THE BEHAVIOUR AND ECOLOGY OF DOMESTIC CATS (FELIS CATUS L.)

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THE BEHAVIOUR AND ECOLOGY OF DOMESTIC CATS (*Felis catus* L.)

by

Roger Panaman

[illegible] for the degree of

[illegible] research [illegible] and

[illegible] under Ordinance

A thesis submitted to the Psychology Department, St Andrews University.

DECLARATION

This thesis is a report of my own work and has been written entirely by me. It has not been previously submitted, in whole or in part, for a degree.

[redacted]

It is submitted to St Andrews University for the degree of Doctor of Philosophy. I was admitted as a research student and as a candidate for the degree in October 1979 under Ordinance General No. 12.

CERTIFICATION

We hereby certify that Roger Panaman has completed nine terms of research under supervision after being admitted as a research student under Ordinance General No. 12. He has fulfilled the conditions of the resolution of the University Court, 1967, No. 1 and is qualified to submit the accompanying thesis in application for the degree of Doctor of Philosophy.

[redacted] [redacted]

R.G.W. Prescott A. Whiten

Research supervisors

November 1983

To BONEY, alias Fm1,

c. 1978-1981 (missing),

and to the honour and greater glory

of all cats.

ACKNOWLEDGEMENTS

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Abstract

This thesis is a reconnaissance of the behavioural ecology of domestic cats. The principal subjects were two groups of farm cats. There was also a group of captive cats and a house cat. The study differs from all previous ones in that the cats were tame and therefore could be shadowed and observed for long periods at all hours. It deals with (1) activity patterns and activity budget, (2) use of space and social behaviour, (3) scent communication, (4) foraging and (5) population dynamics.

Summary

This thesis is a reconnaissance of the behavioural ecology of domestic cats. It deals with (1) activity patterns and activity budget, (2) use of space and social behaviour, (3) scent communication, (4) foraging and (5) population dynamics. The principal subjects were two groups of farm cats. The study differs from all previous ones in that the cats were tame and therefore could be shadowed and observed for long periods at all hours. There was also a group of captive cats and a house cat.

(1) Cats were mainly active during the day, some were equally active during the day and night and two became mainly active at night. Cats had similar activity curves. I hypothesise they might be entrained to the mean daily variation in solar radiation and air temperature. The mean time spent in different behaviours by the farm cat groups was similar. Cats slept considerably less than has been reported in sleep studies.

(2) Farm cats did not use all available space; home ranges were clumped together and greatly overlapping. Males generally had larger home ranges than females. Cats shared the same core area. Males sometimes walked about it in an apparently aimless manner, a behaviour not shown by females. Females only left their core area to forage but males also left it for non-foraging purposes. Cats travelled up to 4 km per day, males more than females.

Farm cats were genetically related to each other, some with long lineages, so were not temporary aggregations. There was no evidence of territoriality among females and little among males in a group. Females seemed to have a non-linear social hierarchy and males a linear one. There was no evidence to support a relative hierarchy. Sometimes a cat would intervene in the fight of two other cats. Cats were not solitary but generally tolerant, friendly and peaceful to each other. They had a social organisation in many ways like lions. Infanticide occurred.

(3) Spraying was the most obvious mode of scent marking. On average males sprayed a magnitude more frequently than females. The frequency of spraying among females varied greatly. Sprays were not clumped but distributed along routes throughout the home range. Males sprayed most frequently inside their core area and never moved far without spraying. Females sprayed most frequently outside their core area and at longer spatio-temporal intervals than males. Most sprays by females occurred when hunting; a few occurred after agonistic interactions, at sleeping places, and after sniffing a spot. The majority of sprays were made after negligible to no sniffing which suggests they occurred in response to a familiar odour or that odour was not significant in eliciting them. Spray sites did not appear to regulate or prevent movement. Spraying did not seem to be closely associated with dominance. Evidence does not appear to support (or refute) the view that spraying allows intruders to assess the quality of the marker. Males, but not females, also scent marked by 'scuff-spraying' and 'squat-spraying'.

In a test of whether cats could distinguish sprayed and urinated urine odours from different cats, subjects appeared to find most samples of little interest or repulsive. However, evidence suggests odours from different cats might be distinguished. Evidence did not suggest that cats preferred sprayed to urinated urine.

Scats were of communicatory significance. Half the scats were scraped-over and half left exposed. There was a tendency to scrape-over scats inside core areas and leave them exposed outside core areas. Scat and urinated urine sites were distributed along routes close to steadings without being clumped or prominently sited.

(4) Principal prey were rabbits and rodents. Birds, contrary to popular belief, were secondary and insects were rarely eaten. There was no evidence of a 'killing neck bite'; rodents did not appear to be deliberately killed before eating. Rabbits were killed by a prolonged bite at the side of the neck. All rabbits caught were juveniles or diseased. Sometimes partly consumed rabbit carcases were returned to for a second meal on another day. Some prey were abandoned, possibly because they were unpalatable, but sometimes other prey were also left uneaten. Cats stopped hunting after catching four rodents or one rabbit in a day. Some females relied more on farm food than on hunting.

Some cats were diurnal hunters, some were diurnal and nocturnal and others were nocturnal. Females generally hunted close to steadings and males generally hunted further away but evidence did not suggest that males and females hunted for a longer distance or duration than each other. Cats shared hunting areas with each other, hunting singly but sometimes close together. Hunting was significantly more stationary than mobile and mobility was positively correlated with home range area. All prey ambushed by three cats were caught in less than 10 min but there was a low ambush success rate (observer interference?) and half the time spent ambushing was on ambushes longer than 10 min. Ambush data do not appear to support two hypotheses predicting giving-up times by foragers.

During hunts by three cats, the distance moved between consecutive minutes and the angles between consecutive moves were measured. Hunting search paths on the large scale were not random; search paths of two cats rarely covered already searched ground, although the search path of another did, and the cats kept mainly to areas where there were prey. On the small scale, for each cat, the turn-angles were normally distributed and the mean turn-angle was close to zero degrees, apparently showing that cats tended to avoid large turns and avoid the direction from which they came. The median straight-line-travel (move-length) was similar for each cat, falling just below the mean. No evidence was found of a pattern to move-lengths, turns and turn-angles.

(5) In a census of 100 sq km of rural Fife there were 3.7 cats per sq km (0.3 per human), with farm cats in the majority. Farm cats lived in significantly larger groups than house cats. The sex ratio of sexually intact farm cats significantly favoured females, possibly due to male emigration. House cat sex ratio was unity which suggests selection for house cats might not be based on sex. Cats suffered a high mortality in their first year. Survivorship appeared to decline steeply until about age

five and then level off. However, few farm cats survived beyond age five. Neutered male and female house cats survived equally well. The maximum age reached was 17 years. House cats were about four times more likely to be neutered than farm cats. A quarter of the censused population had been imported into the census area but most immigrants were neutered so probably few contributed to the population's gene pool.

Perhaps the single most important conclusion from this study is that, contrary to all previous work, it shows that close observation of the behaviour of free-ranging domestic cats can be achieved at all hours and therefore domestic cats are ideal for research in behavioural ecology. Furthermore, they are of interest to conservation for through them we may better understand other more difficult-to-observe small cat species and thus contribute to small cat conservation.

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CHAPTER 1

INTRODUCTION

This thesis is a reconnaissance of the behaviour and ecology of a few tame cats (Felis catus) observed directly by following them wherever they went.

Research Background

Of approximately 4,000 species of mammals, about 240 are carnivores and of these about 35 species are cats. Cats are top carnivores so are not normally numerous but domestic cats, because of their association with humans, outnumber all other cats put together. They are also the most widely distributed being found in Africa, Eurasia, the Americas, Australasia and in most places humans inhabit. But their behaviour and ecology has barely been studied.

There is much scientific and non-scientific literature on domestic cats but little on their behavioural ecology. What there is can be divided into two kinds. The first, which comprises the least number of studies, is based on direct observation of cats for as long a period as possible. It is the method used in this study. Direct observation means a wide range of topics can be researched like activity patterns, space use and social behaviour. This approach dates from the 1950's, when Leyhausen and Wolf (1959) published their paper on the behaviour of Welsh farm cats. The next paper was published a generation later (Laundre 1977) but was quickly followed by another three papers (Dards 1978; Macdonald and Apps 1978; Liberg 1980), two Ph.D. theses (Corbett 1979; Dards 1979) and the circulation of a dissertation by Liberg (1981) based on his Ph.D. thesis. The second kind of study has more literature but is less relevant to this thesis. It is based on dead cats and on signs and brief sightings of live ones so is limited in the kinds of data it can yield, for instance diet, reproduction and density. It had its beginnings between the world wars. One of the first papers published was Errington (1936) and recently Derenne (1976), Jones (1977), Van Aarde (1978) and Fitzgerald and Karl (1979). The results and conclusions of the first approach and those of the second which are relevant are dealt with as they logically arise in the body of this thesis.

Whichever the study, however, they all have the common factor that the cats were not observer tolerant and therefore could not be followed but only observed, often intermittently, from a distance. The study reported in this thesis differs from any previous one in that the cats were tame, that is they could be followed, which made possible detailed, direct and continuous observation at all hours wherever they went. For instance, Liberg (1981) recorded 104 h of cat activity in 3,500 h spent in the field whereas by shadowing a cat from 1 to 10 m away I could record 24 h of activity in 24 h.

Need for Research

Why study domestic cats? About a seventh of carnivore species are felids. Most ecological research on them has concentrated on the large species like lions, tigers and cheetahs. But the small species constitute at least two thirds of the cat family; therefore in order to understand the evolution, ecology and range of behaviour of felids it is important to pay more attention to small cats and a good start is with the most numerous and most easily accessible one. Moreover, the study of small felids is particularly important now that they and their habitat are coming under increasing human pressure.

Although called 'domestic', domestic cats may not have been selectively bred, like dogs and cattle but may have adapted by natural selection to a new niche created by humans who tolerated them about their settlements and grain stores and who began to keep them in their households (Todd 1978). Research on domestic cat behaviour and ecology may therefore help us better to understand the processes of domestication. The domestic cat-human relationship is a symbiotic one. The extent to which one side has manipulated the other remains to be seen.

Research Objectives

There were five basic avenues of research.

(1) Activity Patterns and Activity Budget (Chapter 3)

The activity patterns of domestic cats are shrouded in mystery. In popular belief cats are crepuscular or nocturnal, yet house cats may sleep a lot at any time of day (they are looked upon as lazy) and are generally considered to be much influenced by human activity patterns. But are they? This chapter examines what cats do, when they do them and how long they spend doing them.

(2) Space Use and Social Behaviour (Chapter 4)

The domestic cat is commonly described as 'the one who walks alone'. But this view is contradicted by the frequent observation that house cats amicably share the same house, eat from the same bowl and sleep together. Are cats really solitary or are they socially flexible as is now realised for a growing number of other carnivores, for instance red foxes, <u>Vulpes vulpes</u> (Macdonald 1977), golden jackals, <u>Canis aureus</u> (Macdonald 1979) and brown hyaenas, <u>Hyaena brunnea</u> (Mills 1983). Social organisation should be reflected in the land tenure system; if cats are solitary they might have discrete home ranges or a method of avoiding each other. There are a few studies on the home ranges of cats but not on detailed movements. This chapter describes cats' movements in some detail and takes a look at their social behaviour in general. Foraging movements are continued in the chapter on foraging.

(3) Scent Communication (Chapter 5)

Many mammal species use scent as an important mode of communication. So in order to understand them a through knowledge of their chemical communication is important. Chemical communication in mammals is complex and difficult to investigate because the same scent mark may have a number of different meanings for different individuals, whose reactions are often latent and not apparent. Many authors have suggested possible functions of scent marking: to aid the marker's orientation and memory, increase his confidence and reassurance, allow his social quality to be assessed, deter or intimidate conspecifics from his area, regulate traffic, prevent encounters, act as sex attractants or stimulants and to impart information about sex, age, sexual and social status. However, little is known about chemical communication in domestic cats and one of the greatest needs at the moment is simply good data on where and how frequently cats mark their environment. This chapter first reports on the observation of the spatial patterns of scent marking and second on reactions to scent in a scent discrimination experiment. Cats were presented with samples of sprayed urine and urinated urine from different cats to find whether they could distinguish between the odours and thus whether they could identify individual cats by odour.

(4) Foraging (Chapter 6)

How do cats harvest their food? Cats are perhaps at the height of their crypticity when hunting and only three authors have so far presented data on hunting cats (Gibb, Ward and Ward 1978; Corbett 1979; Liberg 1981). But they have been impeded by having to work at a distance on cats who soon passed out of view. I had the advantage of close observation for as long as hunts lasted and in this chapter their hunting habits are reported in full. Furthermore, observation of their hunting movements is described in terms of their foraging search paths.

Although foraging paths of a variety of species have been plotted there are only two papers on mammals.

(5) Population Dynamics (Chapter 7)

In this chapter data are presented on the population dynamics of farm and house cats living in 100 sq km of Fife. There are many pitfalls in obtaining data suitable for estimating mortality patterns, not least an adequate sample size and an accurate method of ageing individuals. But, while acknowledging these two stumbling blocks and although originally collected as preliminaries to a radio tracking study, the data indicate a general trend in cat survivorship, a subject still waiting to be fully explored.

The unifying factor behind such diverse subjects was the method of data collection - that of following and directly observing tame cats; it permitted the simultaneous recording of a number of different activities and proved to be a very effective means of illuminating the behaviour and ecology of a familiar yet little known carnivore. The final chapter (Chapter 8) discusses the merits of this method and some possibilities of its use in future work.

CHAPTER 2

GENERAL METHOD

Subjects and Study Areas

I gave each cat a threefold name. (1) A capital letter shows a cat's address and status: C - Cornish farm, F - Fife farm, B - captive cat and H - house cat; (2) a small m or f shows thesex; and (3) a number. Thus Cf2 is Cornish female two, Bm3 is captive male three and Hm1 is house male one. Cats came from five sources. Those who were followed are presented in Table 2.1.

(1) Cornish farm cats: These lived at Lower Lanherne, a dairy and arable farm, 8 km north east of Newquay, Cornwall. The farm was typified by large stone and earth walls, thickly covered with vegetation, which separated fields of kale, turnip and grass. The cats' genealogy is shown in Fig. 2.1. Five females were the principal subjects: Cf1, Cf2, Cf3, Cf4 and Cf5; brief notes were kept on the others. The cats were descended from one female, except Cf5, an adult about 3 years old, who immigrated in 1977 so was probably unrelated to the other cats. Cf6 emigrated in 1977 but briefly turned up a few times at the farm during the study. Cm2 was castrated four months before the study began.

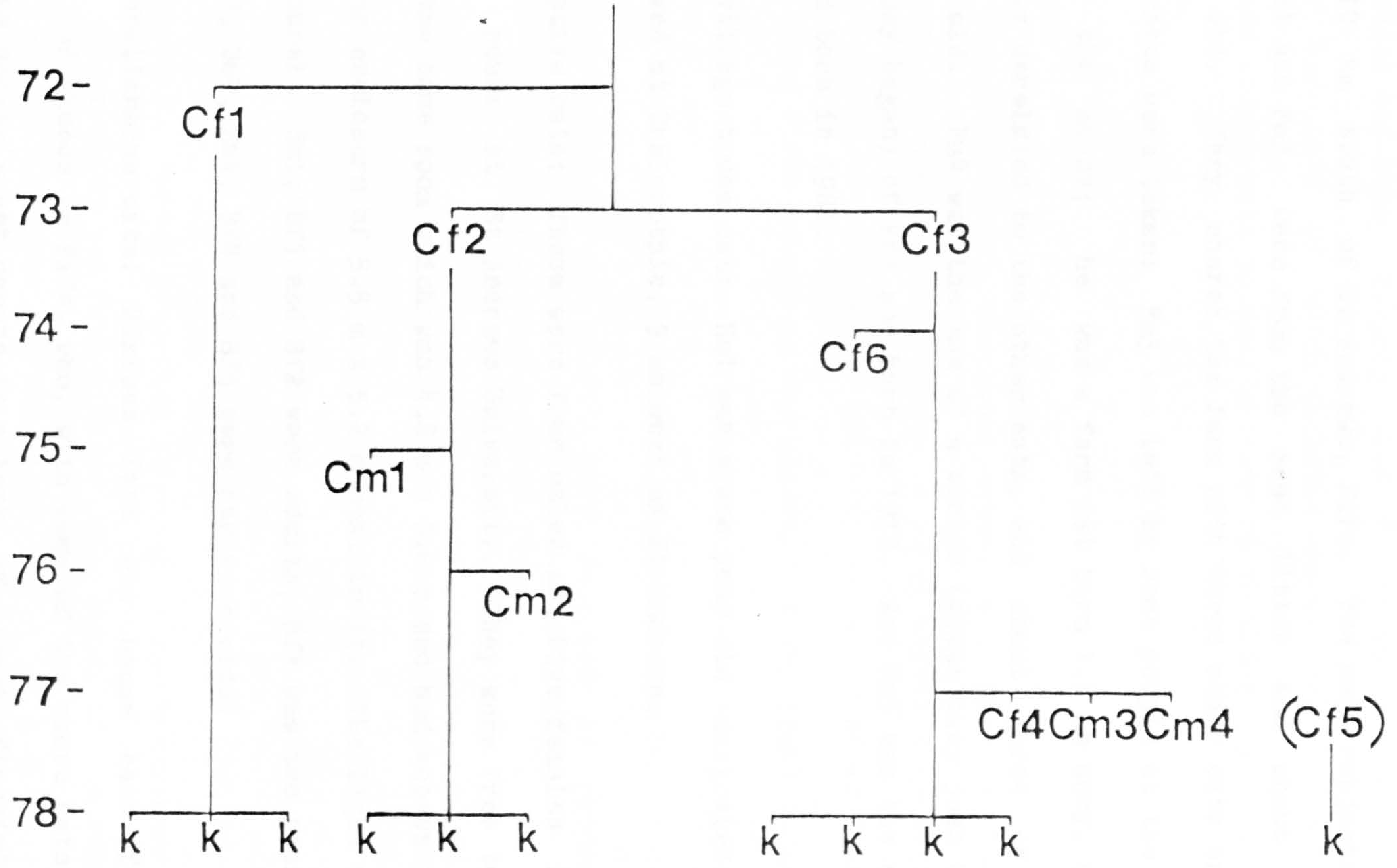


Fig. 2.1 Genealogy of Cornish farm cats present at the time of the study. Year of birth on left. Cf5 immigrated in 1977. k denotes a kitten.

(For more details see under Genetic Relatedness in Chapter 4.)

(2) Fife farm cats: These cats lived at Wester Kellie, an arable farm 10 km south of St Andrews, Fife. The main subjects were Ff1, Fm1 and Fm2. were from the same litter and about three years old. They shared the farm with three other cats on whom brief notes were taken: Fm3 was left by some people at the farm during the study; he was a farm cat born 1.3 km away, so was probably unrelated to the other cats, and about three or four years old. Fm4 was the son of a sister (given away just before the study began) of Ff1 and born in 1979. And Fm5 was the son of Ff1 and born in 1980.

(3) A village house cat: Hm1 was a one year old castrated male who lived at Craigrothie, 9 km west of St Andrews.

(4) Captive cats: These were four males and five females in an animal house at St Andrews University. They were free to move about the same room which was 4.8 m x 6.0 m and had access to an out door enclosure of 5.5 m x 5.2 m next to it. The light regime was natural. Bm1, Bf1 and Bf2 were adults, Bf3 was two years old and Bm2, Bm3, Bm4, Bf4 and Bf5 were one year olds.

(5) Miscellaneous cats: Sixteen farm and house cats from a number of places in Fife, who, with some of the above cats, were subjects and/or scent donors in a test of scent discrimination (see Scent Discrimination Experiment, Chapter 5).

I was directly introduced to the Cornish cats and to Hm1, but drove 3,000 miles in Scotland searching for other places and farms which had cats. Roughly 10.0 % of about 200 farms I visited had cats of which at least one was tame but only five farms had enough cats to make a study worth while. I chose the closest.

Procedure

A free-ranging cat, the focal animal, was observed for the whole of an observation period. A focal animal's activity was recorded as one of a number of mutually exclusive categories (see below) every fifth minute on the minute. If the focal animal was not in sight at the moment of making a record he was recorded as lost to view. During recording intervals other behaviours and routes were noted. Focal animals were selected at random and followed at distances between 1 m and 10 m.

The activity of captive cats was recorded by scan sampling. After recording the activity of the first cat I looked up and recorded the activity of the second one at that instant and so on in a set order of cats until the activity of each individual had been recorded. During recording intervals other behaviours were noted. Observation was from a chair in a corner of the room. At night a veiled lamp provided dim light.

Data were recorded using a wrist watch, pen and note book. A pocket tape recorder was used when following Cf3 in 1980, the Fife cats and Hm1. The behaviour of the captive cats was recorded on a check sheet. A pocket torch projecting a 20 m white beam was used to observe at night. Observation days were selected in advance and adhered to whatever the weather.

Dawn and dusk were estimated as the time, to the nearest five minutes, when the light was just too poor to be able to read with ease from a page of print.

Observation Periods

Each of the five Cornish females was followed three times from the beginning of the first complete hour to the end of the last complete hour of daylight and twice for 24 consecutive hours, from October 1978 to February 1979. The four males were approachable when they were stationary but when followed they were soon lost to view and as their data were mainly limited to stationary situations I stopped following them. Cf3 was followed in February 1980 from 09.00 to 17.00 h for 13 consecutive days.

The Fife cats were observed from April to June and to some extent in July 1981. Ff1, Fm1 and Fm2 were each followed once for 24 consecutive hours. Further following was disrupted because Ff1 gave birth to kittens and Fm2 went missing. Therefore Ff1 and Fm2 were subsequently observed in blocks to make up composite 24 h periods (Ff1 after she had lost her litter, see Infanticide in Chapter 4).

The captive cats were observed in 3 h blocks over 7 days to make up one composite 24 h period in November 1981.

There was a pilot study of 40 h on the Cornish females, 6 h on the Fife cats and 3 h on the captive cats during which the cats became accustomed to me and I to their habits. These data were not used in the analysis. Table 2.1 lists the number of observation hours, excluding pilot study hours, on each cat or group. Free-ranging cats were lost to view for 5.7 % of the time. In addition, the four Cornish males were observed for 59.7 h before I stopped following them. Therefore cats were in sight for a total of 950 h.

Behavioural Categories

All behaviour was classified under eight exclusive categories. (1) Sleeping: when the head was resting on the body or ground. (2) Resting: when stationary. (3) Hunting: a) making a roving search of the environment, that is travelling alertly by walls, long grass and buildings, stopping every few metres and appearing to look and listen intently; b) stationary, attentive and orientated towards a locus, often between bouts of roving searches; and c) pouncing during a) or b). (4) Grooming. (5) Travelling: when locomoting but not when hunting. (6) Feeding. (7) Other activities: everything else, for instance suckling, playing, excreting, clawing, spraying, fighting and allogrooming. (8) Lost to view: when out of sight at the moment of making a record. Categories (3) to (8) are also called 'active behaviour' (that is everything except sleeping and resting) and, for analysis, categories (5) to (7) are sometimes lumped and called 'all-other'.

	Total	Lost to view
Cf1	77.0	7.5
Cf2	76.0	3.7
Cf3	180.0	13.8
Cf4	77.0	6.7
Cf5	76.0	4.0
Ff1	102.0	1.3
Fm1	115.0	6.8
Fm2	61.0	3.1
Fm3	24.0	0.0
Hm1	29.3	0.3
B cats (N = 9)	24.0	0.0
Total	841.3	46.6

Table 2.1 The number of hours cats were observed. The total includes time lost to view, which is also shown separately.

Social Interactions

Three exclusive categories of social interaction were distinguished, based on the behaviour of the male, female or independent kitten initiator. (A) Agonistic: growling, hissing, spitting, swiping, ear flattening, piloerection, and fighting. (B) Amicable: allogrooming, sniffing towards or touching the nose of another cat, playing with another cat, sleeping within 30 cm of another cat, approaching to linger by another cat who was otherwise alone and not near food. (C) Exploratory: sniffing another cat so that the nose of the initiator was less than 5 cm from the other cat, the initiator appearing to be neither agonistic nor amicable.

Home Range Estimation

The maps used to delineate home ranges were Ordnance Survey maps of 4 cm to 100 m (1:2500). The convex polygon (Mohr and Stumpff 1966) and the grid square (Siniff and Tester 1965) methods were used to estimate home range configurations. For the polygon method, the outer positions of a cat's routes were joined to form the smallest convex polygon. The area was estimated by tracing the polygon on a sheet of paper, cutting it out, weighing it on a sensitve balance and calculating its area by simple proportion to a similar piece of papar of known weight and area. For the grid square method, each square represented 20 m x 20 m; the squares through which a cat's routes passed were taken to be the cat's home range and their sum was taken to be the home range area.

Food

The main feeding place of the Cornish cats was two bowls in a 400 sq m area by the farm house. The farmers put out cow milk for them at irregular intervals but often between 07.00 h and 09.30 h, 12.00 h and 17.30 h, and 20.00 h and 01.30 h. Milk was also put out in two bowls at the dairy at midmorning and occasionally at other times. About 5 l of milk were dispensed per day. Meagre table scraps were sometimes put out, and the cats had access to cattle feed in the form of dry pellets.

The feeding place of the Fife farm cats was one bowl in a small byre near the farm house. Their usual fare was a mean of 0.5 l of powered and/or cow milk and a mean of about 200 g of table scraps a day. They also had access to dry pellet cattle food and about eight times a year meat was butchered and they were given scraps. They were usually fed in the afternoon around 14.00 h to 17.00 h.

Hm1 was given up to about 200 g of tinned cat food a day plus cow milk.

The Captive cats were given a mixture of tinned cat food and fruit in three bowls, plus water. They were usually fed in the afternoon around 16.00 h.

Human Activity Times

Humans were active at the Cornish farm between 07.00 h and 01.00 h, at the Fife farm between 08.00 h and 22.00 h and at the captive cat animal house between 09.00 h and 17.00 h.

Definitions

Dawn and dusk: the time, to the nearest five minutes, when the light became just too poor to read with ease from a page of print.

Home range: the area in which an animal goes about his routine daily activity (Ewer 1973).

Territory: the area "occupied more or less exclusively by an animal or group of animals by means of repulsion through overt defence or advertisement" and may be a part or all of the home range or may be limited to the immediate area around an animal wherever he goes (Wilson 1975).

Core area: an area constantly and more frequently used than any other part of a home range and which contains the principal resting sites and dependable food sources (Kaufmann 1962).

Solitary: a cat who lives alone without associating with other cats except for breeding and raising offspring.

Farm cat: a cat who lives at a farm but not with the household and is given little or no human-provided food.

House cat: a cat who lives with a household and is given all or most of his food.

Group (of domestic cats): all the cats attached to one farm or household.

Chapter 3

ACTIVITY PATTERNS AND ACTIVITY BUDGET

Preamble

Little is known about domestic cat activity patterns. Basic questions are to what extent are cats active throughout the day and how much are they influenced by human activity patterns. Even the amount of time they spend asleep is open to question. In this chapter I will examine the activity distribution of cats, compare the activity patterns of different groups of cats and try to find patterns which may go some way towards explaining them, and look at activity budgets and make group comparisons.

The following is a brief description of the method used in this chapter. A more detailed account is given in General Method, Chapter 2.

Subjects

Five female Cornish farm cats: Cf1, Cf2, Cf3, Cf4 and Cf5; one female and three male Fife farm cats: Ff1, Fm1, Fm2 and Fm3; and four male and five female captive cats.

Procedure

Behaviour was recorded as one of a number of mutually exclusive categories (see under Behavioural Categories in the General Method, Chapter 2). A farm cat was followed and directly observed for the whole of an observation period (see below) and the cat's behaviour was recorded every fifth minute on the minute. If the animal was not in sight at the moment of making a record he was recorded as lost to view. The behaviour of the captive cats was recorded every fifth minute by scan sampling; immediately after recording the behaviour of the first cat the behaviour of the second cat was recorded and so on in a set order of cats until the last cat's behaviour had been recorded.

Observation Periods

Each Cornish cat was followed three times from the begining of the first complete hour to the end of the last complete hour of daylight and twice for 24 consecutive hours. They were observed from October 1978 to February 1979. Cf3 was followed in February 1980 from 09.00 h to 17.00 h for 13 consecutive days. Each Fife cat was followed once for 24 consecutive hours and thereafter followed in blocks to make up composite 24 h periods. They were observed from April to June 1981. The captive cats were observed in 3 h blocks, over seven days in November 1981, to make up one composite 24 h period.

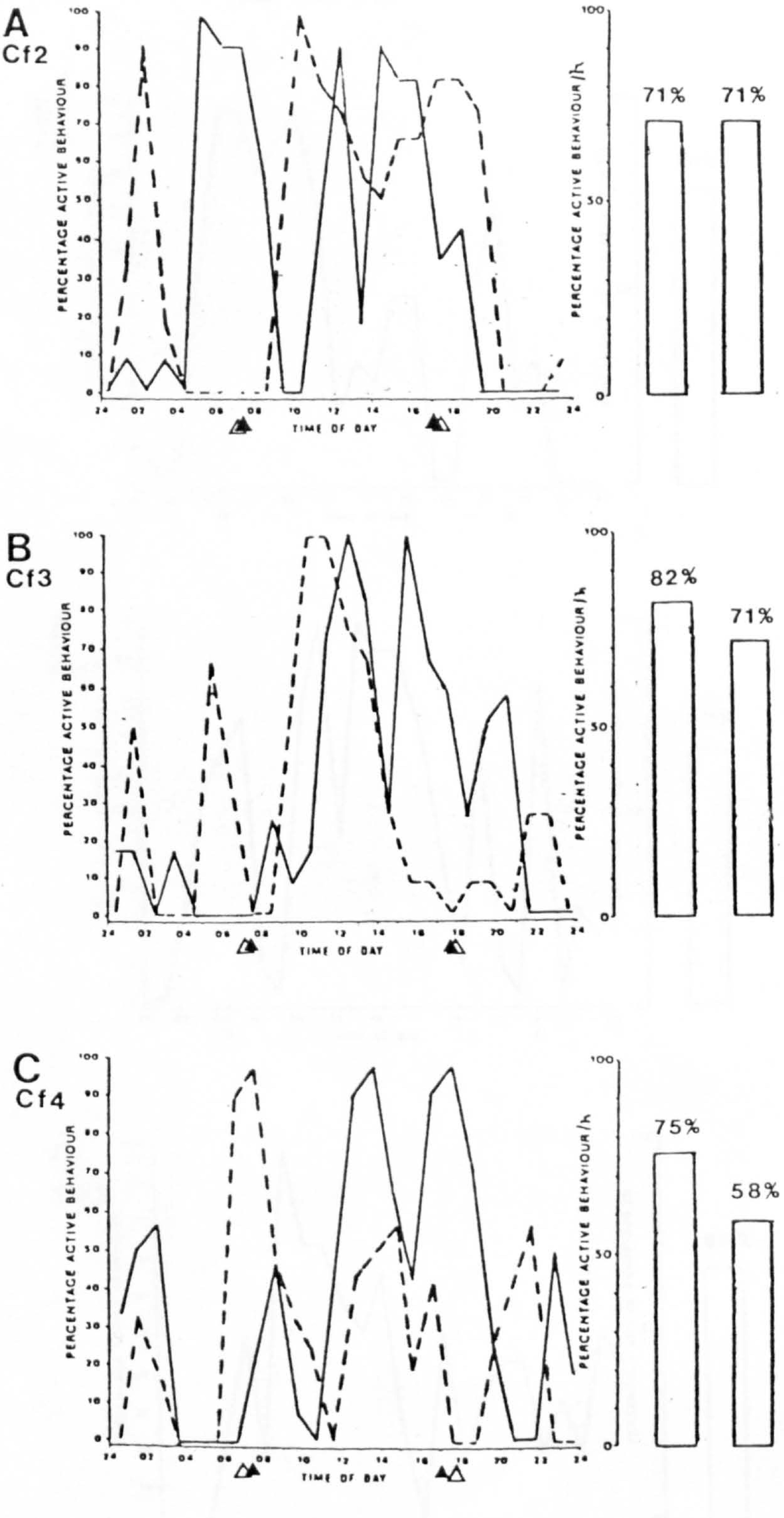
Active Behaviour: 24 h distribution

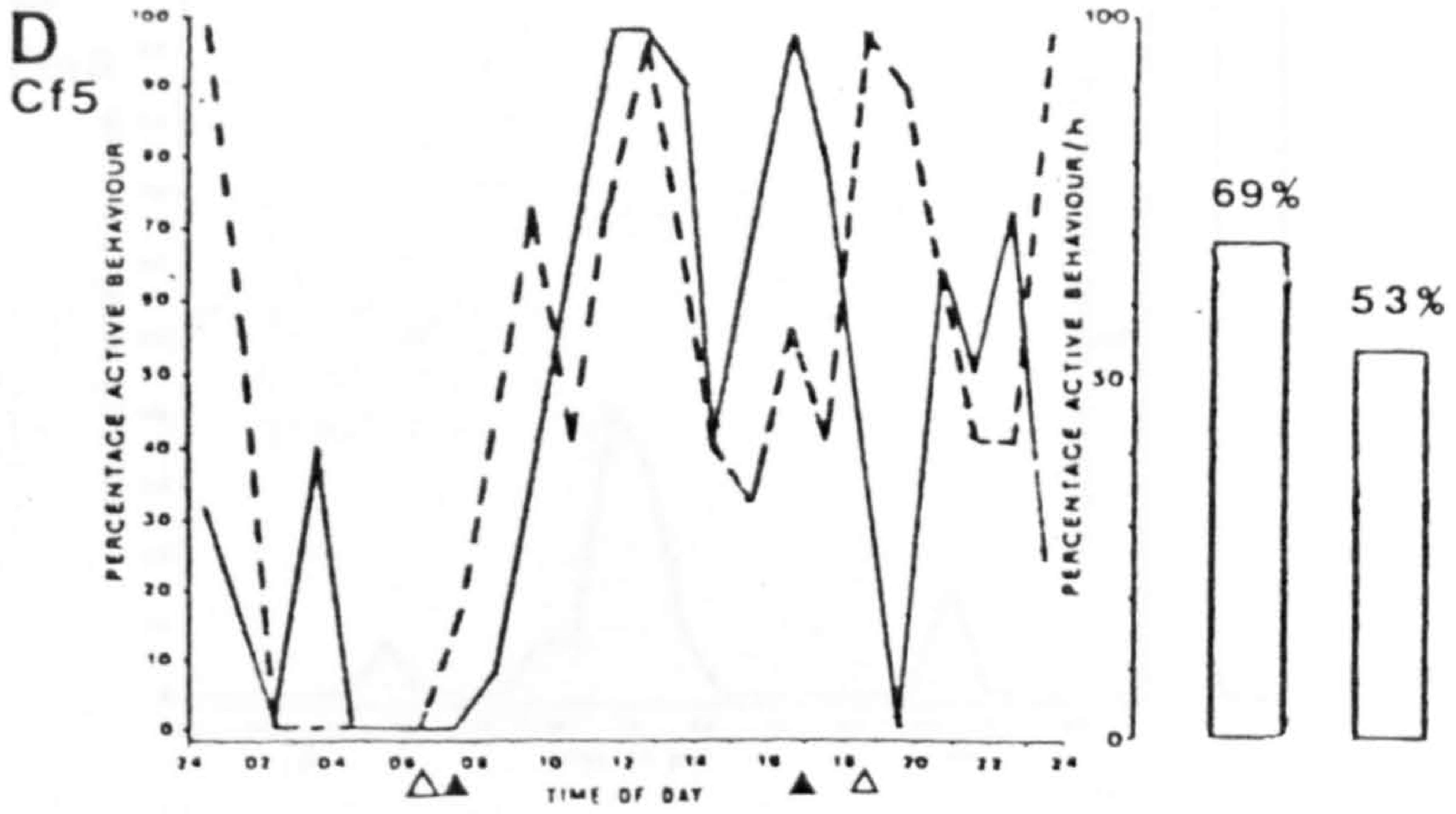
Fig. 3.1 shows the 24 h activity distribution of Cornish, Fife and captive cats. Graphs A to D: four Cornish females

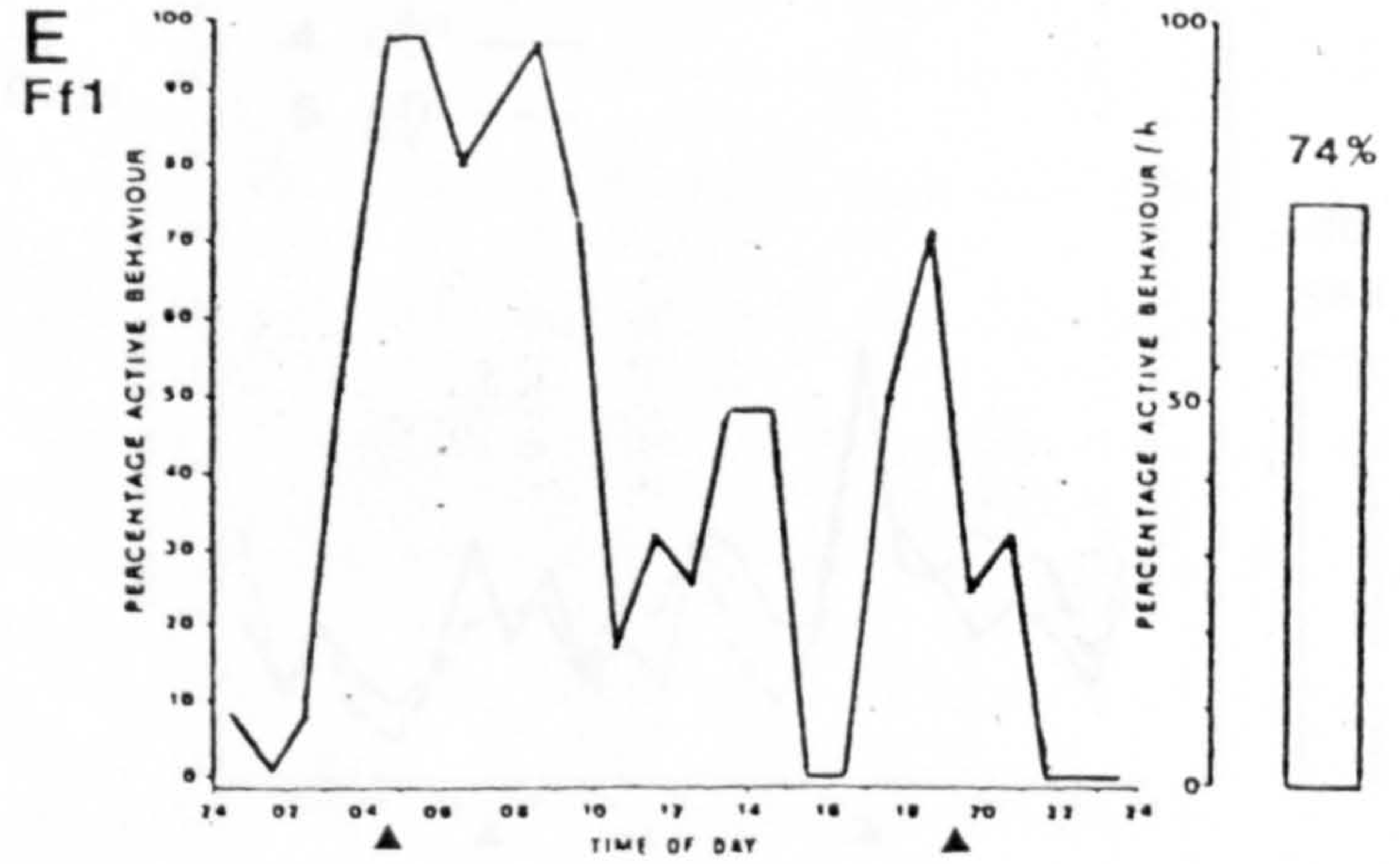
(Cf2, Cf3, Cf4 and Cf5) were active mainly during the day (mean percentage of active behaviour per hour between dawn and dusk 69 %, range 53 % to 82 %). Graphs E to H: the Fife cats (Fm1, Fm2, Ff1 and Fm3) were also mainly active by day (mean percentage of active behaviour per hour between dawn and dusk 77 %, range 65 % to 100 %). The graph of Fm3 shows that he was active very little; he was unkempt, so must have been ill. Graph I: the captive cats were about equally active day and night (mean percentage of active behaviour per hour between dawn and dusk for males 56 %, range 42 % % to 53 %; mean for females 52 %, range 38 % to 53 %).

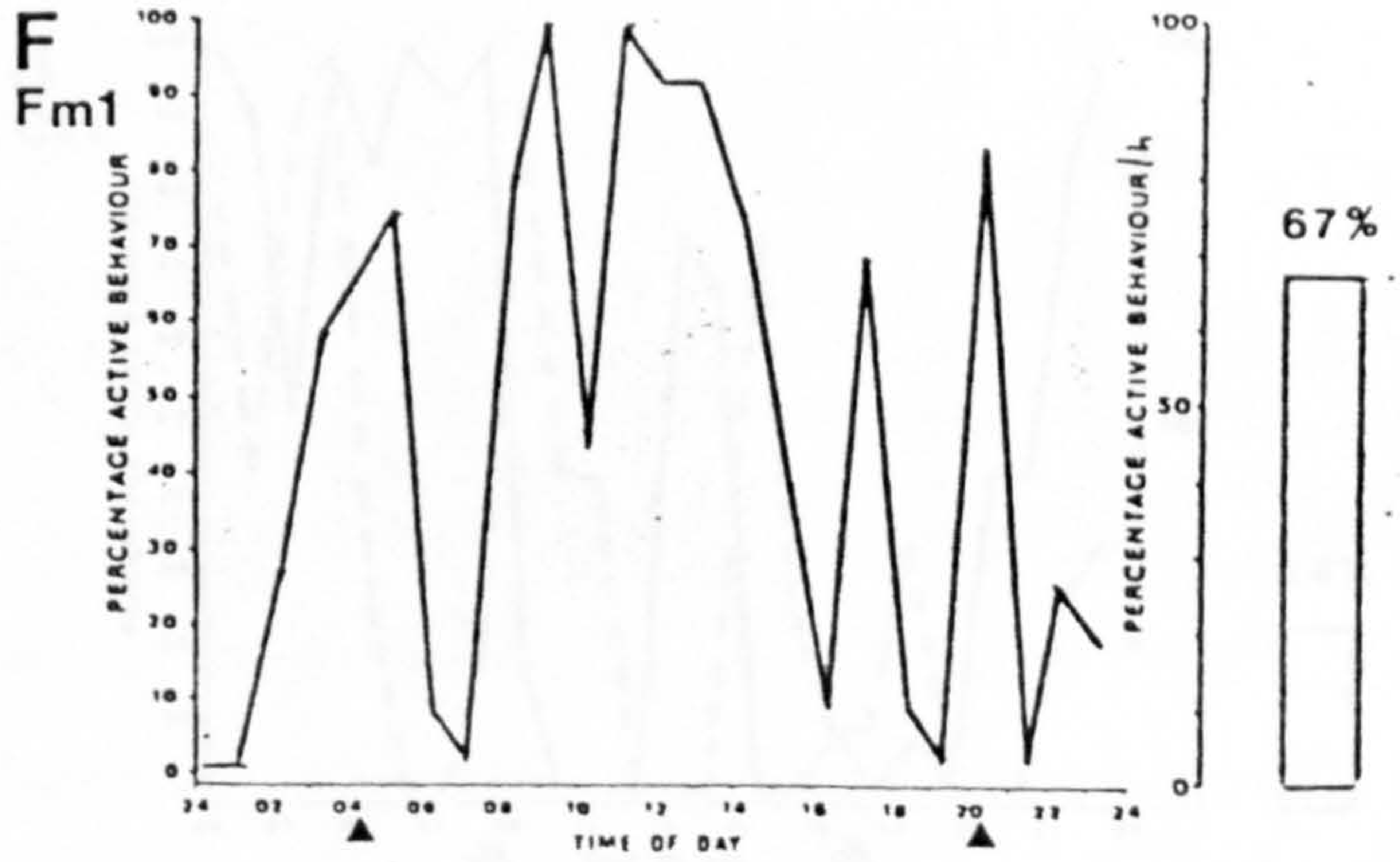
Two females at first had activity patterns like the other cats but changed them during the study. Cf1 hunted but did not sleep during daylight observations and therefore was active mainly by day. But during 24 h observations she had clearly become more active at night (graph J): a mean of 65 % of her activity per hour was at night (53 % and 76 %). Ff1 also became more active at night after the observation shown in graph F. Their activity patterns are superimposed in graph K for comparison. The curve of Cf1 is the mean of her activity from graph J and the curve of Ff1 is the mean of the three composite 24 h periods after her change. The curves are strikingly alike, even though the cats were separated by more than 1,000 km and observed more than two years apart. A correlation of the mean activity level of each hour was $r = 0.730$, $p < 0.001$, $df = 22$. The graph shows that both cats were active mainly from 23.00 h to 04.00 h, when other cats were least active. Much of the curves consist of hunting behaviour (see Fig. 6.1 H).

Fig. 3.1 Percentage of active behaviour by five Cornish females, four Fife cats and nine captive cats. Left: percentage of active behaviour for each hour of the day: solid curve is the first observation for cats observed twice. Right: percentage of active behaviour per hour between dawn and dusk, left bar is for the solid curve. Arrow heads indicate dawns and dusks, solid arrow heads for solid curves. Data are from 24 consecutive hour observations: two on each Cornish female and one on each Fife cat. Observations on other cats are composite 24 hour periods. See text for details.




D
Cf5
PERCENTAGE ACTIVE BEHAVIOUR
100
90
80
70
60
50
40
30
20
10
0
24
02
04
06
08
10
12
14
16
18
20
22
24
TIME OF DAY
PERCENTAGE ACTIVE BEHAVIOUR/h
100
50
0
69%
53%


E
Ff1
PERCENTAGE ACTIVE BEHAVIOUR
100
90
80
70
60
50
40
30
20
10
0
24
02
04
06
08
10
12
14
16
18
20
22
24
TIME OF DAY
PERCENTAGE ACTIVE BEHAVIOUR/h
100
50
0
74%


F
Fm1
PERCENTAGE ACTIVE BEHAVIOUR
100
90
80
70
60
50
40
30
20
10
0
24
02
04
06
08
10
12
14
16
18
20
22
24
TIME OF DAY
PERCENTAGE ACTIVE BEHAVIOUR/h
100
50
0
67%

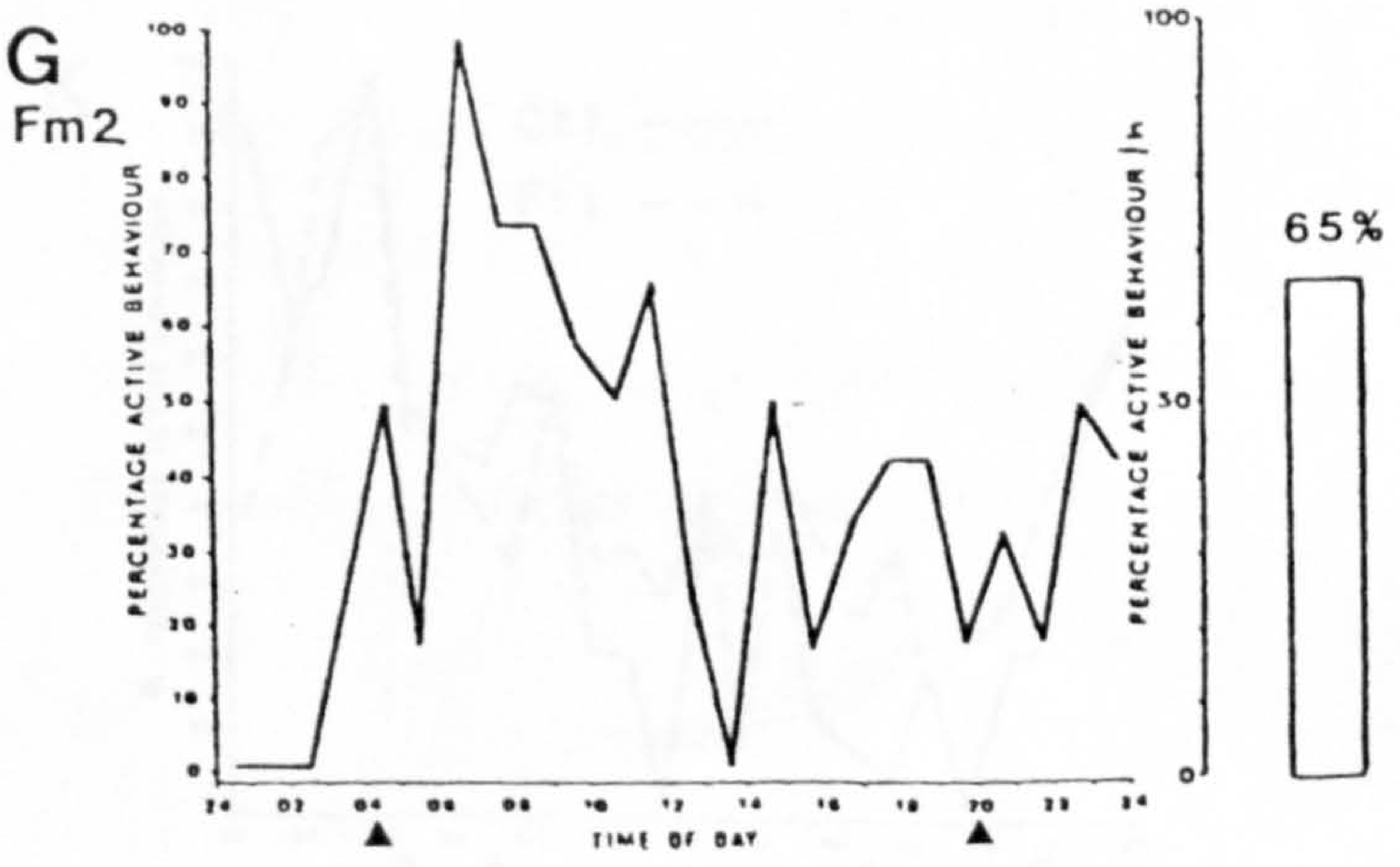

G
Fm2
PERCENTAGE ACTIVE BEHAVIOUR
100
90
80
70
60
50
40
30
20
10
0
24
02
04
06
08
10
12
14
16
18
20
22
24
TIME OF DAY
PERCENTAGE ACTIVE BEHAVIOUR/h
100
50
0
65%

Fig. 3.1 continued

Summarising, cats were active at all hours. However, comparing day versus night activity, the cats were mainly active during the day - contrary to the common belief that cats are nocturnal - but two females did become mainly active at night. The captive cats were equally active during the day and night.

Active Behaviour: activity cycles

An attempt was made to analyse 24 h activity patterns for cycles of activity. The data were regarded for each cat as the number of times a cat was active out of 12 records per hour. (Activity was all behavioural categories except sleeping and resting.) Thus, one 24 consecutive hour observation yielded 24 consecutive observations from a binomial distribution with parameters 12 (the number of records per hour), and θ_t, where θ_t is the probability that a cat was active at time t. The variance of the binomial distribution is not constant but depends on its mean so that the traditional form of spectral analysis which assumes constant variance is not appropriate in this case. The data were analysed by fitting the first nine harmonics as fourier series by iterative maximum likelihood estimation. The G.L.I.M. package (GLIM System Release 3 Manual, General Linear Interactive Modelling, Numerical Algorithm Group, 1978) was used to carry out the fitting. In GLIM terms, the error structure was binomial and the default link for binomial error (logit) was used. The adequacy of fit of any model can be tested objectively. If its deviance exceeds the upper five percent point of the chi-squared distribution with corresponding degrees of freedom the model is inadequate. The contribution of an individual harmonic is significant if it exceeds the upper one percent point of the chi-squared distribution with two degrees of freedom, that is 9.2.

Table 3.1 shows the number of cycles (k) each 24 h observation was found to be composed of. Only the values which reached significance ($p < 0.01$) are shown for clarity. The size of each value per column equals its contribution to the activity curve, for example in the first column 178.7 accounts for 178.7/305.5 or 58.5 % of the curve. Comparisons among cats and between observations of a cat observed twice may be made using the two values in each column which contributed most to a cat's activity (marked with an asterisk). The Table shows that most harmonics were of low frequency and that almost all cats showed one and two cycles per 24 h. No activity curve was found to be composed of more than nine cycles. The locations of the two largest values per column suggest there was much variation between cats; comparing the same Cornish cat on both observation days, Cf3 was the most consistent, with the same pattern on both days, and Cf1 was the most variable.

