coast) was delineated more quickly, suggesting its importance. It was therefore used to look at differences in range size between sexes and between months.

21. Male home range length (2650m) and area (12.3ha), was significantly greater than that of females (1240m, 4.9ha).

22. Significant changes in range length between months resulted primarily from an increase in the home range of male mink during the rut. Females may have been restricted in their movements through care for their dependent kits during May and to a lesser extent, June.

23. Home ranges were probably intrasexually distinct for most of the year. Intersexual range overlap was extensive during the rut, but was mainly evidenced by trapping results outside this period.

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24. In December, trapping indicated that the degree of overlap between male ranges increased. This corresponded with the onset of testicular development.

25. In late January, sub-adult males often vacated their ranges. This could have been voluntarily, but it might have been due to competition with adult males in adjacent ranges.

26. Females first came into oestrus, and first matings occurred in mid-February.

27. In March, there was an influx of new males, and some of the resident males left. Many adult residents remained however, suggesting the existence of more than one male mating strategy. Such strategies could not be successfully classified by age or body size.

28. The mink mating system was classified as promiscuous. However, the observation that many adult males remained close to their pre-rut ranges suggested that the scope for mating many different females was constrained, probably by the unusual female reproductive physiology, and possibly by high levels of competition from resident males in other areas as well.

29. The major influx of new males, occurring at the end of the rut instead of at the beginning, suggested that it that it was not due to a roaming mating strategy, but due to the decreased availability of receptive females as the rut came to a conclusion.

30. Parturition occurred in early May. Females tended to use one den for many days at a time and foraged for short periods (often less than 10 minutes). The duration of activity bouts increased as the kits grew. Kits were first observed playing out of den on the 8th July and by the last week of July were seen foraging for themselves in the sea. The average reproductive output (kits surviving to independence) was approximately three per female.

31. Observations suggest that the kits become independent due to increasing degrees of intolerance on the part of the mother.

Conclusions

32. Sex-related differences were the consequence of two separate factors; the different reproductive roles of the sexes; and the marked degree of sexual dimorphism in body size.

33. Sexual dimorphism lead to niche separation in the diet, habitat utilization and temporal distribution of activity. This possibly lead to a reduction of exploitation competition and interference competition. The extent of the niche separation could not be determined due to the lack of simultaneous radio-tracking of a male and female mink in overlapping ranges.

34. Competition for females during the mating season was evident, thus providing the impetus for sexual selection. The mating success of male mink was thought to be well below that of similarly dimorphic cervids, suggesting that some other factor was responsible for the extreme size difference between the sexes.

35. It has been suggested that selection favours small females, because, by minimizing their own requirements, more energy can be channeled into reproduction. The finding that foraging efficiency increases with size could have implications for such models, as they tend to assume that foraging efficiency is independent of size. However, being small may be advantageous to a female if it reduces the time she spends away from her kits, as this may decrease the chances of mortality through hypothermia or predation.

36. The increase in foraging efficiency with increased size also has implications for the evolution and development of large size in male mink and perhaps other male mustelids. The increase in foraging efficiency associated with predation of larger prey by larger individuals reduces the energetic constraint acting on the development of a larger body size.

37. The short lifespan of mink and other mustelids was advanced as a reason for greater than expected levels of dimorphism. The low probability of surviving to future mating seasons may have selected for males who invested particularly heavily in adaptations designed to increase mating success, in this case increased body size.