The fact that the curves can be explained in terms of harmonics does not necessarily mean the cats' activity was cyclic, because random generated curves may also be shown to be built of harmonics. The lack of a consistent pattern between cats and between observations of the same cat suggests the cats' activity did not occur in cycles. However, the data fall below the amount needed for an adequate statistical analysis, for which at least 60, and preferably more than 100, consecutive hours of

k	Cf1	Cf1	Cf2	Cf2	Cf3	Cf3	Cf4	Cf4	Cf5	Cf5	Ff1	Fm1	Fm2
1	178.7*	24.2	63.0*	68.3*	55.6*	100.2*	55.7*	15.3	84.3*	40.2	33.9*	35.4*	-
2	95.0*	19.1	83.9*	10.0	29.8	-	25.3	9.2	37.6*	50.7*	102.3*	-	37.6*
3	-	36.4*	10.5	101.6*	16.3	-	11.9	24.8	-	21.8	29.9	50.3*	9.2
4	31.8	27.0*	20.6	-	10.8	-	17.8	28.7*	24.9	42.2*	22.2	20.8	-
5	-	26.4	14.9	-	21.8	12.1	60.0*	24.9*	-	-	24.3	13.8	-
6	-	16.4	18.9	-	31.8*	34.9*	-	12.4	16.0	-	-	29.6	10.3*
7	-	24.0	-	-	12.2	-	-	-	-	-	9.5	-	-
8	-	-	18.4	-	-	12.8	-	-	-	-	-	33.4	9.6
9	-	-	-	-	-	-	-	-	9.2	-	-	-	-

Table 3.1 The binomial powers for the first nine significant harmonics (k) of each 24 h observation per cat. The data are from 24 consecutive hour observations: two on each of five Cornish cats and one on each of three Fife cats.

observation per cat are necessary, which might be why a consistent pattern of cycles was not detected.

Active Behaviour: other studies

Almost all the minuscule data on the activity patterns of other domestic cats, whether free-ranging or captive, has been gleaned during the course of studies on behaviour other than activity patterns.

In free-ranging cats, Derenne (1976) observed feral cats living on Kerguelen archipelago which were active during the day but especially active at night. Laundre (1977) observed a group of farm cats in Wisconsin which were active to some unknown extent during the daylight. Macdonald and Apps (1978) studied a male and three female cats at a farm in Devon which spent most of the daylight in their core area and travelled outside it after dark. Rabbits (Oryctolagus cuniculus) living in a large enclosure in New Zealand were studied by Gibb, Ward and Ward (1979) who noted the activity of cats which preyed upon them; the cats hunted by day but were more active in the afternoon and were seen hunting at all times of night. Fitzgerald and Karl (1979) set up cat live-traps in a New Zealand forest during daylight hours and a few feral cats were caught indicating there was some diurnal activity. Finally, on the largely uninhabited Heisker Island in the Outer Hebrides, Corbett (1979) observed that feral cats hunted mainly in the evening. These studies used direct observation but Macdonald and Apps (1978) also used radio telemetry.

In captive cats, Sterman et al (1965) recorded the sleeping patterns for 23 h periods of eight cats of both sexes with chronically implanted electrodes. The cats were free to move about in chambers in stable environmental conditions. Light was turned on from 08.00 to 20.00 h. The cats were most active just before light onset and just after light offset. Most sleep was in the middle of the light period and a bit less in the middle of the dark period. For 22 h periods Ursin (1970) monitored the cortical electrical activity of 12 adult cats of both sexes who were free-moving in constant light in a chamber. The cats showed an awake peak around 22.00 h and a sleep peak around 13.00 to 17.00 h.

These data (also see Dards (1979) below) support my own in that it may be concluded that domestic cats may be active during the day as well as night.

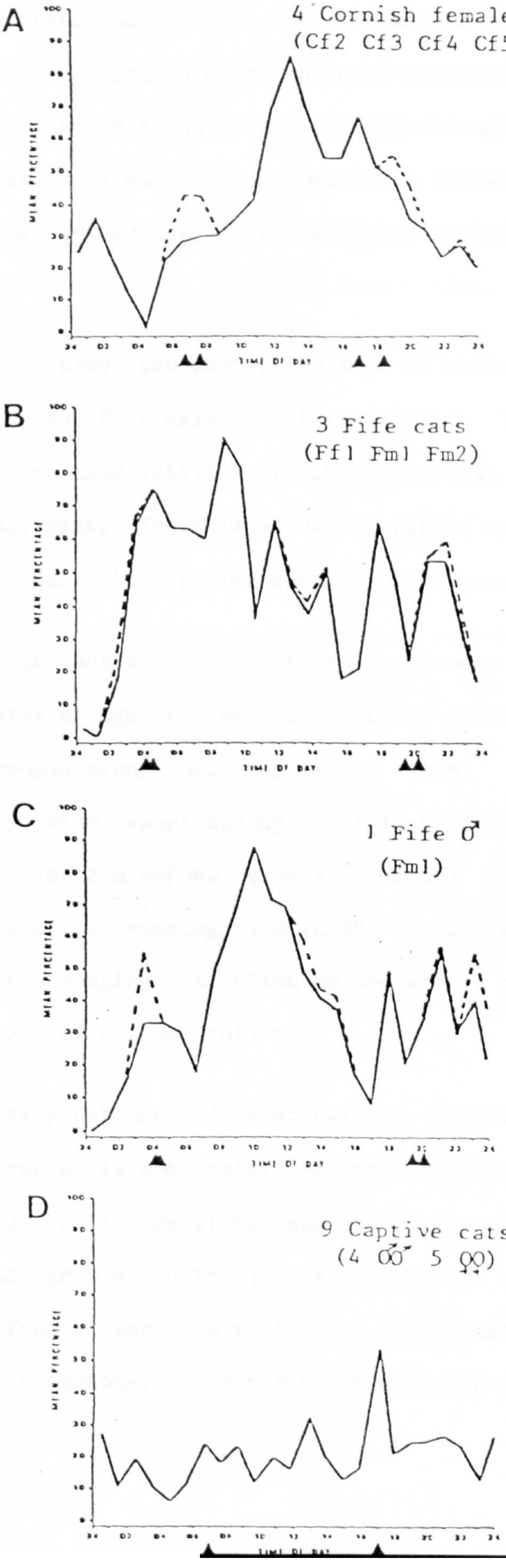
The only data on other small felids which have been published is on wildcats (<u>Felis silvestris</u>), which are similar to domestic cats so might reflect activity patterns of feral cats. Schuh, Tietze and Schmidt (1971) observed wildcats in the Harz area. The peak of activity was in the evening. Kolb (1977), taking most information from de Leuw (1957), states wildcats are nocturnal with dawn and dusk peaks but in the summer they hunt in the daytime. Schauenberg (1981), in a review of diverse authors, concludes that wildcat activity is irregular but the main periods are at dawn and dusk; late at night they are inactive. The most detailed study of wildcats has been carried out by Corbett (1979), using radio telemetry. He interpreted radio signals as indicating wildcats were active in every hour of the day but predominantly between 16.00 and 02.00 h. Summer activity was almost exclusively within this period but winter activity was spread over more of the day. The wildcats did not show a bigeminus pattern, in which there are two activity peaks with the first higher than the second (Aschoff 1966), as reported for some (non-felid) carnivores. Again, one may conclude that wildcats, like the cats in my study, may keep flexible hours, although they appear to emphasise evening activity.

Comparison of Activity Patterns

Fig. 3.2 shows a comparison of the mean activity patterns of Cornish, Fife and captive cats. Fig. 3.2 A shows the mean percentage of active behaviour by the four dirunal Cornish females (Cf2, Cf3, Cf4 and Cf5) for each hour of the day. There is a trough of activity in the early hours (around 04.00h) and a peak of activity around midday. More tenuously, and assuming the cats were active when lost to view (dashed curve), there are minor peaks of activity around dawn and dusk.

Fig. 3.2 B shows the mean percentage of active behaviour of two males and a female (Fm1, Fm2 and Ff1) at the Fife farm. There is an early morning trough of activity before dawn (around 01.00 h) and a midday period of activity (11.00 h to 15.00 h). The dawn activity (03.00 h to 05.00 h) extends till late morning (up to 10.00 h); there is an active period around dusk (17.00 h to 22.00 h).

Fig. 3.2 Mean percentage of active behaviour per hour by four Cornish, three Fife and nine captive cats. Dashed curves show additional percentage lost to view. Arrow heads indicate the earliest and latest dawns and dusks. Data are from two 24 consecutive hour observations on each Cornish cat and one on each Fife cat; captive cats were observed in 3 h blocks to make up one 24 h period.



More data are available for one male (Fm1). (The other male went missing and the female changed her activity patterns, see above.) The distribution of his active behaviour from Fig. 3.2 B and from three composite 24 h periods were averaged and are shown in Fig. 3.2 C. There is an early morning trough of activity before dawn (24.00 h) and a midday peak. An active period occurs around dawn and another active period (three peaks) occurs around dusk.

Fig. 3.2 D shows the mean percentage of active behaviour of the captive cats, four males and five females. This graph also shows an early morning activity trough before dawn (around 04.00 h) and a midday peak. There is an active period around dawn (two peaks) and another active period around dusk.

Thus all the activity patterns are similar in that they show an early morning trough and peaks of activity around midday, dawn and dusk. Troughs occur about 3 h before dawn. Midday peaks, however, vary from about midday (that is half way between dawn and dusk) to about 2 h before midday. Midday peaks are more obvious in the free-ranging than in the captive groups possibly because the free-ranging cats often hunted around midday whereas the captive cats of course could not.

The activity patterns of feral cats in Portsmouth Dockyard have been studied in some detail by Dards (1979). She directly observed two groups in the winter and one of the groups in the summer. Both groups consisted of four females. Their activity was recorded from a car every 5 min in blocks to make up composite 24 h periods, one for the summer group and two for the winter groups. Mature males were less sedentary than other cats and were impossible to follow because of their evasive behaviour. She found that females in winter were active at most hours but mainly during the daylight (80 % between 06.00 and 18.00 h, from her Fig. 8.3); there was a peak around dawn at 07.00 h and another before dusk at 15.00 h. In summer the females appeared to be arrhythmic. Dards (1979) also observed three immature males (19 to 26 months old) and four kittens in the winter. Their activity patterns reflected the females' but with a third small peak between 22.00 and 01.00 h.

Like all but two of my farm cats, the Portsmouth Dockyard cats observed in winter were mainly active by day and showed a dawn activity peak. However, the mean distributions of active behaviour of the dockyard and farm cats were otherwise different. Living in a different habitat may not account for this because the mean activity distribution of the farm cats did not differ greatly from the captive cats', who lived in very different ecological circumstances. In the discussion I shall go on to consider how the farm cats' activity distribution may be explained but will now turn to a comparison of behavioural categories.

Comparison of Behavioural Categories

Fig. 3.3 shows the mean percentage of behavioural categories for the four Cornish females, three Fife cats and nine captive cats. The various behaviours occurred at all hours but were concentrated into certain periods. Fig. 3.3 A shows that all three groups slept most during three to four hours before

Fig. 3.3 Mean percentage of behavioural categories per hour by four Cornish females, three Fife cats and nine captive cats. A - sleeping and resting, B - hunting, C - grooming and D - all other and lost to view. Arrow heads indicate earliest and latest dawns and dusks. Data are from two 24 consecutive hour observations on each Cornish cat and one on each Fife cat; captive cats were observed in 3 h blocks to make up one 24 h period.

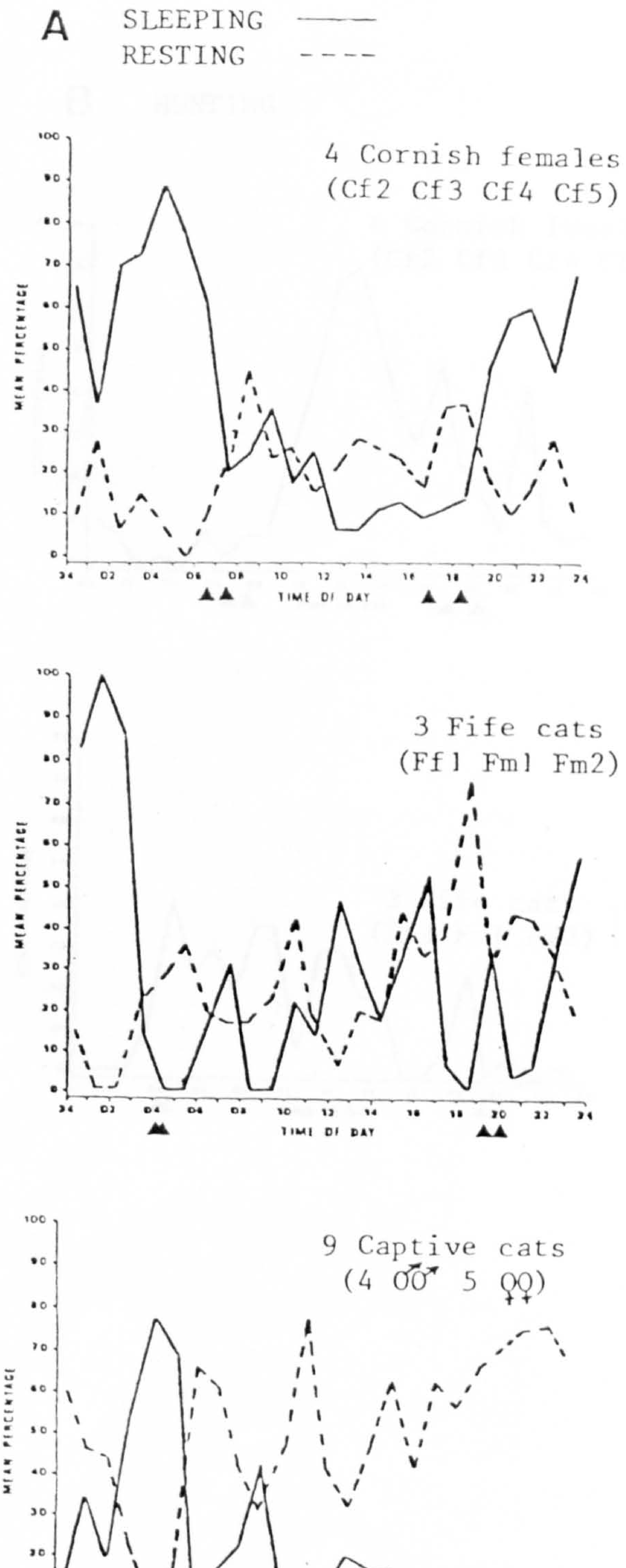
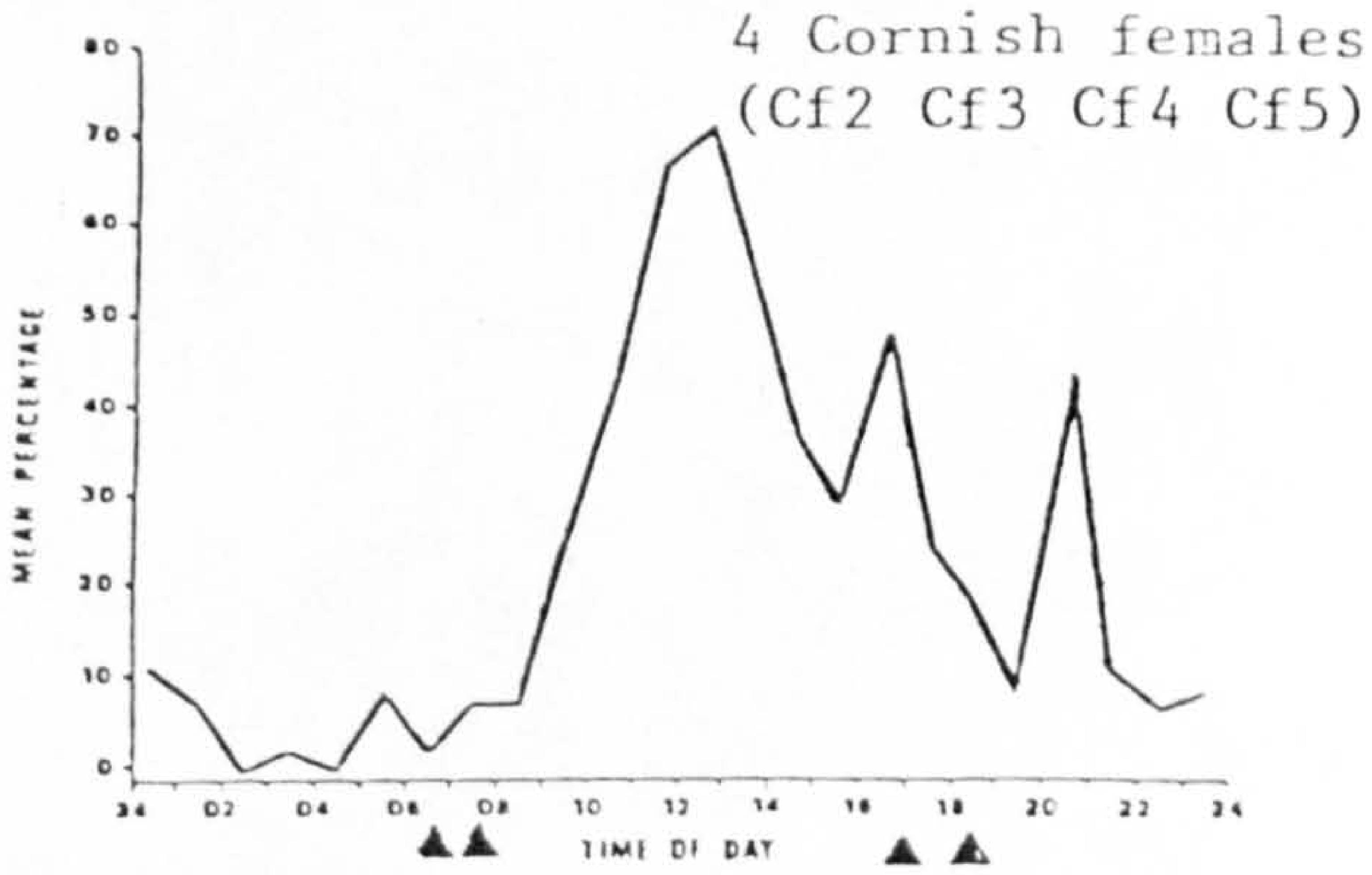
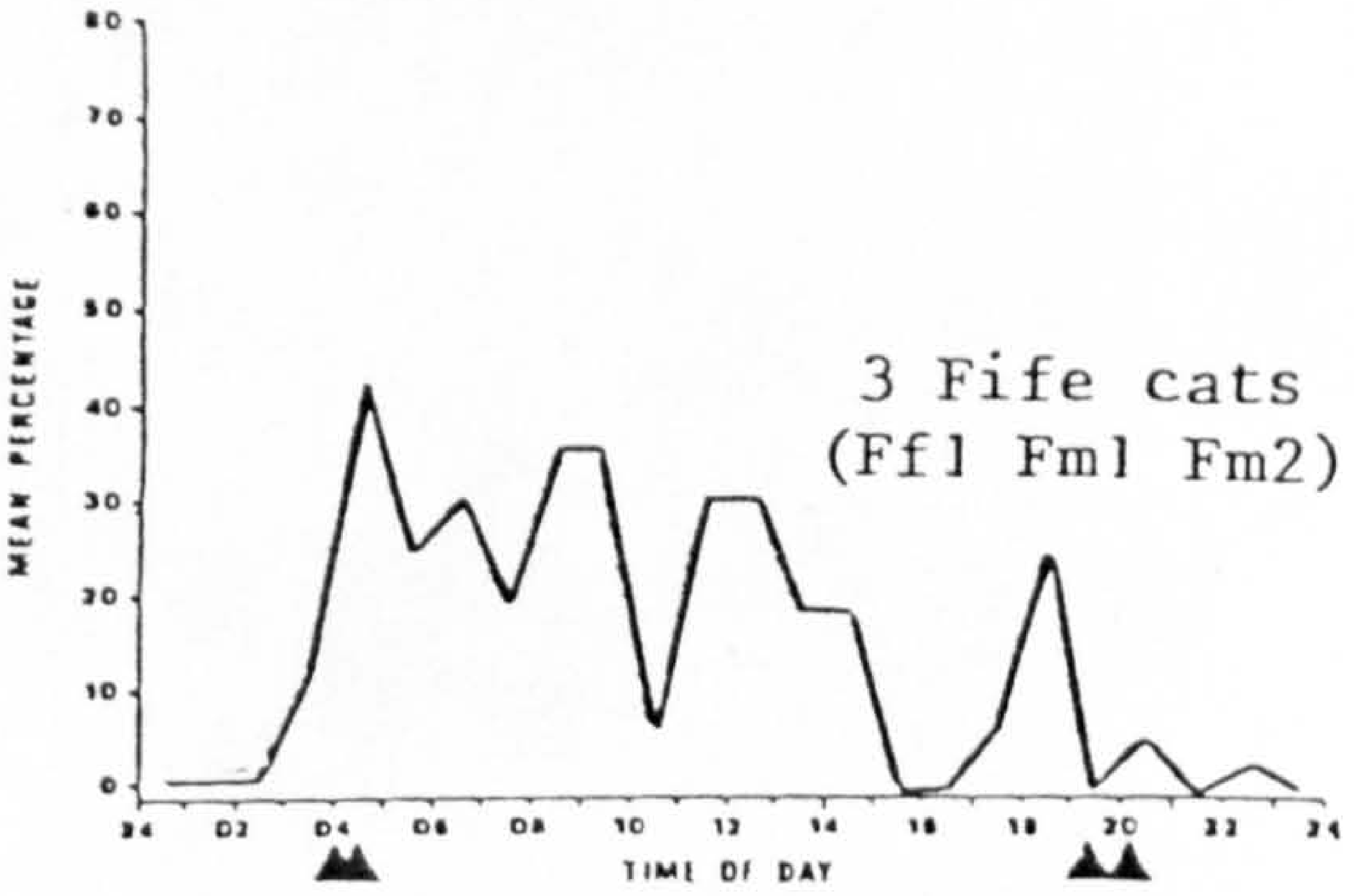


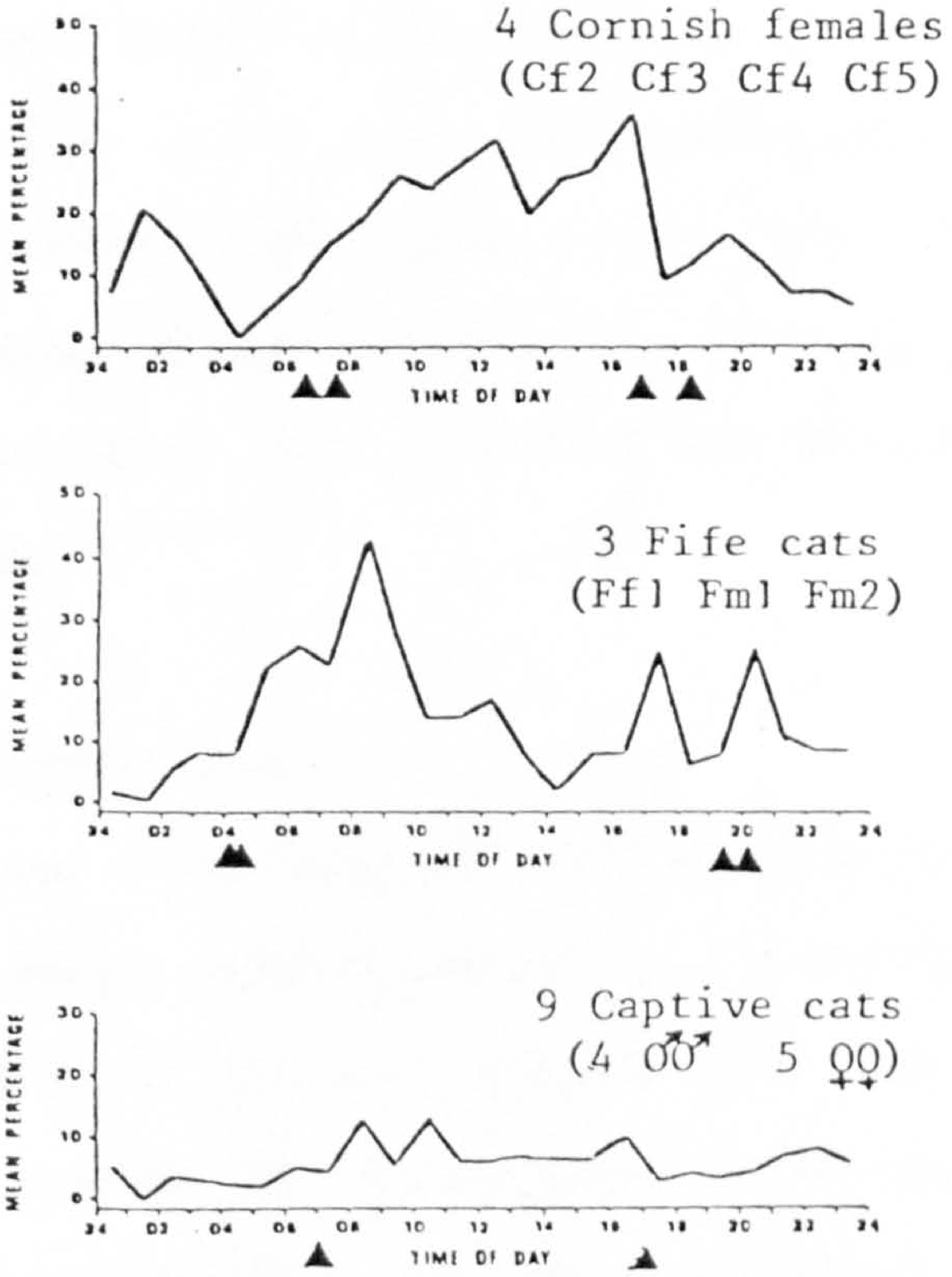
Fig. 3.3 continued

B HUNTING





C GROOMING

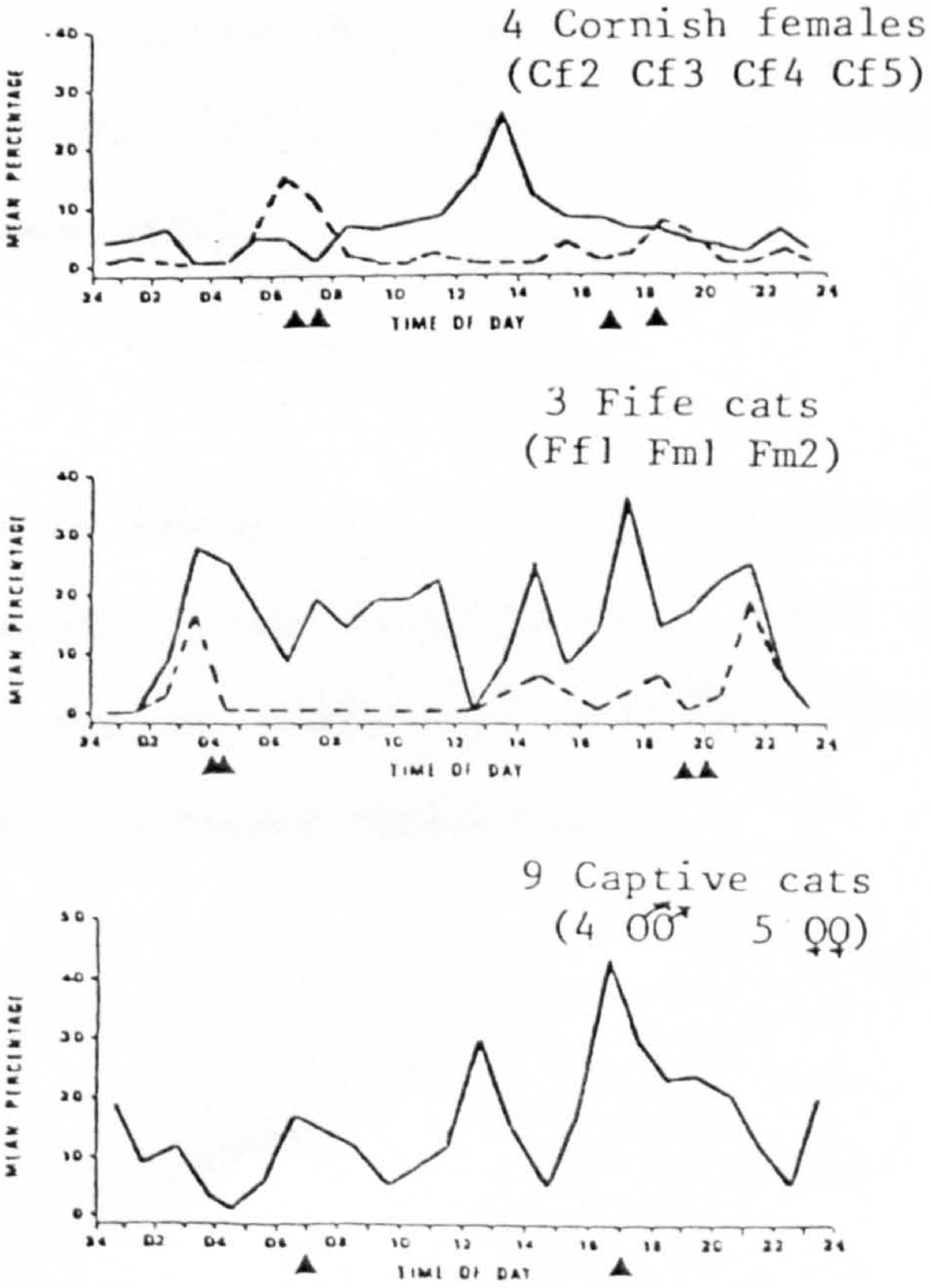


4 Cornish females (Cf2 Cf3 Cf4 Cf5)

3 Fife cats (Ff1 Fm1 Fm2)

9 Captive cats (4 ♂♂ 5 ♀♀)

D ALL OTHER ———
LOST TO VIEW - - - -



4 Cornish females (Cf2 Cf3 Cf4 Cf5)

3 Fife cats (Ff1 Fm1 Fm2)

9 Captive cats (4 ♂♂ 5 ♀♀)

dawn. Resting was least during this time and erratic for the rest of the day. Fig. 3.3 B shows that free-ranging cats hunted during the day, particularly after dawn (for Fife cats), at midday and to a lesser extent around dusk. Grooming (Fig. 3.3 C) and all-other (Fig. 3.3 D) occurred most frequently during the daylight hours.

Variability of Activity Levels

The correlation of the mean level of activity for each hour by captive males versus captive females was $r = 0.758$, $p < 0.001$, $df = 22$; Fig. 3.1 I); the mean activity level for males and females during a week of observation, therefore, was highly synchronised. As a comparison, the same correlation for the two days each free-ranging female was observed (Fig. 3.1, graphs A to D and J) ranged from $r = 0.023$ to 0.375. Even when blocks of three consecutive hours were averaged, starting arbitrarily at 24.00 h, the correlation was low, $r = 0.016$ to 0.627. Thus a free-ranging female's activity level was poorly synchronised on days about two weeks apart.

Activity budget

Fig. 3.4 shows the mean 24 h percentages spent in each behavioural category by the three groups of cats: five Cornish females, two male and one female Fife cats (Fm1, Fm2 and Ff1), and four male and five female captive cats.

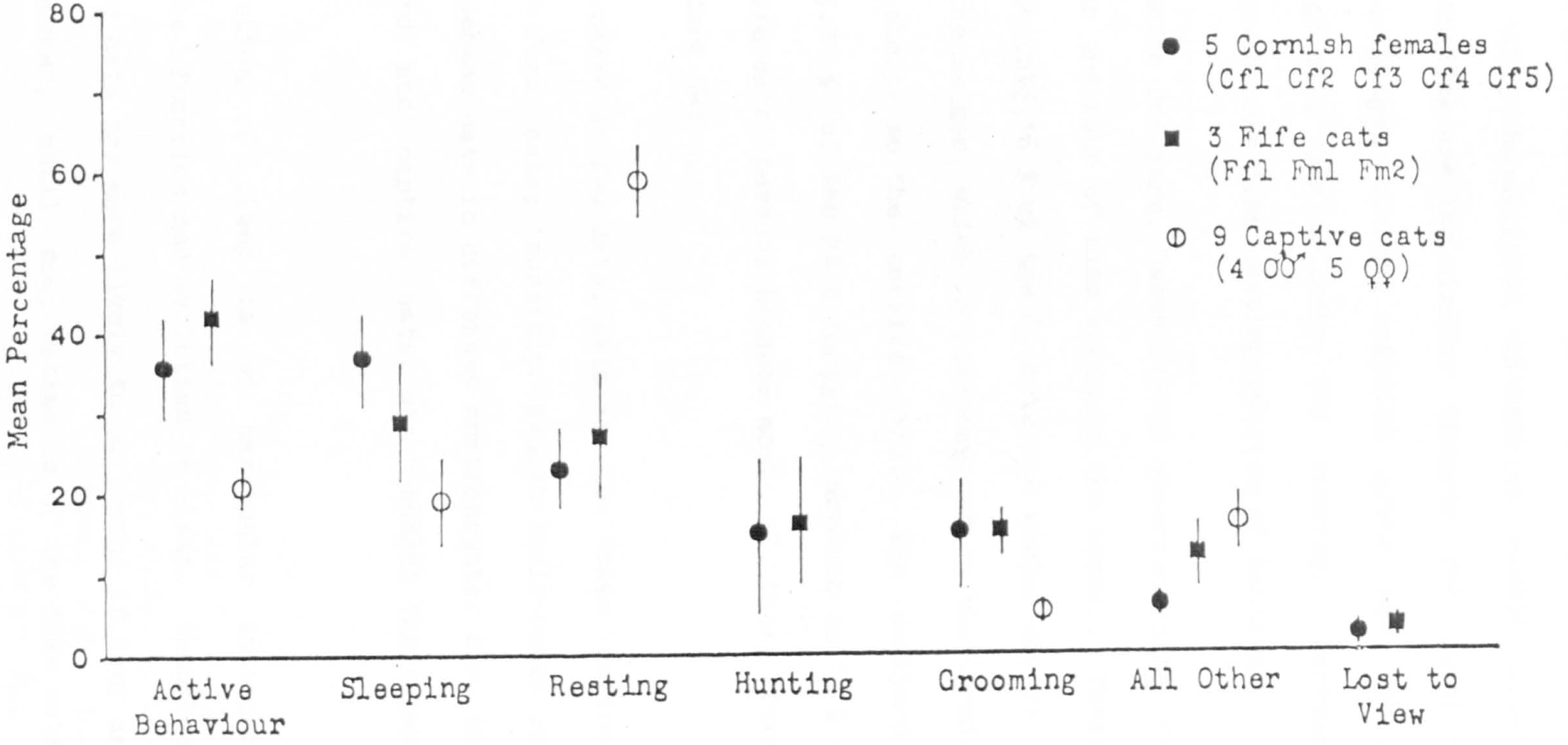


Fig.3.4 Mean percentage ± standard deviation of behavioural categories of three groups of cats. Data are from 24 consecutive hour observations: two on each of five Cornish females and one on each of three Fife cats. The group of captive cats was observed in 3 h blocks to make up one composite 24 h period.

The mean and variation of both free-ranging groups are similar for all behavioural categories except all-other. Particularly striking are the similar budgets for hunting and grooming. The budget of the captive group was unlike the free-ranging groups, particularly for resting. Perhaps the captive cats spent more time resting in lieu of hunting.

In Portsmouth Dockyard, Dards (1979) observed eight females in the winter and four of them again in the summer. These cats were active for only 16 % of the 24 h in the winter and 24 % of the 24 h in the summer, which is low compared to the Cornish and Fife cats but closer to the captive cats. The dockyard cats spent only 3.2 % of the 24 h foraging compared to 15 % by the Cornish and Fife cats, perhaps because most of their food was found in builders skips.

Although based on few data, cats in the same environment, for instance farm cats, possibly budget their behaviour in a similar way whereas cats in different environments, for instance farm, dockyard and captive cats, might budget their behaviour differently.

The duration of sleep is of particular interest for explaining the function and evolution of sleep. Theories based on comparative data are more likely to be useful if they are well founded. However, until now, estimates of the time cats spent asleep have been based on sleep studies of laboratory cats, who have spent 55 % to 66 % of the 24 h asleep (Sterman et al 1965; Jouvet 1967; Ursin 1970). This has led to a belief that all domestic cats sleep for most of the day (for instance Jouvet

1967). But the Cornish and Fife cats respectively slept a mean of 8.9 h and 6.9 h (Fig. 3.4), which is comparable to the time humans sleep. Extrapolating data from captive to free-ranging cats might therefore be wrong. I cannot say whether the mean of 4.6 h (Fig. 3.4) the captive cats slept was usual or the result of my presence. They did not appear to be especially active because of me but even if they had been the figure still suggests they spend a lot less than half the day asleep.

The captive group spent much less time grooming than both free-ranging groups, perhaps because the captive cats' environment was cleaner. However, the Portsmouth Dockyard cats studied by Dards (1979) spent only 4.8 % of the time grooming (including allogrooming and excreting) so this might not be the explanation.

The percentage of the 24 h spent by Cornish, Fife and captive groups respectively in the three behavioural categories comprising all-other was 2.3 %, 5.3 % and 5.4 % travelling; 2.3 %, 2.6 % and 3.8 % feeding; and 1.5 %, 3.6 % and 6.8 % other.

Discussion

Far from being nocturnal, as domestic cats are generally presumed to be, all free-ranging cats were active at all hours but were mainly active during the day. However, one female in both free-ranging groups became mainly active at night. This happened to Cf1 in December and the reason was not apparent. She shared the same physical environment as the other cats at her farm and appeared to be in good health. It may have been social because she was attacked periodically by Cf5 and might have tried to avoid her. But this is just speculation. Another female, Cf4, was also periodically attacked by Cf5 but did not become more night-active.

Ff1 became mainly active at night in May and again the reason was not evident. I tried observing her brother, Fm1, in late June and in July but had difficulty finding him. His activity pattern seemed to have changed because instead of hunting around midday he appeared to hunt in the hours before dawn when earlier in the spring he had been asleep. Consequently he may have become mainly active at night. Thus some cats might change their activity patterns towards summer and become more night-active; Ff1 might have changed too, before Fm1.

The distributions of the mean percentage of active behaviour by the three cat groups were too similar to have occurred by chance. Why? The captive cats did not hunt and the free-ranging cats were probably not responding to prey activity peaks (see the discussion in Chapter 6). Nor, probably, were the cats responding to feeding times or to activity patterns of humans because these were different at each place. The three groups were separated in space and time so the similarity is probably due to global factors: they may have been entrained to aspects of the climate.

Fig. 3.5 is a representation of the mean hourly variation of solar radiation and air temperature (adapted from Geiger 1965; Rosenberg 1974; Gates 1980). Solar radiation is at a minimum when the sun is below the horizon at dawn and dusk and is at a

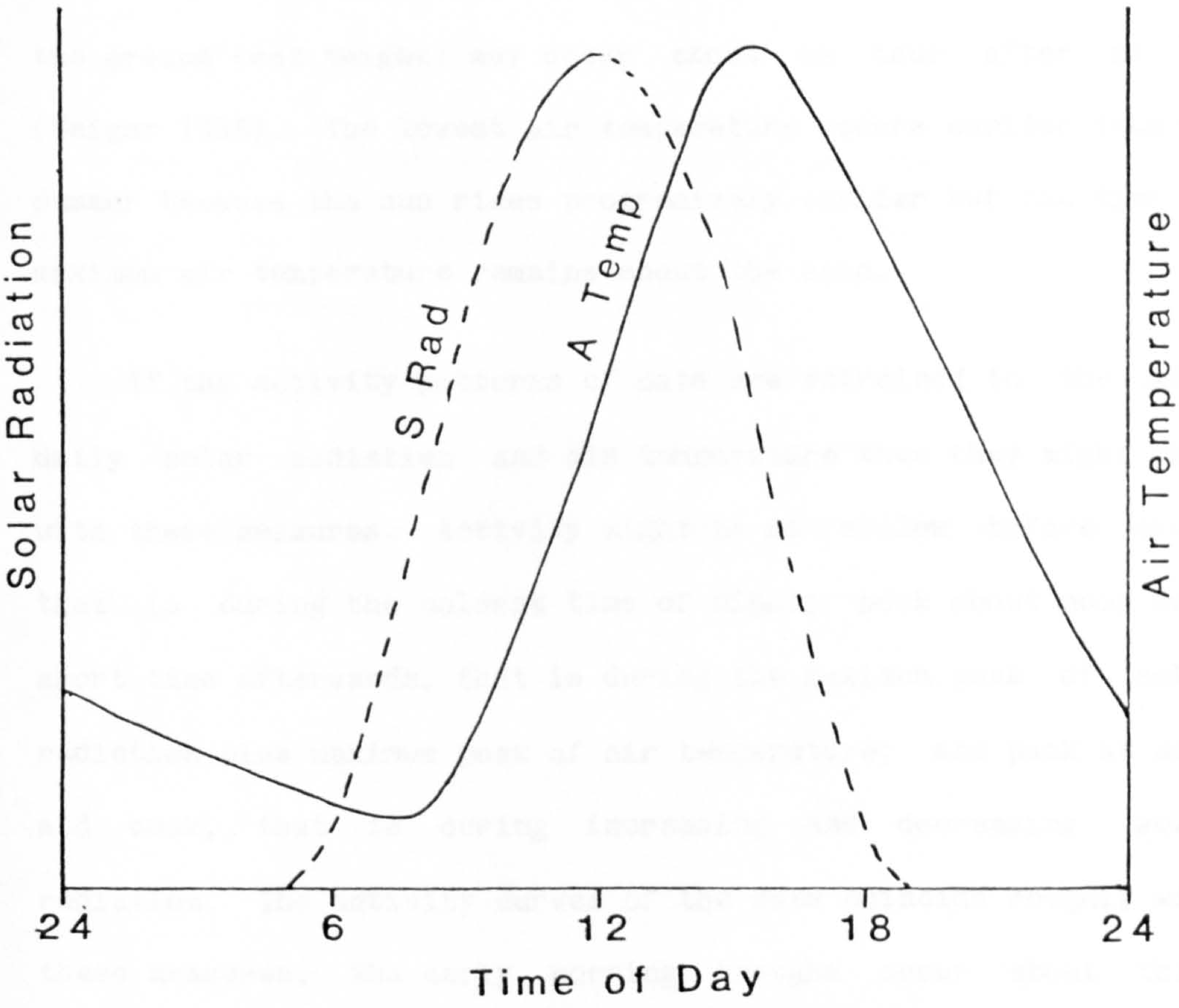


Fig. 3.5 Mean hourly distributions of solar radition and air temperature.

maximum when the sun is overhead at midday. It is more intense in summer than in winter but peaks about the same time. The mean air temperature is lowest just after dawn and is at a maximum some time after midday; the maximum air temperature 10 cm above the ground (cat height) may occur about an hour after midday (Geiger 1965). The lowest air temperature occurs earlier towards summer because the sun rises progresively earlier but the time of maximum air temperature remains about the same.

If the activity patterns of cats are entrained to the mean daily solar radiation and air temperature then they might vary with these measures. Activity might be at a low before dawn, that is during the coldest time of night; peak about noon or a short time afterwards, that is during the maximum peak of solar radiation plus maximum peak of air temperature; and peak at dawn and dusk, that is during increasing and decreasing solar radiation. The activity curves of the cats coincide roughly with these measures. The early morning troughs occur about three hours before dawn but the midday peaks occur at, or one to two hours before, midday. Dawn Dusk peaks are weak and variable.

Being least active during the coldest time of day and most active during the warmest might function to save energy. The purpose of activity around dawn Dusk could be partly to catch prey, although most hunting occurred around midday (Fig. 3.3 B). Day to day variations of the cats' activity patterns might be caused by short term influences, for instance interactions involving weather, degree of hunger and social pressures.

The mean activity curves of the mainly night-active cats, like those of the mainly day-active cats, were too similar to be the result of chance. Therefore the two cats who were mainly active at night might have been entrained to the same, although unknown, global factors.

This is the first evidence, known to me, that cats may be entrained to any environmental factor. Rudnai (1979) compared the daily temperature variation with the activity of lions (<u>Panthera leo</u>) in Nairobi National Park but found little correlation. Given that domestic cats might be entrained by easily manipulated physical variables a controlled study would be useful.

Chapter 4

USE OF SPACE AND SOCIAL BEHAVIOUR

Animals occupy space and therefore information on the size, shape and use of the space they occupy is important for understanding many aspects of their behaviour - for instance feeding strategies and social organisation - for assessing environmental influences on them and for their conservation and management. The first part of this chapter looks at the use of space by farm cats. The second part looks at farm cat social behaviour. Lions (Panthera leo) are called the only truly social cats (Schaller 1972; Rudnai 1973) and a group is called a pride. In contrast, domestic cats are considered to be solitary (Baron, Stewart and Warren 1957; Rosenblatt and Schneirla 1962; Fox 1975) and a group is called a clutter because it is an assortment of unrelated solitary individuals. Is this true? The main sections here look at farm cat genetic relationships, social interactions and social hierarchy.

The following method is an outline for this chapter. A more detailed description is in Chapter 2.

Subjects

The subjects were five female Cornish farm cats: Cf1, Cf2, Cf3, Cf4 and Cf5; and one female and two male Fife farm cats: Ff1, Fm1 and Fm2. A male house cat, Hm1, was also followed and notes were kept on the four male cats and eleven kittens at the Cornish farm and two males - Fm4 and Fm5 - at the Fife farm.

Procedure

A cat was followed and directly observed for the whole of an observation period (see below). The cat's behaviour was recorded as one of a number of mutually exclusive categories (see under Behavioural Categories and under Social Interactions in the General Method, Chapter 2) every fifth minute on the minute but if the animal was out of sight he was recorded as being lost to view. Other behaviours and the routes the cat travelled were noted during recording intervals.

Observation Periods

Each Cornish cat was followed three times from the beginning of the first complete hour to the end of the last complete hour of daylight and twice for 24 consecutive hours, from October 1978 to February 1979. Cf3 was followed in Februray 1980 for 13 consecutive days from 09.00 h to 17.00 h. Each Fife cat was followed once for 24 consecutive hours and thereafter observed in blocks to make up composite 24 hour periods; they were observed from April to June 1981.

Home Range Estimation

Home range areas were calculated using the smallest convex polygon connecting all outlying points of a cat's routes and by grid squares (20 m x 20 m), taking the home range to be the squares in a grid of squares through which a cat's routes passed.

Review of Home Range Estimations

As yet no single method has been found which can adequetly describe the use of space by an animal and hence a number of methods have been used. These have evolved from trap-capture and radio telemetry data in which spot locations of an animal's postion are taken. For the purpose of this review (based partly on Macdonald, Ball and Hough 1980; Voigt and Tinline 1980; Wolton 1982) the main methods are grouped into three broad categories.

(1) Probability Method (for example Hayne 1947). This is a statistical concept of a home range which assumes there is a probability of finding an animal within certain boundaries, for instance within a 95 % boundary. The boundaries may be drawn in either concentric, elliptical or assymetrical circles around a 'centre of activity' but do not necessarily have any behavioural or ecological significance. The centre of activity, as defined by Hayne (1947), is the locus given by the means of the x and y co-ordinates of all the locations of an animal. Like boundaries, it does not necessarily have any behavioural or ecological significance but Dixon and Chapman (1980) devised one which falls in the densest collection of locations and may reflect a real activity centre. A disadvantage of this method is that large

unused areas may be included in the home range and highly frequented areas may be left out. Furthermore, unlike the next method to be discussed, it does not show the frequency of usage of areas.

(2) Grid Method (for example Siniff and Tester 1965). A grid of squares is superimposed over a map of all the locations of an animal's movements and the squares which contain locations are taken to represent the home range. The range area is taken to be the combined squares in which locations occur. The number of locations per square is taken to be an indication of the frequency of use of the squares, which may be highlighted by projection in the vertical dimesion. Grid squares can indicate areas which are used frequently and eliminate large areas which are not used. But size, shape and the pattern of use of the home range may vary with the size of the grid. A grid size is chosen intuitively and different sizes are chosen by different workers which may make comparisons difficult.

(3) Polygon Method (for instance Mohr and Stumpff 1966). The outermost locations of an animal's movements are connected to make the smallest convex polygon and the area within the polygon is taken to be the home range. It is useful insofar that it has been widely applied so comparisons between studies can be made. Like grid squares, it imposes a definite boundary on a home range but can include large unused areas because it emphasises the importance of a few outlying locations, for instance made by sallies (occasional brief excursions away from the frequented areas). Attempts to overcome this problem include restricting

the line joining the outermost locations so that it does not exceed a certain length. For instance, Harvey and Barbour (1965) use lines which do not exceed a quarter of the home range length and Dards (1978; 1979) uses a line which is half the distance from the centre of activity to the furthest location from it. Locations which cannot be joined to the resulting 'restricted polygon' are joined to it by narrow lanes, considered to be sallies. Compared to the convex polygon, it minimises large areas which may be unused but the choice of the maximum length of the line connecting outlying locations has no behavioural or ecological significance and different choices give different results.

The probability method and reduced polygon are not used in this study because they are calculated from point locations. My data consist of routes the cats took and are suitable for convex polygons and grid squares. Both these methods are used. The former because, although it includes large unused areas, it has been employed by many cat observers so can be used for comparisons; and the latter because, although it has not been reported in a previous cat study, it minimises unused areas and therefore should provide a better estimate of a home range area and shape than a convex polygon.

Home Range Area and Overlap

The cats were observed a limited number of times, so have their home ranges been fully observed? A way to establish this is to plot the observation-area curve (Odum and Kuenzler 1955); that is, the cumulative new area an animal enters against each observation. If observed a sufficient number of times the curve will rise steeply then reach an asymptote and the value at whcih the curve levels off may be taken to be the full home range area. Fig. 4.1 shows the cumulative number of new grid squares entered by the Cornish cats against days they were observed. The curves have probably not reached a definite asymptote and hence the cats' home ranges had probably not reached their maximum areas by the end of the study. The curve of Cf3 when she was followed in 1980 looks as though it reached an asymptote after four days of observation but on the ninth day the number of new squares she entered nearly doubled. Therefore perhaps as much as nine days of observation are necessary to establish whether home range areas have reached a maximum. Curves are not shown for the Fife cats because they were not observed for as long as Cornish cats; Fm2 went missing early in the study and Ff1 only once travelled outside the farm steading. Like the Cornish cats, their home range areas would probably have increased with further observation.

The extent of home ranges estimated by convex polygons are shown in Figs. 4.2 and 4.3 and by grid squares in Figs. 4.4 and 4.5. The area of each home range is shown in Table 4.1 with the percentage difference between the convex polygon and grid square estimates and with the furthest straight-line distance each cat travelled from his core area. Females had smaller home ranges than males and, naturally, travelled less far from their core areas. But one female (Cf3) had an unusually large home range which was an order of magnitude greater than the other females' and comparable in size to the males' home range. Figs. 4.2 and

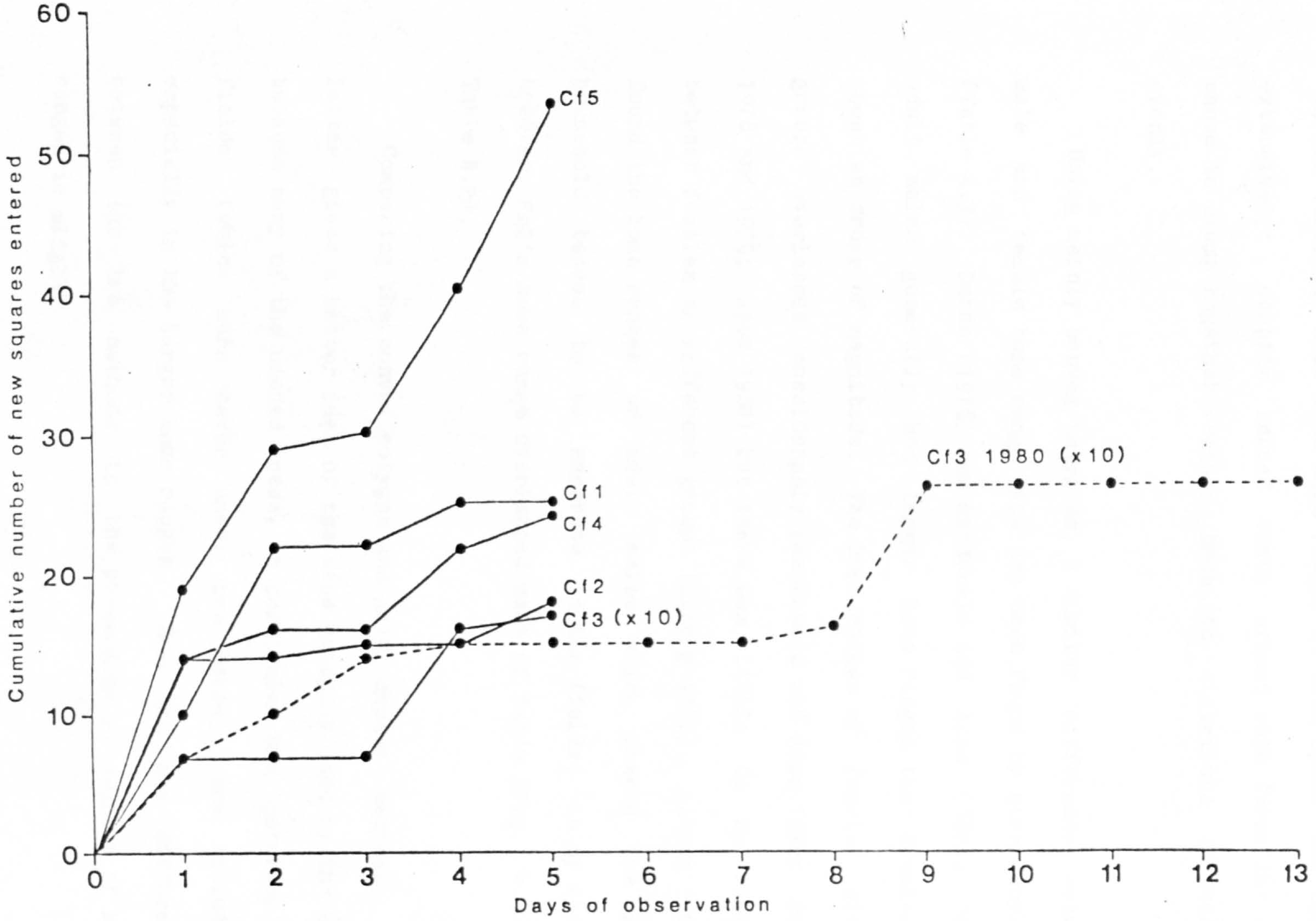


Fig. 4.1 Cumulative number of new squares entered per observation for each Cornish cat. The curve of Cf3 is also shown for 1980. The data are from three daylight and two 24 consecutive hour observations per cat and 13 daylight observations on Cf3 in 1980.

4.3 and Table 4.2 show that home ranges at both farms overlapped extensively; despite unused space around both farms the cats chose to clump together rather then to distribute themselves evenly.

Using mainly convex polygons, a similar difference between male and female home range size has been found by other workers (Table 4.3). Dards (1978) and Macdonald and Apps (1978) found adult males generally had larger home ranges than females by about an order of magnitude. The home ranges of females within groups overlapped considerably (Macdonald and Apps 1978; Dards 1978 and 1979; Apps 1980) but there was little to no overlap between females of different groups (Liberg 1980). Liberg (1980) found the home ranges of adult males which shared the same household tended to be separate in the fields; in my study, however, Fm2's home range overlapped most of Fm1's (Fig. 4.4 and Table 4.2).

Comparing the convex polygon and grid square methods, the latter gives a better idea of the area actually used by the cats because many of the unused areas, in particular the interior of fields (which were never used, see below), are excluded, especially in the larger home ranges. However, the difference between the two methods in the percentage of overlap of home ranges is slight.

Core Areas

The home range of each cat consisted of a core area and surrounds. The core areas of the Cornish females coincided and

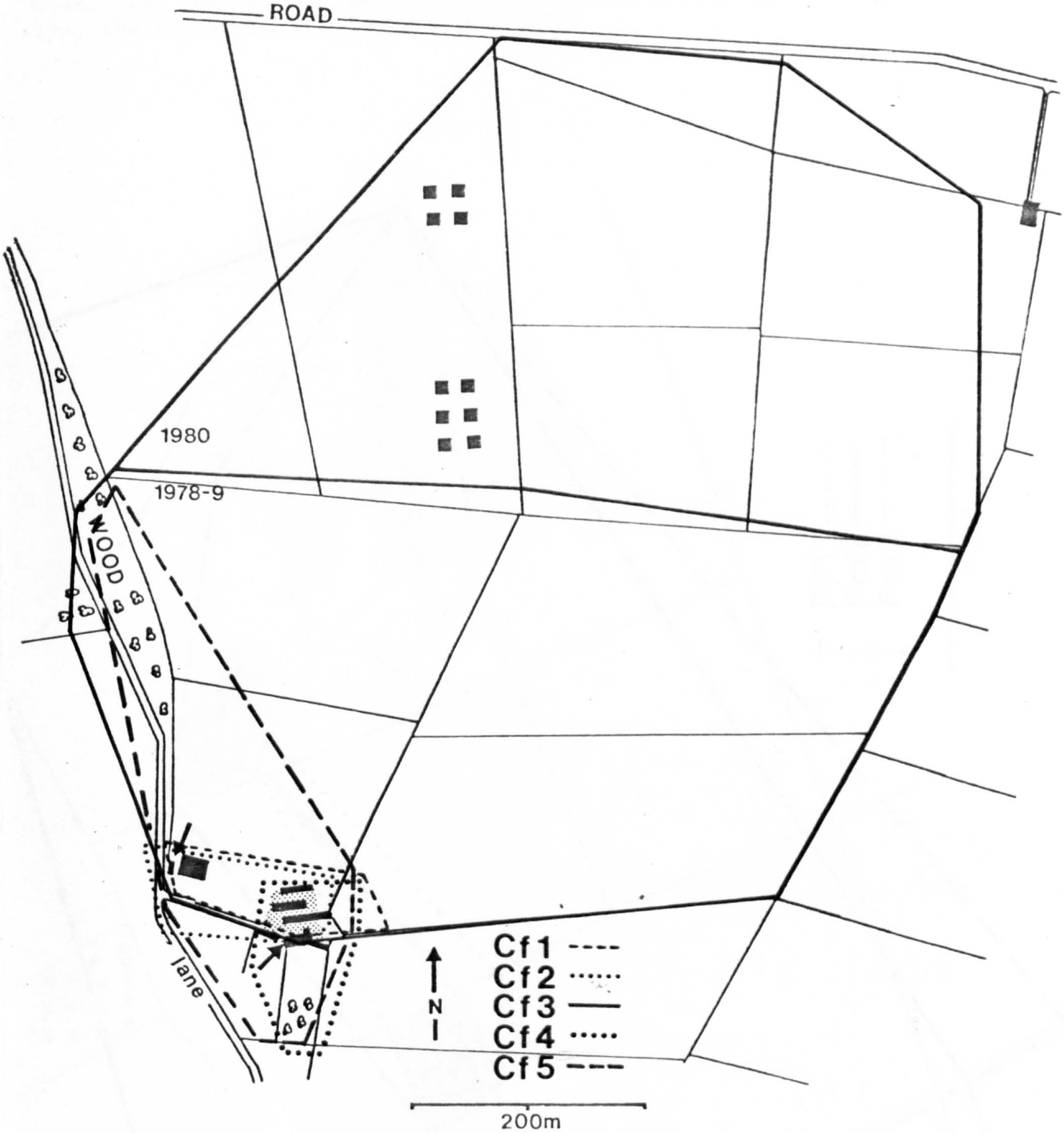
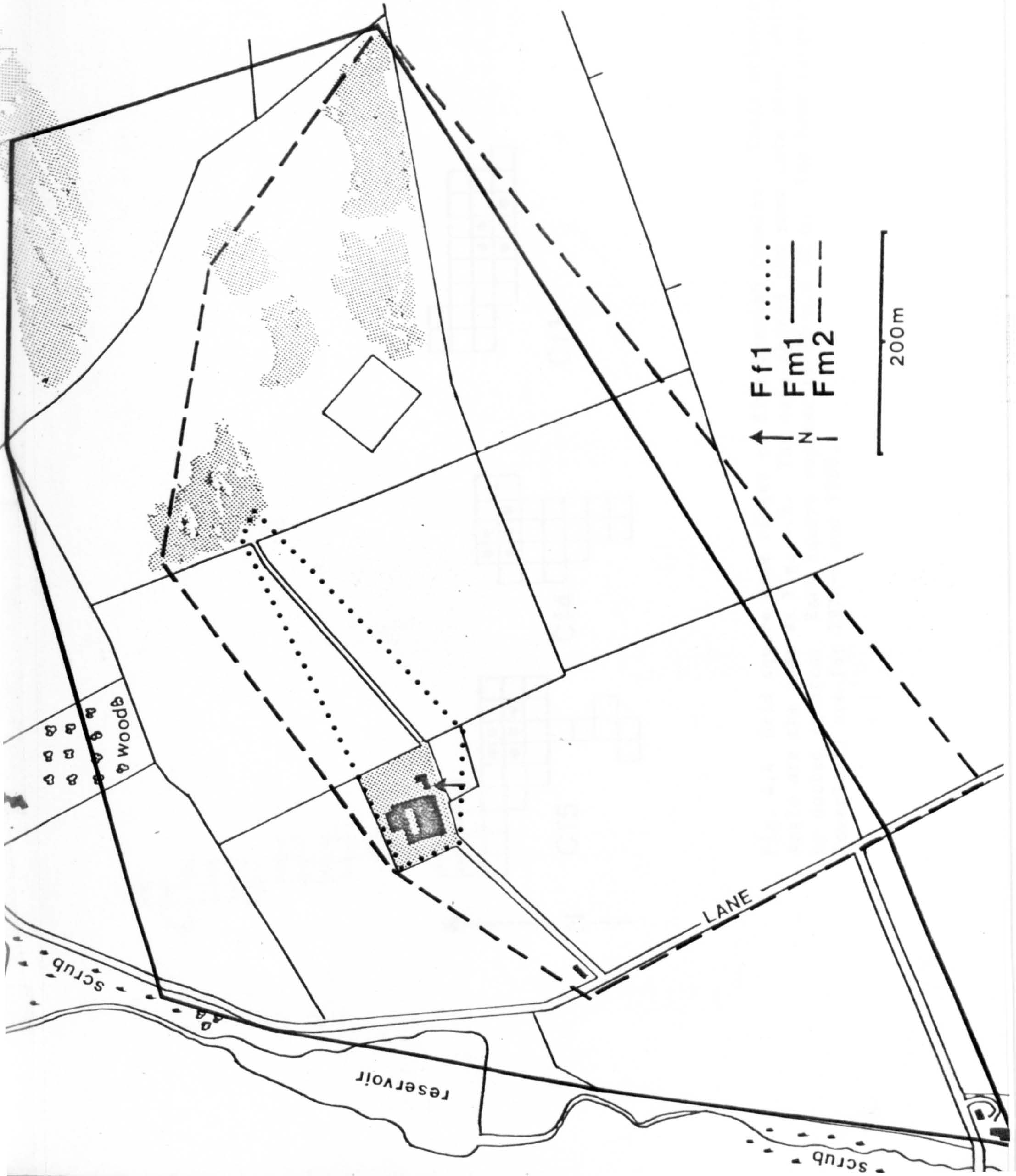


Fig. 4.2 Plan of the Cornish cats' farm drawn to scale (1:2500) from an Ordnance Survey map. The overlay shows convex polygon home ranges. The shaded area is the cats' core area, which they all shared. Arrows point to the dairy (left) and the farm house (right).

Fig. 4.3 Plan of the Fife cats' farm drawn to scale (1:2500) from an Ordnance Survey map. The overlay shows convex polygon home ranges. The shaded area on the left is the cats' core area, which they all shared; arrow points to the farm house. The shaded areas on the right are gorse patches in the males' hunting area; the rectangle is a covered reservoir.



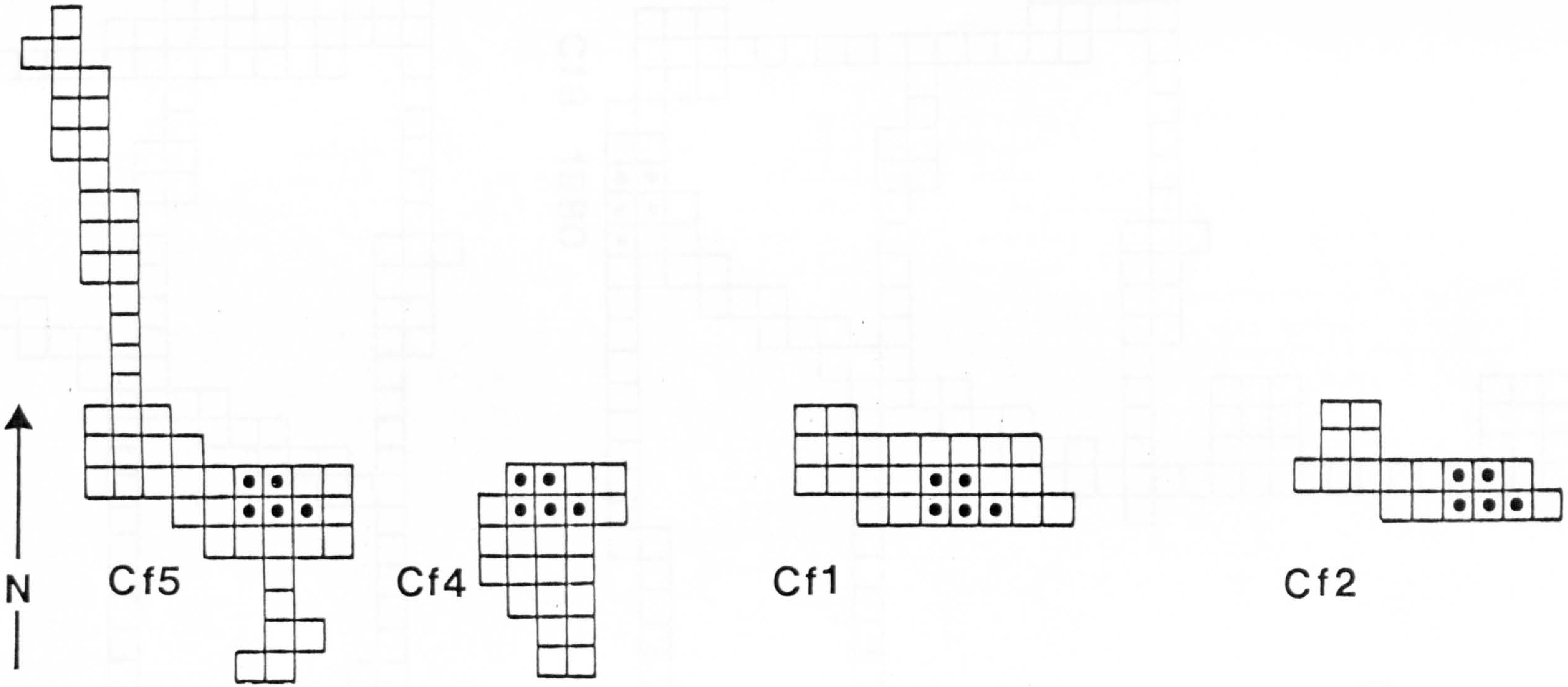
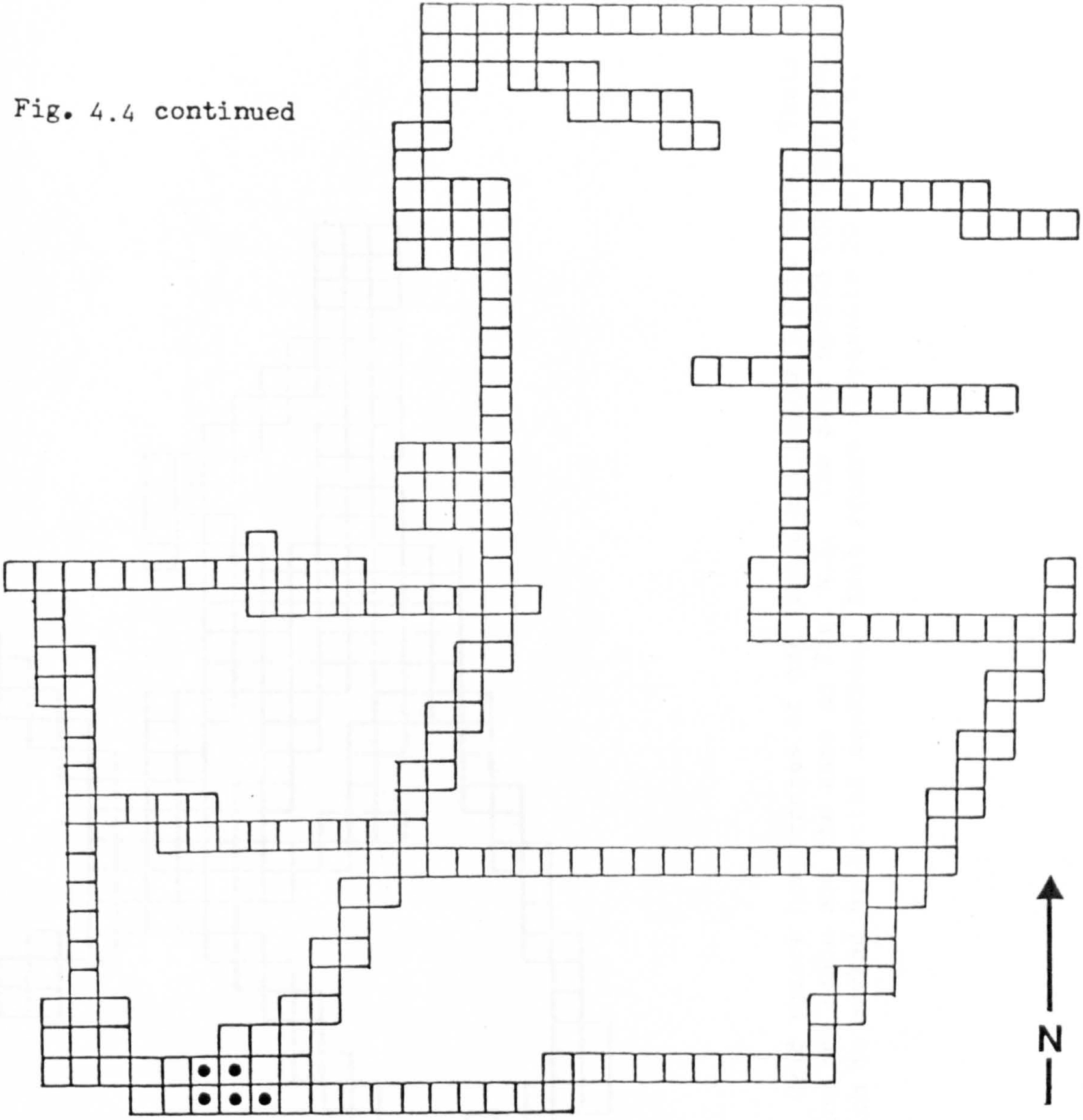
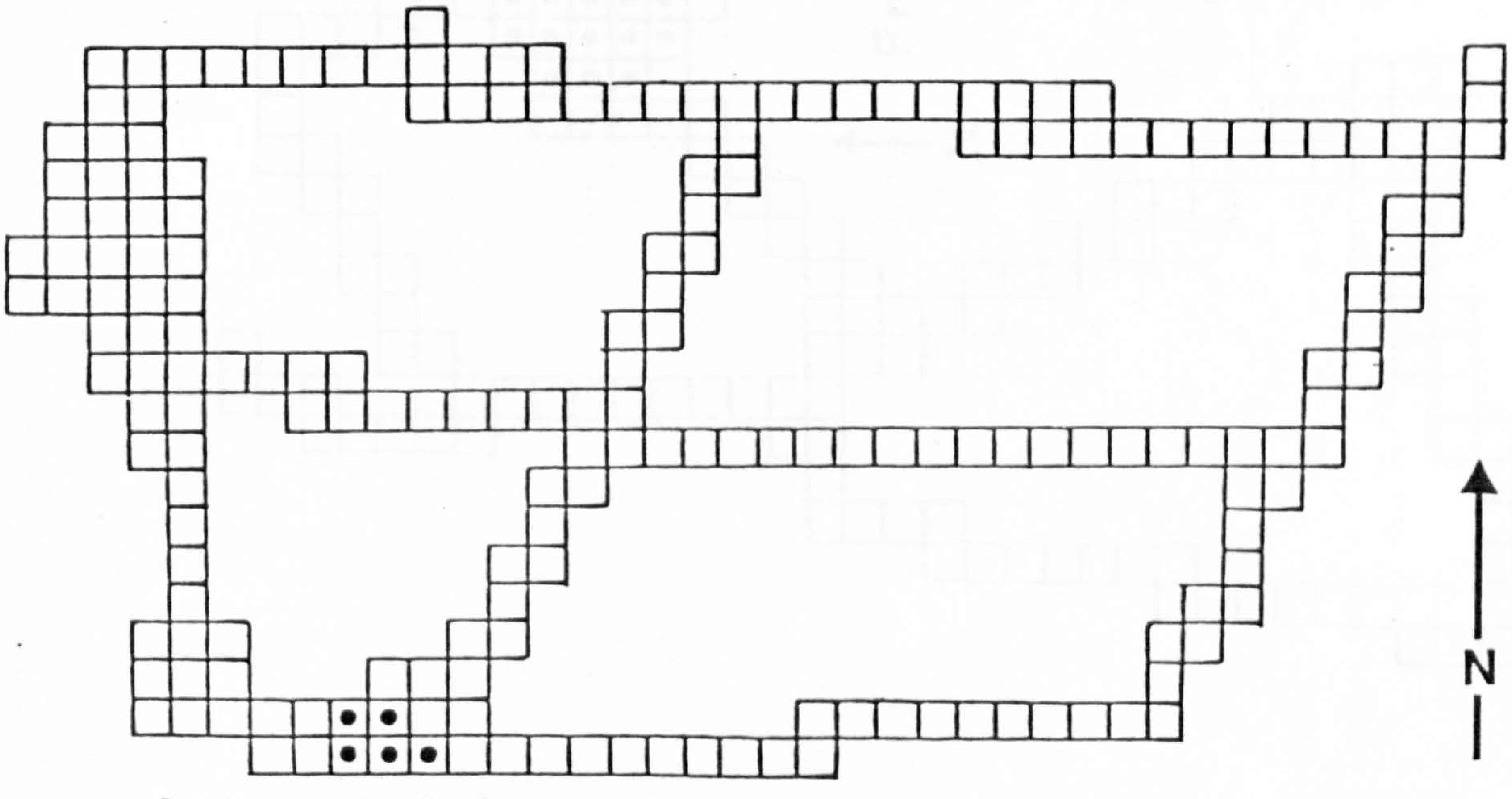


Fig. 4.4 Grid square home ranges of five Cornish females. Their orientation and scale are the same as Fig. 4.2. The cats shared the same core area, which is marked by dotted squares. Each square represents 20 m x 20 m. The home ranges of Cf3 (overleaf) are for 1978-9 and 1980.

Fig. 4.4 continued



Cf3 1980



Cf3 1978-9

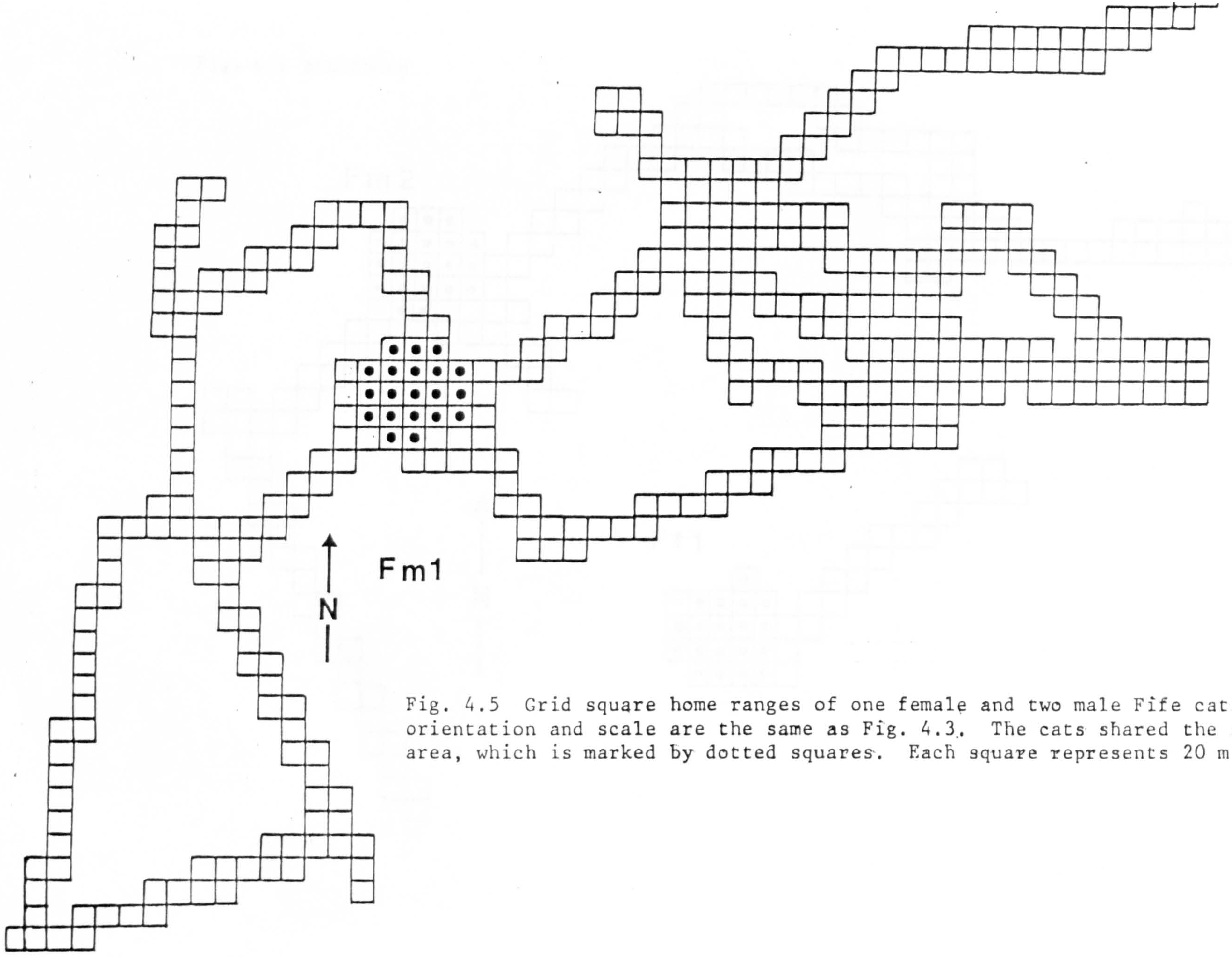
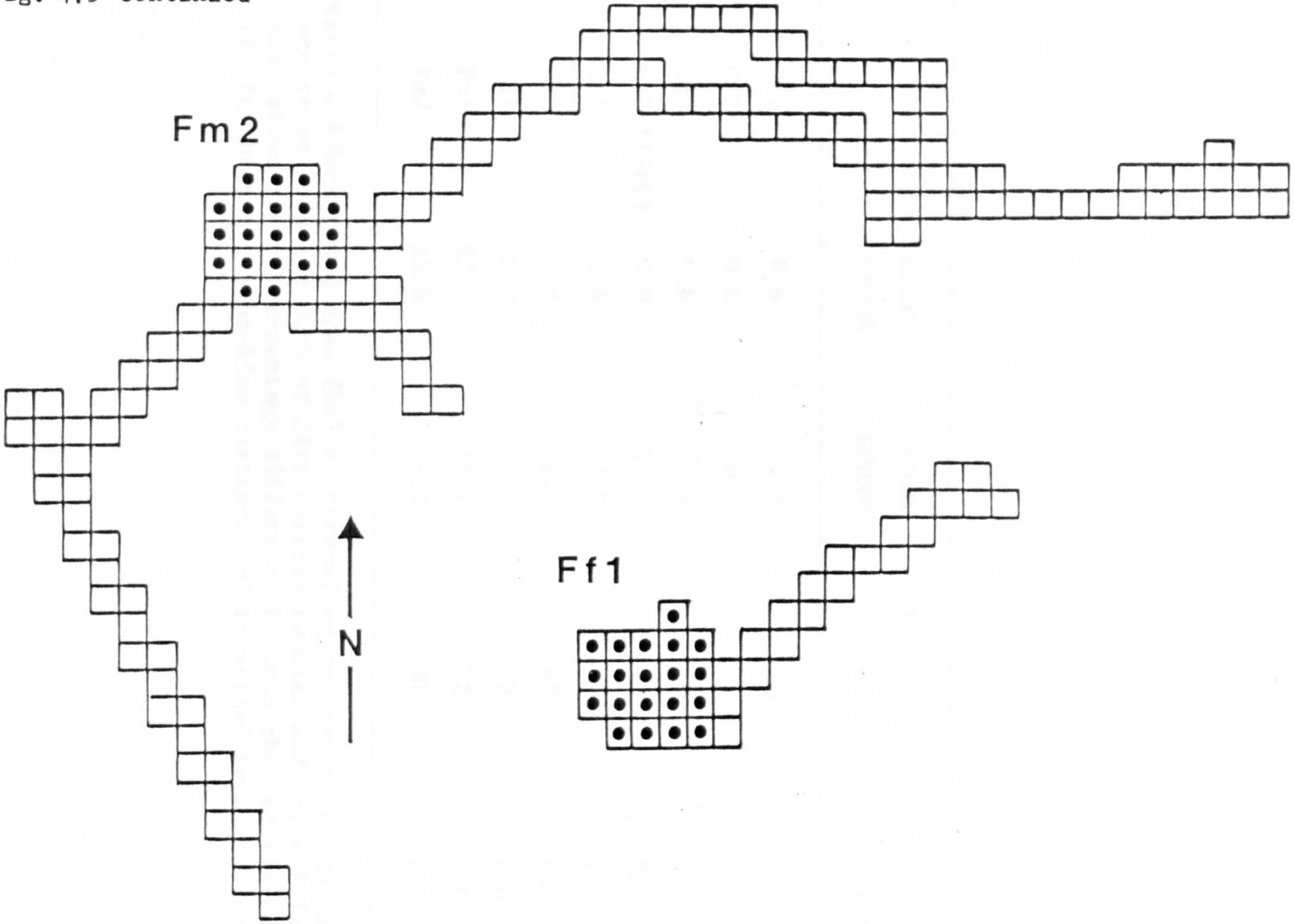


Fig. 4.5 Grid square home ranges of one female and two male Fife cats. Their orientation and scale are the same as Fig. 4.3. The cats shared the same core area, which is marked by dotted squares. Each square represents 20 m x 20 m.

Fig. 4.5 continued



	CONVEX POLYGON	GRID SQUARE	PERCENTAGE DIFFERENCE	FURTHEST DISTANCE
Cf1	0.6	1.0	40	120
Cf2	0.6	0.7	14	120
Cf3	19.6	7.9	60	625
Cf3 (1980)	39.0	10.9	72	825
Cf4	0.6	1.0	40	100
Cf5	3.8	2.1	45	400
Ff1	2.2	1.6	27	230
Fm1	53.1	15.1	72	750
Fm2	32.6	6.2	81	750

Table 4.1 Home range area (ha) as determined by convex polygon and grid square methods for each of five Cornish females and three Fife cats. Also shown is the percentage difference between the two estimates and the furthest straight-line distance (m) travelled from the core area.

	Cf1		Cf2		Cf3		Cf4		Cf5		Ff1		Fm1		Fm2	
	CP	GS	CP	GS	CP	GS	CP	GS	CP	GS	CP	GS	CP	GS	CP	GS
Cf1	-	-	76	68	100	88	47	40	98	80						
Cf2	80	94	-	-	94	100	53	44	94	100						
Cf3	5	12	4	9	-	-	5	5	18	21						
Cf4	48	42	30	30	47	38	-	-	87	75						
Cf5	21	19	23	34	79	79	21	34	-	-						
Ff1											-	-	100	100	100	100
Fm1											8	11	-	-	47	40
Fm2											15	26	87	89	-	-

Table 4.2 Percentage of the home range of the cats on left overlapped by the home range of the cats at top. Estimates are given for convex polygon (CP) and grid square (GS) methods.

HOME RANGE AREA (ha)		NUMBER		CAT TYPE	HOW OBSERVED	HOME RANGE DETERMINED BY	AUTHOR
♀♀	♂♂	♀♀	♂♂				
0.7 - 10.9	6.2 - 15.1	6	2	farm	vis	grid square	This study
0.6 - 39.0	32.6 - 53.1	6	2	farm	vis	convex poly	This study
0.03 - 4.2	0.8 - 24.0	68	32	dockyard	vis	convex poly	Dards 1978; 1979
4.9 - 30.3	3.7 - 63.2	<20		farm	vis rt	convex poly	Corbett 1979
24.0 - 60.0	not observed	2	-	feral	vis rt	convex poly	Corbett 1979
up to 40.0	>females	not stated		farm	vis rt	convex poly	Liberg 1980
not observed	2-4 km across	not stated		feral	vis rt	convex poly	Liberg 1980
2.0 - 7.0	60	3	1	farm	vis rt	not stated	Macdonald & Apps 1978
50.0 - 100.0	>females	not stated		farm	vis	not stated	Leyhausen 1979

Table 4.3 Home range areas (ha) of adult domestic cats. Also shown is the number of cats observed, type of cats, how they were observed (direct visual observation or radio telemetry), how the home range areas were determined (convex polygon or otherwise) and authority.

were about 0.2 ha in area. The Fife cats' core areas also coincided and were about 0.7 ha.

The Cornish females and Fife cats, respectively, spent a maen of 82 % and 89 % of the 24 h in their core areas (Table 4.4). Cats tended to aggregate in certain places within them. Cornish females gathered at the main feeding place and spent there a mean of 2.2 h (range 0.3 to 6.6 h). They also gathered in an area next to it to sunbathe and groom and often slept in the dutch barn - where hay and straw were copious - and in the feed store - where there were many sacks of cattle feed on which they lay. In addition to spending time in the core area, four females visited the dairy to feed, rest and sometimes sleep, spending there a mean of 0.8 h (range 0.0 to 1.5 h).

The Fife cats, perhaps because they were given milk less frequently and more regularly and therefore knew with more certainty when to be present for food, spent very little time at their feeding place but were found nearby over a wider area. Most sunbathing was in the yard north of the farm house and all sleep was on hay and straw in buildings around the yard.

In Portsmouth dockyard, females spent much time in their core areas some of which were little bigger than the skips from which they scavenged their food; males spent more time in a broader area and in visiting different female groups (Dards 1978 and 1979). One male and three female farm cats, observed by Macdonald and Apps (1978), spent most of the daylight hours in 0.8 ha. Corbett (1979) located most radio collared wildcats (Felis silvestris) in small areas of their home range; therefore

	h		h
Cf1	15.2	Ff1	24.0
	21.7		-
Cf2	21.4	Fm1	18.9
	20.0		-
Cf3	19.7	Fm2	21.1
	19.8		-
Cf4	19.2		
	22.0		
Cf5	20.0		
	16.2		
$\bar{X} \pm$ SD	19.5 + 2.2		21.3 ± 2.6

Table 4.4 Number of hours cats spent in their core areas. Data are from 24 consecutive hour observations: two on each Cornish female and one on each Fife cat

wildcats also probably use core areas.

The reasons for choosing a place to be a core area are suggested to be good shelter and the abundance of food (Dards 1978 and 1978; Liberg 1980). But food is probably the overriding factor because cats are small and so should be able to find good shelter almost anywhere.

Core Area of Non-focal Cats

Casual observation at both farms showed that the other farm cats shared the same core area as focally observed cats. They were most often seen to rest, groom and sunbathe there and were regularly observed to sleep there at night. They were not observed to sleep elsewhere so probably spent a large part of the 24 h there. Mature males, however, were seen there less often than younger males. When seen outside the core area non-focal cats were usually travelling or hunting.

All the farm cats at both farms, therefore, appeared to share the same core area with every other cat at the farm but in Cornwall two cats chose a different one. In the summer of 1978 Cf5 bore at least three kittens by the dairy, which was 80 m west of the farm cats' core area (Fig.4.2), and raised them there. Only one survived but unlike the other kittens at the farm, which had been born and raised in and around the core area, it remained centred on the dairy. The following year Cf5 bore and raised more kittens near the dairy. Again only one survived and again it remained centred on the dairy. Both appeared to be good hunters and the farmers provided them with extra milk in the evening to encourage them to stay. Even in adulthood the two cats were rarely seen in the core area of the other cats even though milk could be found there frequently and the other cats were not agonistic towards them. Thus, they probably took a different core area from the other cats because they had been raised at the dairy and moreover were later able to get adequate and regular food there. Individuals of both 'groups' mixed as peacefully in the one core area as they did in the other.

Surrounds

Some hunting was in the core area but most occurred in the surrounds. The percentage of hunting time outside the core area is shown in Table 4.5. Only Cf5 and Ff1 hunted substantially within their core area.

Females were relatively sedentary compared to males. They only left their core area for getting food but the males (Fm1 and Fm2) left their core area for hunting and non-hunting purposes. Fm1 visited a female a number of times at a house about 400 m south-west of the farm (Fig. 4.3). She later bore a litter of kittens - one kitten exactly like him. He also once travelled north west of his core area around a field and along the road (Fig. 4.3) before he gradually slowed and eventually stopped, whereupon he rested a while before he returned to his core area. In a similar manner, Fm2 twice travelled part way to the nearby village (1 km away) before returning. The males were travelling quickly without hesitating so probably were not exploring and became ambivalent about continuing.

	%		%
Cf1	100.0	Ff1	0.0
	65.5		-
Cf2	100.0	Fm1	100.0
	100.0		-
Cf3	100.0	Fm2	100.0
	94.0		-
Cf4	84.4		
	66.3		
Cf5	33.3		
	41.1		
$\bar{X} \pm SD$	78.5 ± 25.6		-

Table 4.5 Percentage of hunting time each cat spent outside his core area. Data are from 24 consecutive hour observations: two on each Cornish female and one on each Fife cat.

Using mainly casual observation, Leyhausen (1965 and 1979) concluded that a cat's core area is used for resting, sunbathing and keeping watch and that beyond it are areas used for hunting, courting and contesting, which agrees with my own observations.

Movements

The detailed movements of cats within their home ranges are largely unknown. The home ranges of feral cats in Portsmouth Dockyard were small (Table 4.3) yet the cats did not completely cover them in one day (Dards 1979). For comparison, a female bobcat completely covered her territory of less than 13 sq km in one to four days (Provost, Nelson and Marshall 1973).

Not all parts of a home range of the cats I studied were used: individuals kept to routes near long grass, hedges, thickets, fences, walls and buildings avoiding large open spaces; the interiors of cultivated fields were never travelled across (for instance Figs. 4.2, 4.3, 4.4 and 4.5). For this reason the outlines of home ranges were largely determined by linear artifacts such as hedges, walls, fences and roads. Rural cats in Sweden also kept to such routes (Liberg 1981).

Fig. 4.6 is a scheme of the routes of Cf6 when she was followed in 1980. All routes were taken when hunting. For clarity, routes used more than once a day and routes within and by the steading are not shown. She hunted for the first four days (routes 1 to 4), did not hunt the next two days, hunted another four days (routes 5 to 8) and did not hunt the last three days. Therefore she did not visit her home range every day or travel throughout all of it on any one day. She kept almost entirely to cover (hedges and building) and did not use part of the same route on more than three consecutive days.

Cf3 had the largest home range and, although observed on consecutive days, was observed only during daylight. Cf4 had one of the smallest home ranges and was observed also at night. Fig. 4.7 is a scheme of all her routes (when hunting and not hunting) when observed twice for 24 consecutive hours eight weeks apart. For clarity, routes used more than once in 24 h are not indicated. During one observation (dotted path) she was fairly sedentary and did not travel far outside her core area. Like Cf3, she kept close to cover (hedges, walls, buildings and scrub) and did not visit all her home range in one day.

A similar pattern of movement applied to Cf2 and Cf5 but not to Cf1 and Ff1. Cf1 used almost all parts of her home range during daylight and 24 h observations and Ff1 rarely left her core area, almost always hunting the same places within it or within 25 m of it, covering much the same ground every day.

As stated above, the males left their core area to hunt and travel and in the case of Fm1 to visit a female. Fm1 always hunted the same hillside taking roughly the same routes (Fig. 6.5) but did not cover all the area during any one hunt (Appendix Fig. A1). Fm2 hunted exactly the same area and used much the same routes (Fig. 6.6). Hm1 used a smaller area and covered much of it during a hunt (Figs. 6.7 and Appendix Fig. A1). Fm1 and Fm2 left their core area on only three occasions to travel with apparently no destination (see under Surrounds, above). Fm1

Fig. 4.6 Routes taken when hunting by Cf3 in 1980.

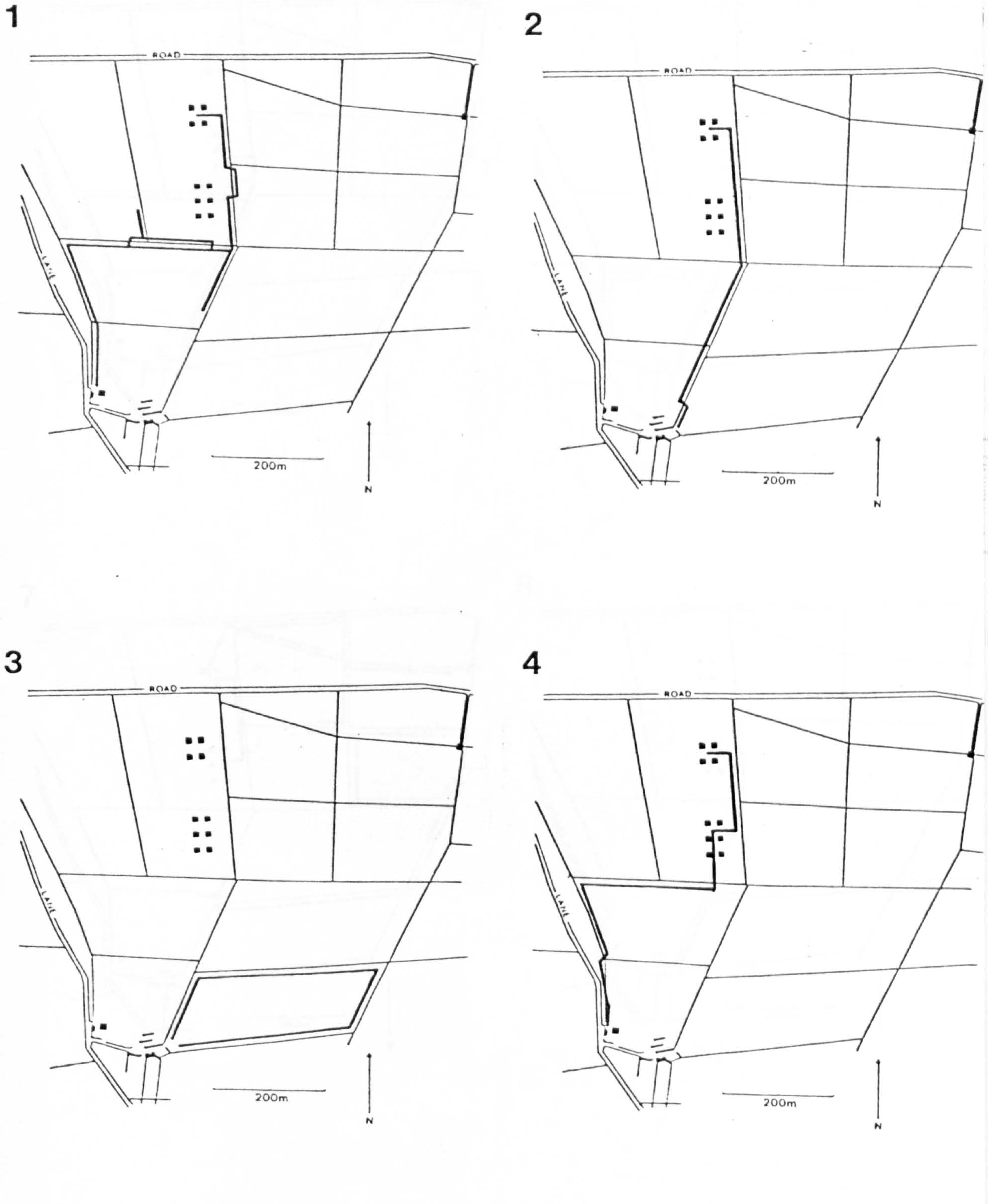
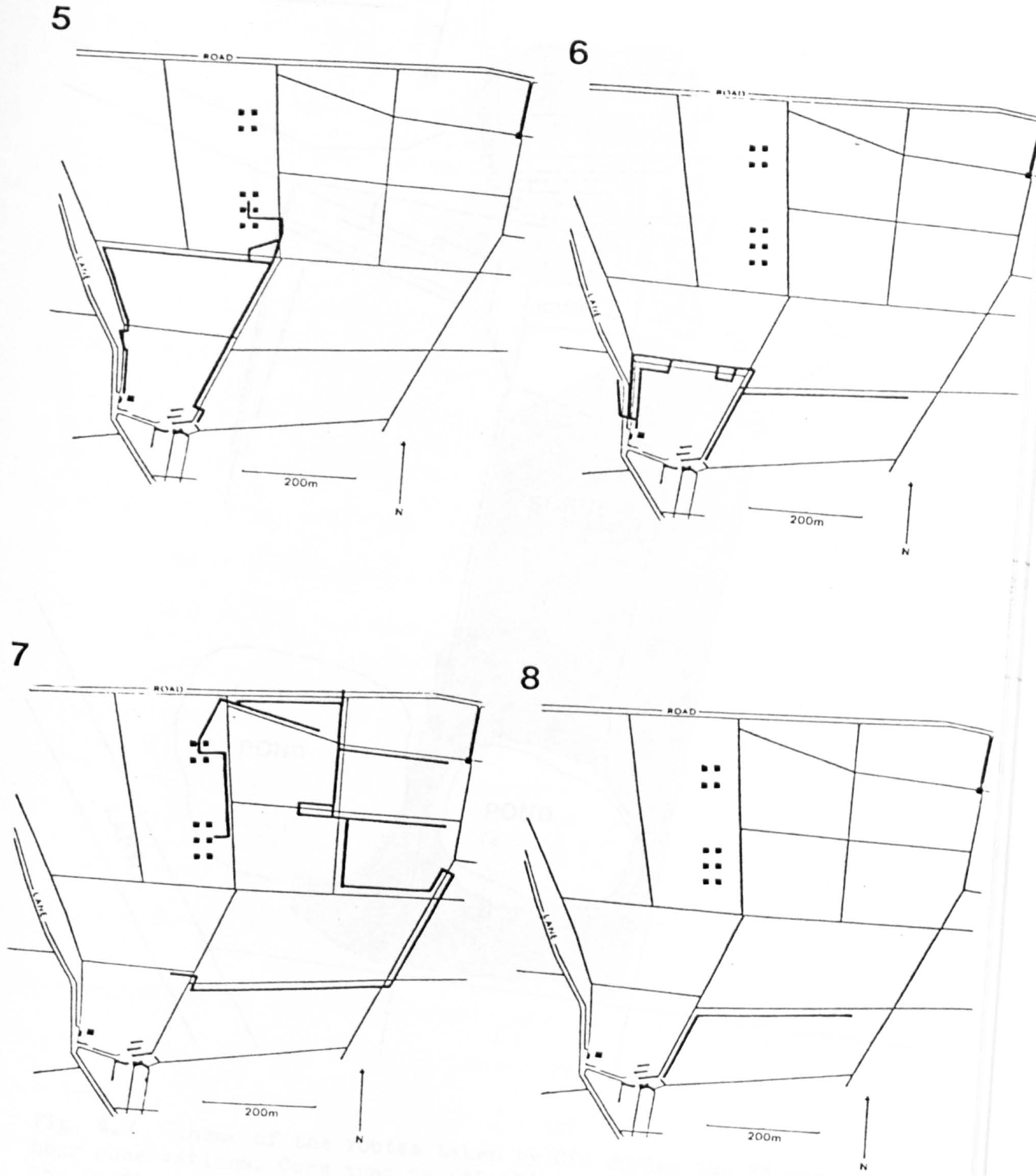


Fig. 4.6 continued.



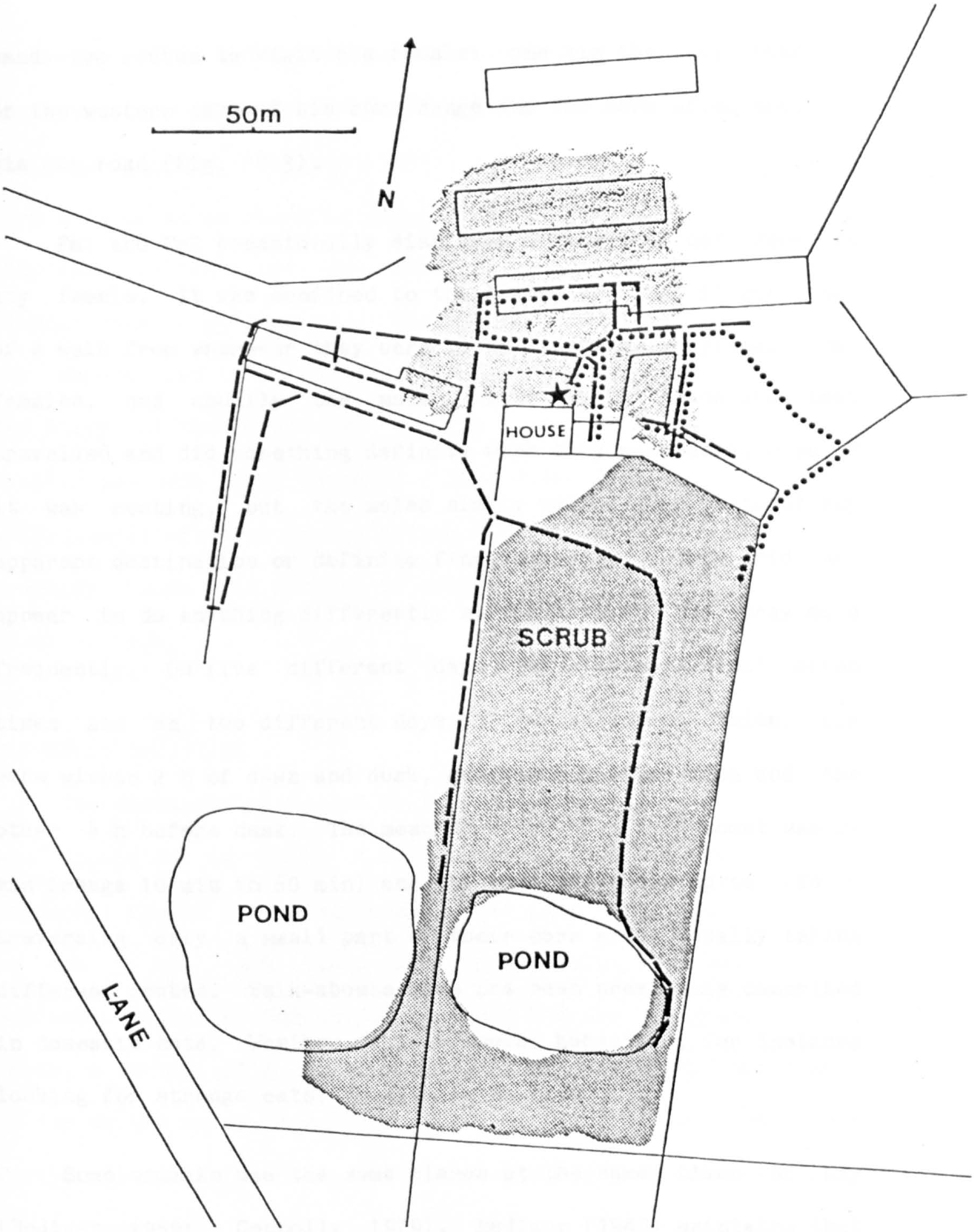


Fig. 4.7 Scheme of the routes taken by Cf4 during two 24 consecutive hour observations. Core area is stippling north of house. Star marks the feeding area.

used two routes to visit his female: one via the field boundary on the western edge of his home range and the more often used one via the road (Fig. 4.3).

Fm1 and Fm2 occasionally displayed a behaviour not seen in any female. It was confined to their core area and it consisted of a walk from wherever they were to no particular place. The females, and usually the males, went to a place when they travelled and did something definite when they got there, even if it was resting, but the males simply walked about without any apparent destination or definite final activity. They did not appear to do anything differently at these times like spray more frequently. On five different days Fm1 'walked-about' seven times and on two different days Fm2 'walked-about' twice: six were within 2 h of dawn and dusk, one was 4 h after dawn and the other 4 h before dusk. The mean duration of a walk-about was 27 min (range 10 min to 60 min) and the cats travelled up to 120 m traversing only a small part of their core area, usually taking different routes. Walk-abouts have not been previously described in domestic cats. Whether it is a social behaviour, for instance looking for strange cats, remains to be seen.

Some mammals use the same places at the same times of day (Hediger 1950; Connolly 1979). Hediger (1949) maintains that their movements appear to be organized according to a 'time schedule', which may serve to maintain spatial separation. Time scheduling has been reported to occur in captive domestic cats: an individual uses a certain place at a certain time of day and all other individuals give way to him at that time only

(Leyhausen 1965). But this has not been observed in free-ranging domestic cats (Leyhausen 1965, 1979; Laundre 1977) or tigers, Panthera tigris (Schaller 1967). However, to some extent the farm cats could be found in approximately the same place doing the same activity at the same time but it did not involve displacement of another cat. For instance, during the start of one observation Cf2 was grooming in a certain place, ambled to the dairy and then went down the lane to hunt. 23 h later exactly the same thing happened. This kind of situation occurred sufficiently often to become noticeable but not often enough to quantify. Some cats seem to be creatures of habit, at least over short periods.

Distances Travelled

The distances travelled by each cat during 24 h observations are tabulated in Table 4.6. Roughly, the females travelled between 1 km and 3 km a day whereas the males travelled between 3 km and 4 km. But these are minimum distances because they exclude meanderings for which, allowing for the topography of the farms, a further 20 % could be added. The females did not travel as far as the males probably partly because they did not make forays into the surrounds for non-hunting purposes (see above under Surrounds).

The mean daily distance travelled by two feral cats, each snow tracked for three days in rural Michigan, was 2.1 km and 4.0 km (Gill 1975), which are the same order of distance my farm cats travelled (Table 4.6).

	Cf1	Cf2	Cf3	Cf4	Cf5	Ff1	Fm1	Fm2
	2685	755	2835	1440	1465	1400	3095	3680
	1480	1405	2850	930	1785	–	–	–
$\bar{X}$	2080	1080	2840	1185	1625	–	–	–

Table 4.6 Distances (m) travelled by each cat. Data are from 24 consecutive hour observations: two one each Cornish female and one on each Fife cat.

Genetic Relatedness

During the census (Chapter 7) of Fife cats, a few farmers said their farm cat groups had existed for many years. At one farm the cat group had been present for 70 years with two short gaps. Unfortunately no records of genealogies have been kept. However, it was possible to construct the genealogy of the cats I studied in Cornwall. This was because the farmers were expert at recalling the names and personal history of their 100 milk cows and since they took an interest in their cats they were able to recall their history too. Checking the details with each farmer over a period convinced me of its accuracy.

Fig. 4.8 shows the genealogies of the two lines of cats at the Cornish farm. Cf5, the founder of the smaller line, immigrated to the farm so was probably not related to the cats of the older line, who were all descended from a female the farmers abandoned at their old farm when they moved to their present one. The figures show the cats were not a haphazard collection of individuals but that each cat was genetically closely related to a large number of other cats in a lineage extending back for generations. A similar close genetic relationship existed at the Fife farm (see subjects in Method, Chapter 2).

Dards (1978) and Macdonald and Apps (1978) each studied the same groups of free-ranging cats for at least a year and Laundre (1977) and Liberg (1980) describe a group of genetically related free-ranging cats whose lineage extends back a number of generations; these groups, therefore, were not temporary aggregations either. Males between one and three years of age

Fig. 4.8 Genealogy of 46 cats from one line and 6 from another at a Cornish farm. Only cats who survived past about two months of age are shown. Year of birth on left. Male marked with an asterisk may be his mother's sister's son. Two females marked with an asterisk may each have bore a kitten or either female may have born both kittens. C - castrated, D - died, F - went feral, G - given away, L - left at previous farm, M - went missing and R - run over.

tended to emigrate from their natal group but young females tended to remain (Dards 1978 and 1979; Liberg 1980); therefore group structure is largely based on mother-daughter lineage. However, Laundre (1977) and Macdonald and Apps (1978) observed that different lineages and non-genetically related individuals may share the same core area.

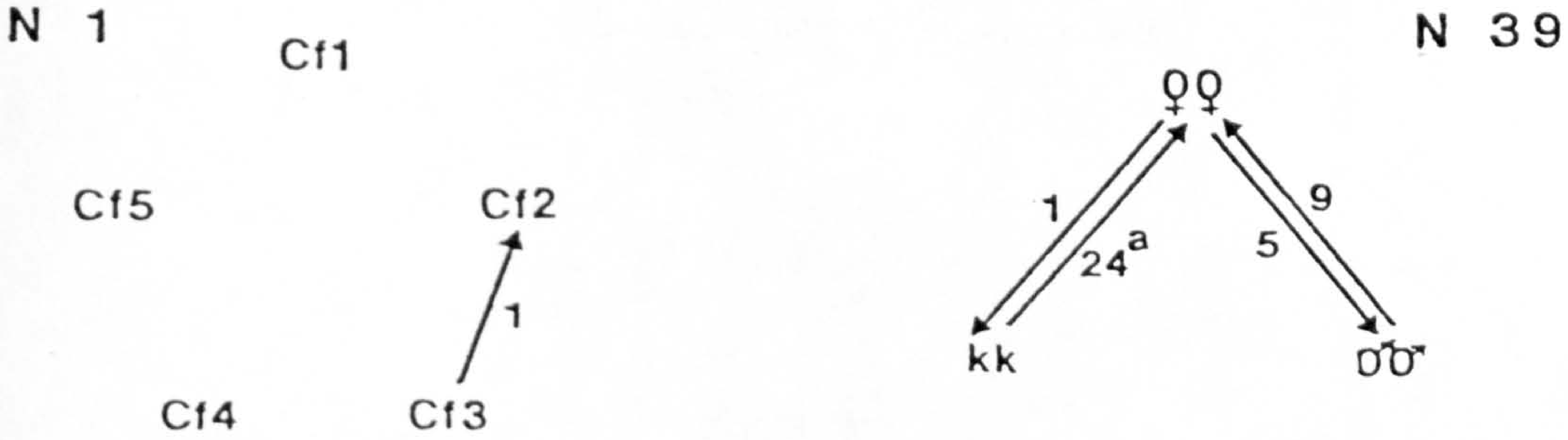
Social Interactions

Figs. 4.9 and 4.10 show the number and direction of social interactions of the farm cats over a sample period. The Cornish kittens were very amicable to the females who were very agonistic to the kittens (Fig. 4.9); the kittens were newly independent and were still attached to their mothers, who were rejecting them. The males were sometimes wary of me so my presence may have led to fewer Cornish male-female interactions. Macdonald and Apps (1978) observed 1,200 interactions in 480 h among a group of one male and three female adults. During all my observations (over 800 h, Chapter 2) I noted only 541. Macdonald and Apps (1978) do not state their criteria for social interaction but since our rates differ so much their criteria must be different from mine and therefore our results cannot be compared.

Table 4.7 shows percentages and locations of social interactions among Cornish females and between them and other cats at the farm. 87.4 % of interactions occurred in the core area. 60.7 % of interactions happened at the two feeding places. Competition for milk was slight, partly because there were two bowls at each feeding place so that each cat was able to get a

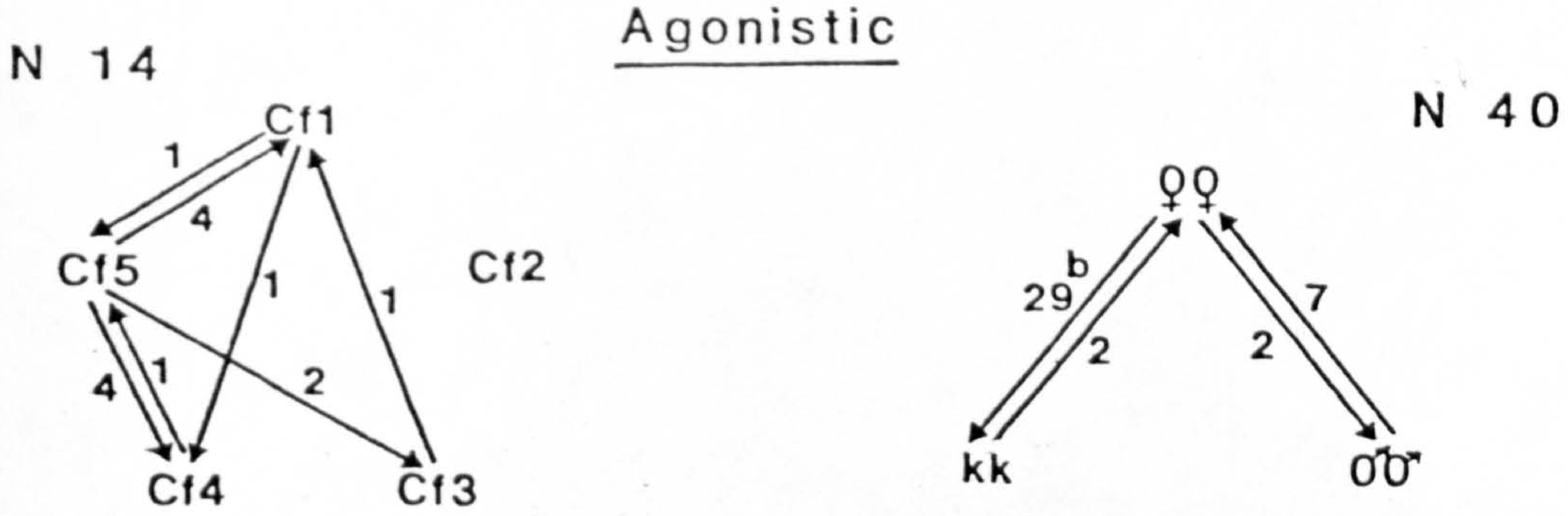
Fig. 4.9 Type, number and direction of social interaction among five Cornish females and between the females, four males and ten kittens. Data are from two 24 consecutive hour observations on each female.

Amicable



a - 15 were by one kitten

Agonistic



b - 17 were by Cf1

Exploratory

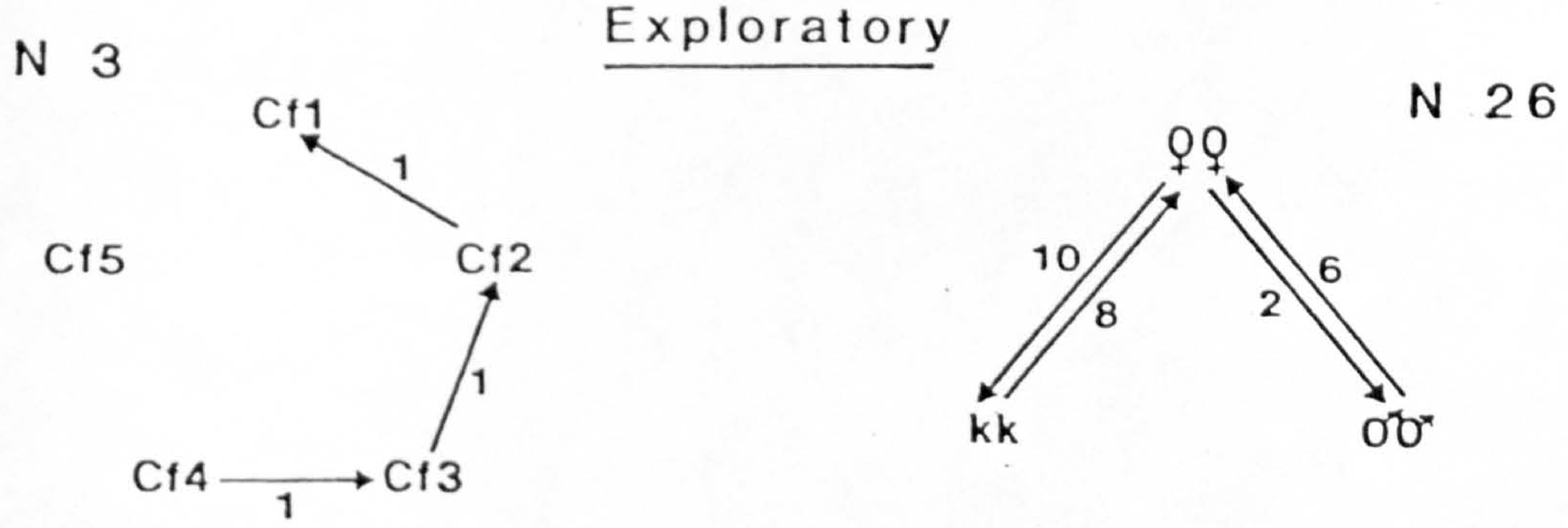
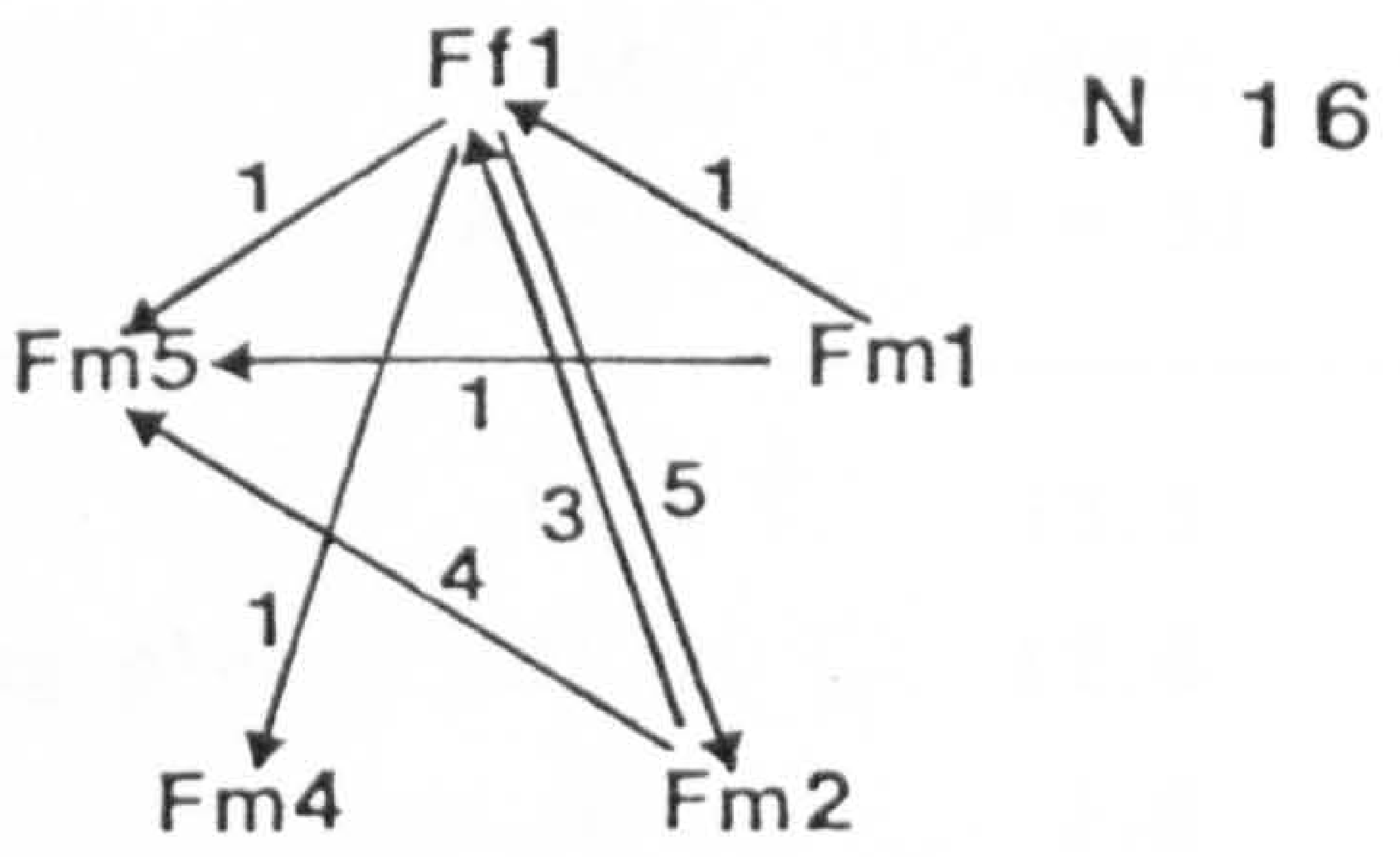
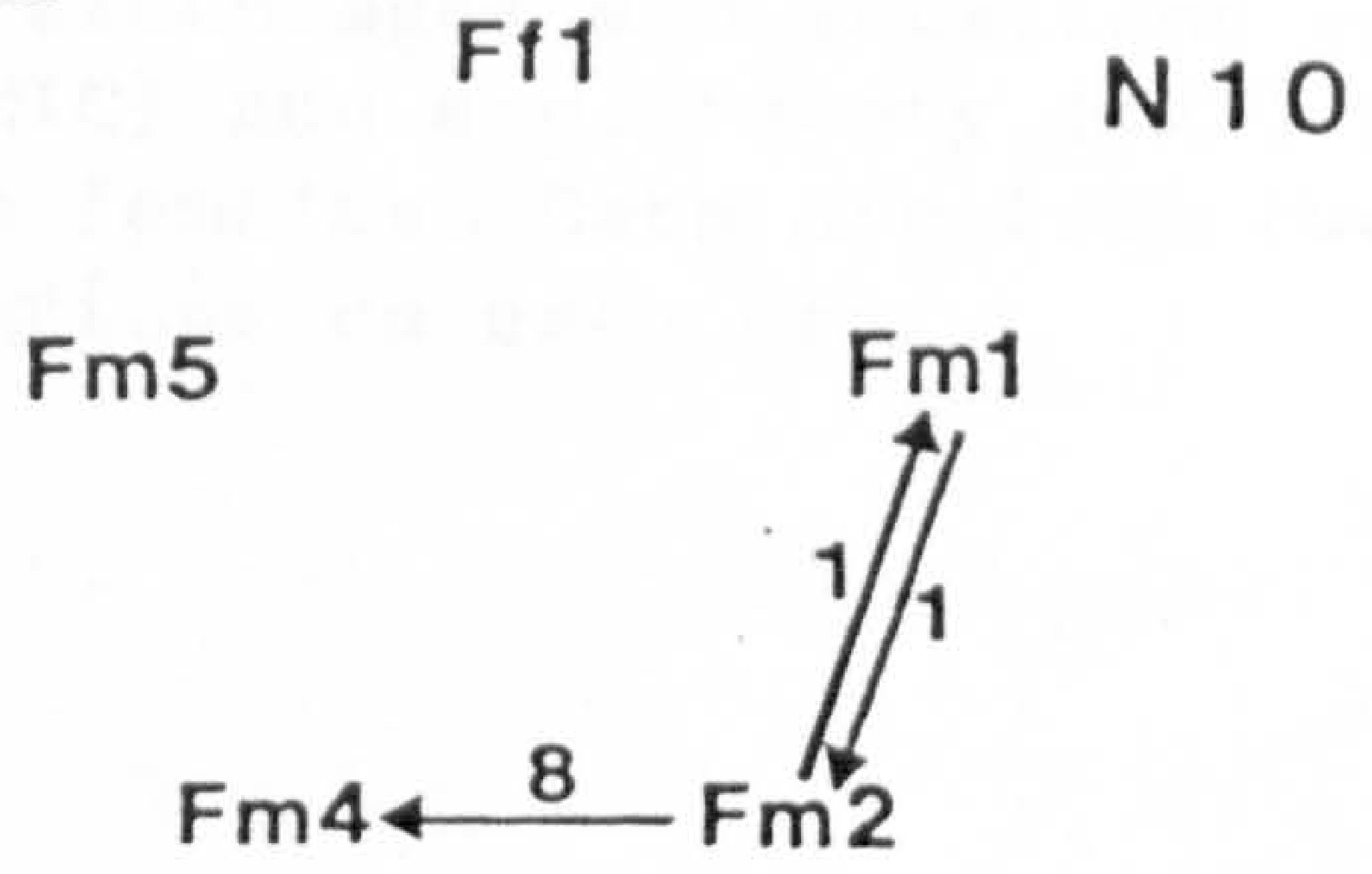


Fig. 4.10 Type, number and direction of social interactions among five Five cats. Data are from one 24 consecutive hour observation on each of Ff1, Fm1 and Fm2.

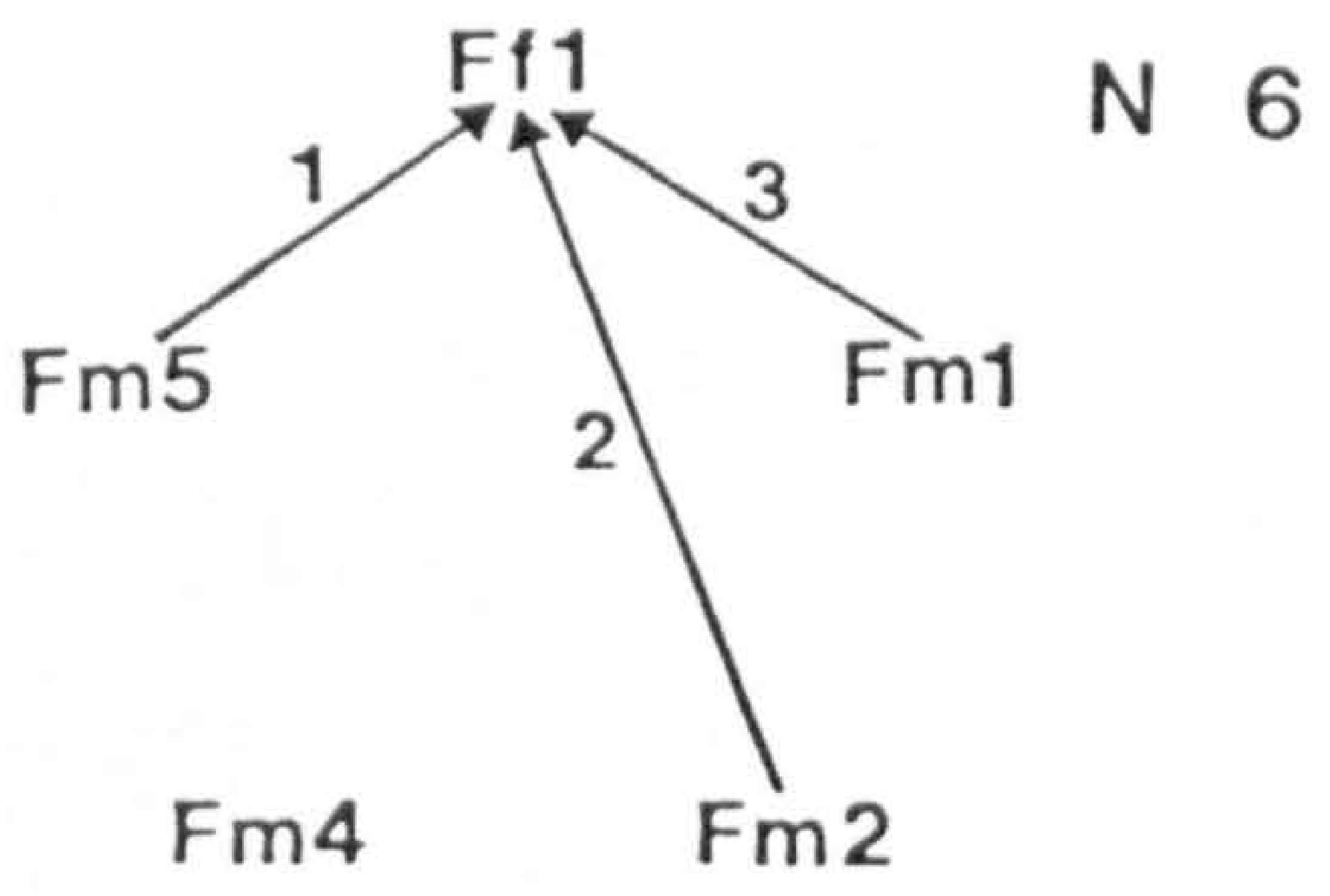
Amicable



Agonistic



Exploratory



	AG	AMIC	EXPL	TOTAL
	N = 79	N = 51	N = 37	
Core area	17.4	13.1	2.4	32.9
Main feeding place	25.1	12.6	16.8	54.5
Dairy	3.6	1.8	3.0	8.4
Other areas	1.2	3.0	0.0	4.2
Total	47.3	30.5	22.2	100.0

Table 4.7 Percentages and locations of agonistic (AG), amicable (AMIC) and exploratory (EXP) interactions by five Cornish females. Data are from two 24 consecutive hour observations on each cat.

share. Agonistic behaviour, however, often arose when cats crowded into a small space when food was expected and it was often precipitated when one individual suddenly but apparently unintentionally advanced towards another, who then attacked the oncomer. But it was brief and never fierce.

There were 17 interactions and near passes (up to 7 m) among Cornish females and between them and other cats outside the core area and dairy. Ten occurred when one or both cats were hunting, six involved physical contact but only two were agonistic. Leyhausen (1965 and 1979) and Liberg (1980) have also observed that females of the same group sometimes hunt close together, even when prey are available elsewhere. And George (1978) describes the amicable behaviour to each other of male and female neutered house cats from the same house when hunting in the same area.

At the Fife farm, all but two interactions by the cats were within their core area. The two interactions which happened outside occurred when Fm1 and Fm2 were hunting; Fm1 chased Fm2 who ran away. During the whole study this was the only behaviour which could be interpreted as territorial. Liberg (1980) noted that males tended to keep separate outside their core areas. 11.2 % (42) of interactions at the Fife farm occurred at the feeding place, fewer than for the Cornish cats (60.7 %). There were also fewer agonistic interactions: 12.6 % compared to the Cornish cats' 47.3 %. The reason why both percentages are relatively much lower compared to the Cornish cats' is probably because the Fife cats spent less time gathered in a small confined area at their feeding place. But like the Cornish cats, agonistic behaviour was not fierce or prolonged.

While waiting for milk the cats at both farms would often sit within a radius of 1 m, sometimes in contact with one another, and when not waiting for food they would often gather within a small area to sunbathe and groom. Cats used each others' vacant sleeping places. Cornish females did not sleep together, but the two young males and the castrated male (Cm2) sometimes slept in contact with a female. Cornish males showed preferences for particular females and only they were seen to initiate a contact by approaching an already resting female. At night the independent kittens slept in a heap. In Fife all the farm cats except Fm3 sometimes slept in contact.

Other observers have found that interactions between group.s are less frequent than within a group. For instance, females of different groups tend to avoid each other (Dards 1979; Liberg 1980). Generally, members within a group interact peacefully, allogroom and sleep together (Macdonald and Apps 1978; Dards 1979) but adult males may fight, avoid or tolerate but rarely be amicable to each other (Dards 1979; Liberg 1980). Males may spend most time with one group or visit a few groups (Dards 1979).

Social Hierarchy

A social or dominance hierarchy is physical domination by some individuals in a social group over others in the group (Wilson 1975) in order to get priority of access to resources

(Clutton-Brock and Harvey 1976). It is maintained by aggression and raises the genetic fitness of the dominant animals (Wilson 1975).

Domestic cats are reported to form social hierarchies. Masserman and Siever (1944) describe a linear hierarchy emerged when captive cats were tested in pairs. Winslow (1938), Baron, Stewart and Warren (1957) and Leyhausen (1979) report that among captive cats held in a group a dominant animal may emerge, with no apparent ranking order among the other cats. In free-ranging cats, Laundre (1977) reports that a female hierarchy existed, with an alpha and beta female, around the milk bowl of a group of farm cats during milking time; and Liberg (1981) found that only a few of the male cats he studied in a rural area performed most copulations. However, the details of cat social hierarchies as well as the changes they might undergo in different ecologial circumstances are unknown.

The data on social interactions among the farm cats were too few to analyse (Figs. 4.9 and 4.10) so my description of a social hierarchy must be largely subjective. Cf5 was the most agonistic female at the Cornish farm. She initiated 16 of the 23 agonistic interactions among the females, including all the six serious fights. She was also the female who sprayed the most frequently (see When and Where Cats Spray and Table 5.1 in Chapter 5). A high rate of scent marking is reported to be associated with high social rank in many mammal species (Ralls 1971; Johnson 1973) and in a study of rural free-ranging cats, Corbett (1979) found dominant cats sprayed significantly more frequently than subordinate ones. Therefore on the basis of agonistic interactions and frequencies of spraying she appeared to be the dominant female. There was no clear ranking structure below her.

However, Cf5 never molested Cf2 and always gave way to her in accidental confrontations. Furthermore, during one confrontation Cf2 sprayed in front of Cf5 (apparently a sign of dominance, see the discussion of spacial patterns of scent marking, Chapter 5). Therefore Cf2 might have been the dominant of the two. Yet she was the lightest and most sedentary of the females and sprayed the least. Cf2's apparent dominance over Cf5 might have been established when she had been more robust and remained unchanged despite a decline in vigour. However, Leyhausen (1979) and Baron, Stewart and Warren (1957) note that the characters of dominant captive cats are often inconsistent with characteristics typically associated with dominance, for instance activity, size and sex, and conclude respectively that character, and motivation and learning were more important determinants of dominance. This was also my impression when observing the females.

Males appeared to have a linear social hierarchy. The order was Fm1, Fm2 then Fm4. Without apparent cause and about once a day for about a minute, a higher male aggressed the males below him by chasing them and swiping at them. Males below did not aggress those above them like this. Therefore this kind of aggression may have been to maintain dominance. Dominance within the group did not appear to be maintained by scent marking, as suggested by Corbett (1979). The dominance order corresponded to weight and age. Liberg (1981) surmises that although weight was important among the rural cats he observed, age was the most important factor in determining social status because no male less than three years old became a dominant breeder.

Males and females at both farms did not interact agonistically, except occasionally at the feeding bowl, so that my impression was that their hierarchies were separate.

Leyhausen (1965 and 1979) believes domestic cats have a relative social hierarchy dependent on place and time; one cat may be dominant at one place and time but not at another. There was no evidence to support this among the farm cats.

Food Provisioning

Cf2 gave up her four kittens which then joined the kittens of Cf3, who caught prey for both lots. The largest and most robust of these kittens was one of Cf2's and he usually took the first prey brought back. One of Cf3's male kittens of the previous year once took the prey. Cf3 never offered resistance to whoever took her prey but gave it up almost immediately. On one occasion, before she could get it to her two lots of kittens, Cf1 took the prey and gave it to one of her own.

Other females are reported also to provision food in a wider sphere than the mother-kitten unit: females may suckle each others' kittens (Dards 1978; Macdonald and Apps 1978) and provision a nursing mother with prey (Macdonald and Apps 1978).

Intruders

I saw a strange male one night in the core area of the Fife farm. Fm1 passed him 3 m away and probably saw him but showed no indication. Another male, a mature whole house cat living 700 m north of the core area, was seen on three nights. Fm1 confronted him on two nights but there was no apparent agonistic behaviour.

Territoriality

There did not appear to be any defended areas among Cornish and Fife farm cats. The agonistic interactions initiated by Cf5 did not appear to be connected with any place. The only evidence of territoriality occurred on the two occasions when Fm1 aggressed Fm2 on encountering him when they were hunting. Sprayed scent marks and scats seemed to be ignored (see Chapter 5, on scent communication).

As stated above, in the discussion on space use, there is some observational evidence of active spacing in free-ranging cats. A breeding female may tolerate a male, possibly her mate, but attack other cats near her den (Corbett 1979). Resident adult males may attack young transient males, who do not settle in the resident males' home ranges (Corbett 1979; Dards 1979; Liberg 1980) and young cats may avoid confrontation by changing course or hiding (Corbett 1979).

Breaking-up Fights

A behaviour at the Fife farm, not observed at the Cornish farm, was 'breaking-up fights'. It occurred five times which was sufficient to bring it to light as a distinct recurring behaviour. One cat would attack another and a third cat would approach the attacker and (subjectively) appear and try to inhibit him from further aggression. For instance, Fm4 was attacked by Fm1. Ff1 quickly approached the aggressor, reared up and flung out both fore paws at him and got in his way. On another occasion Fm3 attacked and chased Fm4 for 20 m. Fm1 immediately chased the aggressor and the two cats spent 10 min howling at each other. As a last example, Fm3 chased and cornered Fm4 behind some bales and started howling at him. Fm2 ran behind the bales and a few seconds later ran out being chased by the aggressor. Breaking up a fight sometimes led to the attacked cat getting away and sometimes to the intervening cat being attacked. Like 'walk-abouts' above, it has not previously been described in cats. Could it be altruism? Its function was not obvious.

Infanticide

Ff1 gave birth to three healthy kittens during the night of 6/7.5.81 and 18 days later during the night they were killed in their nest. According to the farmer one kitten was partly eaten by Ff1. The following day I examined the other two. They weighed 245 g and 265 g. One kitten had two punctures, one on the neck near the spine and the other 17 mm away towards the throat and both about 1 mm x 2 mm in area. There was also a haemorrhage 2 mm to the right of the windpipe which was not punctured. The other kitten had a small puncture at the base of its right ear, four small punctures close together in a straight line, 14 mm long, on the neck to the right of the spine and two punctures, 14 mm apart and each 1 mm x 2 mm, by the windpipe, which was not punctured. No other wounds were evident. These wounds were similar to those inflicted on rabbits killed by Fm1, Fm2 and Hm1 which suggests the kittens were killed by a cat. The 1 mm x 2 mm wounds may have been caused by canines and the four small punctures in a row may have been caused by incisors. The distances between wounds are compatible with the distances between a cat's teeth.

Males are popularly thought to kill kittens and the general belief is that it is in order to mate with the female again (for instance Topsell 1607). This would make evolutionary sense if the infanticidal male were not related to the father and succeeded in making the female bear his offspring, which would increase his reproductive success (Hrdy 1974; Bertram 1975). Infanticide by males is reported to occur in a numer of mammal species, for instance primates (Hrdy 1979) and lions (Bertram 1975), but has not so far been reported in the literature to occur in domestic cats.

Discussion

There was little difference in the estimation of overlap of home ranges using convex polygon and grid square methods. The former method provides an estimate of the minimum perimeter of a home range and shows the approximate direction and extent of movements of a cat and of cats relative to each other. However, only the latter method was able to show an effect of the environment on the shape of a home range. Cats did not cross fields but travelled along and kept close to linear features, for instance roads and hedges, and these clearly determined the configuration of the larger home ranges (Cf3, Fm1 and Fm2). Furthermore, grid squares present a more accurate estimate of area actually used by a cat. Although the difference was slight for small home ranges it became increasingly important for the larger ones. For both these reasons, therefore, home ranges are better estimated using grid squares.

Each cat spent most of the 24 h in a small core area which was used mainly for sleeping, resting and grooming. Core areas overlapped extensively and cats passed each other frequently. Surrounding a core area, and partly within it, were areas where hunting was the main activity. These areas were not used uniformly by females, who appeared to have a few places in which most hunting occurred. Males had larger home ranges than females. Home ranges overlapped considerablly but no part within an overlapping area, for instance routes, hunting areas and even sleeping places, was exclusive; within a group there was no defence of any area. This picture of space use agrees well with reports by other workers (Leyhausen 1965; Laundre 1977; Macdonald and Apps 1978; Dards 1979; Liberg 1980).

Within both groups of farm cats there was no obvious territoriality. However, there is some observational evidence of overt territoriallity in free-ranging cats. A breeding female tolerated a male, possible her mate, but attacked other cats near her den (Corbett 1979). Resident, adult males attacked young transient males, who did not settle in the resident, males' home ranges (Corbett 1979; Dards 1979; Liberg 1980) and young cats avoided confrontation with adults by changing course or hiding (Corbett 1979). Dards (1979) and Liberg (1980) believe aggression may play a role in dispersal and Corbett (1979) believes aggression, possibly reinforced by spraying and leaving prominent scats, plays a major role in spacing. However, within both groups of farm cats there was no obvious territoriallity.

Nor did there appear to be any covert teritoriality. It has been suggested that urine marking may facilitate prevention of encounters between felid conspecifics (Leyhausen 1965; Schaller 1967; Hornocker 1969; Eaton 1970). But there was no evidence that the movements of the cats were inhibited by urine marks. The cats did not change course abruptly or retrace their steps as a possible response to a conspecific's urine mark; conversely, they occasionally hunted close by and within sight of each other and females sometimes approached and greeted each other and males when travelling and hunting.

Domestic cats have been considered to be solitary animals (for instance Baron, Stewart and Warren 1957; Rosenblatt and Schneirla 1962; Fox 1975) but the farm cats showed more than a tolerance for each other. They gathered in close proximity within their core area, slept with each other, and females greeted each other and males when hunting and travelling. Despite unlimited space they favoured a loose cohesion. Non-solitary behaviour has also been reported in other free-ranging cats: sleeping together, communal suckling and food provisioning (Macdonald and Apps 1978) and small groups of non-breeding adults (Dards 1978 and van Aarde 1978).

The farm cats were not a clutter of unrelated vagrants. My data support the prediction of Fagen (1978a) that groups of domestic cats may live for generations with humans, with genetic relationships comparable to lions (Bertram 1976) and hanuman langurs, Presytis entellus (Hrdy 1977). Thus kittens may have social contacts with litter mates, older siblings, cousins, aunts, uncles and perhaps fathers, which also occurs in social primates, social dogs and lions (Fagen 1978a). Laundre (1977) and Liberg (1980) have also described individuals in groups of genetically related domestic cats who have lived together for generations.

Lions have been upheld as the only social cats (for instance Schaller 1972; Rudnai 1973; Bertram 1975) but this view is no longer tenable because the similarities of farm cats with lions are too close: the females of both species may live with offspring in long lived groups wherein individuals share the same area, are genetically related, interact peacefully within the group and agonistically to other groups and tend to remain in their natal area; the males in the group may also be genetically related, associate with more than one female group and tend to emigrate from their natal area. But there are also contrasts; male lions hunt together and together control female groups whereas male domestic cats do not. (Domestic cats: this study; Laundre 1977; Macdonald and Apps 1978; Dards 1979; Liberg 1980. Lions: Schaller 1972; Rudnai 1973; Bertram 1975).

The primary reason why domestic cats live in groups is probably to feed on the human-provided food supply. During the cat census I found three farms which had had cats who all left in a few weeks when the food provisioning stopped. None returned. That canrnivores may alter group structure in response to food supply has been recorded in other carnivores. For instance, golden jackals (Canis aureus) usually form pairs and eat small dispersed prey but groups of up to 20 individuals feeding from human garbage by the Dead Sea have been studied (Macdonald 1979). Spotted hyaenas (Crocuta crocuta) live in small groups or hunt singly when the herds they prey on are migratory but form large groups when the prey become non-migratory (Kruuk 1972). Red foxes (Vulpes vulpes) in rural areas are solitary, eating rabbits, rodents and birds but in urban areas may live in small groups eating earthworms (Lumbricus terrestris) and garbage (Macdonald 1977).

Liberg (1980) believes the social organization of domestic cats evolved from a solitary to a gregarious life style through the differential survival of offspring at human settlements; survival of offspring who remained with their mothers at a human-provided food source was greater than for those who dispersed and fended for themselves, so grouping was favoured. However, the ability to alter group structure is now recognised as being inherent in the same species; as Macdonald (1979) writes, we should not think of a species social system but of its social systems. All the small felid species are presumed to be solitary, as the domestic cat has been, but when their free-ranging behaviour is elucidated they too will probably show a large capacity for social behaviour, depending on their ecological circumstances.

Selective advantages favouring grouping might include observational learning (Adler 1955) within a social group. Advantages might also arise from the human provided food and from food supplied by other individuals in the group (for instance Cf3's behaviour, above). Communal suckling of kittens and provisioning of food to nursing mothers was observed by Macdonald and Apps (1978) who propose cooperative defence of a (human-provided) food source and of kittens. However, although cats sharing an area may react agonisticly to an intruder, it is likely they are acting independently, giving a specious impression of cooperation. My cats did not obviously cooperate or even obviously defend anything. For instance Fm3, an outsider introduced to the Fife farm, ate freely from the food bowl used by the other cats.

Selective pressures against grouping include transmission of disease and inbreeding. In 1981 all the kittens at the Cornish farm died, perhaps from an epidemic of cat flu, except one kitten who lived at the dairy so had minimal contact with the other cats. It has been argued that males are selected to leave their natal birth place to avoid inbreeding (Dards 1979; Liberg 1980) but the adult males at the Cornish and Fife farms were present during the breeding period.

Chapter 5

SCENT COMMUNICATION

Preamble

Many species of cats are reported to use urine and faeces as means of scent marking (Wemmer and Scow 1977). But although odours used in mammal scent communication have been chemically analysed, little is known about their behavioural significance. One of the greatest needs at the moment is for data on the spatial patterns of scent marking in free-ranging animals (Mech and Peters 1977) and this is particularly true of domestic cats, where very little is known (Corbett 1979; Dards 1979; Liberg 1980). In the first part of this chapter I report on my field observations of the spatial patterns of scent marking, that is the distribution of sites where urine and faeces were deployed and the frequency with which they were deposited, and attempt to relate them to the activities of the cats. I then continue in the second part of the chapter with an experiment intended to show that cats can distinguish between odours from different cats in order to demonstrate they can recognise scent marks as having been made by different individuals.

The following is an outline for the section dealing with the spatial patterns of scent marking. A more detailed description is presented in Chapter 2. The method for the experiment on odour discrimination is dealt with in the section on odour discrimination.

Subjects

Five female Cornish cats: Cf1, Cf2, Cf3, Cf4 and Cf5; and one female and two male Fife farm cats: Ff1, Fm1 and Fm2.

Procedure

A cat was followed and directly observed for the whole of an observation period (see below). The cat's behaviour was recorded as one of a number of mutually exclusive categories (see under Behavioural Categories in the General Method, Chapter 2) every fifth minute on the minute. But if the animal was out of sight he was recorded as being lost to view. Other behaviours and the routes the cat travelled were noted during recording intervals.

Observation Periods

Cornish cats were each followed three times from the beginning of the first complete hour to the end of the last complete hour of daylight and twice for 24 consecutive hours. Cf3 was followed for 13 consecutive days from 09.00 h to 17.00 h. Fife cats were each followed once for 24 consecutive hours and thereafter in blocks to make up composite 24 h periods. Cornish cats were observed from October 1978 to February 1979 and Cf3 observed again in February 1980. Fife cats were observed from April to June 1981.

Spraying Frequencies

Spraying is directing a jet of urine rearwards on to an object. The number of sprays by each Cornish female is shown in Table 5.1 and the number of sprays by the Fife farm cats is shown in Table 5.2. The frequency of spraying by the Cornish females varied greatly between and within individuals. Cf5, for instance, sprayed on average twice as frequently as the other females and Cf3 sprayed 36 times during one observation and only twice during another.

Sprays by Fm1 and Fm2 confirm the observations by de Boer (1977) on captive cats and Liberg (1980) on free-ranging cats that mature adult males spray more frequently than females. During 24 consecutive hour observations their frequency of spraying was an order of magnitude greater than that of the females: the mean number of sprays by the males was 124.5 and by the Cornish females 11.1.

The only time the Fife female (Ff1) was seen to spray was at the end of May when she came into oestrus after her kittens were killed (see Infanticide, Chapter 4). Fm3 did not spray, probably because he was ill. He was inactive for most of the day (see Activity Patterns, Chapter 3).

Dominant animals in many mammal species are reported to mark more often than subordinates (Ralls 1971; Johnson 1973). Corbett (1979) found dominant rural cats he studied sprayed significantly more frequently than subordinants. However, Cf5 sprayed the most frequently but appeared to be subordinate to Cf2, who sprayed the least frequently; furthermore, the

Day	Cf1	Cf2	Cf3	Cf4	Cf5
1	10	4	20	8	4
2	20	2	2	6	21
3	7	1	36	0	10
4	11	5	6	11	42
5	10	2	2	0	22
$\bar{X}$	11.6	2.8	13.2	5.0	19.8

Table 5.1 The number of sprays by five Cornish females each observed on three daylight (days 1-3) and two 24 consecutive hour observations (days 4-5).

Day	Ff1	Fm1	Fm2
1	0	126	123
2	20	152	134
3	0	263	-
4	1	117	-

Table 5.2 The number of sprays by one female and two male Fife cats each observed on one 24 consecutive hour observation (day 1) and on composit observations to make 24 h periods.

	INSIDE	OUTSIDE	% OUTSIDE
Cf1	23	35	60.3
Cf2	1	13	71.4
Cf3	0	66	100.0
Cf4	4	21	84.0
Cf5	35	64	64.6
$\bar{x}$%	24	76	76.1

Table 5.3 The 262 sprays by five Cornish females inside and outside their core area. Data are from three daylight and two 24 h observations per cat.

subordinate male farm cat (Fm2) sprayed the same number of times as his dominant brother (Fm1) (Table 5.1 and Social Hierarchy in Chapter 4). Therefore spraying frequencies in cats do not always appear to be a sign of dominance.

When and Where Cats Spray

Of the total 262 sprays by the Cornish females 46.2 % (121) occurred when hunting and a further 15.3 % (40) occurred within one record (that is 5 min) of showing obvious hunting behaviour and in the absence of other activity (for instance, feeding and social behaviour). Therefore as many as 61.5 % of sprays may have been made when hunting. Percentages per cat were Cf1 62.1 %, Cf2 21.4 %, Cf3 87.9 %, Cf4 52.0 % and Cf5 51.5 %.

18.3 % (48) of their sprays were not associated with hunting. Ten of these sprays were at sleeping places and nine sprays occurred after sniffing a spot. However, nearly half (23) of these were by Cf5 (who was unusually agonistic towards other females; see Chapter 4, on social behaviour): most occurred when she was in the presence of other females or at places where they had recently been, four occurred at the end of four of the six serious agonistic interactions initiated by her against females, and one occurred after an unexpected encounter with a female in which she was at a disadvantage and withdrew. The six remaining sprays could not be associated with anything.

The males, Fm1 and Fm2, also sprayed when hunting but proportionally less frequently than the females. During nine hunts, Fm1 sprayed a mean of 25.4 ± 12.7 times (range 12 - 51, N

= 209). Thus if his average number of sprays in 24 h was about 130 (Table 5.2) then about 20 % of sprays occurred when hunting.

The Cornish females usually sprayed outside their core area. Table 5.3 shows their total number of sprays and in all cases more occurred outside than inside their core area (sign test, N = 5, $p < 0.03$, one tailed). The positions of sprays were noted for Cf3 in 1980 and Fig. 5.1 shows the position of all her 27 sprays; all were outside her core area. The few sprays (Table 5.2) by Ff1 when she came into oestrus after her kittens were killed, however, were inside her core area.

Contrary to female behaviour, most sprays by the two males, Fm1 and Fm2, occurred in their core area, when walking about it. For instance, during both males' 24 consecutive hour observation 84 % (106) and 75 % (96) of sprays occurred there (Fig. 5.2).

Males and females left their core area to hunt but only males left their core area to travel. Fm1 sometimes visited a female 650 m away, spraying as he travelled there and back along the same route. The males also sprayed when following Ff1 when she was in oestrus.

Fig. 5.3 shows the spatial distribution of all the 209 sprays during nine hunts by Fm1 in his hunting area and the track leading to it. The positions of sprays were noted in relation to markers along fences and hedges and to pegs at the intersection of 12.5 m squares in the hunting area (see Procedure, Chapter 6). Fig. 5.3 shows that many sprays appear to be concentrated within gorse patches. This can be explained if Fm1 used the patches

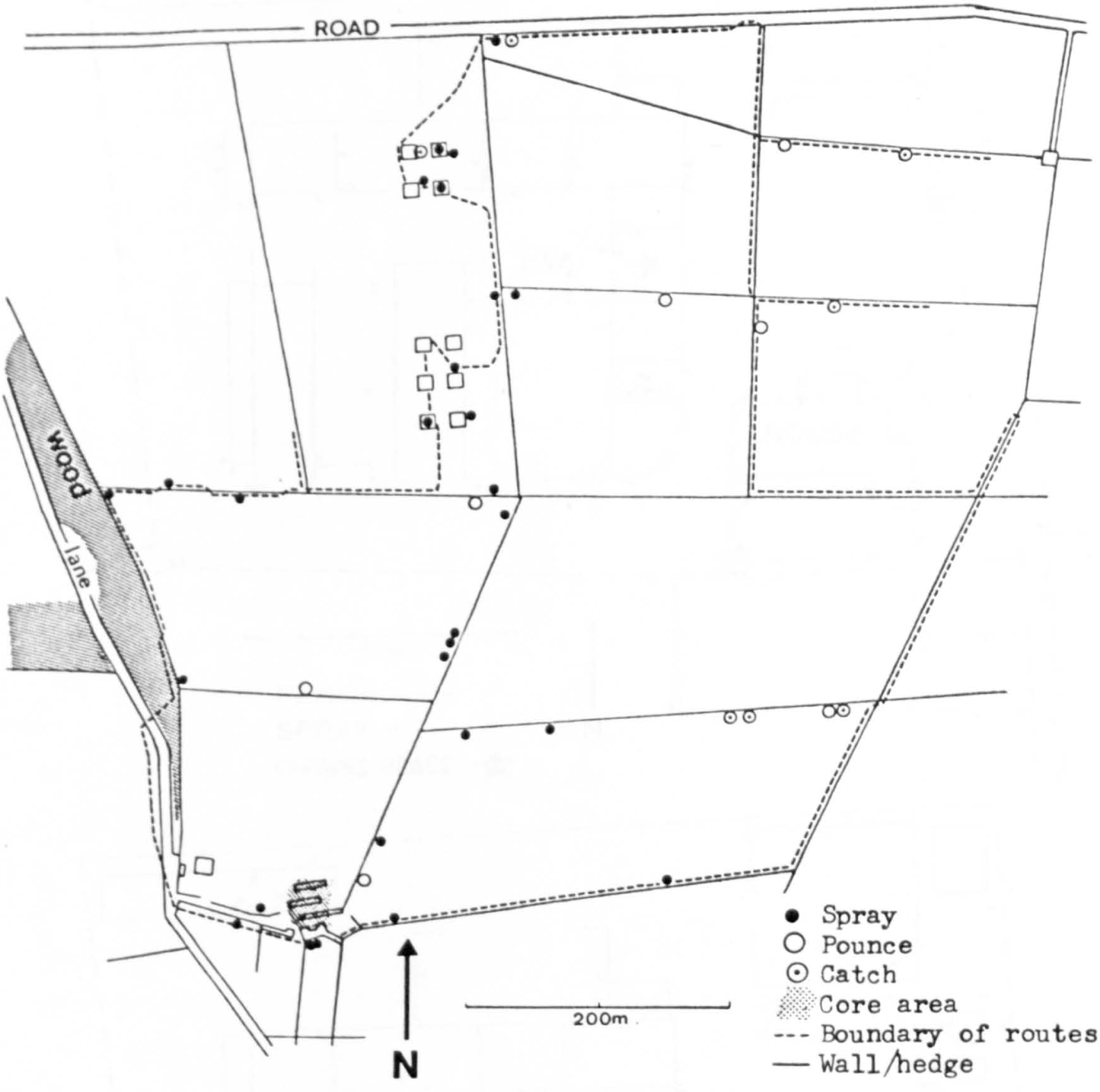


Fig. 5.1 27 spray and 14 pounce and catch sites of Cf3 in 1980.

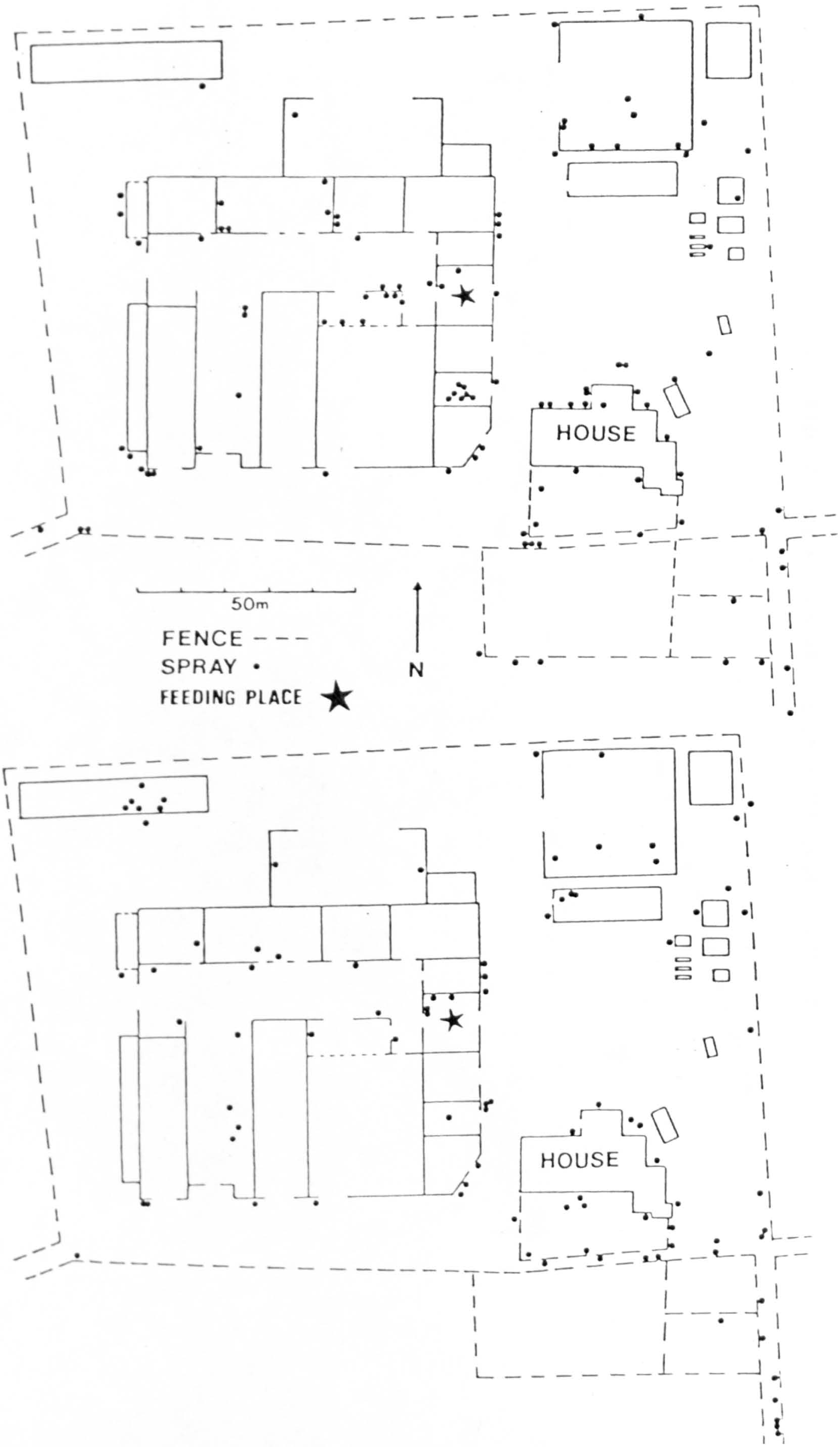


Fig. 5.2 Positions of 106 sprays by Fm1 (top) and 96 sprays by Fm2 in their core area. Data are from one 24 consecutive hour observation on each cat.

Fig. 5.3 Distribution of 209 sprays by Fml on nine hunts.

more than the area outside them and Fig. 6.5 (Chapter 6), of his search paths throughout the area, shows this is what he did. Thus most sprays may occur within the patches simply because they were used more. A nearest neighbour statistical test (for instance Clark and Evans 1954) can be used to find whether the sprays within a gorse patch were randomly distributed, spaced relative to each other or clustered together. However, due to the uneven terrain and dense vegetation some pegs were not always evenly spaced. Furthermore, the distance of a spray to a peg was guessed and sometimes the nearest peg was obscured by vegatation so that the next nearest peg was used, which was sometimes as much as 25 m away. Consequently, to avoid spurious accuracy the distances between sprays should be lumped into 20 m steps. But Fig. 5.3 shows that the majority of sprays were less than this distance apart, so a nearest neighbour test cannot be used.

Fig. 5.3 also shows that sprays do not usually occur where Fm1 had located prey, tried to catch or caught them or where he found and ate rabbit carcases. Therefore they do not appear to be related directly to prey. Fm1, however, did keep close to rabbit holes within the patches (Fig. 6.5). Corbett (1979) suggests that domestic cats he watched hunting in sand dunes in the Hebrides often sprayed near rabbit holes. If Fm1 frequently sprayed close to rabbit holes then sprays should be proportionally more concentrated in squares which contained one or more holes. In the field with gorse patches, 51 sprays occurred inside and 92 sprays occurred outside the squares with rabbit holes, which was significantly different from an expected random distribution (chi-squared 11.189, df = 1, $p < 0.001$). So

Fm1 sprayed proportionally less frequently near rabbit holes than at other places in the field.

Summarising Figs. 5.3 and 6.5, most sprays were consentrated in gorse patches, possibly because these patches were used more than other areas; however, sprays did not usually occur where prey had been located and the majority of sprays occurred away from rabbit holes.

Fig. 5.1 shows the spatial distribution of all sprays by Cf3 when she was followed in 1980 for the eight days when she hunted. Like the sprays of the males, they do not appear to be related to sites where prey were located and are distributed throughout the area she hunted. The spatial distributions of the sprays of the other Cornish females were not recorded but they appeared to be similar to Cf3's.

Spraying Rate

During nine hunts Fm1 sprayed once per 5 min and 44 m and during one hunt Fm2 sprayed once per 15 min and 64 m. During all their hunts the Cornish females sprayed once per 22.2 min and 79 m. These durations include time spent ambushing. On four observations, when travelling to a female 650 m from his core area, Fm1 sprayed once per 1.6 min and 41 m. And when observed on one occasion travelling outside his core area Fm2 sprayed once per 23 min and 43 m. These durations include time spent resting.

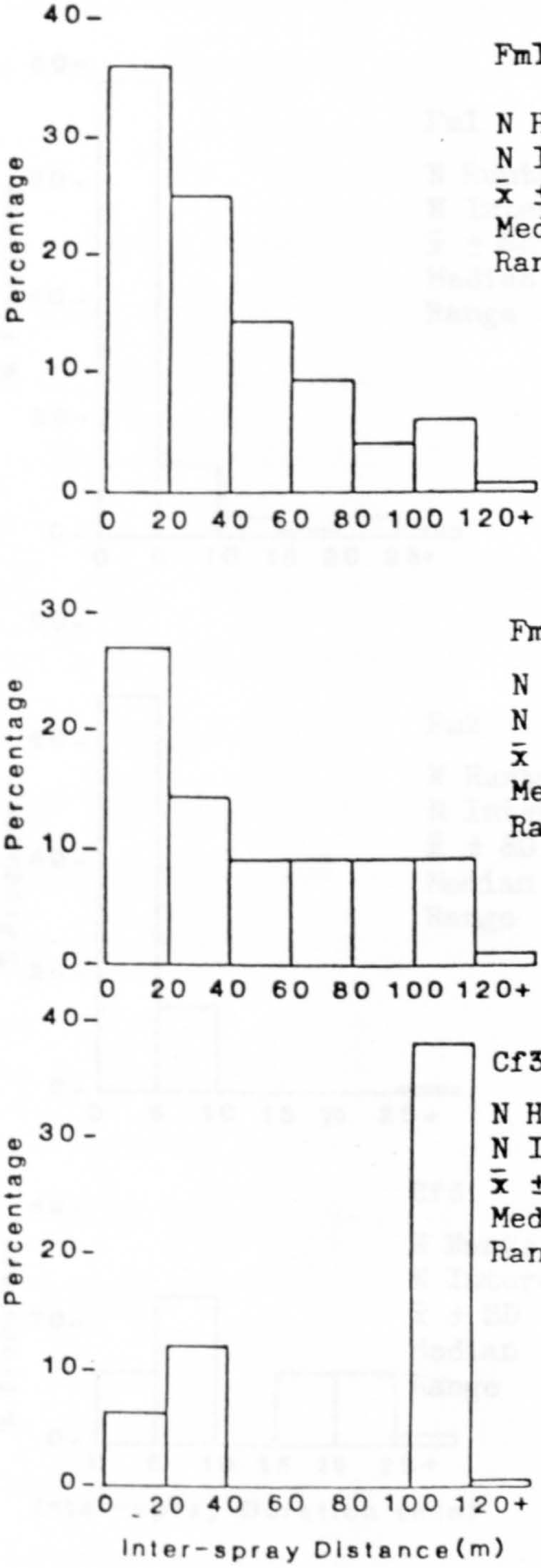
Corbett (1979) quantified the spraying rate of domestic cats he observed as the number of sprays per 'walking minute', that is when cats were mobile. His method of quantification means our data are difficult to compare because my data include time spent stationary. However, for 22 cats seen walking he calculated the rate was 1 spray per 5.4 walking minutes.

Fig. 5.4 shows the frequency distributions of interspray distances by Fm1, Fm2 and Cf3 when hunting. The distribution for both males is monomodal and strongly right skewed but for the female it is bimodal and strongly left skewed. The interspray distances of the males are usually short but for the female they are usually long. Schaller (1972) noted that lions (<u>Panthera leo</u>) sometimes travelled for some distance without spraying and the farm cats also did this when hunting. The males sometimes travelled up to 485 m without spraying and the female travelled up to 1,595 m.

Fig. 5.5 shows the frequency distributions of the three cats' interspray time when hunting. The distributions for the males reflect those for interspray distance; they are monomodal and strongly right skewed, most interspray times are within 5 min. The distribution for Cf3 might be bimodal and, compared with the males' distribution, most interspray times are of relatively longer duration.

Thus the males usually sprayed at short spatio-temporal intervals whereas the female usually sprayed at longer ones. Data are not available for the other Cornish females but their spraying frequencies appeared to be like Cf3's.

Fig. 5.4 Distances (m) between sprays by two males and one female.



Fm1

N Hunts	9
N Inter-spray distances	159
$\bar{x} \pm SD$	45 ± 46 m
Median	29 m
Range	2 - 319 m

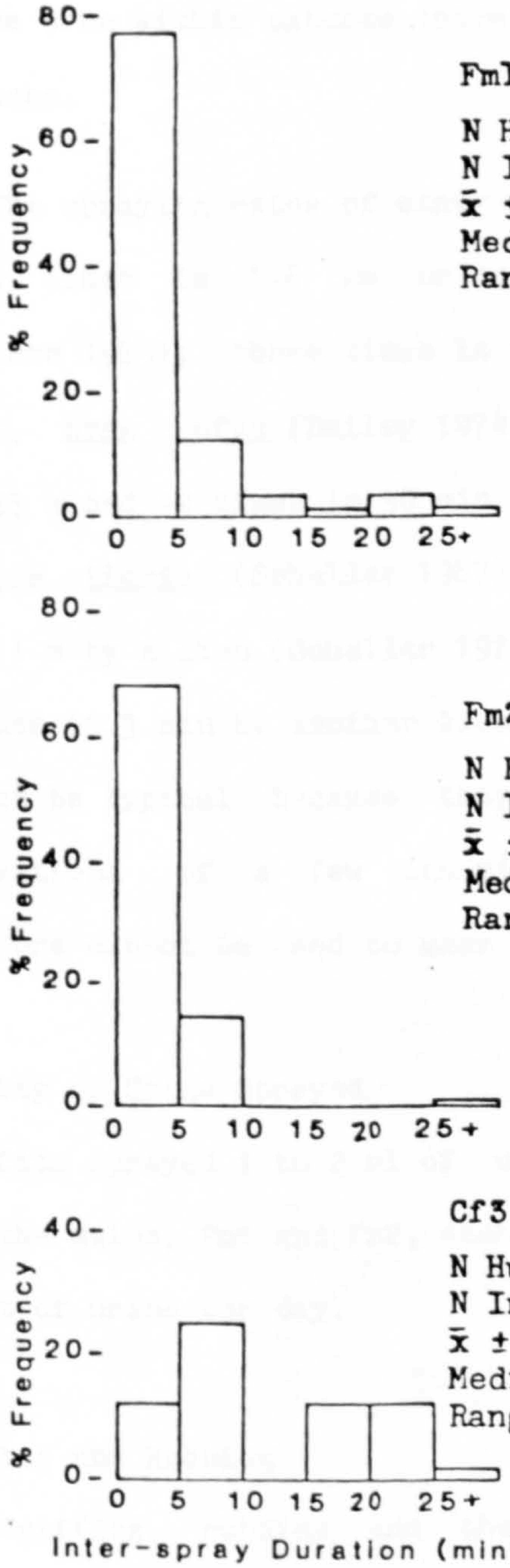
Fm2

N Hunts	1
N Inter-spray distances	22
$\bar{x} \pm SD$	98 ± 121 m
Median	54 m
Range	7 - 485 m

Cf3

N Hunts	6
N Inter-spray distances	16
$\bar{x} \pm SD$	264 ± 387 m
Median	115 m
Range	15 - 1595 m

Fig. 5.5 Durations (min) between sprays by two males and one female.



Fm1

N Hunts	9
N Inter-spray durations	159
$\bar{x} \pm$ SD	5 ± 9 min
Median	2 min
Range	0 - 52 min

Fm2

N Hunts	1
N Inter-spray durations	22
$\bar{x} \pm$ SD	23 ± 64 min
Median	2 min
Range	0 - 294 min

Cf3

N Hunts	6
N Inter-spray durations	16
$\bar{x} \pm$ SD	34 ± 36 min
Median	20 min
Range	1 - 62 min

Fig. 5.6 shows the spatial distribution of sprays by Fm1 and Fm2 in relation to a single search path when hunting (see Search Paths, Chapter 6). Long interspray distances cannot be completely accounted for by the long spaces between gorse patches because even within patches there are sometimes long interspray distances.

The spraying rates of other felids have also been noted: 17 to 20 times in 1.6 km or once per 80 m by lynxes, *Lynx lynx* (Saunders 1963); three times in 1.6 km or once per 533 m by a bobcat, *Lynx rufus* (Bailey 1974); three times in 700 m or once per 233 m and 12 times in 30 min or once per 2.5 min by tigers, *Panthera tigris* (Schaller 1967); seven times in 1.9 km or once per 271 m by a lion (Schaller 1972) and 13 times in 2 h 40 min or once per 12.3 min by another lion (Rudnai 1973). But these rates may not be typical because they are based mainly on chance observations of a few individuals over brief periods and therefore cannot be used to make comparisons.

Quantity of Urine Sprayed

Cats sprayed 1 to 2 ml of urine per spray, rarely more. Thus the males, Fm1 and Fm2, each sprayed about a quarter to half a pint of urine per day.

Sniffing and Rubbing

Sniffing, rubbing and then spraying by cats sometimes occurred consecutively. A cat would briefly sniff a spot, rub it once or a few times with the side of the head and then spray within 30 cm of it. Sniffing was not always followed by rubbing

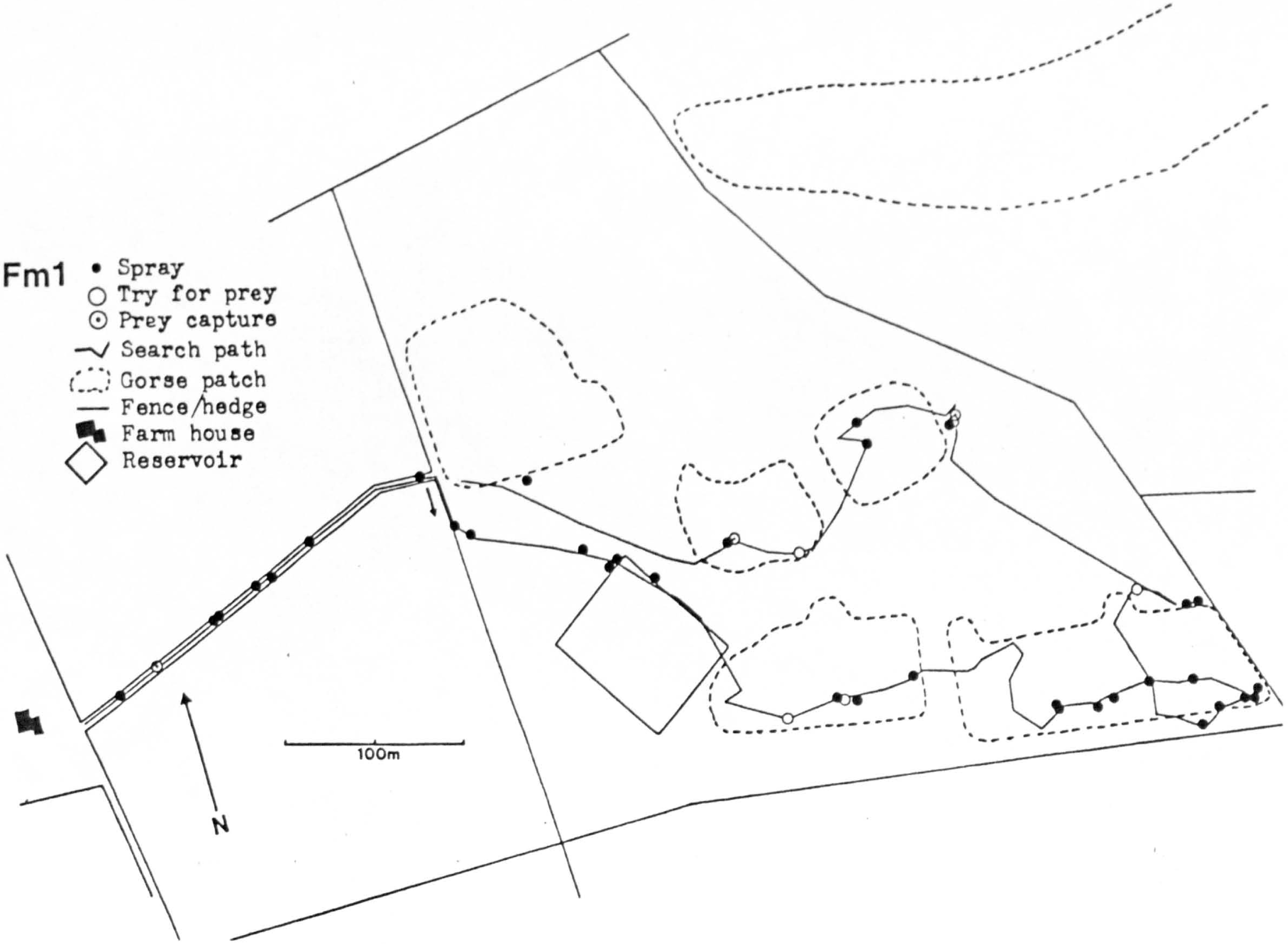
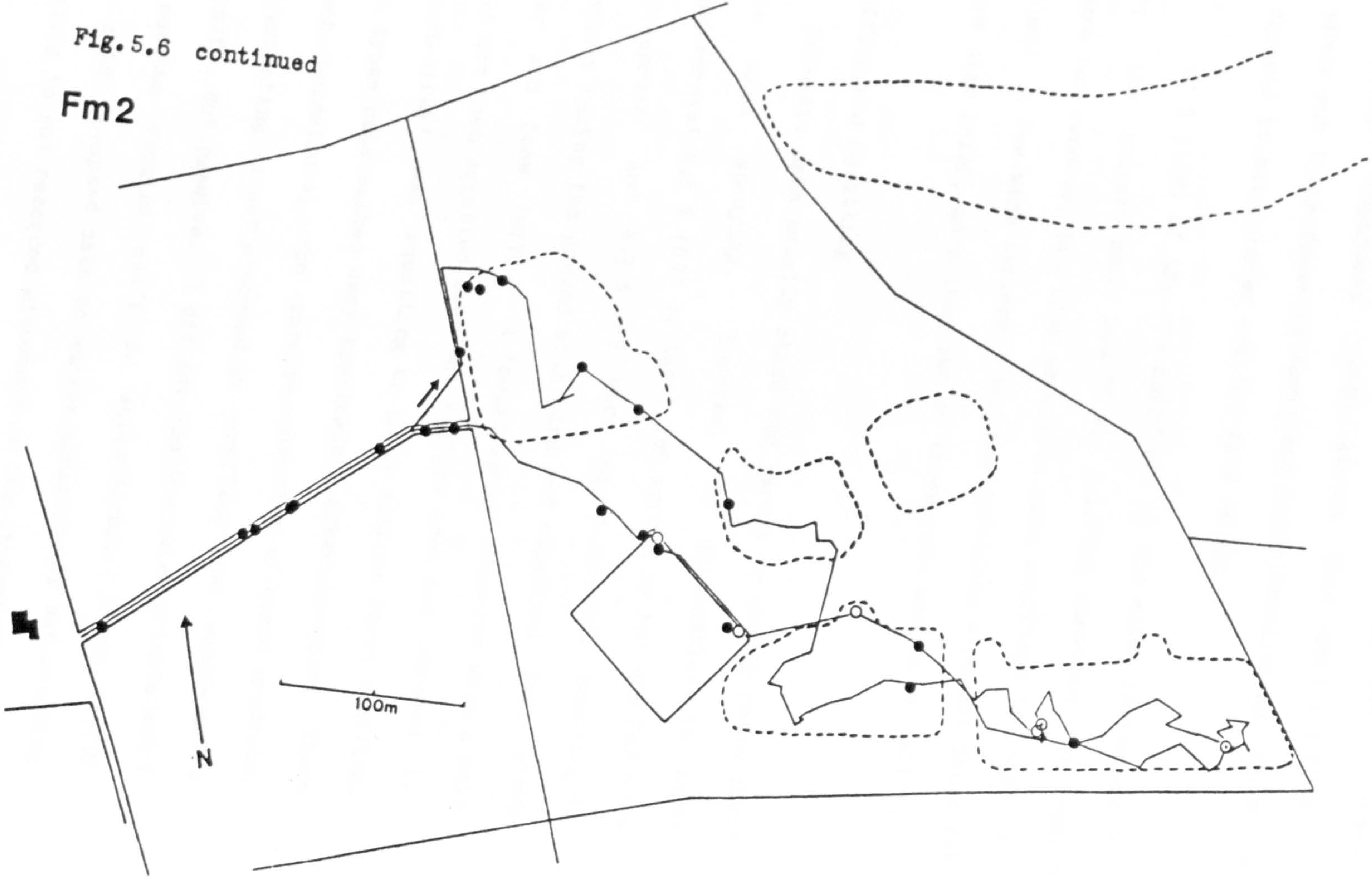


Fig. 5.6 A hunting search path of Fm1 and of Fm2 showing the distribution of sprays.

Fig.5.6 continued

Fm2



before spraying but in every case rubbing was preceded by sniffing. Leyhausen (1965) states that male and female cats often rub their faces in their own urine immediately after they sprayed it but I never saw the cats do this.

87 % (499) of the 575 sniffings by the males lasted about 1 s; the longest sniff was 75 s. Sniffing durations for females were not recorded but they were like male sniffings in that all except a few were cursory. Rubbing durations were not noted but were also brief, more than two or three rubs was an exception.

Scuffing and Squatting

Domestic cats usually stand and partly or wholly raise their tails when spraying. However, in distinction to these 'stand-sprays' 4.7 % (64) of the 1,365 sprays by Fm1 and Fm2 were 'scuff-sprays' and 4.3 % (59) were 'squat-sprays'. Scuffing is vigorously raking the ground with hind and sometimes fore claws (Wemmer and Scow 1977). A 'scuff-spray' occurred when a male scuffed and then squatted over the scuffed area and sprayed it. A 'squat-spray' was squatting to spray without first scuffing. In both types cats walked away immediately after spraying. These were not urinations, the passive excretion of waste products, because urinating is not preceded by scuffing and squat-sprays were forceful not passive. I did not see the males urinate and I did not see the females scuff or squat-spray. Dards (1979) observed male dockyard cats to scrape occasionally but scuffing and squatting is not recorded elsewhere in the literature.

Frequency of Defaecating

The defaecations of the Fife cats were too few to quantify. However, the mean number of defaecations in 24 h by Cornish females was 3.2 ± 1.5 (N = 32). They often had diarrhoea, probably because of the large quantities of milk they drank (after eating prey a cat had fairly firm scats), so this figure is probably higher than cats on a more solid diet.

Scraping-over Scats

Table 5.4 shows the number of defaecations per Cornish female. Half the scats were scraped over and half left exposed. The cats tended to scrape-over scats inside the core area and tended to leave them exposed outside (but this was not consistent, sign test, N = 5). The table also shows the number of scraped-over and exposed scats by Cf3 inside and outside her core area during 13 consecutive days of observation in 1980. Again, half the scats were scraped over and half left exposed and she tended to leave more scats scraped-over inside the core area and leave more exposed outside it.

Scats appear to have communicatory significance but like sprays their purpose is not clear. Bailey (1974 and others cited therein) found bobcats scraped over half their scats. Lynxes (Lindermann 1955), wildcats (*Felis silvestris*) (Ragni 1978) and rural domestic cats (Liberg 1980) tend to scrape over scats within relatively more frequented areas and leave them exposed outside them. But Corbett (1979) found farm cats and subordinate feral cats and Dards (1979) found dockyard cats usually scraped over theirs. Lions leave theirs exposed (Rudnai 1973).

	INSIDE		OUTSIDE		TOTAL
	SCRAPED	EXPOSED	SCRAPED	EXPOSED	
Cf1	1	0	7	0	8
Cf2	3	2	0	4	9
Cf3	3 (8)	1 (3)	3 (6)	7 (10)	14 (27)
Cf4	5	2	2	6	15
Cf5	0	2	5	5	12
% TOTAL	20.7	12.1	29.3	37.9	100.0

Table 5.4 The number of scraped-over and exposed scats by five Cornish females inside and outside their core area. Data are from three daylight and two 24 h observations per cat. Scats in brackets are by Cf3 observed in 1980 and not included in the percentage total.

Prominence and Clumping of Scats

Scats may be deposited in prominent places by lynxes (Saunders 1963), tigers (Schaller 1967), cheetahs, Acinonyx jubatus (Schaller 1972; Bertram 1978) and bobcats (Bailey 1974). And Corbett (1979) observed that wildcats and feral cats left their scats in prominent places. The farm cats did not do this. Scats left lying in prominent places have not been observed in other farm cats (Corbett 1979) and dockyard cats (Dards 1979). Schaller (1967; 1972) and Rudnai (1973) did not observe it in lions.

Bobcats (Bailey 1974) and adult feral cats (Corbett 1979) leave scats singly but may also leave them in clusters. The farm cats were somewhat like this. Data for the spatial distribution of scat and urine loci were collected only for Cf3 when she was followed in 1980 (Fig. 5.7) but her data seem typical of the other male and female farm cats. Some sites were relatively concentrated: north and south of the dairy and by the house, where she waited for milk, and some were clumped in a leanto (the third building north of the house), where she slept during this time. Clumping might have occurred because bowel movements may have started which led her to excrete when she got up and became active. Thus some clumping might be due more to physiology than behaviour and occur near dens and resting places. But generally, scat and urine loci were distributed along the routes without being clumped.

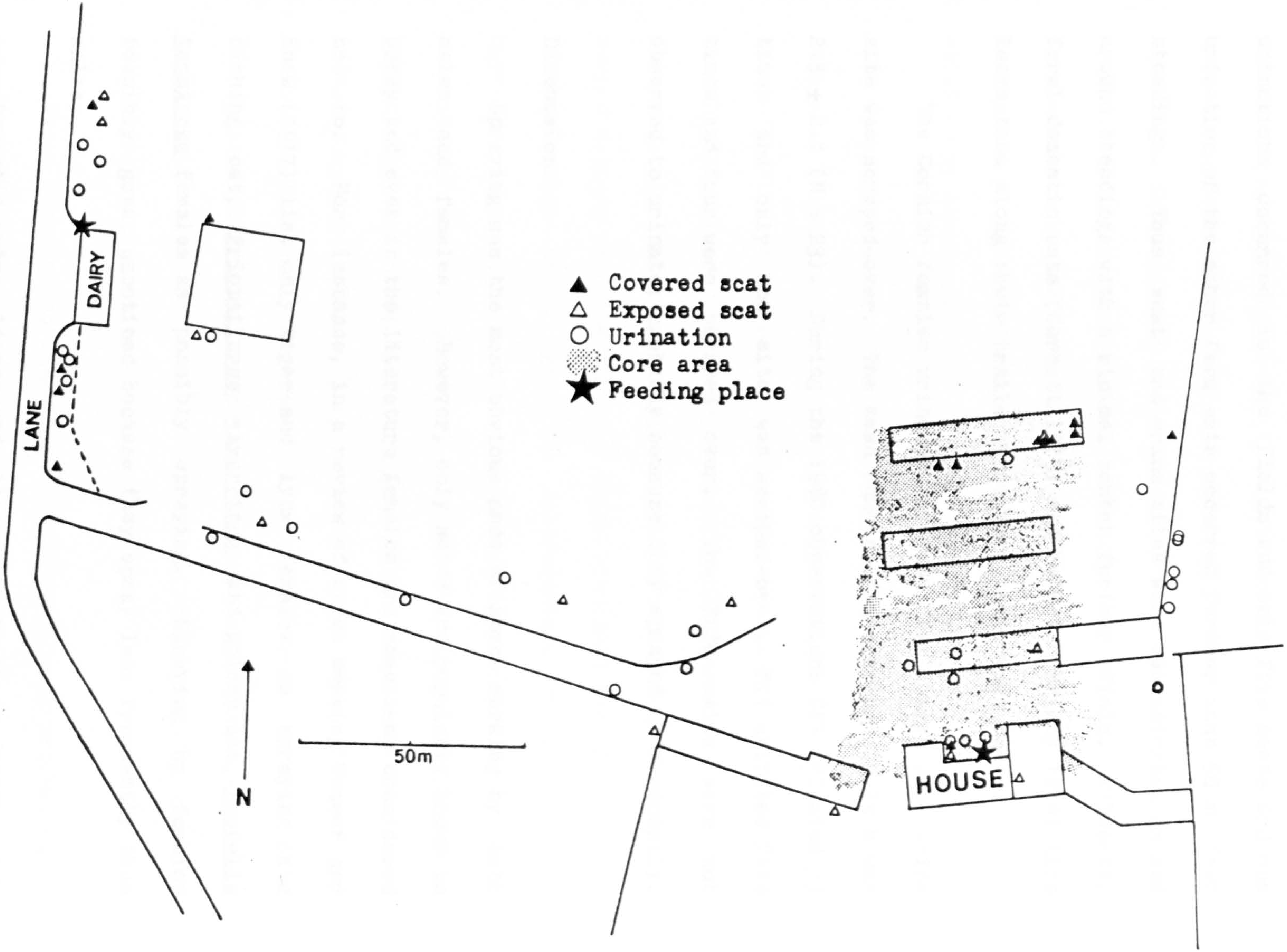


Fig. 5.7 Positions of 25 scat and 30 urine sites by Cf3 in 1980.

Interestingly, however, only one of her scats and three urinations occurred in the fields and only five scats and one urination of the other farm cats occurred further than 50 m from steadings. Thus scat and urine sites were concentrated on and around steadings with a minimal number further afield. Wildcats, feral domestic cats (Corbett 1979) and bobcats (Bailey 1974) also leave them along their trails throughout their home range.

The Cornish females urinated 33 times but only one urine site was scraped-over. The mean number of urinations in 24 h was 2.3 ± 2.1 (N = 23). During the 1980 observations Cf3 urinated 33 times and only one site was scraped-over. Ff1 urinated five times and four were scraped over. The Fife males were not observed to urinate, probably because they sprayed so frequently.

Discussion

Spraying was the most obvious mode of scent marking by both males and females. However, only males are popularly known to spray and even in the literature females are sometimes considered not to. For instance, in a review of scent marking Wemmer and Scow (1977) list only tiger and lynx females as spraying and fishing cat, Prionailurus viverrinus and golden cat, Profelis temmincke females as possibly spraying. Spraying by females possibly goes unnoticed because they spray less frequently than males.

Domestic cats, lions and leopards, Panthera pardus are considered to spray in response to existing scent (respectively Leyhausen 1965; Schaller 1972; Eisenberg and Lockhart 1972).

Eaton (1970) watched cheetahs spend much time searching for odours and marking them. But the majority of sprays of the farm cats occurred after no or a seemingly negligible amount of sniffing. This suggests most sprays may have been in response to a familiar odour which did not need inspection or that odour may not have been significant in eliciting them. Strange cats were not seen at the Cornish farm so sprays there were probably not elicited by strange odour.

Spraying did not occur indiscriminately but in a limited number of circumstances: (1) by males marking their own and/or a female's (Ff1) core area; (2) when cats were hunting; (3) next to sleeping places, which may be analogous to marking den sites; (4) a few times after sniffing a place, which was possibly in response to an existing odour; (5) by agonistic cats in front of attacked cats after agonistic interactions, which has been reported to occur in other domestic cats (Leyhausen 1979; Corbett 1979; Liberg 1980), leopard cats, <u>Prionailurus bengalensis</u> and servals, <u>Leptailurus serval</u> (Leyhausen 1979) and lions (Schaller 1972); (6) by males when they were travelling, also reported in other domestic cats (Macdonald and Apps 1978; Liberg 1981) and (7) spraying next to oestrus females, a well known male cat behaviour (for instance Leyhausen 1979; Corbett 1979; Dards 1979; Liberg 1981).

Urine marking has been suggested to facilitate prevention of encounters between conspecifics (Leyhausen 1965; Schaller 1967; Hornocker 1969; Eaton 1970; Corbett 1979) and to regulate traffic in a shared area (Leyhausen 1965 and 1979; Hornocker

1969) but the movements of the farm cats did not appear to be inhibited by each others' sprayed urine. For instance, cats did not appear to respond when passing centimetres from urine marks I knew had been sprayed by males and females within the hour or sprayed by cats directly in front of them. Leyhausen (1965 and 1979) and Laundre (1977) have also noted a lack of inhibition. However, although group members appear not to be inhibited by spray odours, outsiders may be, as apparently observed by Corbett (1979) and Liberg (1980) on a few occasions. Unfortunately, the opportunity for observing the reactions of cats who were not part of the farm groups did not arise.

Spraying in front of another cat after agonistic behaviour and spraying when following oestrus females is almost certainly social in nature. Gosling (1982) suggests scent marks serve a social function in that they reduce the cost of territorial defence to the marker and allow intruders to assess his quality and therefore avoid conflict if the marker is superior. However, this does not explain why Fm2 sprayed as frequently as the dominant Fm1; it would have been advantageous not to spray and let Fm1 defend the area alone. On the other hand, Fm2 could have been scent marking in order to take over the area quickly if Fm1 were to disappear. The data are unfortunately to few to draw any conclusions.

There was a clear spraying sexual dichotomy. Males sprayed most frequently inside their core area whereas females sprayed most frequently outside their core area. Both sexes sprayed frequently when hunting but the females sprayed proportionately more. These data have not previously been reported in the literature and future hypotheses must take them, and the differential frequency of spraying between the sexes, into account. Sprays inside the core area served no foraging purpose and sprays when hunting did not appear to be directly associated with catching prey. Together they constituted about 80 % of sprays.

Scats were probably used in communication - olfactory and/or visual - but their effect on the behaviour of the cats was not discernible.

Scuffing has been observed in tigers (Schaller 1967; Sunquist 1981), pumas, Felis concolor (Hornocker 1969; Seidensticker et al 1973), cheetahs (Eaton 1970), leopards (Schaller 1972; Eisenberg and Lockhart 1972; Bertram 1978) and lions (Schaller 1972; Rudnai 1973). Schaller (1967 and 1972) states spraying and scuffing supplement and reinforce each other in tigers and lions and that scuffing lions smear the urine of the scuff site onto their feet which enables them to track one another; or as Bertram (1978) puts it, "to leave a trail of scented footsteps" so that a lion's territory becomes faintly but definitely odorous. The farm males sprayed on the scuff but then walked away without wetting their feet so they did not leave a scented trail and therefore scuffing was not a trail marking activity. Its purpose remains to be fathomed.

Odour Discrimination: Introduction

Previous behavioural experimentation on scent cues in cats has been by Whittle (1981) on zoo tigers; he found that flehmen was not restricted to the assessment of oestrus. And by Verberne and de Boer (1976) and de Boer (1977) on domestic cats who concluded respectively that males sniffed and flehmed urine more frequently than females and that fresh urine marks were examined before older ones.

Experimenting to test what information is received by an animal who sniffs a conspecific's scent mark is difficult because the sniffer may not show an immediate overt response but a change in behaviour at a later date. The simplest experiment, however, is to show whether odours from different individuals can be distinguished and this is the aim of the experiment here. It is the last of three to be tried after two previous ones failed. I shall briefly explain the two which failed and speculate why before passing on to describe the third experiment.

The first experiment was after Halpin (1974) who tested mongolian gerbils (<u>Meriones unguiculatus</u>) individually in small cages. Odour A is presented to an animal for a few minutes, it is then removed and presented again with a different odour (B) a distance from it. The rationale is that the animal will habituate to odour A in the first presentation and if the two odours are perceived to be different then, when both are presented together, odour B will be sniffed significantly longer than odour A. The second experiment was after Gorman (1976) who worked with captive Indian mongooses (<u>Herpestes auropunctatus</u>) An animal is presented with an odour and trained to select it from a series of different odours. On sniffing the correct odour the experimenter says 'yes' and the animal returns to him for a food reward. During the experimental trials no vocal cues are given and the last odour to be sniffed before returning to the experimenter is taken to be the animal's choice. Halpin (1974) and Gorman (1976) obtained positive results but the results of my experiments, working with three male and three female captive cats, were haphazard. Perhaps this was because scent cues might have little meaning for cats who have spent all their lives together in confinement; they lacked the every day experience of cats in the outside world, where scent cues would be important. None of the captive cats sprayed and the main use of scent for them might have been to identify the sexual status of females.

The tests of the third experiment were limited to two parts: sprayed urine versus sprayed urine and urinated urine versus urinated urine on free-ranging and captive cats.

Subjects and Material

Urine donors were 13 male and five female farm and house cats, some whole and some neutered; also a wildcat and two male clouded leopards (Neofelis nebulosa) from zoos. Subjects were 12 male and nine female farm, house and captive cats, some whole and some neutered. Free-ranging subjects were not restrained during testing, being free to come and go as they chose. Captive cats were also unrestrained but confined to their living quarters of two rooms (see under Subjects in the General Method, Chapter 2). Ages varied from about one year to at least three years.

Urine was collected by following a donor cat till he/she sprayed or urinated when the urine was immediately caught in an aluminium foil container and 1 to 2 ml samples were syringed into plastic-capped soda glass vials. Samples were frozen in carbon dioxide within 3 h then later transferred to a freezer and stored for 10 months. Cross-contamination was minimised by using the same foil containers and syringes for a particular cat. Samples were presented to subjects on slightly odorous pine wood pegs of 33 cm x 2 cm x 2 cm from the same block of wood.

Nomenclature

Subjects were presented with three odours. The first was water or the first odour, the second was urine A or the second odour and the third was urine B or the third odour.

Procedure

Urine samples were thawed at ambient temperature. 1 to 2 ml of water or urine were placed near the end of each of three pegs and allowed to sink in: peg 1 bore water, peg 2 cat urine (urine A) and peg 3 urine from a different cat (urine B). The time a cat spent sniffing each odour was recorded using a stop-watch and a cat was judged to be 'sniffing' when he held his nose within 2 cm of an odour, whether or not he appeared to be sniffing. Cats were not tested more than once a day.

Pegs were presented to a cat in the order 1 to 3. Peg 1 was repeatedly presented until by turning his head or by moving away for at least 60 s a cat showed he was not interested in it. Immediately, peg 2 was substituted for peg 1 and the procedure repeated; peg 3 was then substituted for peg 2 and the procedure repeated again. This procedure constituted one trial.

Rationale

If a cat does not sniff a following odour it probably means that he has found it to be either (1) the same as the preceding odour and was not interested in it or (2) different from the preceding odour and was not interested in it or was repelled by it. If, however, the cat sniffs the following odour it probably means that he has found it to be (3) different from the preceding one and is interested in it or was repelled by it. Thus if the following odour is not sniffed it may or may not be perceived as the same as the preceding one but if it is sniffed then it is probably perceived as different.

Proviso

An odour was not always sniffed intently on its first presentation; often it would pass within 2 cm of a cat's nose without any reaction from the cat and/or it would be sniffed cursorily and the cat would move away. Only after a peg had been shown a few times and some seconds of 'sniffing' had been recorded would the cat suddenly start sniffing intently at the odour. Often as much as 10 s would elapse before this stage was reached. Therefore I take the first 10 s of sniffing time not as odour exploration but as time during which a cat came to realise he was being offered something to sniff.

Pilot Study

There was a pilot study using three male and three female free-ranging cats, each tested once. No cat sniffed the first odour (water) more than 10 s. Males sniffed the first urine from 50 s to 65 s and females sniffed it from 35 s to 45 s. Males sniffed the second urine odour (donated by a different cat) from 45 s to 60 s and females sniffed it from 30 s to 45 s. This led me to believe that the experiment would yield unambiguous positive results.

Results

Table 5.5 a and b shows the results of the sprayed and urinated urine tests and Table 5.6 shows the percentage of trials in which odours were sniffed greater than 10 s. There were few clear positive results, unlike those which the pilot study had suggested would occur. However, it is clear that the cats were more interested in the sprayed and urinated urine than the water. Most odours were sniffed less than 10 s and therefore they appeared to be of no interest or might have been repulsive to the cats. Nevertheless, a quarter of urine A and urine B odours were sniffed greater than 10 s which is evidence for the assertion that the cats could possibly discriminate between sprayed urines and between urinated urines from different cats.

Table 5.5 a and b show no cat sniffed all the odours greater than 10 s and therefore the odours seem not to be of universal interest. Also, no particular odour appeared to be of interest to all the cats because none was sniffed greater than 10 s by all the cats; therefore interest probably depended on the individual who perceived it. Whittle (1981) had similar results when he offered their own scent to nine male and female tigers. The

SPRAYED URINE TESTS	MALES												FEMALES								
	Farm				House				Captive				Farm		House		Captive				
	1	2	3	4	1	2	3	4	1	2	3	4	1	2	1	2	1	2	3	4	5
Control	0	0	1	1	1	0	1	0	0	1	0	1	0		0	0	0	1	1	1	
Whole ♂ 1	1	▬	1	1	▬	1	1	1	0	1	▬	1	1		▬	1	1	1	1	1	
Whole ♂ 2	1	1	1	1	▬	0	1	1	1	1	0	1	1		0	1	1	0	▬	1	
Control	0	0	1			0	0		0	1	1	1		0	0		0	1	1	1	
Whole ♂ 3	1	▬	▬			1	1		1	1	▬	1		▬	▬		1	0	1	1	
Whole ♂ 4	1	1	1			1	1		▬	0	▬	0		1	▬		1	1	1	1	
Control			1		0	▬		0	0	0	1	1	0		0	▬		1	1	0	
Neut. ♂ 1			1		▬	▬		▬	0	0	1	1	▬		1	▬		0	▬	1	
Neut. ♂ 2			▬		▬	▬		▬	1	0	▬	1	▬		0	▬		1	1	▬	
Control	1	1	1		0	1	0		0	0	1	1	0		1	1	1	1	1		1
Whole ♂ 1	1	1	0		1	1	1		0	0	1	1	0		1	1	1	0	1		1
Neut. ♂ 3	▬	0	0		1	▬	1		1	0	1	0	0		1	1	1	0	1		1
Control	0	0	1	0	0	0	0	1	1	0	1	▬	1		1	0	1	1	1	1	1
Whole ♀ 1	▬	▬	▬	▬	1	1	1	1	0	1	1	1	▬		▬	0	1	1	1	1	1
Whole ♀ 2	▬	1	▬	1	1	1	1	▬	0	0	▬	1	▬		1	0	1	0	1	1	0
Control		0	0	1	1	0	1		1	0	1	0	0		0	1	1	0	1	1	▬
Whole ♀ 3		▬	1	1	1	▬	1		▬	1	1	1	1		▬	1	1	1	1	1	▬
Whole ♀ 4		▬	1	1	▬	▬	1		1	0	1	1	1		▬	1	1	1	1	0	▬

Table 5.5a Sprayed urine tests. 0 = sniffed 0 s; 1 = sniffed < 10 s; ▬ = sniffed > 10 s. Empty boxes occur because some cats could not be found to be tested. All farm and captive cats were whole. All house cats (except house female 1) were neutered. Ages ranged from 1 to about 4 years. Whole male 6 was a zoo wildcat and whole males 7 and 8 were zoo clouded leopards. Some donors were also subjects: whole male 4 = farm male 1, neutered male 4 = house male 3, whole females 3 and 5 = farm female 1 and captive female 3.

URINATED	MALES												FEMALES								
URINE	Farm				House				Captive				Farm		House		Captive				
TESTS	1	2	3	4	1	2	3	4	1	2	3	4	1	2	1	2	1	2	3	4	5
Control	1	1	0	/	0	/	0	/	0	1	1	0	0	1	0	1	1	1	▬	1	1
Whole ♂ 5	1	1	1		1		1		1	1	1	1	1	▬	1	1	1	1	1	1	1
Whole ♂ 6	▬	1	1		1		1		0	1	▬	1	1	▬	1	1	1	1	1	▬	1
Control	/	0	1	1	0	0	0	/	0	1	▬	▬	0	/	1	1	/	0	▬	1	▬
Whole ♂ 7		1	▬	▬	1	1	1		1	▬	1	▬	▬		▬	1		▬	▬	▬	▬
Whole ♂ 8		0	▬	1	1	1	1		0	1	1	1	1		1	1		0	1	1	1
Control	1	0	1	0	0	/	1	/	1	1	1	▬	1	1	1	0	1	1	1	1	1
Neut. ♂ 1	1	▬	1	1	▬		1		1	1	▬	▬	1	▬	1	1	1	1	1	▬	▬
Neut. ♂ 4	1	1	1	1	▬		1		1	0	1	1	1	▬	0	1	1	1	1	0	▬
Control	1	/	0	/	0	1	1	/	0	1	1	1	0	/	0	1	0	1	1	1	1
Whole ♂ 5	1		1		1	1	1		1	0	1	1	▬		1	▬	0	1	1	1	▬
Neut. ♂ 5	▬		1		▬	1	1		1	1	1	1	1		0	1	1	▬	1	▬	▬
Control	0	1	1	1	0	1	1	/	1	1	1	1	0	0	0	0	1	1	1	1	1
Whole ♀ 2	▬	1	1	1	1	0	1		1	0	1	1	1	▬	0	1	1	1	1	1	1
Whole ♀ 5	1	1	1	1	1	0	1		0	1	0	1	1	▬	0	1	1	▬	1	0	0

Table 5.5b Urinated urine tests. See Table 5.5a for details.

	SPRAY TRIALS n = 103	URINE TRIALS n = 91
WATER	3.9	6.6
URINE A	25.2	25.3
URINE B	24.3	16.5

Table 5.6 Percentages of odours sniffed longer than 10 s.

tigers responded by sniffing and flehming but individuals did not respond equally to all the odours and some odours were apparently ignored.

Although my tests were not designed to show consistency of response by individuals, only two cats (house male 3 and captive female 1) showed an obvious consistency by not sniffing any odour greater than 10 s (Table 5.5 a and b).

A chi-squared test was used to find whether males sniffed more odours greater than 10 s compared to females and whether free-ranging cats sniffed more odours greater than 10 s compared to captive cats. The number of tests in which a urine odour was sniffed more than 10 s and the number of tests in which a urine odour was sniffed less than 10 s by males and by females was entered into a 2 x 2 contingency table and a chi-squared analysis calculated. The result was not significant (chi-squared = 0.009, $p > 0.05$, df = 1, two tailed). Similarly a chi-squared was calculated for free-ranging versus captive cats. The result was not significant (chi-squared = 3.825, $p > 0.05$, df = 1, two tailed). This suggests, but does not prove, that there was no differential interest shown to odours, in terms of the time spent sniffing them, by males and females and by free-ranging cats and captive cats. My opinion, based on watching the cats when they were being tested, is that captive cats were less interested in the urine odours compared to free-ranging ones, perhaps because in their confined environment scent communication was less important than it would be in the outside world.

A chi-squared test was used in the same way to find whether cats sniffed more sprayed urine odours compared to urinated urine odours greater than 10 s. The result was not significant (chi-squared = 0.004, $p < 0.05$, df = 1, two tailed). De Boer (1977) observed the sniffing time and reactions of captive domestic cats introduced into a room containing sprayed and urinated urine. These cats also did not appear to distinguish one kind from the other.

Of urine A and urine B odours sniffed greater than 10 s, 68.5 % were sniffed for less than 20 s and none longer than 60 s. The median sniffing time of sprayed urine odours was 18 s (maximum 60 s) and of urinated urine odours 15 s (maximum 28 s). Hence the cats usually took less than 20 s and not more than 60 s to process an odour.

Discusion

In summary, the odours did not appear to be of interest to all the cats and no single odour appeared to interest all the cats. Cats appeared to be more interested in urine than water but appeared to be no more interested in sprayed than urinated urine. There was no indication of a differential interest for odours between males and females, and between free-ranging cats and captive cats. Cats showed an interest in a sufficient number of urine odours to assert that they might be able to distinguish between odours from different cats and therefore might recognise scent marks by different individuals.

Why did cats appear to show no interest in most odours? The poor results compared to the pilot study are not due to a waning of response because the cats would show more interest in the first tests and less in the subsequent tests but this pattern does not appear in Table 5.5a and b. Much might depend on experience and sexual and social status. Subjects, as well as donors, were a heterogeneous mixture of sex, age, free-ranging and captive, and some may have been dominant and others subordinate. Therefore a first step to improve the test could be to separate these categories. Also, fresh urine might help because deep frozen and long stored samples might lose information which would be of interest to the cats.

Chapter 6

FORAGING

Preamble

Several authors have published data on the type of prey taken by free-ranging domestic cats and attempts have been made to quantify the amount the cats' eat (Jones 1977; Corbett 1979; Fitzgerald and Karl 1979). Almost all these studies have been based on stomach analysis of dead cats. However, in the first part of this chapter I look at the food habits of cats as they go about their daily activities and estimate their food intake. I then pass on to hunting behaviour. Cats are cryptic when hunting and few workers (Gibb, Ward and Ward 1978; Corbett 1979) have observed them at such times but because my cats were tame their hunting techniques are reported in some detail. In the last part of the chapter I analyse their foraging search paths. There have been several studies on foraging paths of insects and birds but only two of mammals: Macdonald (1980) on area restricted search in foraging red foxes (_Vulpes vulpes_) and Sniff and Jesson (1969) on the movements of red foxes (_V. fulva_) and snowshoe hares (_Lepus americanus_).

The following is a brief description of the method for the first two sections dealing with food habits and hunting. A more detailed account is given in the General Method, Chapter 2. There is a detailed method for the third part of this chapter, on search paths, in the last section.

Subjects

The subjects were five female Cornish farm cats: Cf1, Cf2, Cf3, Cf4 and Cf5; one female and two male Fife farm cats: Ff1, Fm1 and Fm2; and a castrated male house cat, Hm1.

Procedure

A cat was followed and directly observed for the whole of an observation period (see below) and his hunting behaviour was recorded as one of a number of mutually exclusive categories on the minute every minute for males and every fifth minute for females. Hunting behaviour was 1) making a roving search of the environment, that is travelling alertly by walls, long grass and buildings, stopping every few metres and appearing to look and listen intently; 2) stationary, attentive and orientated towards a locus, often between bouts of roving searches; and 3) pouncing during 1) or 2). If the animal was out of sight at the moment of making a record then he was recorded as lost to view. Other behaviours and the routes the cat travelled were noted during recording intervals.

Observation Periods

Each Cornish female was followed three times from the beginning of the first complete hour to the end of the last complete hour of daylight and twice for 24 consecutive hours, from October 1978 to February 1979. Cf3 was followed in February 1980 for 13 consecutive days from 09.00 h to 17.00 h. Each Fife cat was followed once for 24 consecutive hours and thereafter observed in blocks to make up composite 24 hour periods, from April to June 1981.

Food Habits and Hunting

Available Food

Prey could not always be identified because small prey were sometimes eaten too quickly and at other times I did not wish to interfere with the cats. But cats were seen to catch the following prey species: pygmy shrew (*Sorex minutus*), common shrew (*Sorx araneus*), harvest mouse (*Micromys minutus*), house mouse (*Mus musculus*), woodmouse (*Apodemus sylvaticus*), field vole (*Microtus agrestis*), brown rat (*Rattus norwegicus*), rabbit (*Oryctolagus cuniculus*), wren (*Troglodytes troglodytes*); as well as flies, grasshoppers and beetles.

The farmers left food for the cats at both the Cornish and Fife farms. In addition, one cat (Cf5) also ate the skins of dried potatoes left in a field and one cat (Fm1) habitually bit open and ate free-range hens' eggs.

The number of prey types caught by each cat is shown in Table 6.8. Rodents (mice and voles) were the staple prey of all females, rabbits and birds were subsidiary and insects were rarely eaten. Rabbits were the principal prey of the males and they caught other prey when the opportunity arose. Only Hm1 and Cf5 caught birds.

Prey Abundance

No attempt was made to sample the prey population at the Cornish farm but birds did not appear to be scarce and there appeared to be few rabbits and rats.

Fm1 and Fm2 hunted many rabbits on a nearby hill. In 18 ha there were 501 rabbit holes in six discrete clumps (suggesting six warrens, Fig. 6.5).

In order to sample the rodents at the Fife farm, 49 Longworth live-traps were left in April for six days and nights (294 trap days) on the steading in places where Ff1 hunted. The traps were baited with rolled oats and peanut butter, the most effective bait tried by Beer (1964) to catch small rodents, and also raw rice, which I found house mice like, and inspected just after dawn and just before dusk. Five house mice and one common shrew were caught. 36 of the traps were then set in pairs for four days and nights (144 trap days) along the 200 m track (Fig. 4.2) leading from the steading to the hunting area of Fm1 and Fm2, along which the cats hunted, and were similarly baited and inspected. Two woodmice, one vole and three pygmy shrews were caught.

Interpreting trapping results is often difficult because of the large number of variables affecting the experimental design (Smith and Gardner et al 1975), but at face value these results suggest that potential prey were few and that the steading and fields appeared to have different proportions of prey species; house mice and common shrews were more frequent on the steading while in the surrounds woodmice, voles and pygmy shrews were more usual. This was supported by the cats' catches I was able to identify on the steading and in the fields: on the steading three house mice, two rats and a common shrew and in the fields four woodmice and two voles.

Amount of Food Ingested

A crude approximation of daily food intake by the five Cornish females can be attempted, based on two 24 h observations of each of the cats. Milk consumption was estimated by noting the mean lapping time to drink 1 ml of milk by one female and five male farm cats, each of whom was tested twice. The mean time was 1.5 s and the time each Cornish female spent drinking was divided by this figure to arrive at their mean milk consumption.

During 24 h they ingested a mean of 470 ml (range 222 ml to 967 ml) of milk, 20 g of cattle pellets and about an equal amount of table scraps, and 1.2 rodents, which weigh about 30 g. Therefore the mean consumption was about 470 ml of milk and 70 g of solid food per female per day. Daily intake by other free-ranging cats was calculated as 170 g by Fitzgerald and Karl (1979), assumed to be 300 g by Jones (1977) and suggested to be 12 rodents by Leyhausen (1976). Future quantifications should take regard of age-sex differences and convert food to energy units for better comparisons.

Table 6.1 shows the weights of the rabbits caught and the weights of the parts eaten by the three male rabbit-hunting cats (Fm1, Fm2 and Hm1). Corbett (1979) calculated, by deducting the weight of the remains of rabbits killed by cats from similar sized rabbits he gutted, that the free-ranging cats he observed ate on average 250 g of rabbit at one sitting. In every case except one the cats in my study ate more than this, consuming a mean of 339 g.

Two of the three heaviest rabbits (1,000 g and 650 g) had myxomatosis. The third (950 g) had a 2 mm diameter puncture behind both ears through to the skull and a 2.5 cm diameter skinless patch behind the ears showing through to the bone. These wounds were clean and looked neither fresh nor old and therefore may or may not have been made during capture. All the other rabbits appeared to be in good health. Rabbits are weaned at about 150 g and are adult around 1200 to 2000 g (Lloyd 1977); therefore most of the rabbits were juveniles and probably not long out of the nest. This conforms to the general view that cats catch young rabbits and diseased adults.

In addition to catching rabbits, Fm1 found the remains of five rabbit carcasses on different days (Table 6.2). They appeared to have been killed by a cat because the remains were those typically left by the cats (Table 6.1) and had been eaten in their characteristic way: from the head along the spine, leaving the limbs till last and not eating the stomach. Other predators have different eating habits (for instance foxes and birds, Corbett 1979). The carcasses were still fresh so had been killed recently. They appeared to be abandoned and not cached because they were left in the open next to gorse bushes, which was where the Fife males left their rabbit catches. Fm1 probably

	RABBIT WEIGHT	WEIGHT EATEN	REMAINS
Fm1	1000	525	Stomach, intestines, part of head, fore leg, kidney, tail, some skin
	950	634	Stomach, intestines, part of head, fore paw, part of body
	650	360	Stomach, part of body
	360	320	Stomach, intestines, some skin
	250	249	Some skin
	250	210	Stomach, intestines
Fm2	285	243	Stomach, intestines, some skin
Hm1	360	290	Stomach, hind legs, tail, some meat and skin
	351	258	Pelvis, hind legs, tail
	305	299	Hind paws, tail, some skin
$\bar{X}$	386	339	

Table 6.1 Weight (in g) of rabbits caught by three male cats, the weight each cat ate at one sitting and the remains.

REMAINS	WEIGHT	WEIGHT EATEN	REMAINS OF REMAINS
Hind quarters	–	–	Not observed
Intestines	not weighed	–	Takes a few bites and leaves
Hind quarters	51	51	None
Intestines, all legs, tail, some skin	150	105	Intestines
Stomach, intestines, half head, all legs, some skin	220	80	Stomach, head
$\bar{X}$ of three rabbits	140	79	

Table 6.2 Rabbit remains (in g) found and eaten by Fm1.

killed them, knew where they were and returned on the following day to eat more. If this is correct it shows he had a good knowledge of his hunting area. Corbett (1979) saw a cat return on three consecutive days to eat from a rabbit carcass.

Uneaten Prey

At both farms, not all captured prey were eaten. Cats caught shrews and a kitten ate one presented by his mother but they were not eaten on other occasions. Cats caught rats but only the tail of one was eaten. A mother gave a wren to her kitten who ate it but none of the cats and independent kittens would eat one I offered them which had been killed by a cat within the hour and abandoned. I found four dead and uneaten wrens in the Cornish farm yard. In terms of energy, a cat who abandons some prey animals is less efficient than one who eats them all because the ratio of energy assimilated by eating them to the energy spent catching them will be lower in the former cat, so in this sense cats were not always efficient. The farm cats were always hungry but not starving; they did not hunt every day and did not always turn up for milk.

What may be considered to be the normal fare of a cat was not always eaten either. I saw two woodmice and a harvest mouse caught and left uneaten by three cats. One cat had previously caught and eaten three rodents so may have been sated but the other two had not eaten for several hours.

Hunting Areas

Most females (Cf1,Cf2,Cf4 and Ff1) hunted on and close to the steading and rarely ventured more than 100 m from the buildings. But one female (Cf5) also hunted in the fields and another female (Cf3) and the males (Fm1, Fm2 and Hm1) hunted exclusively in the fields (see Figs. 4.1 and 4.2 of home range areas).

Females caught only rodents but males also caught rabbits. However, on returning to the farm a year after the field work the two females who hunted in the fields each caught a rabbit showing that rabbit hunting was not the prerogative of males alone. The two females had possibly not caught rabbits earlier because they were scarce. No rabbits or their signs were seen close to the steadings so the females hunting these areas caught only rodents.

All cats shared their hunting areas; home ranges overlapped greatly (Figs. 4.1 and 4.2 and Table 4.2). Cornish females who hunted around the steading appeared to concentrate most hunting in two to four places in which other females hunted little or not at all. But Fm1 and Fm2 frequently hunted the same places.

When Cats Hunt

The percentage distribution of each hour spent hunting by cats is shown in Fig. 6.1. Graphs A to I show a variety of patterns: Cf3 and Fm1 hunted predominantly during the day, Cf4 hunted mainly in the afternoon and evening, Cf5 hunted mainly in the afternoon up till about midnight, Ff1 hunted during the day and around dawn and dusk, Fm2 and Cf2 hunted mainly at dawn and dusk, and Cf1 hunted mainly at night and around dawn.

One Cornish female and one Fife female became nocturnal. During three previous daylight observations Cf1 did not sleep but did go hunting and therefore was mainly active during the day. During the subsequent 24 h observations she slept during the day and hunted mainly at night and therefore had become night active. Ff1 changed her hunting times after her 24 h observation, shown in graph E, to hunting mainly at night. Superimposed in graph H is the mean of the curves of graph G of Cf1 and the mean of all observations on Ff1, after her observation shown in graph E. They are remarkably similar so the cats might have been entrained to the same environmental cues (see Activity Patterns, Chapter 3). Returning to graph E of Ff1, the curve is almost like her curve in graph H, which suggests that during the former observation she might have been in transition from hunting mainly by day (or at dawn and dusk) to hunting mainly at night.

Constancy of hunting time is demonstrated by cats who were observed twice (graphs A, D, F, and G; not C); by Cf3 (graph I) who was observed 12 months later, who kept to the same hunting times as the previous year (compare with graph A); and by Fm1 (graph B) who was observed on a number of hunts and always hunted during the day.

Fig. 3.3B (Chapter 3) shows the mean percentage of each hour spent hunting by four Cornish females (Cf2, Cf3, Cf4 and Cf5) and three Fife cats (Fm1, Fm2 and Ff1). Respectively, a mean of 80.7 % and 92.6 % of hunting per hour occurred between dawn and dusk.

Fig. 6.1 Percentage of time spent hunting by five Cornish females and three Fife cats. Left: percentage of each hour spent hunting. The solid curve is the first and the dashed curve is the second observation. Arrow heads indicate dawn and dusk, solid arrow heads for solid curves. Right: percentage of hunting per hour between dawn and dusk for solid curve (left) and dashed curve (right). Data are from 24 consecutive hour observations: two on each Cornish female (Cf1 Cf2 Cf3 Cf4 Cf5) and one on each Fife cat (Ff1 Fm1 Fm2). See text for details of graphs H and I.

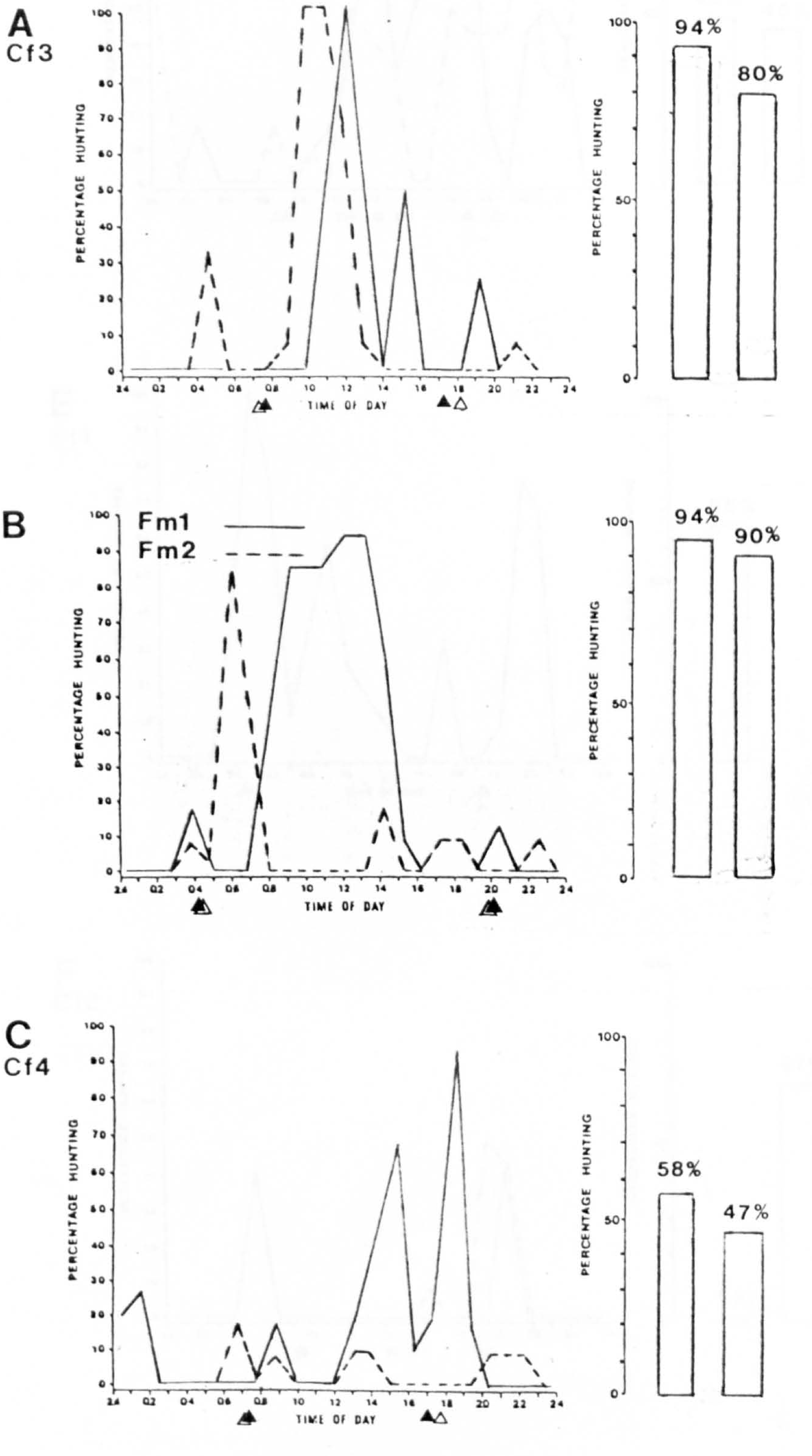


Fig. 6.1 continued

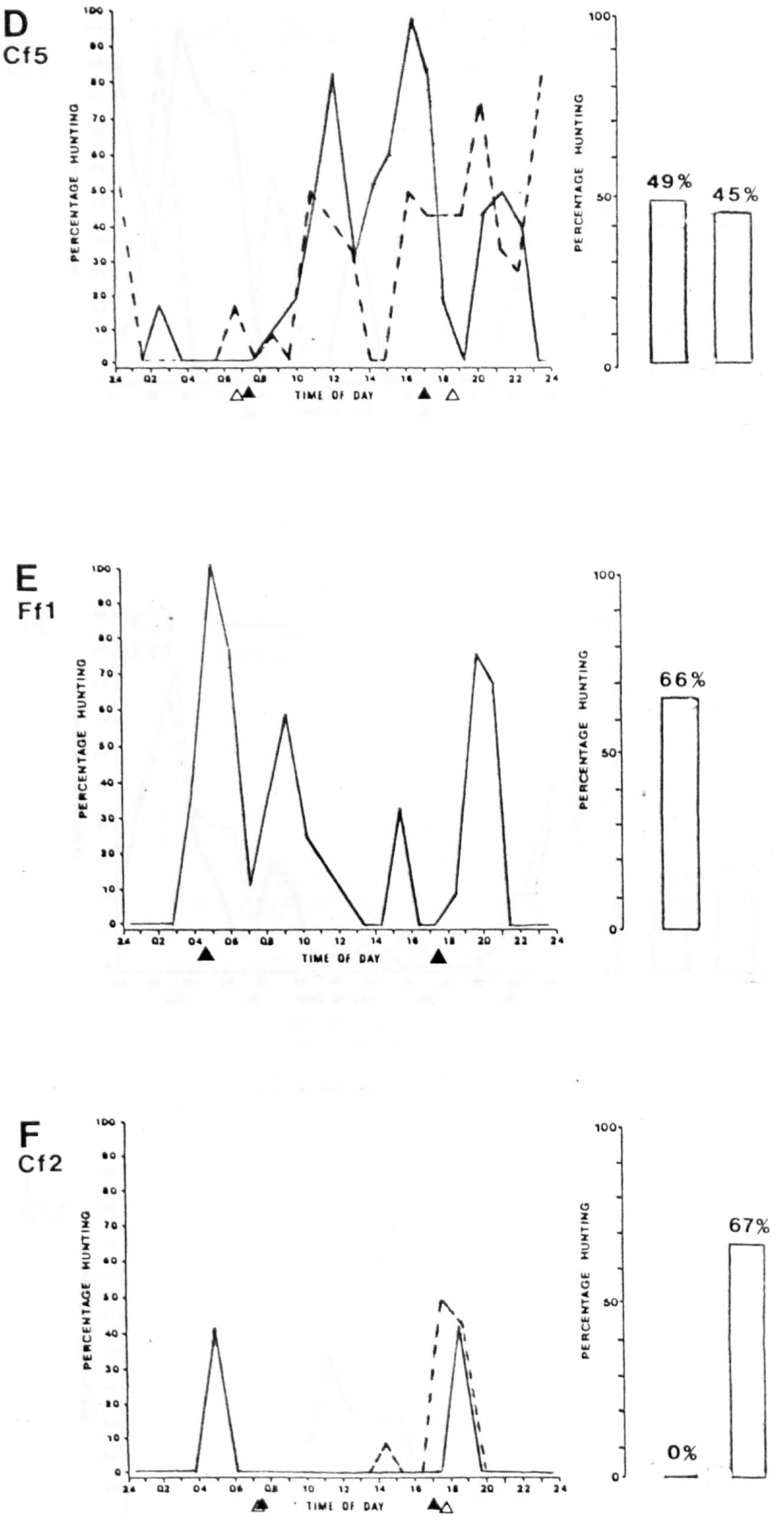
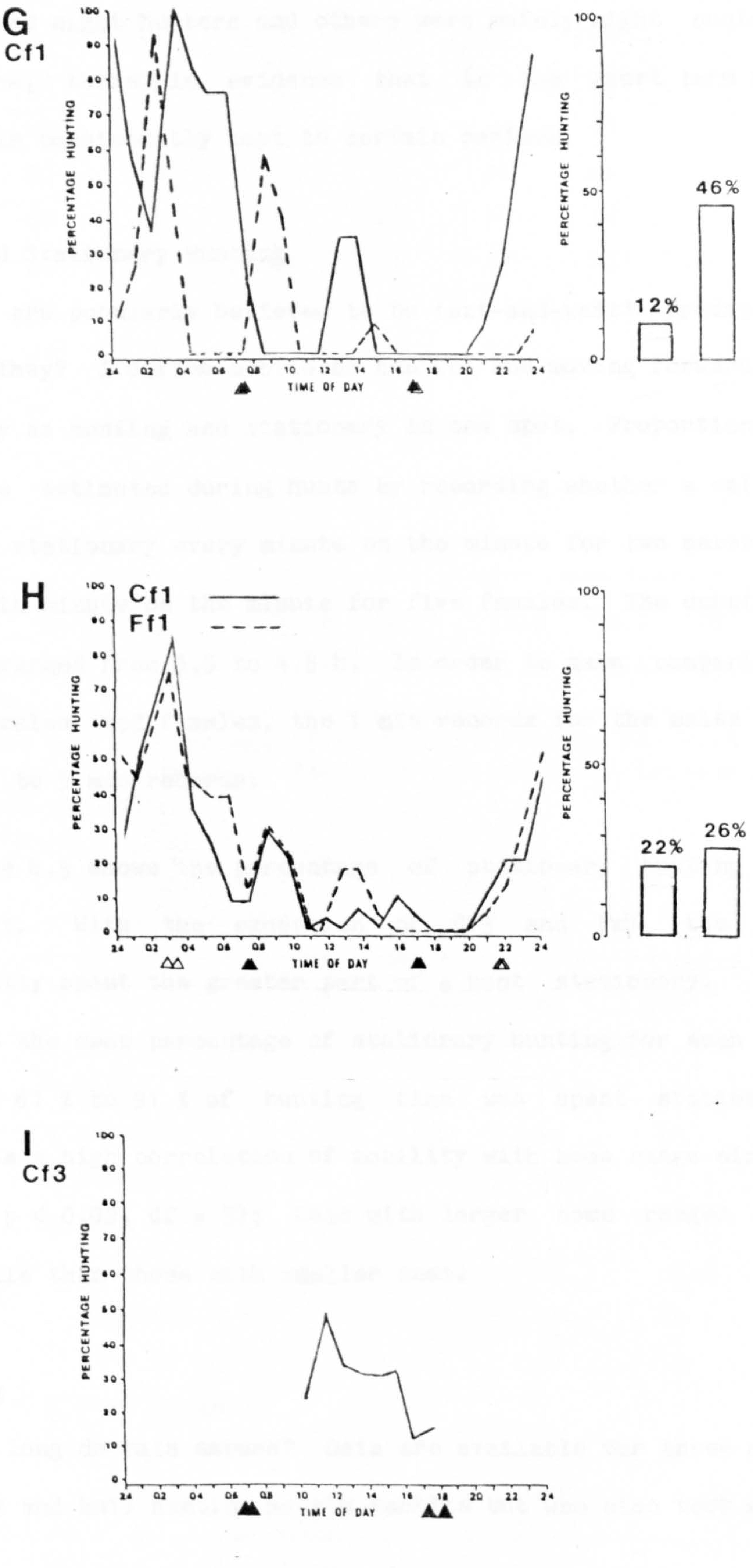


Fig. 6.1 continued



In conclusion, the cats hunted at all hours but particularly during certain periods. Some cats were mainly day hunters, some were day and night hunters and others were mainly night hunters. Furthermore, there is evidence that in the short term most individuals consistently kept to certain periods.

Mobile and Stationary Hunting

Cats are popularly believed to be 'sit-and-wait' predators. But are they? I define mobile as hunting and moving forward and stationary as hunting and stationary in one spot. Proportions of each were estimated during hunts by recording whether a cat was mobile or stationary every minute on the minute for two males and every fifth minute on the minute for five females. The durations of hunts ranged from 0.5 to 4.8 h. In order to make comparisons between males and females, the 1 min records for the males were converted to 5 min records.

Table 6.3 shows the percentage of stationary hunting for each hunt. With the exception of Cf3 and Fm1, the cats consistently spent the greater part of a hunt stationary. Fig. 6.2 shows the mean percentage of stationary hunting for each cat. A mean of 61 % to 91 % of hunting time was spent stationary. There was a high correlation of mobility with home range size ($r = 0.852$, $p < 0.02$, df = 5); Cats with larger home ranges were more mobile than those with smaller ones.

Ambushing

How long do cats ambush? Data are available for three males (Fm1, Fm2 and Hm1) hunting mainly rabbits but who also took other

	Fm1	Hm1	Cf3	Fm1	Hm1	Cf1	Ff1	Cf5	Cf4
N	10	10	13	10	10	8	10	14	5
1	74	84	34	82	47	88	100	100	93
2	74	71	44	73	77	83	100	83	94
3	70	77	33	60	83	100	67	67	88
4	64	81	50	55	76	75	100	100	80
5	54	63	66	46	79	72	83	100	100
6	61	78	100	57	87	67	90	75	
7	80	79	60	80	70	82	75	100	
8	53	74	67	18	77	75	100	67	
9	89	78	65	75	74		92	100	
10	74	76	59	73	62		90	100	
11			75					100	
12			65					83	
13			73					100	
14								90	
$\bar{X}$	69.3	74.8	60.8	61.9	73.2	80.2	89.7	90.4	91.0
SD	11.4	5.3	18.0	19.4	11.4	10.4	11.8	13.0	7.5

Table 6.3 Percentage of stationary hunting for each hunt by two male and five female cats. Based on left on 1 min records and on right on 5 min records.

	Fm1	Fm2	Hm1
N Hunts	9	1	10
N Ambushes	25	14	40
% Ambushes < 10 min	76.0	85.7	77.5
Ambush duration:			
median	5.0	5.5	6.5
maximum	41	59	84
% > 10 min	54	57	58
N Prey caught:			
rabbits	1	1	3
rodents	3	0	0

Table 6.4 Ambush data for three male cats.

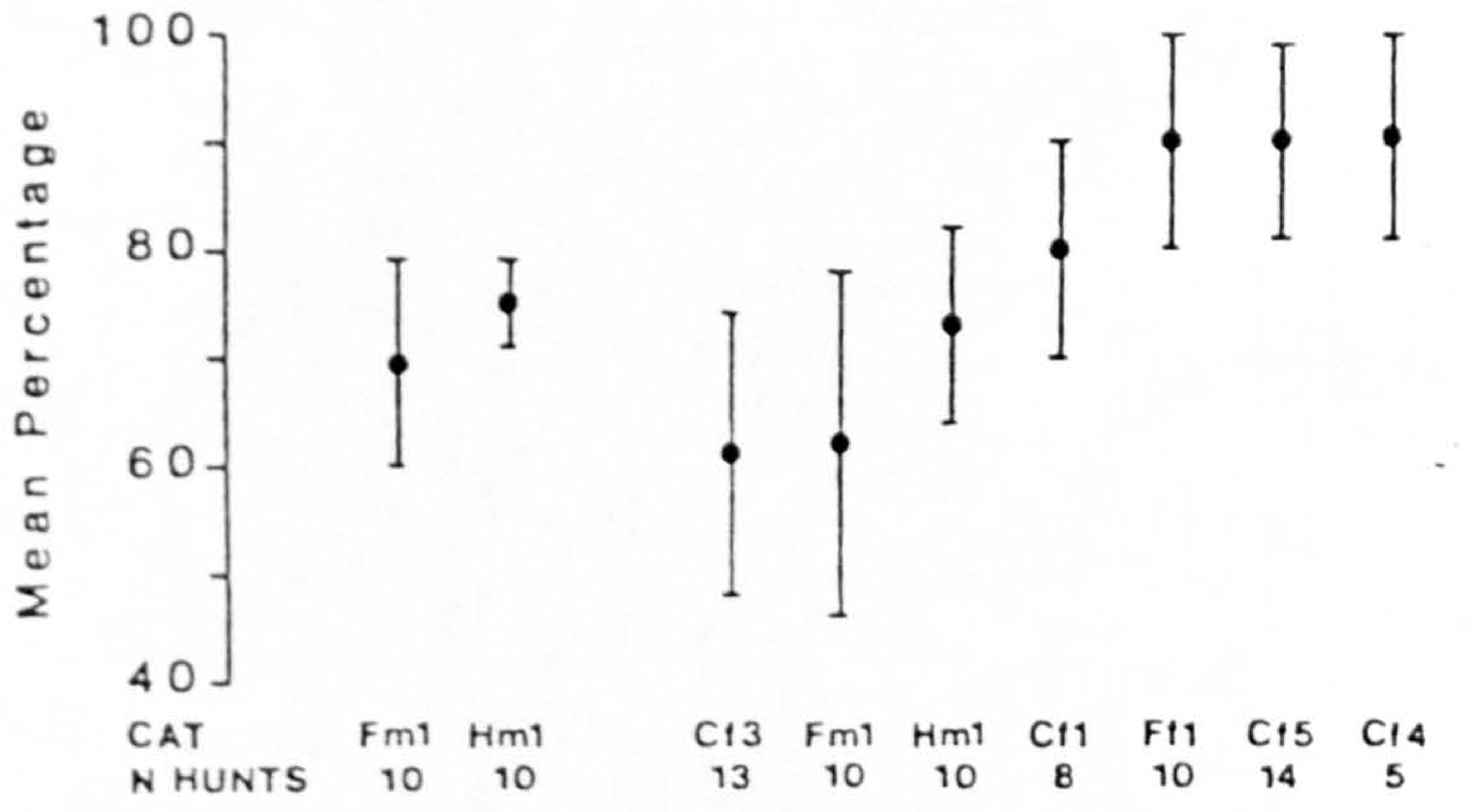


Fig. 6.2 Mean percentage of stationary hunting ± standard deviation for a number of hunts per cat by two males on left and the two males and five females on right. Data are based on 1 min records on left and 5 min records on right.

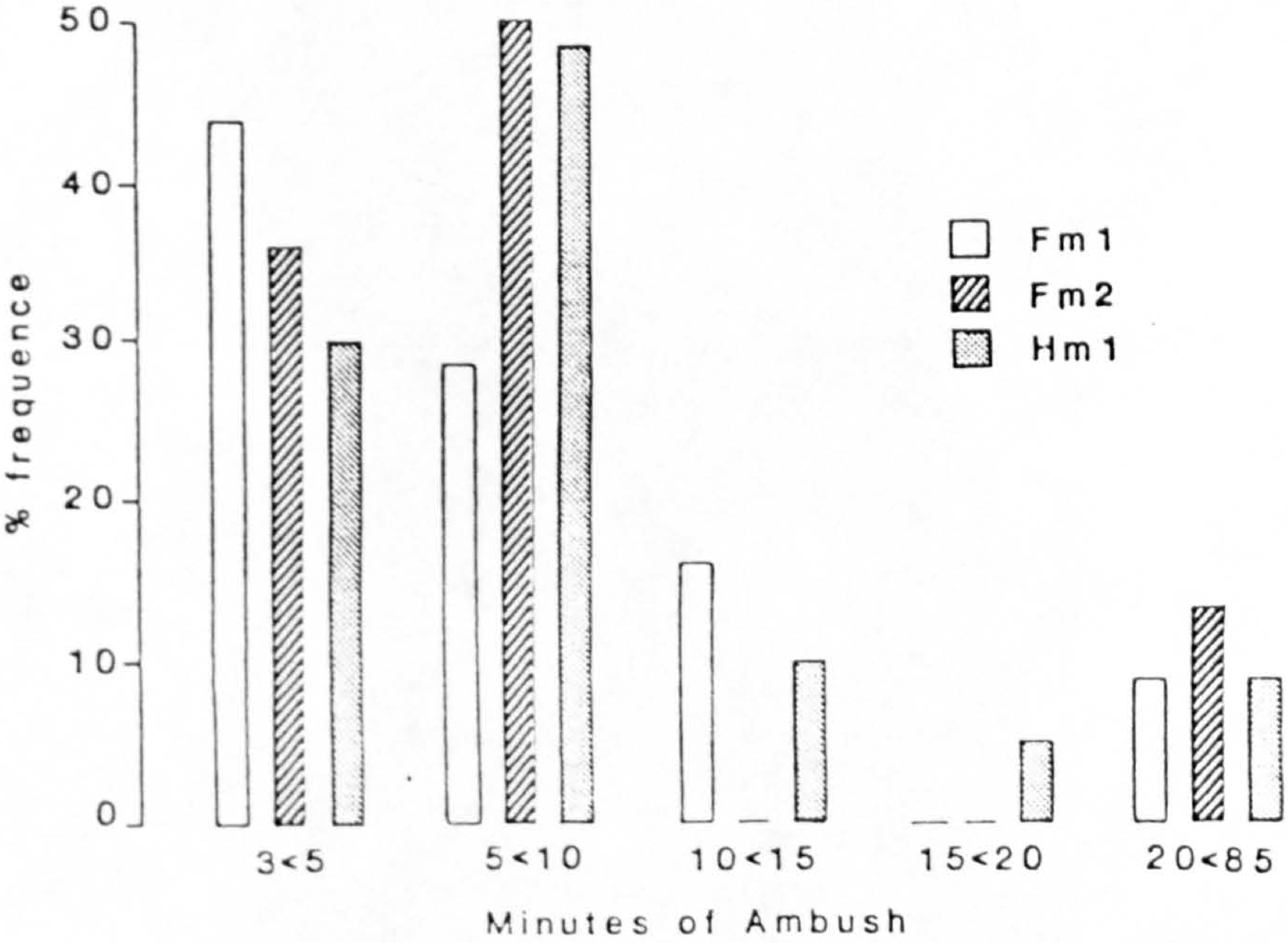


Fig. 6.3 Percentage frequency of 79 ambushes of 3 min and more by three male cats.

prey when the opportunity arose. Their ambush durations were recorded every minute on the minute. Only ambushes of three and more records (that is of at least 3 min) were analysed because I could not always be certain that stationary periods less than 3 min were ambushes. Fig. 6.3 and Table 6.4 show ambush data of the three cats. Most ambushes (62) lasted less than 10 min and the longest was 84 min. Although all the prey were caught in less than 10 min, half the ambush time was longer than 10 min. Only 8 of the 79 ambushes ended in prey capture, resulting in an ambush success rate of 10 %.

Duration and Distance to Catch Prey

Table 6.5 shows hunting data for six females. All the prey they caught were rodents. There was much variation by each female and between females in time and distance spent hunting. Only four females caught prey; but not more than four a day after which they stopped hunting. The other two females (Cf2 and Cf4) did not catch prey and relied heavily on farm food for sustenance.

Table 6.6 shows a similar breakdown for each of the three males. Unlike Table 6.5 it is not based on the total hunting in 24 h but on 20 hunts. However, the males would make one long hunt and seldom hunt again for the rest of the day so that the data in the two tables are roughly comparable. A hunt started when a male left his core area and ended when he returned to it. As for Table 6.5, non-hunting time is excluded, for instance for eating and grooming. Comparing males and females, a Kolmogorov-Smirnov two sample test resulted in no significant

	HUNTING TIME	HUNTING DISTANCE	PREY CAUGHT	TIME/PREY	DIST/PREY
Cf1	8.1	1600	4	2.0	400
	2.9	330	0	–	–
Cf2	0.8	35	0	–	–
	1.0	30	0	–	–
Cf3	2.8	1770	4	0.7	445
	3.3	450	1	3.3	450
Cf4	3.2	170	0	–	–
	0.6	55	0	–	–
Cf5	6.3	485	2	3.2	245
	6.8	265	1	6.8	265
Ff1	3.0	715	1	3.0	715
$\bar{X}$	3.5	540	1.3	3.0	455

Table 6.5 Time spent hunting (h), hunting distance (m) and the number of prey caught by six females. Data are from 24 consecutive hour observations: two on each Cornish female and one on the Fife female.

	HUNTING TIME	HUNTING DISTANCE	PREY CAUGHT	TIME/PREY	DIST/PREY
Fm1	2.0	875	0	–	–
	2.0	710	0	–	–
	2.3	1495	3*	0.8	500
	1.5	1035	1*	1.5	1035
	2.9	1360	1*	2.9	1360
	1.3	830	1*	1.3	830
	1.2	1315	1*	1.2	1315
	1.6	705	0	–	–
	1.1	520	2	1.1	260
Fm2	5.7	1480	2*	2.8	740
Hm1	2.9	1165	0	–	–
	1.9	840	0	–	–
	2.3	1260	0	–	–
	4.4	1210	2*	2.2	605
	2.3	870	1*	2.3	870
	3.8	1290	1*	3.8	1290
	2.7	1070	1	2.7	1070
	1.1	640	1*	1.1	640
	2.1	885	1	2.1	885
	2.3	690	0	–	–
$\bar{X}$	2.4	1010	0.9	2.6	1125

Table 6.6 Time spent hunting (h), hunting distance (m) and the number of prey caught by three males. See text for details. An asterisk indicates one rabbit was among the prey – the rest were rodents and one bird.

difference for the duration of hunting and hunting distance (respectively chi-squared = 1.336, $p > 0.5$ and chi-squared = 0.333, $p > 0.2$, both df = 2 two tailed). Therefore there is no evidence that the males hunted longer and further than the females in the course of a day.

Rabbits were important prey because they constituted the bulk by weight of the males' diet. From Table 6.6 it can be calculated that the mean time and distance to catch one was 4.7 h and 2,025 m. This may be on the high side because my presence probably alerted some rabbits which might have otherwise been caught.

Hunting Speed

Table 6.7 shows the mean hunting speed of the three males for each of their hunts. The data are calculated from Table 6.6 which is based on the duration of each hunt from start to finish and excluds time not hunting, for instance when eating prey and grooming. The speed of Fm1 and Hm1 differed significantly ($t = 2.250$, $p < 0.05$, df = 17). The grand mean speed was 480 ± 190 m per h.

Hunting Success

Table 6.8 shows the number of 'tries', that is pounces and rushes, to catch prey and the number of prey caught by three males and six females during all observations. There were 140 tries, excluding those obviously after insects, and 50 prey captures making 2.9 tries per vertebrate capture. Two cats (Cf2 and Cf4) hunted little and caught nothing. The number of tries

	Fm1	Hm1	Fm2
	438	402	260
	355	442	
	650	548	
	690	275	
	469	378	
	638	340	
	1096	396	
	441	582	
	473	421	
		300	
$\bar{X} \pm SD$	583 ± 223	408 ± 98	-

Table 6.7 Hunting speed per hunt ($m^{-}h$) of three male cats. Based on data from Table 6.6.

per capture by the other cats varied from 1.4 to 6.2. There was less variation in the number of tries for the three prey types, 1.9 to 3.0. As stated under Hunting Success above, there was a success rate of 10 % by the males hunting rabbits.

Gibb, Ward and Ward (1978) observed that adult rabbits often escaped cats hunting them. On three occasions the cats I studied tried running after adults but were out-distanced and left panting after about 10 m. In order to stand a chance of catching rabbits the cats had to stalk to about 3 m of them, which they did on all successful captures.

Fm1 caught six rabbits in nine hunts, Fm2 caught one during the only hunt on which he was observed and Hm1 caught three rabbits in ten hunts making respectively 0.7, 1.0 and 0.3 rabbits per cat per hunt and averaging 0.5 rabbits per hunt. These are minimum ratios as my presence undoubtedly alerted some rabbits, which may otherwise have fallen prey to the cats.

Handling Prey: killing and eating

Captive cats may kill rodents by a 'neck bite', that is the insertion between two vertebras in the neck of a canine which forces them apart and severs the spinal nerve (Leyhausen 1979). The initial few seconds of the capture of a rodent by the farm cats could not be observed and consequently it is difficult to say whether a killing bite was used. I believe it was not because eight of the 35 rodents caught were alive after capture. They were stupefied and most died as a result of being eaten, starting at the head. I examined six rodents and none had a

	RODENTS		RABBITS		BIRDS		UNIDENTIFIED VERTEBRATES		INSECTS		TOTAL		T/C
	T	C	T	C	T	C	T	C	T	C	T	C	
Fm1	11	8	13	6	0	0	1	0	1	0	25	14	1.8
Fm2	4	2	3	1	0	0	0	0	0	0	7	3	2.3
Hm1	3	0	5	4	7	3	1	0	4	0	16	7	2.3
Cf1	7	5	0	0	0	0	0	0	0	0	7	5	1.4
Cf2	0	0	0	0	0	0	1	0	0	0	1	0	0.0
Cf3	41	13	0	0	1	0	0	0	0	0	42	13	3.2
Cf4	0	0	0	0	0	0	0	0	1	0	0	0	0.0
Cf5	23	3	0	0	2	1	0	0	a few		25	4	6.2
Ff1	16	4	0	0	1	0	0	0	1	1	17	4	4.2
TOTAL	105	35	21	11	11	4	3	0	-	-	140	50	-
T/C	3.0		1.9		2.8		0.0		-	-	2.8		-

Table 6.8 The number of tries (T) to catch prey and the number of prey caught (C) by three male and six female cats. Totals are for vertebrates only.

wound at the back of the neck.

All rabbits caught by Fm1 (6) and Fm2 (1) and one caught by Hm1 were killed by a prolonged bite on the side of the neck. Bites were not made over the windpipe but about a centimetre from it towards the spine so that death may have been caused by constricting the blood flow to the brain, not by asphyxiation. The cats stood and held the rabbits in such a way that the rabbits' limbs pointed away from them, either upwards or in the direction the cats were facing; in this way the rabbits could not get a purchase on the ground or strike a cat. Death (rabbits were unconscious, limp and with eyes open) occurred in 5 to 90 s. A cat then released his grip and almost immediately began to eat. Hm1 caught a further three rabbits: one was stupefied by its capture and died when its head was eaten; another died without any apparent attempt to kill it and one escaped when Hm1 was distracted by dogs.

In the light of this evidence doubt must be cast on extrapolating the neck bite from captive to free-ranging cats. The neck bite is a method of killing rodents but seems to be one which is dispensable. The method of killing rabbits was a quick means of dispatching one, which may weigh a third of a cat, exerting a minimum of energy to do so while elegantly keeping clear of a rabbit's legs, which could deal a hefty blow. Its widespread practice is hinted at by the different kinds of cats using it: the male farm cats and the neutered house cat.

Corbett (1979) describes a different method. Cats gripped rabbits using all paws and killed adults with a steady bite on the nape of the neck and juveniles with a bite behind the orbits thereby crushing the skull. However, Corbett (1979) could only observe cats from a distance so might have mistaken a bite on the side of the neck with one on the nape. This may be because the cats in my study started eating adults between the neck and the base of the skull and juveniles at the nose. If Corbett's cats had started eating adult rabbits in this way and juveniles between the orbits then he might have been misled into believing the rabbits had been killed at these places.

The cats I observed ate rearwards and appeared to use the spine as a guide. All parts of rabbits were eaten although not usually the stomach and sometimes not all the intestines. Intestines, limbs and head of larger rabbits were sometimes left but the smaller rabbits were almost totally consumed (Table 6.1). Cats observed by Corbett (1979) ate in a similar fashion but sometimes made a second start by opening the abdomen.

The four birds which were caught (by Hm1 and Cf5, Table 6.8) were not killed at capture but died while or after being played with. Cf5 was the only farm cat to play occasionally with prey. Farm cats on all other occasions either quickly killed prey or killed them quickly as a result of eating them. Hm1, the house cat, played with all captured prey (N = 7) except one rabbit.

Foraging Search Paths

Subjects and Study Areas

Subjects were Fm1, Fm2 and Hm1. Fm2 went missing after his first recorded hunt. Fm1 and Fm2 shared most of the same hunting area of about 12.9 ha and 9.7 ha respectively. It was east of their core area on a grass hillside grazed by cattle and sheep and had five large patches of gorse, one sloping east and the others sloping south (Figs. 4.2, 6.5 and 6.6). The hunting area of Hm1 was about 2.4 ha next to his house on the edge of his village (Fig. 6.7). It was fairly flat and contained large areas of grass, gorse and scrub and was grazed by cattle.

Procedure

A cat was followed from 1 m to 10 m distance and his activity and position recorded into a pocket tape recorder every minute on the minute (sometimes ± 5 s). Activity was everything listed under Behavioural Categories in the General Method, Chapter 2, and whether a cat was 1) mobile, 2) stationary or 3) ambushing. Mobile was hunting moving around; stationary was hunting at rest, for instance pausing to sniff the air and look about, and ambushing (which included stalking). A position or 'fix' was recorded with reference to the distance and direction according to one of the eight cardinal points of the compass to the nearest visible peg in an array of uniquely marked pegs in the hunting area.

Pegs were set out in grids, each peg 12.5 m from its nearest neighbour (Figs. 6.5, 6.6 and 6.7). They were white pine wood of 2 cm x 2 cm x 50 cm hammered about 25 cm into the ground. Short pegs had to be used because longer ones were knocked over by cattle and sheep but 100 cm long pegs were sometimes used where vegetation and grazing animals allowed. In very high gorse where pegs could not be seen strips of yellow PVC sticky tape were stuck to vegetation. In addition, pegs or tape were set out every 12.5 m along fences and field boundaries.

A search path was deemed to have started when a cat started hunting in his hunting area. Search paths shown graphically (Figs. 6.5, 6.6, 6.7 and A1 in the appendix) ended when a cat left his hunting area but for statistical analysis ended when a cat caught a rabbit or, if not, when he stopped hunting.

Analysis of Data

Search paths were analysed in terms of move-lengths, turns and turn-angles (Fig. 6.3.1). A move-length is the straight-line distance between two consecutive fixes. A turn is the direction, left or right, from the direction of a move-length to the direction of the next move-length. A turn-angle is the angle between a move-length direction and the next move-length direction.

Fixes were marked on a plan (1 cm to 12.5 m) of a home range prepared by hand from an Ordinance Survey map and field measurements. A grid of squares on a transparent sheet was placed over the plan and XY coordinates were noted for each fix.

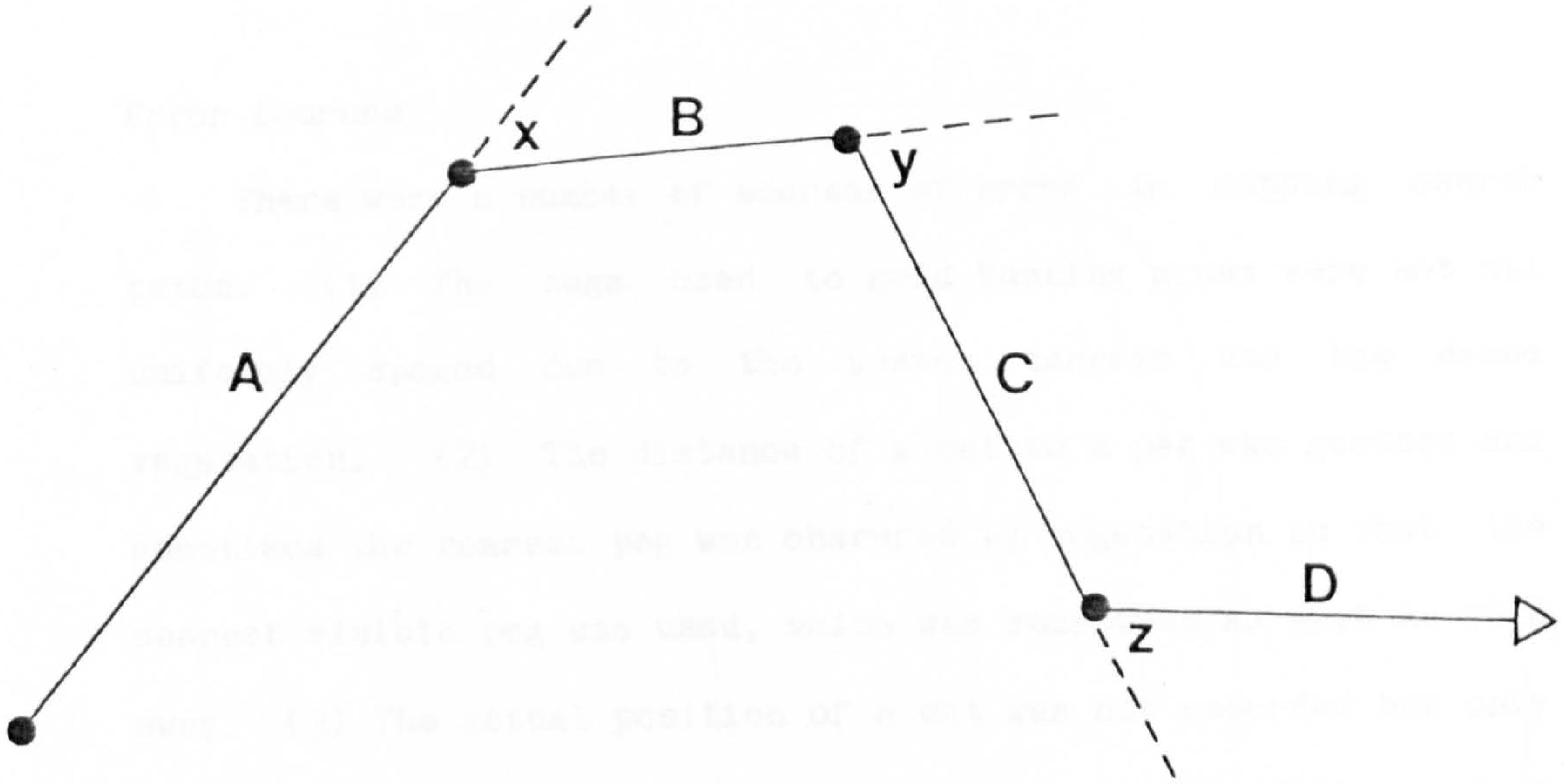


Fig.6.3.1 Scheme of a search path. A: first move-length. B: second move-length making a right turn of turn-angle x. C: third move-length making a right turn of turn-angle y. D: fourth move-length (incomplete) making a left turn of turn-angle z. And so on.

The coordinates were typed into a computer which measured the distance of each consecutive move-length, the value (left or right) of each consecutive turn and the size of each consecutive turn-angle for each search path.

Error Sources

There were a number of sources of error in mapping search paths. (1) The pegs used to grid hunting areas were not all uniformly spaced due to the uneven terrain and the dense vegetation. (2) The distance of a cat to a peg was guessed and sometimes the nearest peg was obscured by vegetation so that the nearest visible peg was used, which was sometimes as much as 25 m away. (3) The actual position of a cat was not recorded but only his position according to one of the main points of the compass with reference to a peg. (5) Fixes were taken at one minute intervals which may have resulted in recording non-existent turns and turn-angles. An example of the last point is Fig. 6.4 which shows a hypothetical search path of a cat and fixes of the cat's position at one minute intervals. The first three fixes record a straight line when the cat has turned left, right then left again. The last fix records a right turn when the cat turned right then left. Shorter interfix intervals could have been used but were not practical (because I had to keep up with the cat, watch for pegs, rabbits and roots, select a path through the gorse, not get caught on thorns or tread on twigs, keep a low profile, manipulate the tape recorder, and so on). (6) Error was incurred converting the field coordinates of fixes into coordinates for the computer.

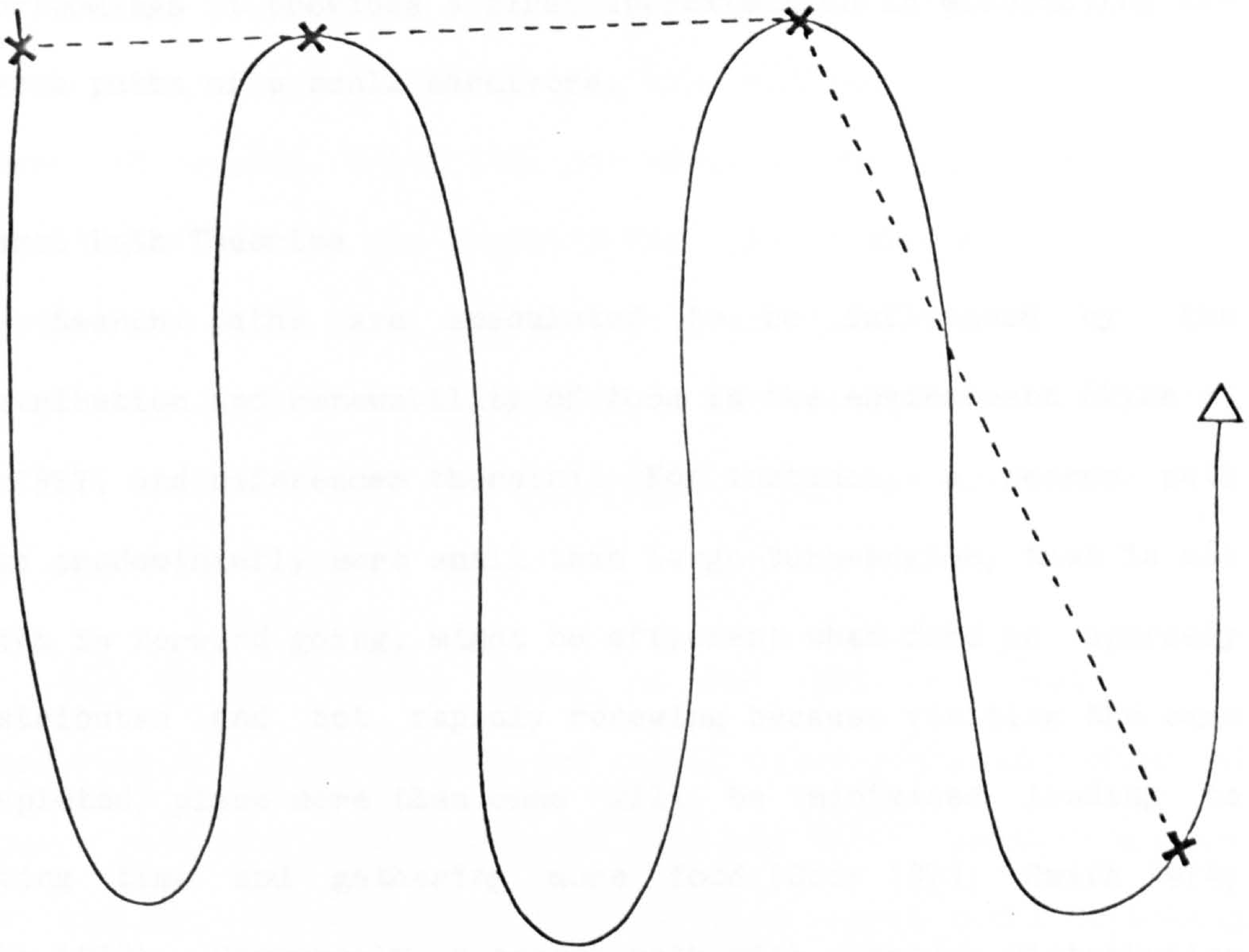


Fig. 6.4 A hypothetical search path.

On the small scale, therefore, the mapped search paths are inaccurate with regard to the exact position of a cat, who might have been misplaced at times as much as 20 m, and with regard to the turns and turn-angles to some unknown extent. But on the grand scale they probably give a good picture of the general appearance of a cat's search path. Although the method has its shortcomings it provides a first approximation in elucidating the search paths of a small carnivore.

Search Path Theories

Search paths are speculated to be influenced by the distribution and renewability of food in the environment (Pyke et al 1977, and references therein). For instance, a search path with predominantly more small than large turn-angles, that is one which is forward going, might be efficient when food is sparsely distributed and not rapidly renewing because visiting the same (depleted) place more than once will be minimised leading to saving time and gathering more food (Cody 1971; Smith 1974; Pyke 1978). Conversely, a search path with a random distribution of turn-angles, that is one which often crosses its own path, might be efficent when food is abundant in all directions and there is little chance of revisiting an already searched place (Zimmerman 1979). Long moves might occur more frequently in an area poor in food until a rich area is encountered when short moves might become more frequent, which should tend to keep an animal in the food rich area (Waddington and Heinrich 1981).

Use of Hunting Area

Figs. 6.5 and 6.6 show nine superimposed search paths of Fm1 and the single search path of Fm2. The overlays show the peg grid pattern and the number of rabbit holes (501) per square. The rectangle represents the wire fence surrounding a covered reservoir. Fig. 6.7 shows ten superimposed search paths of Hm1. The overlay shows the peg grid pattern, the four walls and a stream running through his hunting area and the numbers are the number of rabbit holes (40) per square. The individual search paths of Fm1 and Hm1 are shown in Fig. A1 in the appendix. All graphs have the same scale and a cross indicates the start of each path. Crosses are almost all at the top left in Figs. 6.5 and 6.6 and at top centre in Fig. 6.7; the areas nearest a cat's core area.

Each of the search paths of Fm1 and Fm2 tend to be meandering but forward-going and rarely cover previously searched areas. Both cats hunted the same area and their search paths are very similar. In contrast, although Hm1's search paths have long segments which are meandering and forward-going, they often cover previously searched ground.

Figs. 6.5 and 6.6 show that Fm1 and Fm2 kept mainly to gorse patches and went quickly from one patch to another because paths between patches are straight and only 4.1 % (25) of Fm1's 599 fixes and only 2.1 % (8) of Fm2's 379 fixes occurred outside patches. Their search paths concentrated where rabbits were likely to be found; 61.1 % of Fm1's fixes and 51.7 % of Fm2's fixes fell within squares which contained one or more rabbit

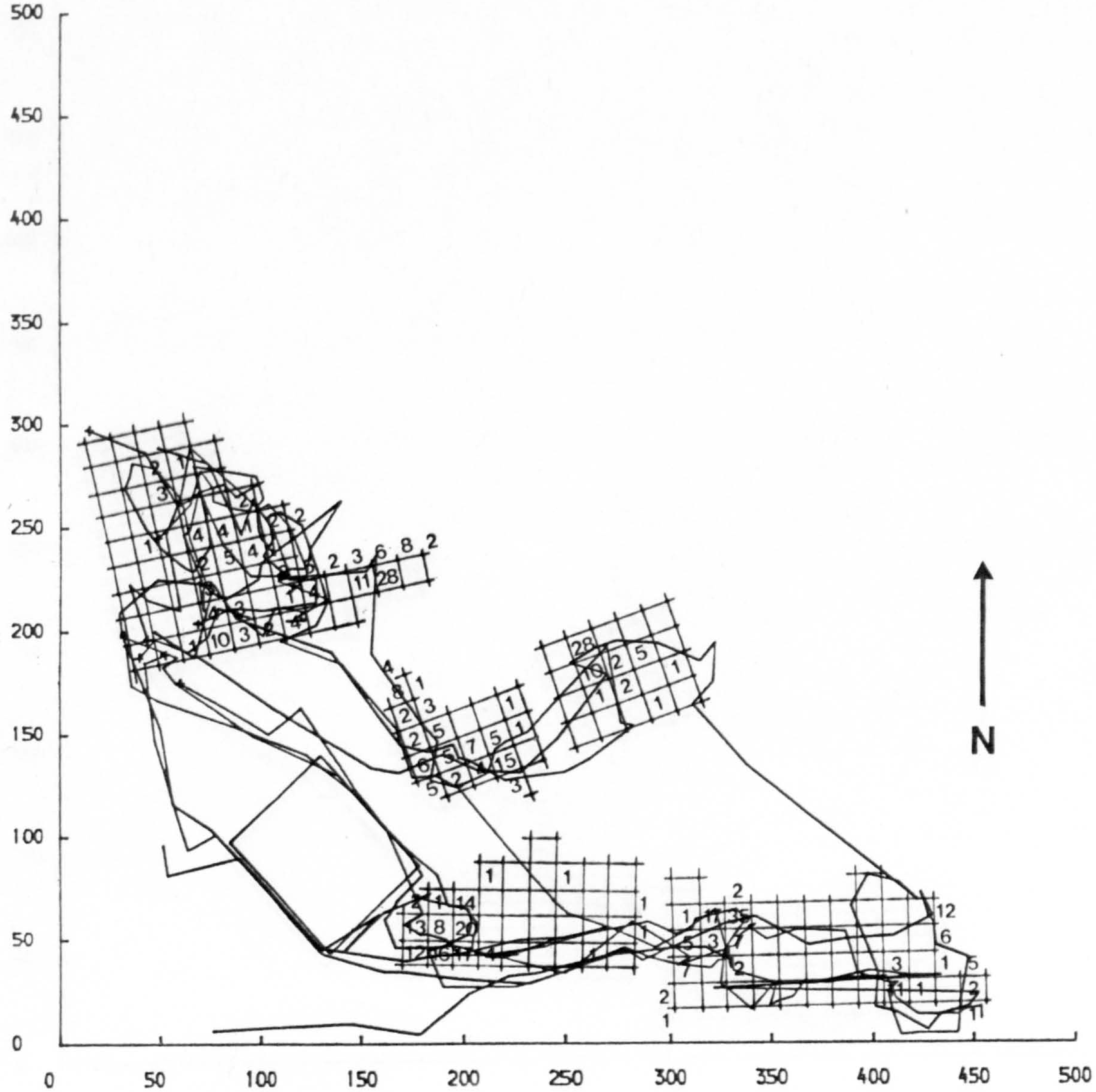


Fig. 6.5 Nine superimposed search paths of Fm1. A cross indicates the start of a path. Scale in metres

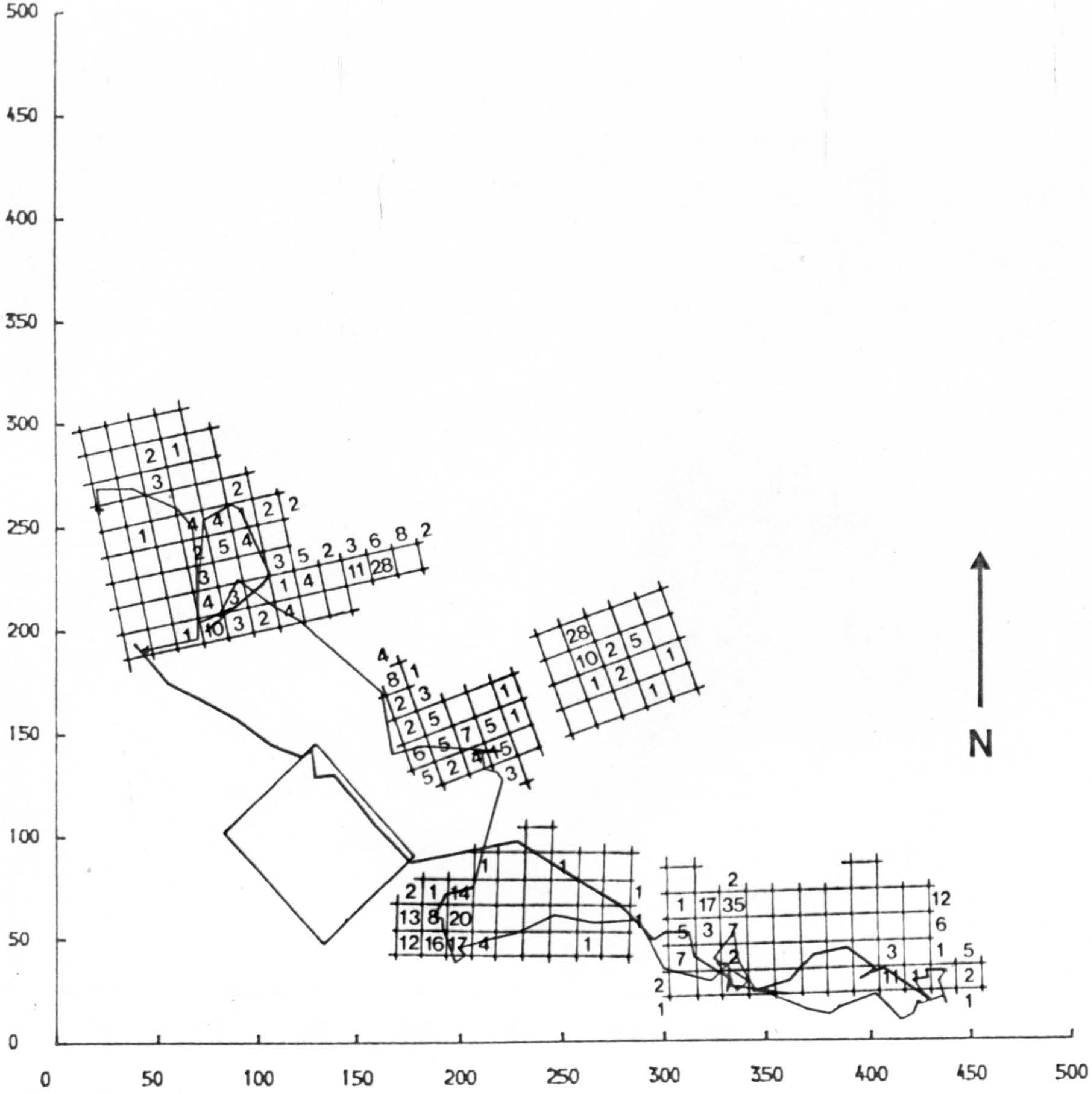


Fig. 6.6 The search path of Fm2. A cross indicates the start of the path. Scale in metres

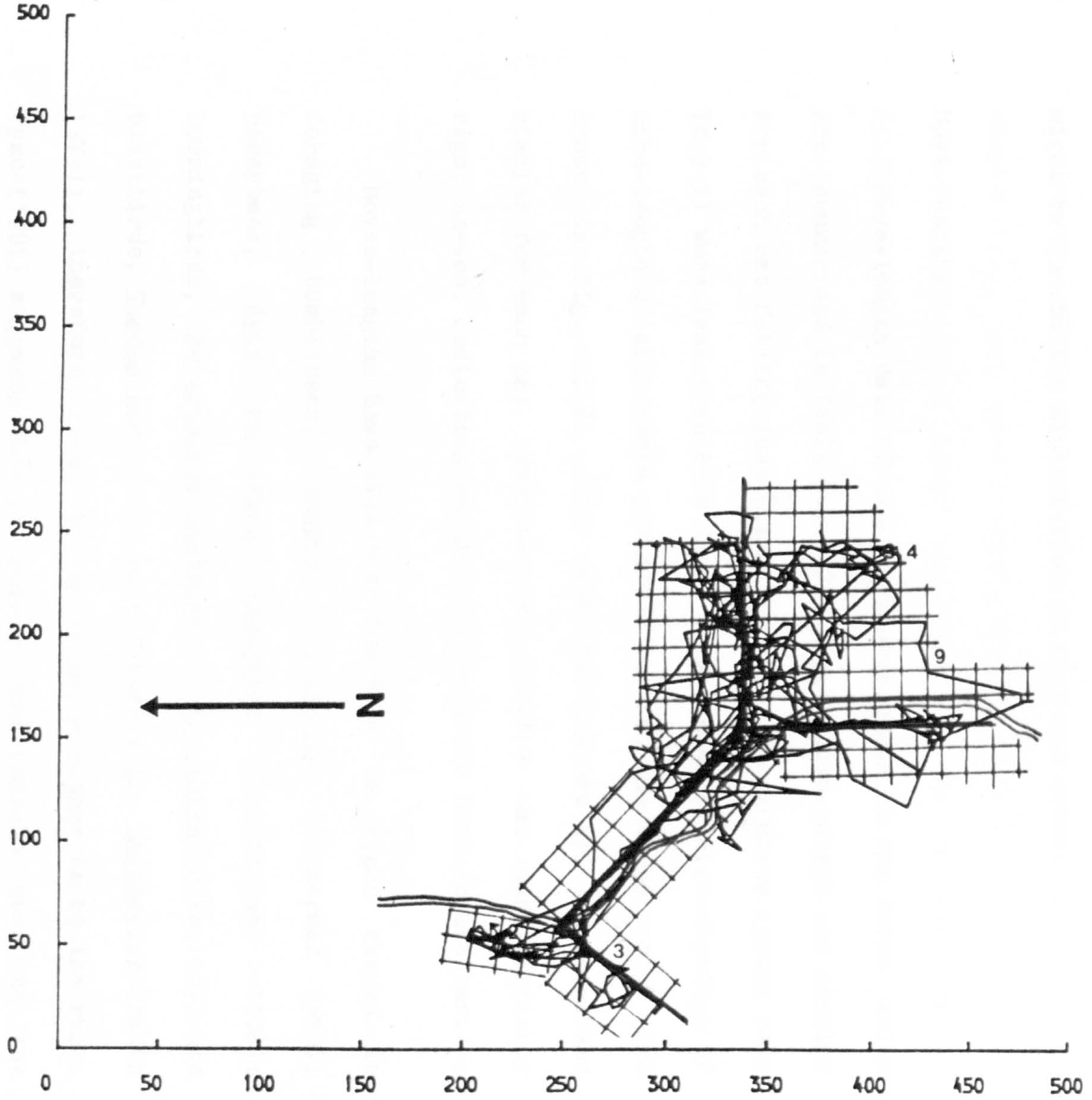


Fig. 6.7 Ten superimposed search paths of Hml. Scale in metres

holes. There were fewer rabbits in Hm1's hunting area compared to the Fife cats': 40 rabbit holes to 501. His search paths (Fig 6.7) concentrated in the vicinity of the walls, particularly the east-west wall; 67.0 % of his fixes fell within one square either side of them. Search paths, therefore, were not random, hunting areas were not used uniformly and the differential use might be due to the distribution of prey and cover.

Move-lengths

Move-length data of all the search paths of the three males are summarised in Table 6.9. The median move-length was similar for each cat falling just below the mean. Most moves (grand mean 78.3 %) were less than 20 m long. The frequency distributions of move-length of all search paths for each of the three males are shown in Fig. 6.8. The distributions are all monomodal and similar for each cat. Each search path of a cat was similarly right skewed, indicating consistency from one hunt to another.

Moves-lengths have also been found to be right skewed in foraging bumblebees, Bombus flavifrons (Zimmerman 1979); honeybees, Apis mellifera ligostica (Waddington 1980); hummingbirds, Selasphorus platycer and S. rufus (Pyke 1981) and blackbirds, Tardus merula and song thrushes T. philomelos (Smith 1974); therefore relatively short moves appear to be the rule. Pyke (1981) suggests this is because the animals move to the closest detected food site. However, this pattern has also been shown by goldfish, Carassius auratus (Kleerekoper et al 1970) which were not foraging and foxes and snowshoe hares (Siniff and Jesson 1969) which may not have been foraging. Consequently this pattern in hunting animals seems to be an aspect of locomotion in general.

Turn-angles

As turn-angle distributions are circular, the mean and standard deviation are meaningless statistics to describe them and therefore the mean angle (L) and angular deviation s, respectively, are used instead (Batschelet 1965). The Rayleigh test z (Batschelet 1965) was used to decide whether a distribution was uniform or significantly unimodal. Batschelet (1965:31) gives three formulas to calculate whether the mean angle of a distribution is significantly different from zero degrees and the decision to use a particular formula depends on the sample size n and a quantity X, which is the component of R in the zero degrees direction (Batschelet 1965:29). These values were different for each cat and therefore formulas were chosen accordingly. The mean angle is significantly different from zero degrees when R is greater than Ro (Batschelet 1965:30).

The frequency distributions of turn-angles of all search paths for each male are summarised in Table 6.10 and shown in Fig. 6.9. The distributions are nearly symmetrical with unimodal peaks which were highly significantly different from an assumption of unifromity (Table 6.10). Mean angles did not differ significantly from zero degrees and the angular deviations ranged from 63 degrees to 68 degrees (Table 6.10). This shows the cats tended to avoid large turns, that is they usually avoided the direction from which they came; a grand mean of 72.3 % of turn-angles were within 90 degrees either side of zero

	Fm1	Fm2	Hm1
N Search paths	9	1	10
N Move-lengths	251	61	668
Move-length (m):			
median	14	12	13
mean	17.5	14.5	13.5
± SD	15.1	10.7	9.6
% Move-lengths < 20 m	70.5	82.0	82.5

Table 6.9 Data on search path move-length for three male cats.

	Fm1	Fm2	Hm1
Rayleigh test Z	40.2	5.5	75.7
Z Critical value ($p < 0.01$)	4.6	4.6	4.6
Mean angle L	+ 7°	+ 2°	- 5°
R	103.5	18.4	223.7
Ro Critical value ($p < 0.05$)	494.0	49.3	224.1
Angular deviation S	63°	68°	66°

Table 6.10 Data on search path turn-angles for three male cats.

Fig. 6.8 Frequency distribution of search path move-lengths of Fm1, Fm2 and Hm1.

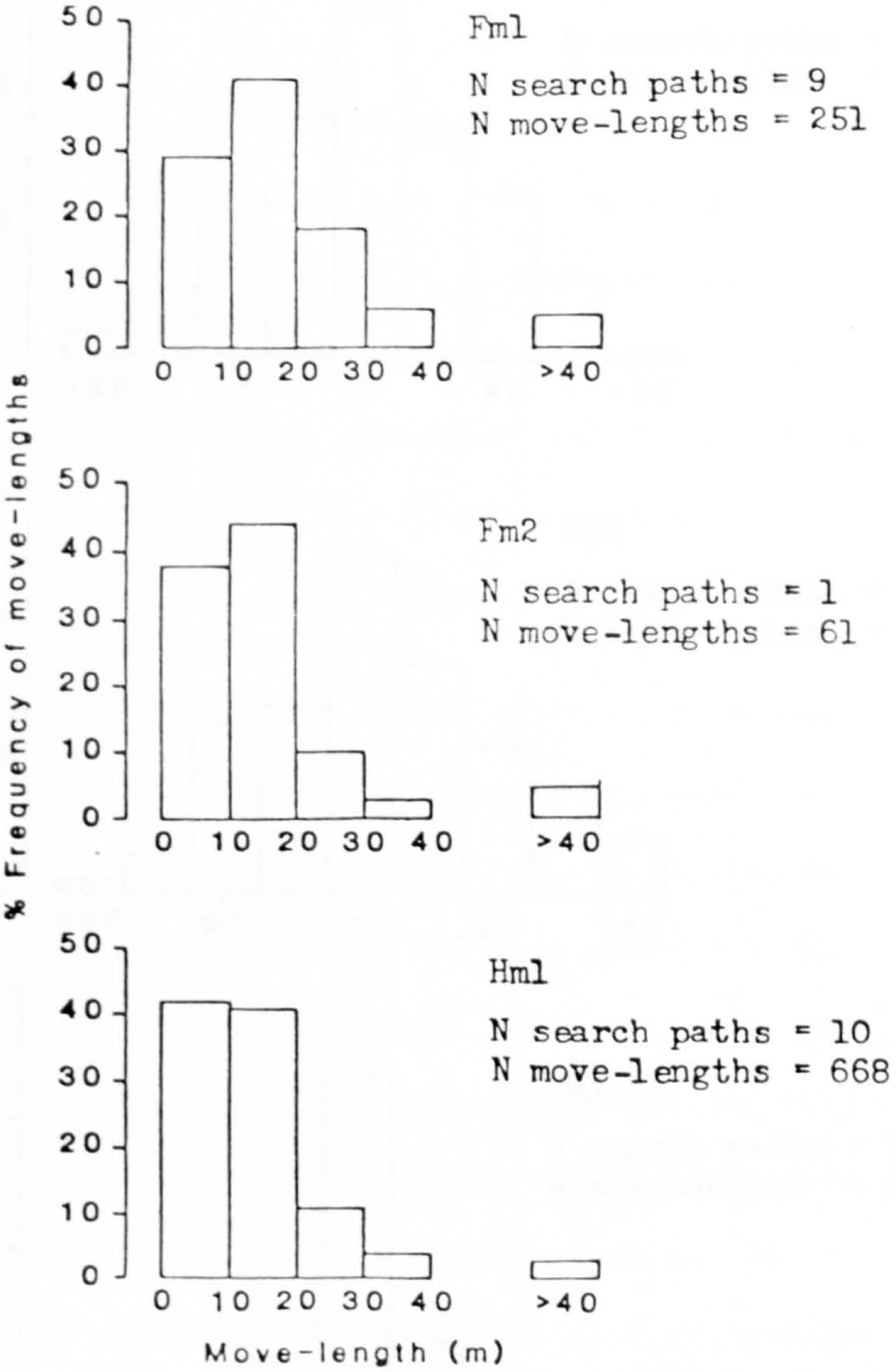
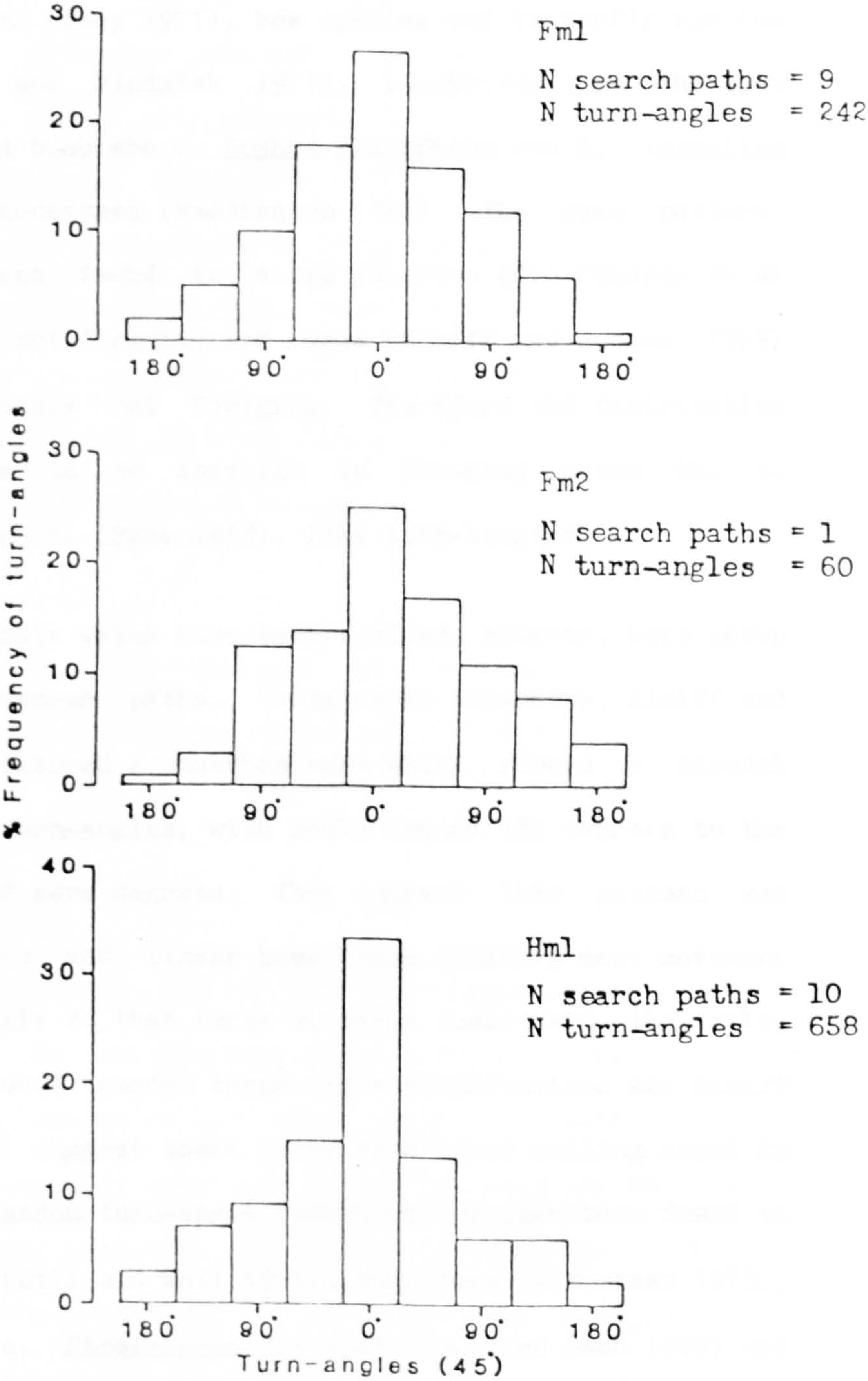


Fig. 6.9 Frequency distribution of search path turn-angles of Fm1, Fm2 and Hm1. Clockwise turns to left, anti-clockwise turns to right.



degrees (Fm1 80.0 %, Fm2 63.9 % and Hm1 70.0 %).

The frequency distributions of turn-angles of a variety of species have been found to be similarly forward going, that is unimodal and symmetric with a mean of about zero degrees: mixed flocks of finches (Cody 1971), bee species and butterfly species (Levin, Kerster and Niedzlek 1971), blackbirds and thrushes (Smith 1974) and bumblebees, Bombus flavifrons and B. appositus (Pyke 1978) and honeybees (Waddington 1980). The same pattern, however, has been found in sated goldfish (Kleerekoper et al 1970) which were not foraging and foxes (Siniff and Jesson 1969) which were possibly not foraging. Therefore the distribution does not appear to be specific to foraging paths but to locomotion in general (Pyke 1978), like move-lengths.

Not all animals which have been studied, however, have shown forward going search paths. Using radio telemetry, Siniff and Jesson (1969) monitored a snowshoe hare which shoeed a bimodal distribution of turn-angles, with peaks around 180 degrees to the left and right of zero degrees. They suggest this pattern was due to a narrow and linear home range limiting most movement about the long axis so that turns of large angle were the rule. Other hares showed random turns angle distributions and Siniff and Jesson (1969) suggest these arose from hares milling about in small areas. Random turn-angle distributions have been found in sunbird species (Gill and Wolf 1977), bumlebees (Zimmerman 1979), caddisfly larvas, Dicosmoecus gilvipes (Hart and Resh 1980) and hummingbirds (Pyke 1981).

Move-length, Turn and Turn-angle Sequence

The sequence of turns and move-lengths may show a regular pattern. Nectar-collecting bumblebees studied by Pyke (1978) showed a significant tendency to alternate left and right turns. Smith (1974) found foraging blackbirds and thrushes tended significantly to alternate left and right turns and to pair moves of short lengths and of long lengths; there was also evidence of higher order sequences. Waddington (1980) found a significant although very low correlation in honeybees foraging for nectar: large turns were paired with long moves and small turns with short moves. Turn patterns are not limited only to foraging animals, however. Sated goldfish studied by Kleerekoper et al (1970) showed a significant tendency to pair turns in the same direction.

The following three sections examine whether there are patterns in the move-lengths, turns and turn-angles of the cats' search paths.

Move-length Sequence

Move-lengths were tested to find regularites in their sequence, that is whether long moves tend to follow long moves and short moves tend to follow short moves, whether long and short moves tend to alternate or whether long and short moves occurred in random sequence. For each search path, therefore, move-lengths were classified as either above or below the median for the path. Consecutive pairs of moves were then entered into a contingency table for observed and expected frequencies of short-short, long-long, short-long and long-short move-lengths and a chi-squared analysis calculated. Chi-squared values for each search path are shown in Table A1 in the appendix and indicate there was no significant difference from a random sequence. This suggests consecutive pairs of moves, classified as either above or below the median, were independent of each other.

Turn Sequence

Left and right turns were tested to find regularities of turning, that is whether there was a tendency to make consecutive turns in the same direction, left-left and right-right, or to alternate consecutive turns left and right. For each search path, the number of times a left turn was followed by a left or right turn and the number of times a right turn was followed by a left or right turn was calculated by entering consecutive pairs of turns into a contingency table and analysing by chi-square. Chi-squared values for each search path are shown in Table A2 in the appendix. They show that the turns were not significantly different from a random sequence. This suggests the direction of a turn was independent of the preceding turn.

Move-length and Turn-angle Sequence

The pattern of moves and their following turn-angles was examined to find regularities in their sequence, that is whether short moves tended to be followed by small or by large turn-angles and whether long moves tended to be followed by small or by large turn-angles. Move-lengths and turn-angles for each search path were therefore classified as either above or below the median for the search path. Each move and its following turn-angle were then entered into a contingency table and chi-squared analysis carried out. Chi-squared values for each search path are given in Table A3 in the appendix and show that the length of turns and the size of their following turn-angles did not depart from a random expectation. This suggests that the length of a move and the size of its following turn-angle were independent of each other.

The same method was used to find regularities in the size of a turn-angle and the length of its following move. Chi-squared square values for each search path are shown in Appendix Table A4. The size of a turn-angle and the length of its following move are not significantly different from chance. Thus, the size of a turn-angle and the length of its following move appear to occur independently of each other.

Discussion

The popular impression of domestic cats is that they hunt at night yet most hunting by the farm cats was between dawn and dusk. Their diurnal hunting does not appear to be a response to their prey's peak activity periods because their prey are reported to be least active during the day: woodmice are crepuscular and nocturnal (Flowerdew 1977); house mice are mainly nocturnal (Rowe 1977); bank voles, <u>Clethrionomys glareolus</u> (Flowerdew 1977) and field voles (Evens 1977) are active throughout the 24 h but mainly at night; most rabbits were seen by Gibb, Ward and Ward (1978) at dusk and most were above ground at night; Lloyd (1977) states rabbits are diurnal if undisturbed but are otherwise crepuscular and nocturnal. The cats' hunting schedules are associated better with climate (see Activity Patterns, Chapter 3).

There was a sexual dichotomy to some extent in that most females hunted close to the steadings whereas males hunted farther away. Because rabbits did not live close to the steadings it led to a major difference in diet in that females caught only rodents but males caught rodents and rabbits. This was not an intrinsic dietary difference, however, because returning at a latter date to the Cornish farm I saw Cf3 and Cf5 each eat a rabbit. Presumably rabbits had not been caught earlier because they had been scarce.

Domestic cats are traditionally believed to be great hunters of birds. The data do not support this belief and are in line with those of other observers, for instance Leyhausen (1979) and Liberg (1981), that birds are not the usual prey of domestic cats. In a review of domestic cat food habits, Fitzgerald and Karl (1979) concluded that predation is mainly on small mammals, particularly rodents and rabbits and that predation of birds is usually minor, except on some small islands with large bird populations. The belief that birds are frequently hunted by cats may stem partly from their conspicuous feathers, which can remain for weeks after a bird has been killed. Rodents in comparison are cryptic and often completely eaten so their killing passes unnoticed.

A problem for the cats is when to give up ambushing; if a cat has not caught a rabbit after a certain time from the start of an ambush then he should give up because he might have success elsewhere. The data from this study is that for each of three cats all prey were caught in less than 10 min and three quarters of the ambushes lasted less than 10 min. However, half the ambush time was spent on ambushes longer than 10 min. This raises the question of why, if all prey were caught in less than 10 min, did the cats spend half their time ambushing longer than 10 min. Two hypotheses about how long a predator should remain in a discrete area containing potential prey are hunting by time expectation (Krebs 1973): a predator learns to expect to catch a prey after a fixed time and should give up after the time has elapsed; and the marginal value theorem (Charnov 1976): some prey will take longer to catch than others and a predator should give up when the ambush time falls below the average time to catch a prey in the foraging area.

Both hypotheses evolved to explain the behaviour of birds predating insects on cones. If they are of general value they should be applicable to cats and in this case 'a discrete area containing potential prey' is a cat's ambush site, for instance a rabbit hole. The data do not support the first hypothesis because the cats gave up ambushing after variable amounts of time and neither hypothesis explains why the cats spent so much time ambushing longer than 10 min. The hypotheses, therefore, do not appear in the light of these data to be of value in predicting the behaviour of cats ambushing. Theoretically the hypotheses may be too simple. They do not take into account the predator himself; for example an ambush may vary in length depending on stimulus intensity of a prey and degree of hunger of a predator.

A major factor directing the search paths of a forager is speculated to be the distribution and availability of food (for instance Pyke et al 1977; Zimmerman 1979): when food is clumped the forager should search where food is most likely to be encountered and if food does not become quickly available again the forager should minimise searching areas recently searched. Failure to do this will lead to a waste of time and energy. The rabbits at the Fife farm were dispersed in clumps within gorse patches and were not quickly available again after a cat had passed because they fled or jumped down holes. Looking at search paths on the grand scale, the two farm cats largely confined their search to the clumps and patches and rarely doubled back to cover previously searched ground. Therefore they are able to distinguish between areas of different prey density and concentrate hunting in profitable areas. They appear to confirm the prediction in that the distribution and availability of the rabbits may have had an effect on determining their search paths. The search paths of Hm1 typically covered areas already searched. Why? He may have been using a different search method in keeping with the distribution and availability of his prey. For instance, his hunting area contained 12 times fewer rabbits and many ambushes were for rodents and birds. Also, as a house cat, he had more human-provided food so may not have needed as great a success rate as the farm cats.

On the small scale, allowing for errors of mapping, the cats' search paths were similar to those of other foragers: thrushes and blackbirds (Smith 1974), bumblebees (Zimmerman 1979), honeybees (Waddington 1980) and hummingbirds (Pyke 1981), in so far as turns were within 90 degrees of straight ahead and most move lenghts were relatively short. But this pattern also appears in animals which were not or probably not foraging: foxes and snowshoe hares (Sniff and Jesson 1969) and goldfish (Kleerekoper et al 1970) and therefore seems not to be peculiar to foraging search paths. The move-lengths, turns and turn-angles showed no other evidence of a regular pattern, perhaps because there was none or because the method was too coarse for one to appear.

It may be argued that the best method of mapping a path is to record its natural features and not impose artificial move lengths, turns and turn-angles. For example, birds make short and long hops and two consecutive hops form a natural angle (for instance Smith 1974). The difficulty is that with cats the only natural features which could be recorded are pauses, ambushes and prey captures and with the exception of the latter even these must be subjectively defined because they are not always immediately obvious. It would be of interest not only to improve the method but also to explore how maturing cats improve their search strategy through experience.

Chapter 7

POPULATION DYNAMICS

Preamble

So far cats have been looked at from close up. But what patterns do they form on the large scale? A cat is a mobile creature. If he travels away from home what kind of conspecific environment, in terms of density, sex ratio, age distribution and so on, would he be likely to encounter? In this last chapter of results I report on a census of cats in Fife and draw together a number of papers which have tackled aspects of domestic cat population dynamics.

Method

A census of cats was conducted from September to October 1980 in two 50 sq km areas of rural Fife by visiting all the houses and farms. The eastern area (Fig. 7.1) enclosed a 4 km radius extending from Wester Kellie farm, 5 km north west of Anstruther. The western area enclosed a 4 km radius extending from Auchindownie farm, 3 km north of Largo, but skewed slightly to include a small area equal in size to Largo and an area of sea which were not censused. The two areas were separated by 0.5 km.

The census scheme was adopted because originally the data were to be part of a radio telemetry study of cats in the two areas.

The questions asked at each visited place were the number of cats and people living there, whether cats were farm cats (live at a farm but not in the house and are fed little or no food) or house cats (live in the house and are fed much food), their age, sexual status, genetic relationships if in a group, whether imported into the census area and, if they had been, the distance from which they came.

Density

Fig. 7.1 shows, as an example of the two census areas, the spatial distribution of 208 cats (130 farm and 78 house cats) in the eastern area. Cats are scattered unevenly because, of course, their distribution is the same as the distribution of dwellings, which were scattered unevenly. For instance, there are no dwellings in the middle north but there is a village just south of the centre. Feral cats were not censused and so are not indicated but my impression, gained by talking to people while censusing (Have you seen any stray cats?), was that feral cats formed a minority of the population, possibly accounting for a further 20 % of cats in the western census area and about a further 5 % in the eastern area. Liberg (1980) found 10 % of resident cats in a rural area of southern Sweden were feral. Therefore Fig. 7.1 probably reflects the distribution of most cats in the area.

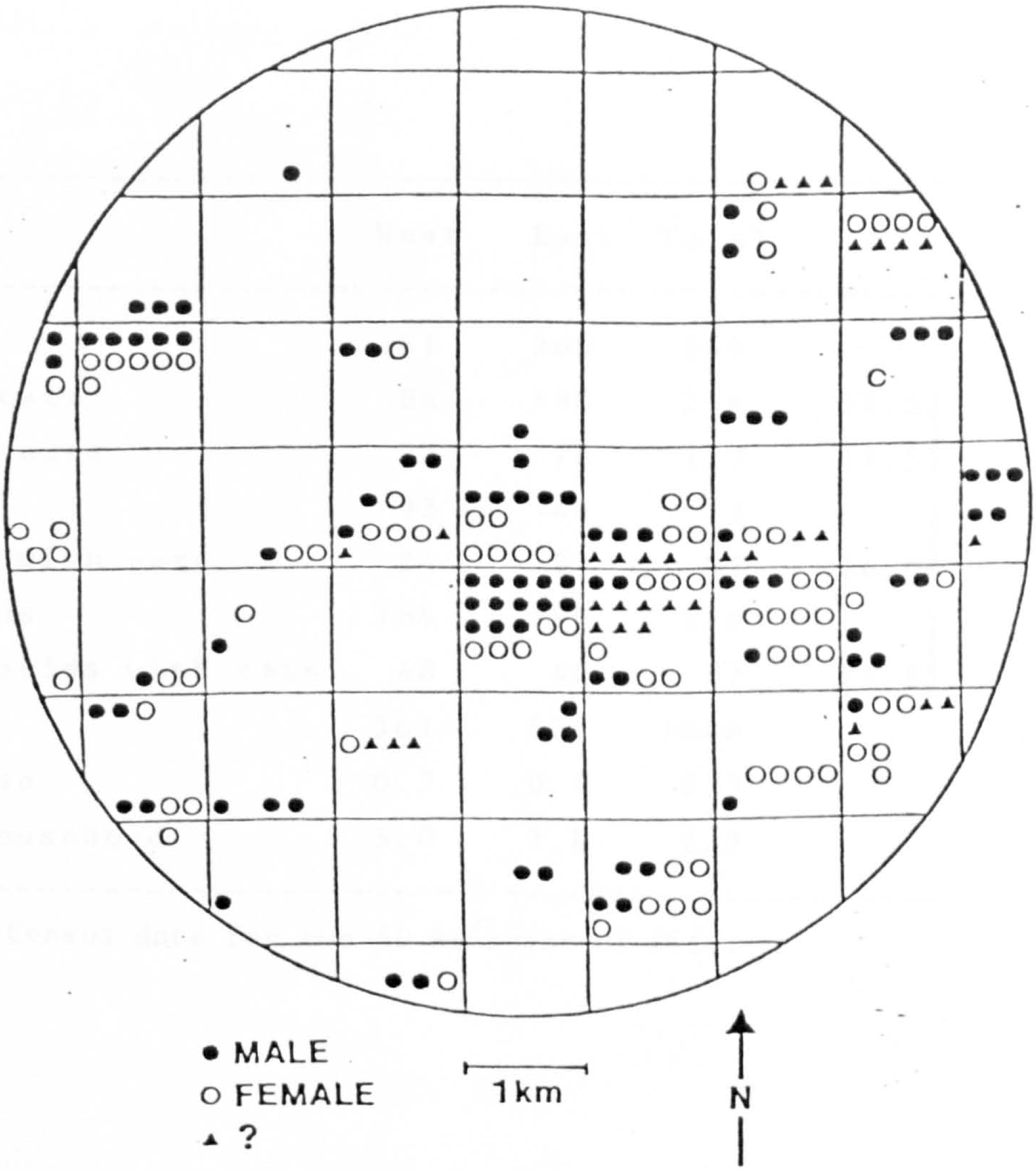
Table 7.1 shows data for the censused 100 sq km. There were 3.7 cats (2.7 dogs) and 10.9 humans per sq km making 0.3 cats per human. These cats were at low density compared to feral cats (Table 7.2). This is surprising because the feral cats are estimated to be at about the same or a higher density to cats supported in part by humans in a highly agricultural area. Possibly, wild areas can support more cats than highly agricultural ones.

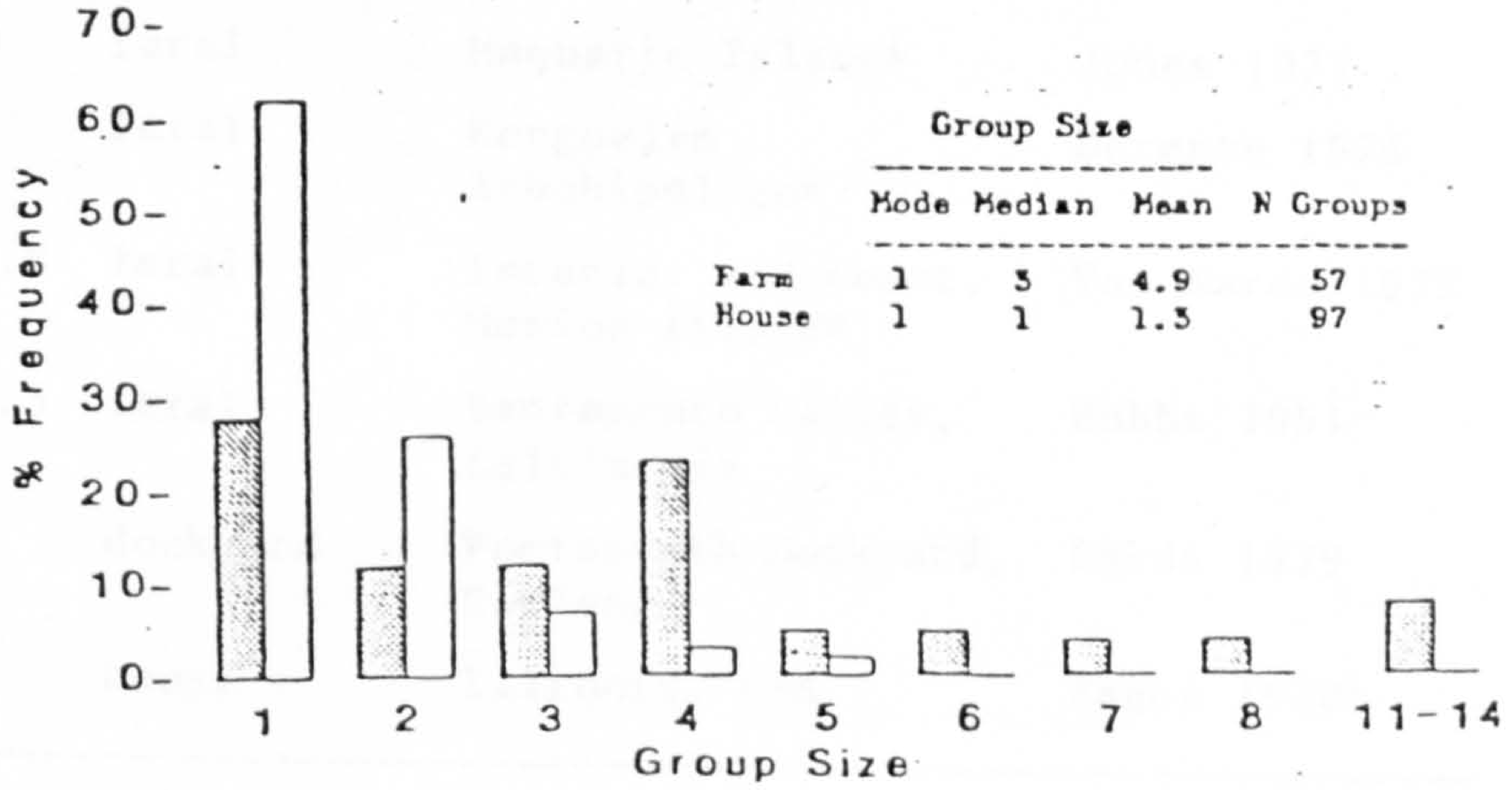
In a review of gene flow of cats in Australian, British and American cities, the percentage of households-with-cats varied from 11.3 % to 60.2 % (Todd 1977). Fagen (1978b) and Clark (1975) estimated respectively that 14.8 % of Illinois and 19.8 % of Glasgow households had cats. In my rural area cats were found at 25.8 % (114) of households (including 17 farm households; Table 7.1). Cats were also found at 74.0 % (57) of farms and although outnumbered by households they contributed the greater number of cats (58.5 %) to the population (Table 7.1). This was because of differences in group sizes.

Group Size

Fig. 7.2 shows the percentage frequency of farm cat and house cat group sizes and their averages. The two frequency distributions were highly significantly different as shown by a Kolmogorov - Smirnov two sample test (chi-squared = 0.325, D = 0.473, $p < 0.001$, two tailed; Table 7.3); cats at farms tended to live in larger groups then cats at households. The largest farm cat groups contained 11 to 14 cats, including some kittens, at four farms and the largest house cat groups had five cats at

Fig. 7.1 Spatial distribution of 208 farm and house cats in 50 km of Fife.





	Group Size			
	Mode	Median	Mean	N Groups
Farm	1	3	4.9	57
House	1	1	1.3	97

Fig. 7.2 Percentage frequency of group size of farm (shaded) and house cats from a census of 100 km^2 of Fife.

	West	East	Total	%
Cats	161	208	369	
farm cats	86	130	216	58.5
house cats	75	78	153	41.5
Farms	33	44	77	
farms with cats	24	33	57	74.0
Households	186	190	376	
households with cats	48	49	97	25.8
Humans	561	527	1088	
Cats/human	0.3	0.4	0.3	
Humans/household	3.0	2.8	2.9	

Table 7.1 Census data for two 50 km^2 areas of Fife.

Density	Cat type	Place	Author
3.7	feral	Monach Isles, Scotland	Corbett 1979
2.0 to 4.0	feral	Maquarie Island*	Jones 1977
6.7	feral	Kerguelen Arhchipelago*	Derenne 1976
5.0 and 13.8	feral	Interior and coast, Marion Island*	Van Aarde 1978
7.8 and 11.5	feral	Sacramento Valley, California	Hubbs 1951
200.0	dockyard	Portsmouth Dockyard, England	Dards 1979
450.0	house	Illinois, USA	Fagen 1978b

Table 7.2 Comparison of cat densities $/km^2$. *Sub-antarctic island.

N cats in group	FARMS N groups	FARMS cumulative frequency	HOUSES N groups	HOUSES cumulative frequency
1	16	0.281	60	0.619
2	7	0.404	25	0.877
3	7	0.527	7	0.949
4	13	0.755	3	0.980
5	3	0.808	2	1.000
6	3	0.861	0	1.000
7	2	0.896	0	1.000
8	2	0.931	0	1.000
9	0	0.931	0	1.000
10	0	0.931	0	1.000
11	1	0.949	0	1.000
12	1	0.967	0	1.000
13	1	0.985	0	1.000
14	1	1.000	0	1.000
N groups	57		97	

Table 7.3 Frequency distribution of farm and house cat group size.

	♂♂	♀♀	♂♂ : ♀♀	Chi^2	p
Whole farm	40	77	1.0:1.9	11.077	<0.001
Neutered farm	12	9	1.3:1.0	0.190	>0.05
Whole house	21	20	1.0:1.0	0.000	>0.05
Neutered house	68	66	1.0:1.0	0.008	>0.05

Table 7.4 Sex ratios of 313 cats of known sexual status.

two households.

Maximum reported sizes of cat groups range from 5 to 19 individuals in rural areas (Laundre 1977; van Aarde 1978; and Corbett 1979) to 10 adults with 15 kittens in Portsmouth Dockyard (Dards 1979). This suggests an upper group size limit which might not exceed much more than 25 adults and kittens although Macdonald and Apps (1978) have seen groups of over 40 cats at Oxfordshire farms.

The average number of cats per household in Australian, British and American cities (Todd 1977) varied from 0.09 to 0.91. Todd (1977) suggests this was connected with the type of dwelling, "composition and age distribution of the household" and its socio-economic status; there tended to be more cats in single family dwellings with children and a professional or semi-professional head of family.

Sex Ratios

Table 7.4 shows the sex ratios of 313 cats of known sex divided into four categories. Only the sex ratio of whole farm cats differed significantly from unity (chi-squared = 11.077, $p < 0.001$, two tailed). The sex ratio of Portsmouth Dockyard cats studied by Dards (1979) also favoured adult females (1:1.5), which she thinks may be due to high mortality among males leaving their natal birth place seeking new areas to live in. Liberg (1980), in a rural area of Sweden, also found the balance favoured females (by 3:5) but, furthermore, found more males than females tended to emigrate from their birth place. Therefore male mortality and emigration in my data are probably confounded because the missing males might have been present as feral cats. Unlike whole males, neutered males are generally considered not to wander so neutered farm cats could be expected to show a 1:1 ratio. Although their numbers are small and therefore might be effected by sampling bias, the neutered farm cats in my census show this ratio and consequently lend support to the missing males hypothesis. The unity sex ratio of whole and neutered house cats can be explained by assuming that both sexes are equally available and on average humans do not choose to have one sex or the other.

Sometimes, however, sex ratios can be biased towards males. On a sub-antarctic island van Aarde (1978) found a sex ratio favouring both adult and sub-adult males (overall 1.9:1). He suggests the ratio may be biased owing to females spending more time than males in lairs during the breeding season; after the breeding season the sex ratio favoured females. Jones (1977), on another sub-antarctic island, also found a sex ratio favouring males for adult and sub-adult classes (overall 2.5:1). There was no evidence to distinguish between a behavioural difference or actual differential mortality but as the samples were small there might have been a sampling bias (Jones 1977).

Survivorship

At least 150 individuals per age distribution are necessary for a statistically adequate analysis of survivorship (Caughley 1977). However, only 268 cats could be classified according to age and dividing this sample into eight categories by sex, and whole/neutered and farm/house status made the numbers inadequately small. Even so, although possibly statistically unrepresentative, an analysis may show a trend to lend support or jog evidence from other population studies.

Table 7.5 shows the age distribution of 268 cats of known age and status. By visual inspection, it shows a steep decline in survivorship (the number surviving to each age) up to about age 5, beyond which only 9.8 % of farm males and 12.1 % of farm females were surviving compared with 24.7 % of house males and 32.1 % of house females. After roughly age 5, the decline in survivorship was uniform. Beyond age 10, no male farm cats and only 3.7 % of whole female farm cats were surviving compared with 16.4 % of neutered male and 15.6 % of neutered female house cats, who were surviving equally well. 17 y was the maximum age recorded.

Survivorship in Table 7.5 appears to be equal for both sexes of whole house cats and for both sexes of neutered house cats but survivorship of whole farm cats appears to favour females. A chi-squared test supports this; it was carried out by pooling the age classes containing most cats (< 2 y) against the total of all the other age classes (2 y and more; Table 7.6). But, as already stated, mortality and emigration in farm males are probably confounded. There were too few neutered farm cats to draw comparisons from them.

Age class (y)	Farm				House				Total
	whole		neutered		whole		neutered		
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	
<0.25	2	0	0	0	0	2	0	0	4
0.25 < 1	11	11	0	0	6	7	6	4	45
1	9	11	1	0	4	1	6	7	39
2	6	8	2	1	5	4	12	7	45
3	2	6	0	0	1	2	10	7	28
4	1	6	1	1	2	0	8	8	27
5	1	5	1	1		1	4	7	20
6	1	3	2	0		0	1	6	13
7		1	0	0		0	1	0	2
8		1	1	0		0	3	3	8
9		0		0		1	3	1	5
10		0		0		0	2	4	6
11		0		0		0	0	1	1
12		0		0		0	3	1	4
13		0		1		0	2	2	5
14		1				2	1	5	9
15		0					1	0	1
16		1					3	1	5
17							1		1
Total	33	54	8	4	18	20	67	64	268

Table 7.5 Age distribution (y) of 268 cats according to status.

This view of cat mortality is corroborated by Hamilton, Hamilton and Mestler (1969) who over a number of years examined more than a thousand cats, mainly house cats, brought for treatment to a Pennsylvania veterinary school. They concluded that, on average, neutered males and whole females lived significantly longer than whole males; neutered females lived significantly longer than whole females (and by implication neutered females lived longer than whole males); and neutered males and neutered females lived as long as each other.

Two conclusions can be drawn comparing the results of Hamilton, Hamilton and Mestler (1969) with mine. Most of the difference in survivorship between farm and house cats might be accounted for by the effects of neutering and not by differences in the farm and house environment. And if neutered males and females live as long as each other then the low numbers of whole farm males in my data might not be because they died but because they emigrated.

Previous workers have observed that kittens suffer a high mortality rate. From Table 7.5 there are 54 whole females more than 12 months old and 49 other cats less than 12 months old. Table 7.7 shows 101 cats who could not be classified as in Table 7.5. In this table there are at least 27 whole females more than 12 months old (maximum of 40 if cats of unknown age and sex are included) and 39 other cats less than 12 months old. Therefore there is a total of 77 (maximum 94) potential female breeders, which constitutes 20.9 % of the population, and 88 cats less than 12 months old, which constitutes 23.8 % of the population. This

Age class (y)	Farm				House			
	whole		neutered		whole		neutered	
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
<2	22	22	1	0	10	10	12	11
>2	11	32	7	4	8	10	55	53
Chi^2	4.897		-		0.000		0.027	

Table 7.6 Chi^2 test for survivorship of cats from Table 7.5.

Age class (y)	Farm						House				Total
	?	?	♂♂		♀♀		♂♂		♀♀		
	?	W	W	N	W	N	W	N	W	N	
<0.25	0	7	0	0	0	0	0	0	0	0	7
0.25 < 1.0	0	32	0	0	0	0	0	0	0	0	32
>1.0	3	2	7	4	23	5	3	1	0	2	50
?	0	12	0	0	0	0	0	0	0	0	12
Total	3	53	7	4	23	5	3	1	0	2	101

Table 7.7 Age distribution (y) of 101 cats who could not be clearly classified according to age, sex and mating status.
W = whole, N = neutered.

suggests a high mortality rate of cats in their first year. On three uninhabited sub-antarctic islands feral cats less than 12 months of age were also estimated to have a high mortality rate: 28 % (Derenne 1974), 20 % (Jones 1977) and 26 % (van Aarde 1978) of the populations.

Ewer (1973), probably from house cat data, cites four as the "usual number" of kittens in a litter. But Dards (1979) found 58 % of litters in Portsmouth Dockyard had only one or two kittens, suggesting high mortality for kittens less than two months old (kittens were first seen at 2 months of age). Mortality between two and six months was high but was relatively lower between six and twelve months. Even in laboratory cats stillbirths are high, for no apparent reason (Scott 1967). Peltz (1976) in a survey of 'pure breeds' calculated a mortality of 31 % of 1,080 kittens.

Comfort (1955) reports on the longevity reached by some cats in Britain, who far outlived the censused cats. Ages ranged from 22 to at least 27 years for six whole males and 19 to at least 21 years for four neutered males. He quotes maximum ages found by Mellen for mainly north American domestic cats: 23 to 26 for three whole males, 21 to 31 for ten neutered males and 21 to 31 for four females. All these were presumably house cats.

Mortality and Emigration

Data on mortality and emigration were not collected during the census but the history of the colony at the Cornish farm is known for nine generations (see Chapter 4). Fig. 4.5 shows the cats' genealogy with their mortality and emigration data, which is tabulated in Table 7.8 for the 35 cats in Fig. 4.5 who died or emigrated. The primary mortality and emigration factors were 'going missing' for unknown reasons, 'dying' and 'giving kittens away' (although one was adult). The six youngest cats in the missing column (Table 7.8) possibly died because females are less likely to go feral than males (Liberg 1980, above) and cats less than 2 y of age are unlikely to go feral because they are not fully mature. I know the oldest female (Cf6) in the missing column of Table 7.8 went feral because, although she went missing initially, I saw her a few times at the dairy the following year when she went missing altogether. This leaves three adult males who went missing and they may have gone feral or died. Therefore perhaps as many as 19 cats died, 11 were given away and 1 to 4 went feral. Although the farm was situated by a fairly quiet lane, about a tenth of the cats in Table 7.8 were killed by motorists. Motorists on a busier road would certainly have killed more.

During a five and a half year study by Reichholf (1982) the annual death rate of cats along 150 km of rural roads in West Germany averaged 0.5 per km. In built-up areas it rose to 1.6 per km. Extrapolating these figures he gives an estimated loss of 94,000 cats a year for the whole country.

Dards (1979) considered the main causes of mortality in Portsmouth Dockyard cats, other than being caught and killed by people when a kitten, were caused by disease. The next major cause was injuries from traffic and machinery. The most common cause of death in "pure breed" kittens was associated with

Age (y)		Missing	Died	Killed on road	Given away	Other	Total
< 1		2	2		10		14
1 < 2	♂♂	1	2				3
	♀♀	3					3
> 2	♂♂	3	1	2			6
	♀♀	1	4	2	1	1*	9
Total		10	9	4	11	1	35

Table 7.8 Emigration and mortality data of cats at the Cornish farm. *Abandoned at previous farm.

delivery and the second most common was disease, mainly infections of the respiratory tract (Peltz 1976).

Hamilton, Hamilton and Mestler (1969) give a breakdown of the causes of death in house cats brought to a veterinary clinic. They do not state the cause of injuries but are specific about the diseases. Injury was a more common cause of death in whole males than in neutered males but whole males were more likely to die from urolithiasis than neutered males, who were more likely to die from cancer; these were the two most common diseases in males. Whole females were more likely to die from pyometra (the most common disease in females) than neutered females. Comparing whole males and whole females, death by injury was equally likely but death from infection was significantly more common in males due to urolithiasis. However, excluding sex-specific diseases, both sexes were equally likely to die, although whole females were significantly more likely to die from cancer. Comparing neutered males and neutered females, death by injury was equally likely but death from infection was more likely in males due to urolithiasis; but after excluding sex-specific diseases the difference was not significant. These results are based on house cats, which have a different dietary regime from non-house cats, and many had been vaccinated and may have received veterinary treatment so extrapolation to non-house cats should be with care.

Risk of neutering

Table 7.9 shows the risk of neutering in 313 cats of known status. The number of whole to neutered cats in each category was highly significantly different; farm cats tended to remain

	Farm				House			
	Males		Females		Males		Females	
	W	N	W	N	W	N	W	N
N	40	12	77	9	21	68	20	66
Chi^2	14.019		52.198		23.775		23.546	
%	76.9	23.1	89.5	10.5	23.6	76.4	23.3	76.7

Table 7.9 Risk of neutering shown by 313 cats of known status: the number of whole (W) to neutered (N) cats, chi^2 value and proportion.

	<10		10 < 50		50<100		100 < 700		Total	
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
N	19	17	22	15	8	3	7	5	56	40
Cum %	37.5		76.0		87.5		100.0			

Table 7.10 Distances (km) from which 96 cats were imported into the census area, showing the cumulative percentage of cats with distance.

	Farm				House					Total			
	♂♂		♀♀		♂♂		♀♀			♂♂		♀♀	
	W	N	W	N	W	N	W	N		W	N	W	N
N	6	4	7	0	12	34	1	32	N	18	38	8	32
%	6.2	4.2	7.3	0.0	12.5	35.4	1.0	33.3	%	18.7	39.6	8.3	33.3

Table 7.11 The status of the 96 cats from Table 7.10.

whole but house cats tended to be neutered. The percentages show the lowest risk was to farm cats; females had a risk of 0.1 but males had a risk of 0.2, possibly partly because they are cheaper to neuter. Male and female house cats each had a 0.8 chance of being neutered; consequently they were about four times more likely to be neutered than farm cats.

Immigration and Gene Flow

26.0 % (96) of the population was imported into the 100 sq km censused area and Table 7.10 shows the distances from which they came. One third arrived from up to 10 km and three quarters from up to 50 km outside the censused area. A few (12.5 %) came from more than 100 km; one from Londonderry, Ireland came the furthest. There were more males than females but the difference was not significantly different (chi-squared = 2.344, $p < 0.05$, df = 1, two tailed). Most immigrants (82.2 %) were house cats (Table 7.11).

Although a quarter of the censused population was imported, Table 7.11 shows that only 26 imported cats, constituting 7 % of the censused population, were not neutered. Most of the cats which were imported and neutered probably did not breed, so not much more than 7.0 % of the population contributed extraneous genes to the population's gene pool.

Chapter 8

DISCUSSION ON METHOD AND FUTURE WORK

The discussion of results is dealt with in the preceding chapters. In this final chapter is a discussion of the method used for observing the cats and possibilities it may hold for future work.

Data were gathered by following and directly observing tame cats. Perhaps the main objection to this method is that tame cats will not act normally. This is probably not the case because any cat who objected to being followed could have disappeared from view and ended the observation. This is what the males at the Cornish farm did and I gave up trying to followthem. But the other cats could be followed, which means they did not object. In fact a cat would occassionally approach me and rub past my leg or one would purr before falling asleep if I made a rustling of straw. They accepted me, enjoyed my company and on the whole ignored me. Of prey, the rabbits were probably sometimes alerted by me but this could not be avoided. I cannot be sure of rodents but they seemed unaware of me and were still caught despite my presence.

Perhaps the single most important conclusion which can be drawn from this thesis is that free ranging domestic cats can be observed in detail at all hours of the day - provided they are tame. And herein lies the clue to observing them. Other workers have had to be content to observe sedentary cats about buildings and to rely on radio telemetry for field sightings (for instance Macdonald and Apps 1978; Dards 1979), or have admitted failure: "To follow a single cat around day and night without losing sight of it, and keep a complete record of all its movements, encounters, etc., requires at least three well-trained, physically fit and inexhaustible observers, plus a lot more equipment than we could command..." (Leyhausen 1965). However, provided cats are tame there are no such problems: they can be observed without expensive equipment; subjects can be located easily because they live in a small area; their numbers can be controlled and they are cheap to keep (just a little milk); and because their life-time is short, perhaps about 5 years for a farm cat, longitudinal studies can estimate life-time fitness. Individual cats in different habitats could be studied or separate groups within range of each other (about 200 m apart) could be set up and a plethora of data accumulated.

Tame free-ranging cats are ideal subjects for researching the behavioural ecology of free-ranging animals in topics as diverse as homing, behavioural development, sexual strategies and energy budgets. Furthermore, by the study of social carnivores, that is species ecologically similar to humans, some of the kinds of selective forces which shaped hominid societies and therefore our own may be elucidated (Schaller and Lowther 1969; Kruuk

1972; Schaller 1972). In the discussion on social behaviour (Chapter 4) it was argued that domestic cats, like lions, are social carnivores. Therefore the study of their behaviour and ecology could help us to understand our own.

Finally, an increasing number of small cat species are under pressure from human exploitation and encroachment on their habitat. Yet knowledge of their behaviour and ecology is largely anecdotal (Guggisberg 1975). Small cats are usually retiring creatures and difficult to observe. But all small cats are alike in morphology and anatomy so different species probably have similar basic ecological needs. Therefore research on easily observed free-ranging domestic cats could contribute to an understanding of the requirements of other small cats and thus to their conservation. Better still, if domestic cats can be observed so easily, why not observe tame individuals of other small (and large) cat species? Setting up tame individuals in a suitable area may take time but once done would generate more data in a week than in the entire observation history of the species.

Specific Names Mentioned in the Text

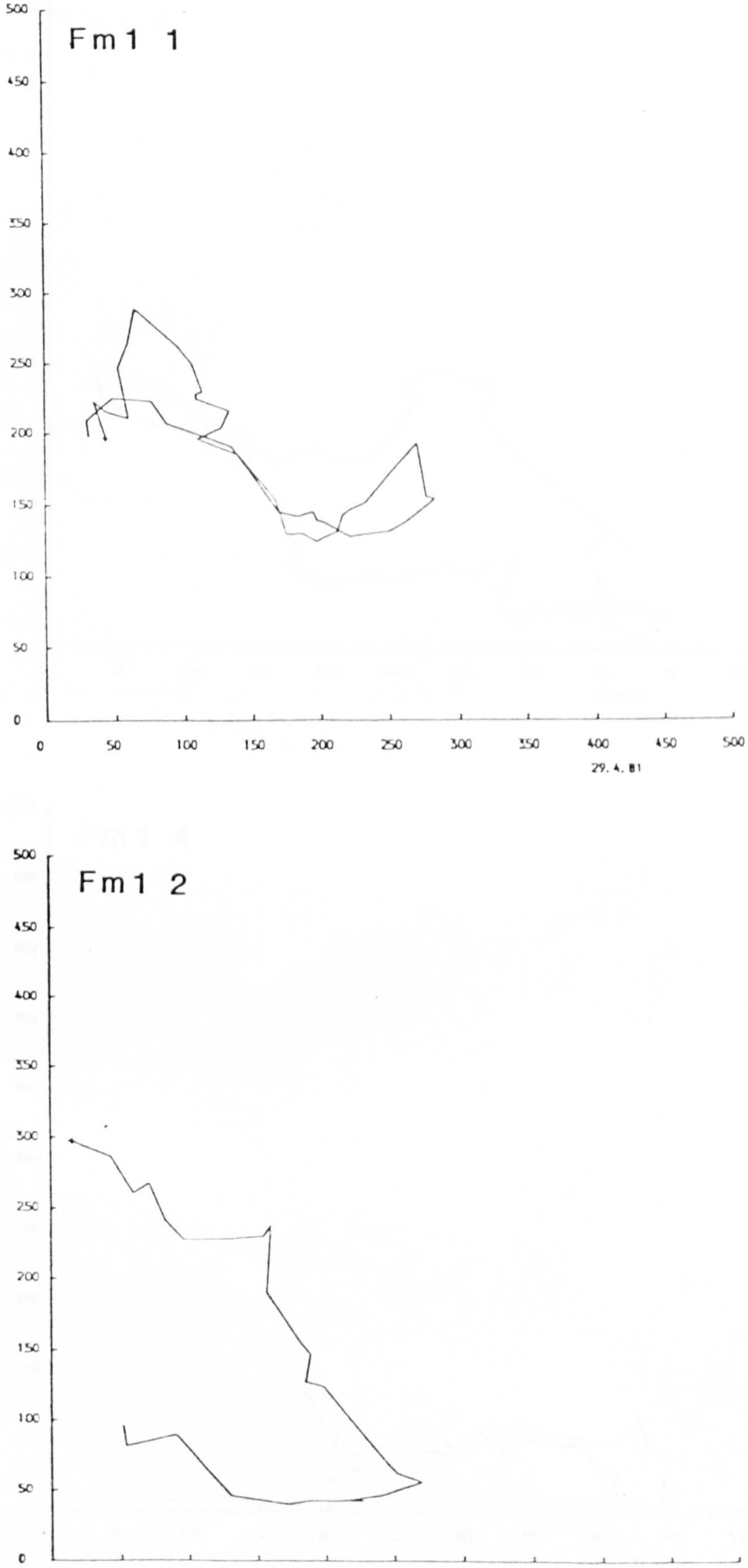
Bank vole	*Clethrionomys glareolus*
Blackbird	*Turdus merula*
Bobcat	*Lynx rufus*
Brown hyaena	*Hyaena brunnea*
Brown rat	*Rattus norwegicus*
Bumblebee	*Bombus flavifrons*
Bumblebee	*Bombus appositus*
Caddisfly	*Dicosmoecus gilvipes*
Cheetah	*Acinonyx jubatus*
Clouded leopard	*Neofelis nebulosa*
Common shrew	*Sorex araneus*
Domestic cat	*Felis catus*
Earthworm	*Lumbricus terrestris*
Field vole	*Microtus agrestis*
Fishing cat	*Prionailurus viverrinus*
Golden cat	*Profelis temmincki*
Golden jackal	*Canis aureus*

Goldfish	*Carassius auratus*
Hanuman langur	*Presytis entellus*
Harvest mouse	*Micromys minutus*
Honeybee	*Apis mellifera ligostica*
House mouse	*Mus musculus*
Hummingbird	*Selasphorus platycer*
Hummingbird	*Selasphorus rufus*
Indian mongoose	*Herpestes auropunctatus*
Leopard	*Panthera pardus*
Leopard cat	*Prionailurus bengalensis*
Lion	*Panthera leo*
Lynx	*Lynx lynx*
Mongolian girbil	*Meriones unguiculatus*
Pygmy shrew	*Sorex minutus*
Puma	*Felis concolor*
Rabbit	*Oryctolagus cuniculus*
Red fox	*Vulpes fulva*
Red fox	*Vulpes vulpes*
Serval	*Leptailurus serval*

Snowshow hare	*Lepus americanus*
Song thrush	*Turdus philomelos*
Spotted hyaena	*Crocuta crocuta*
Tiger	*Panthera tigris*
Wildcat	*Felis silvestris*
Woodmouse	*Apodemus sylvaticus*
Wren	*Troglodytes troglodytes*

***** APPENDIX *****

Fig. A1 Nine search paths of Fm1 and ten search paths of Hm1 with the date of each path. A cross marks the start.



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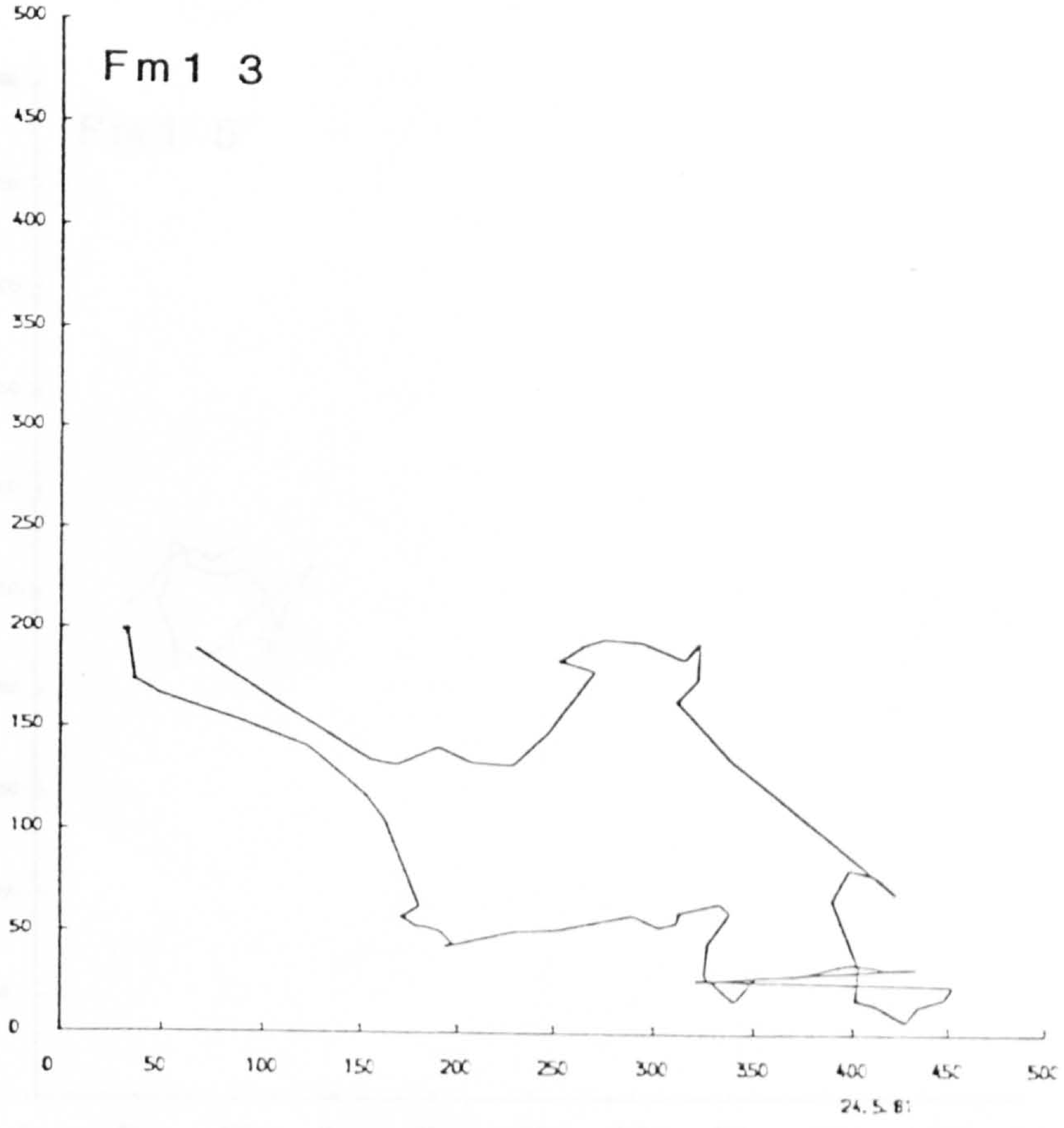


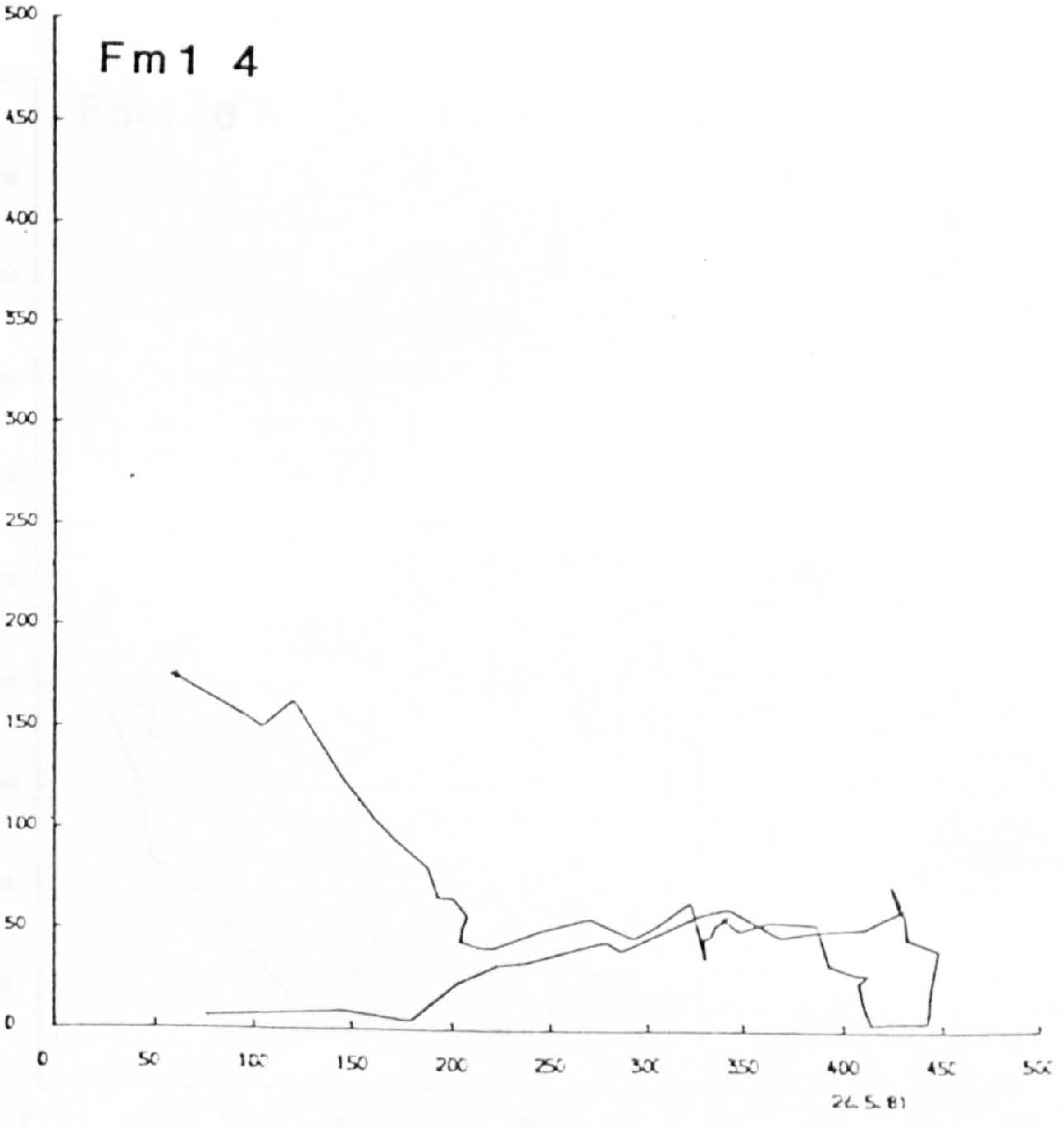
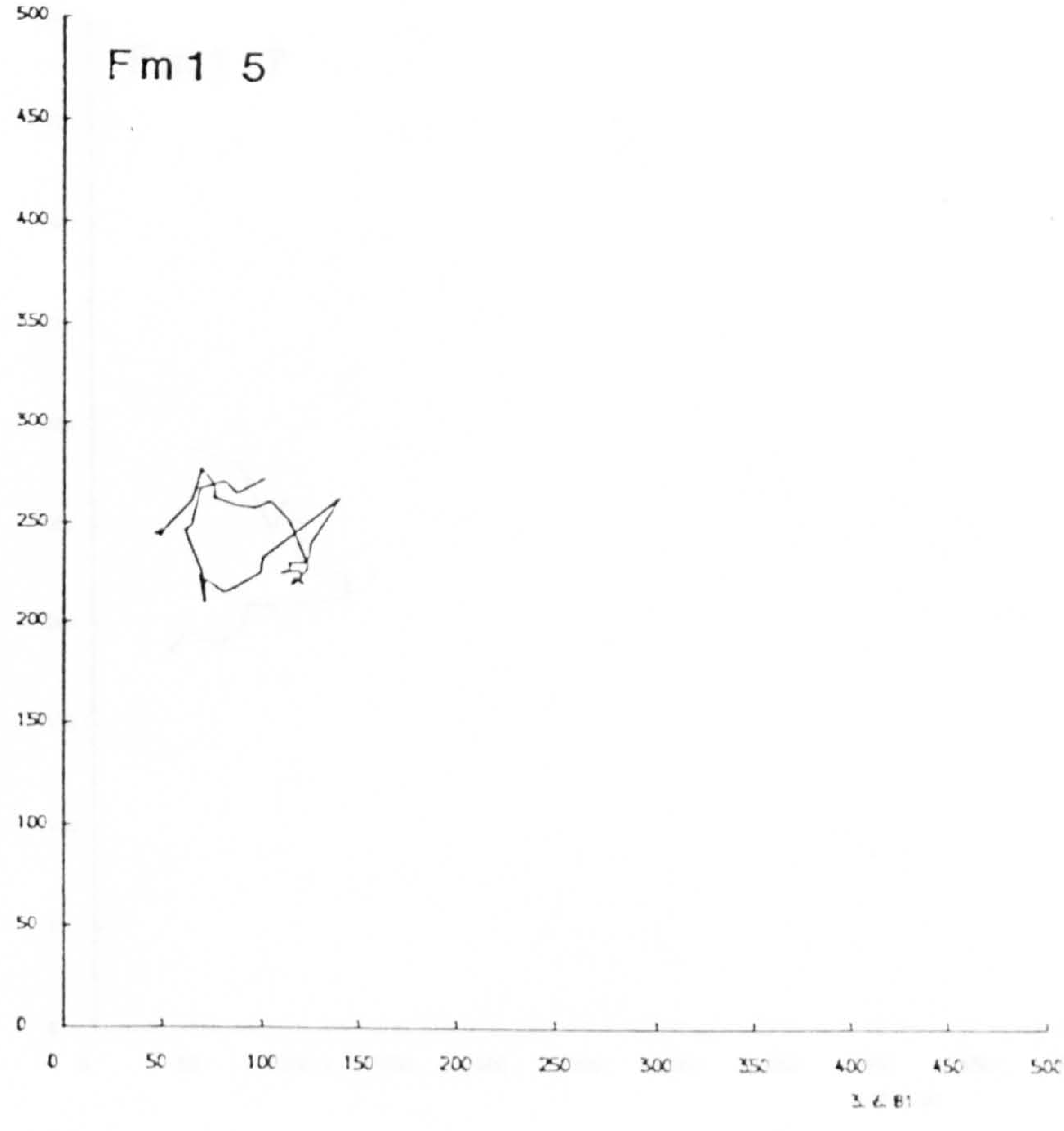
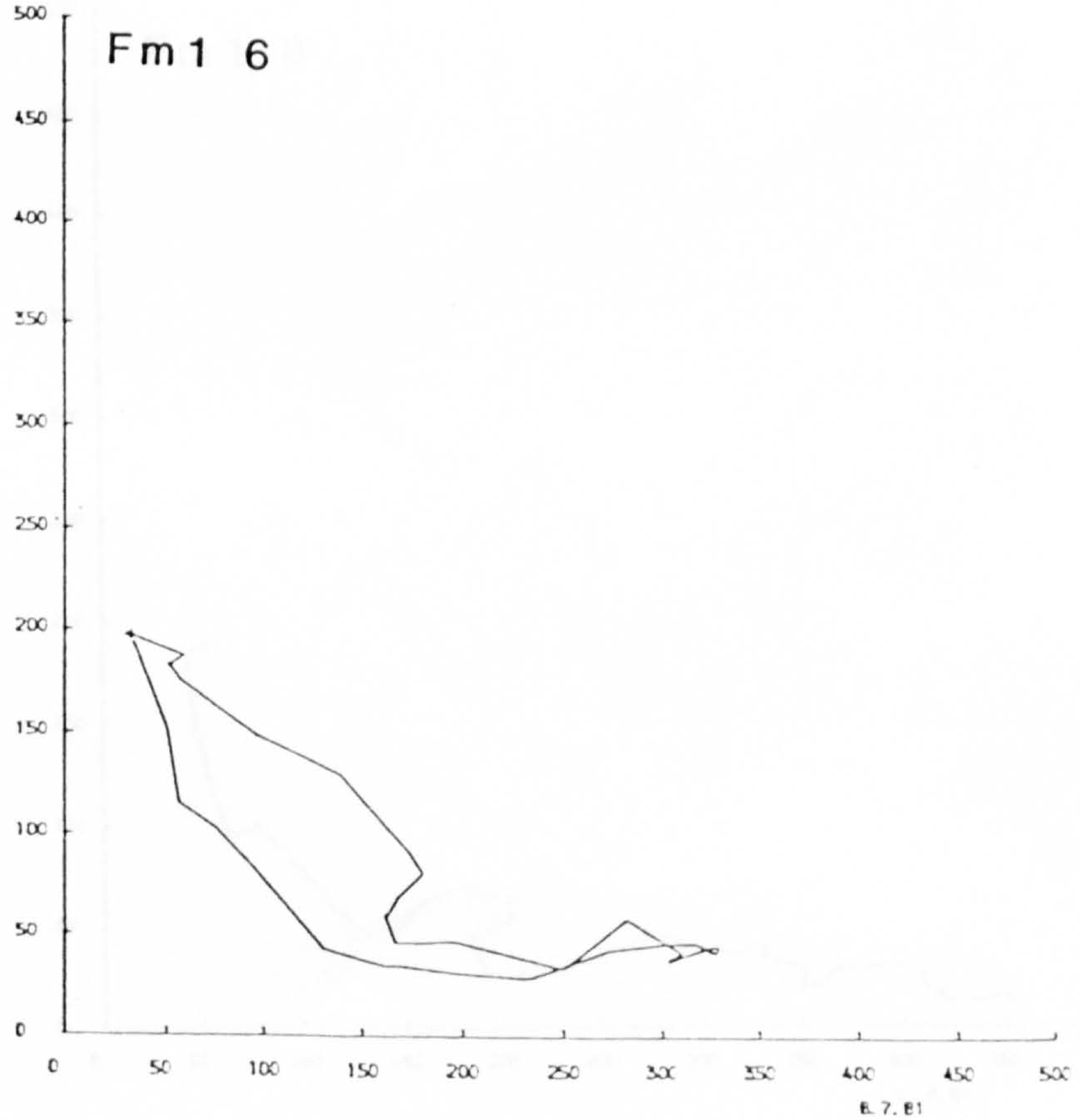


Fig. A1 continued





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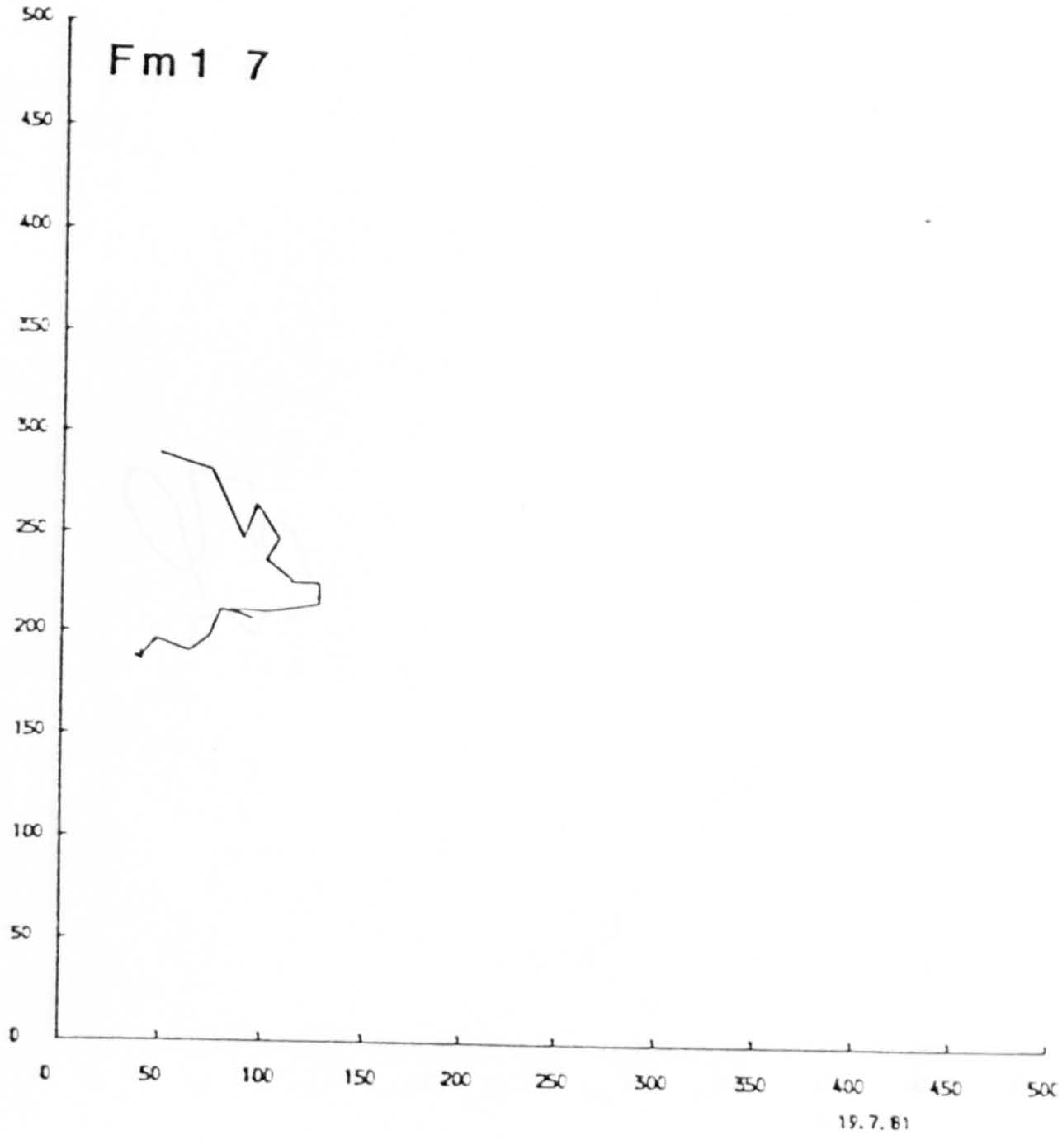


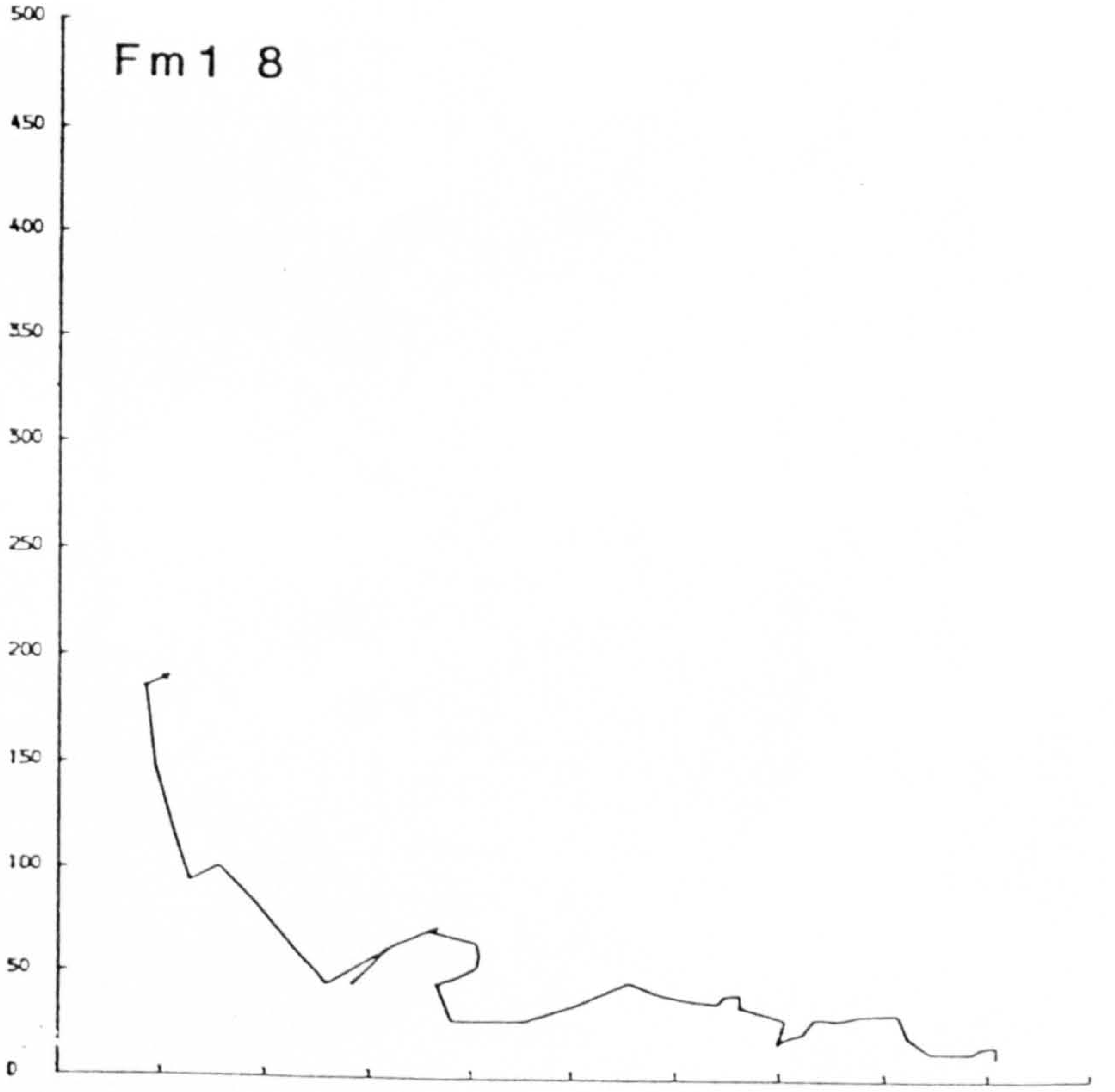
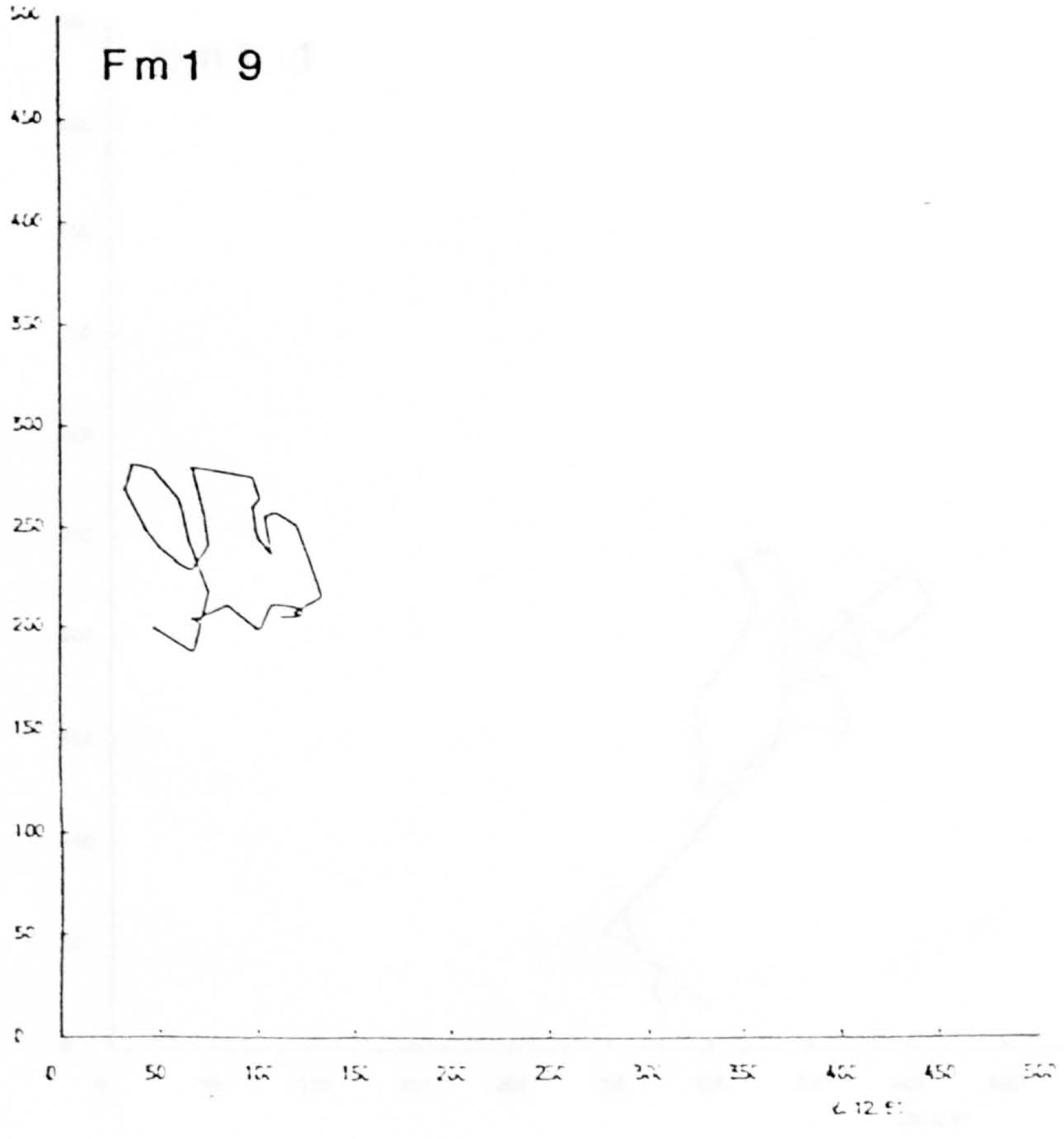


Fig. A1 continued



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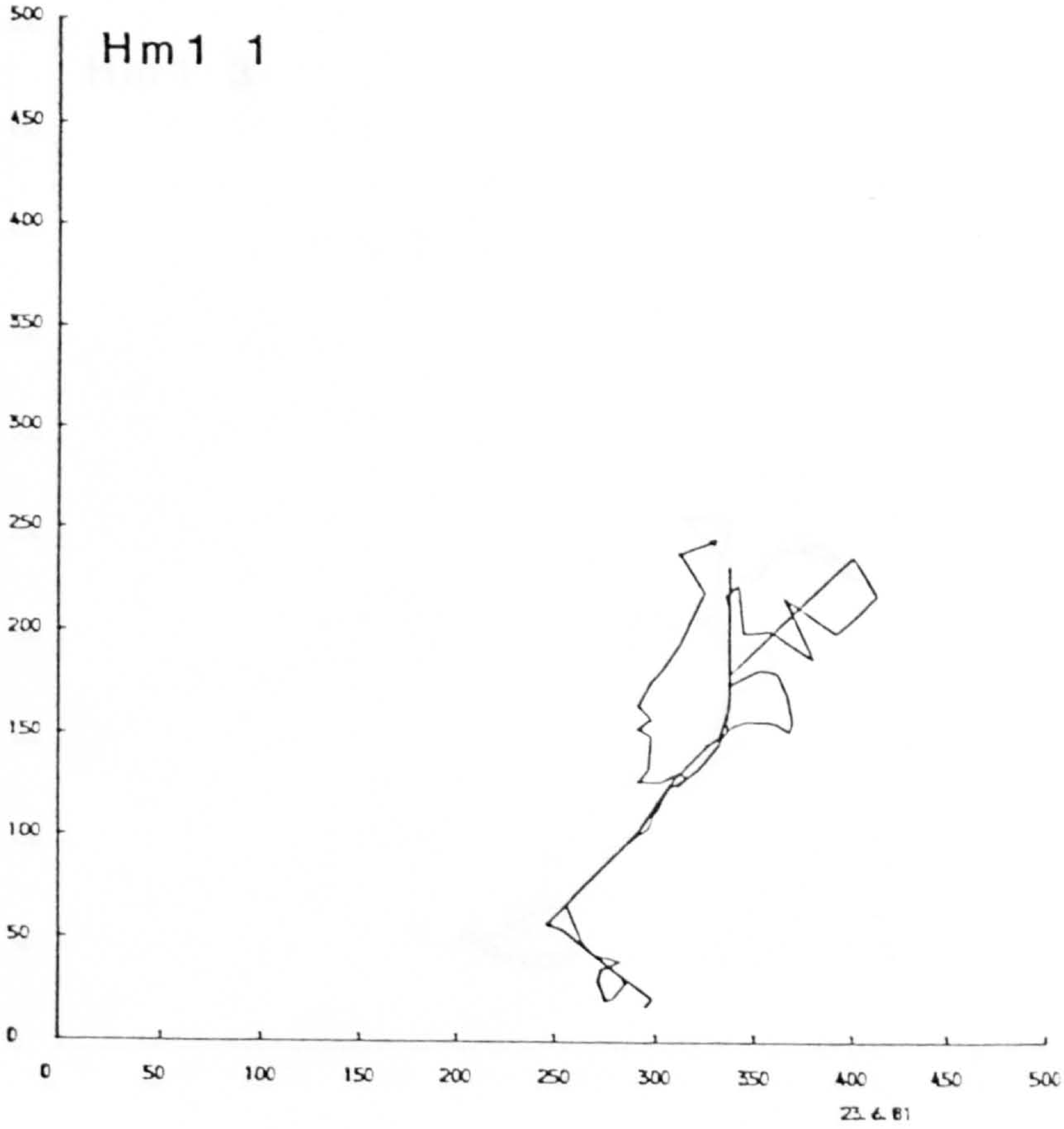

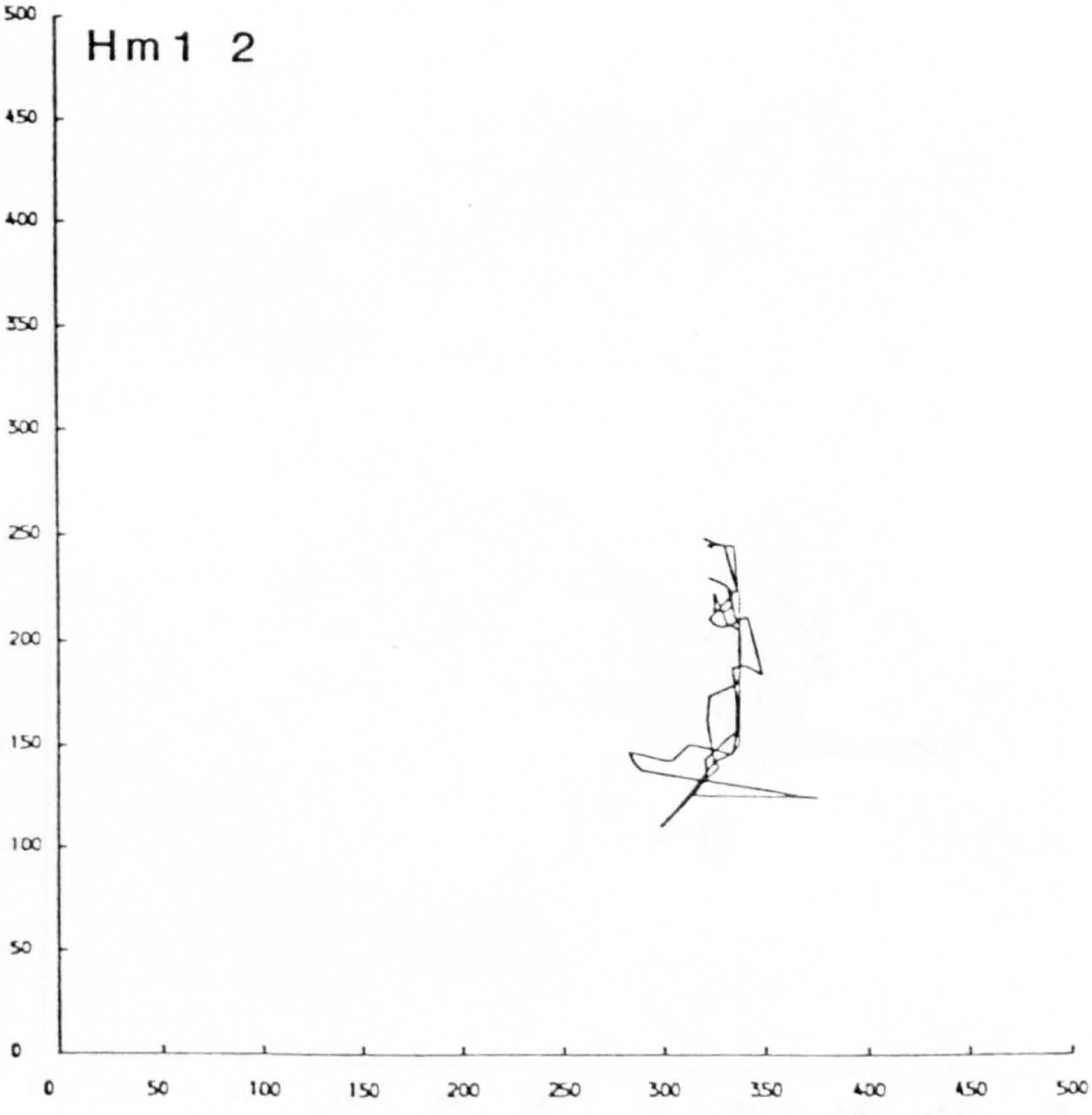

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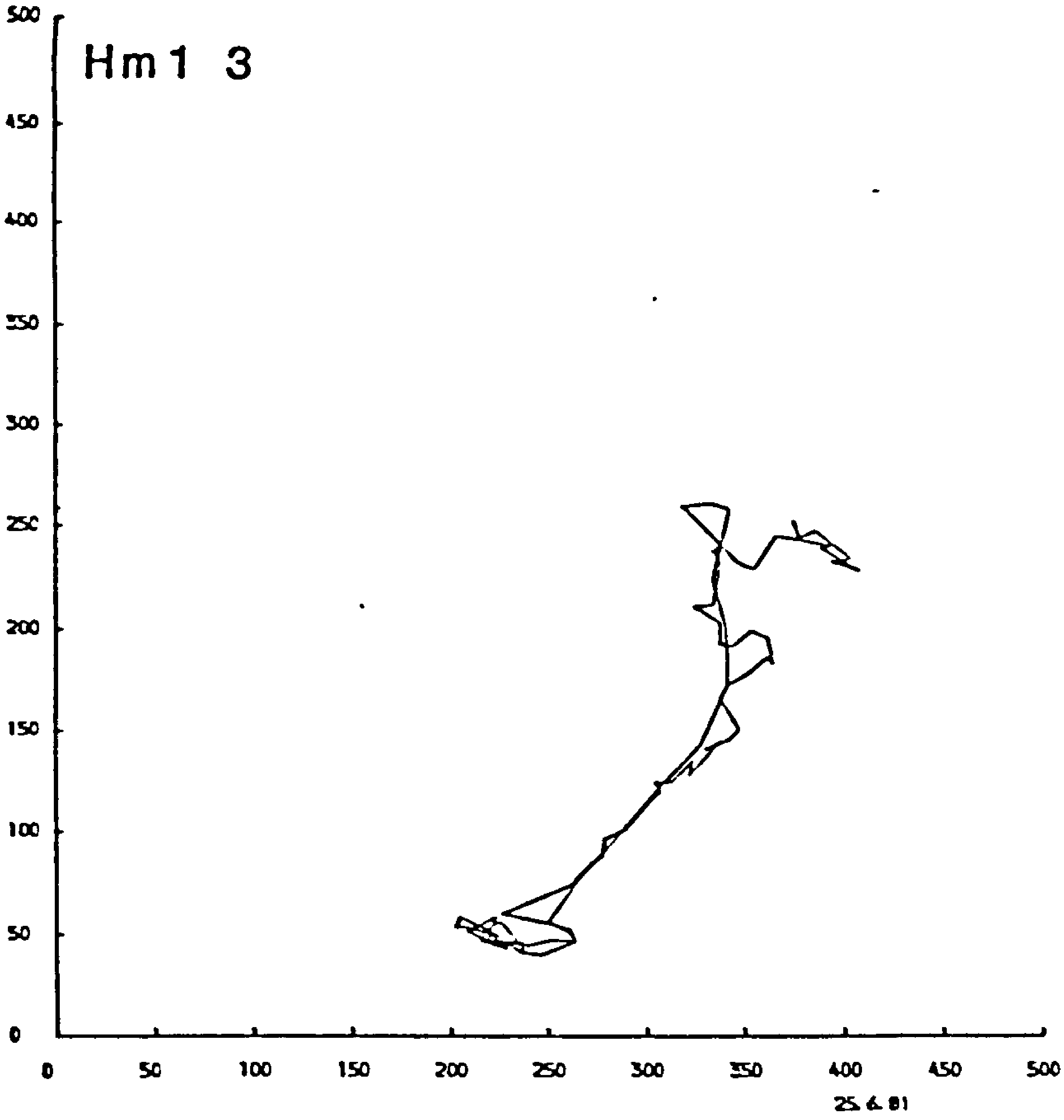

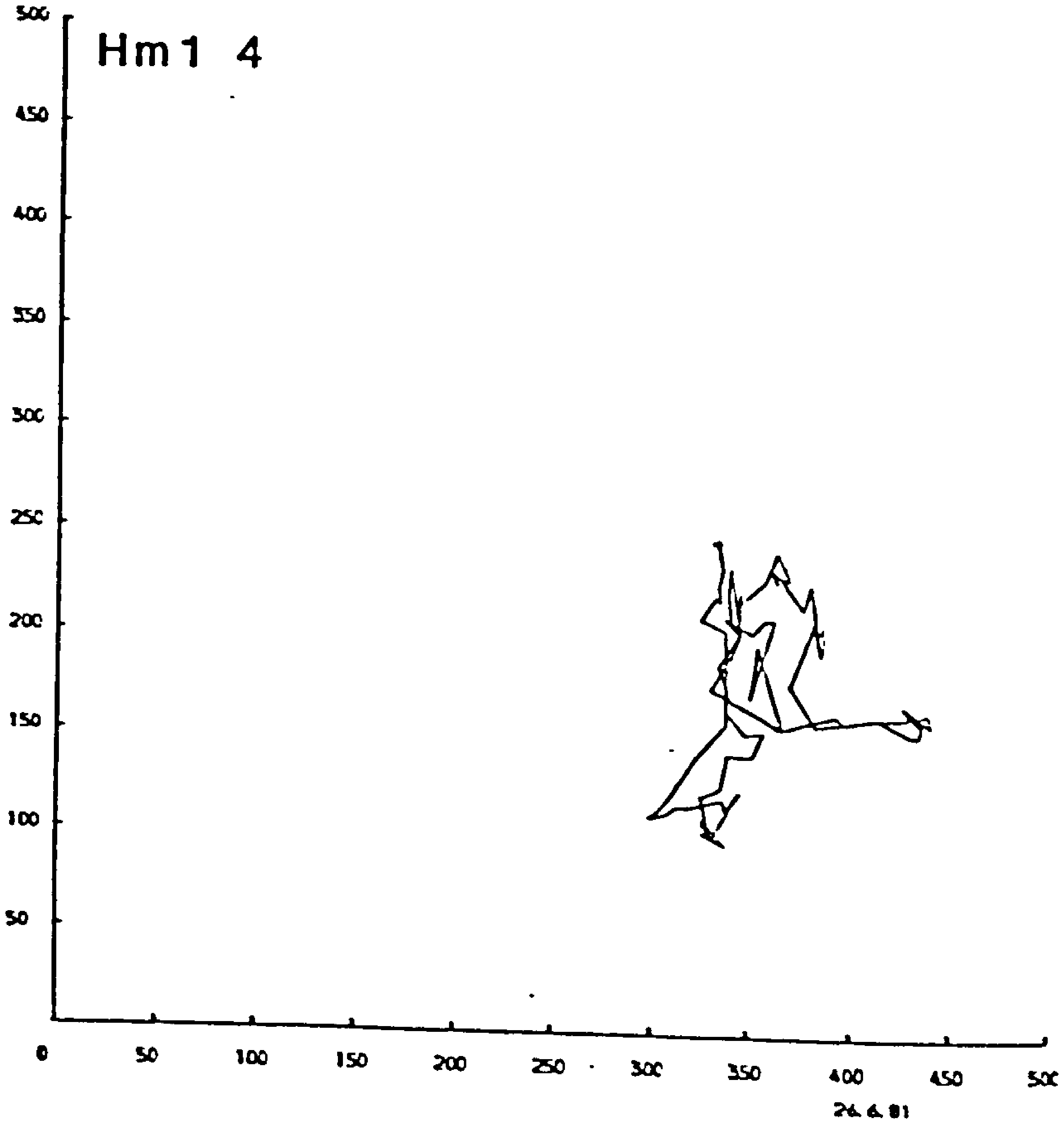

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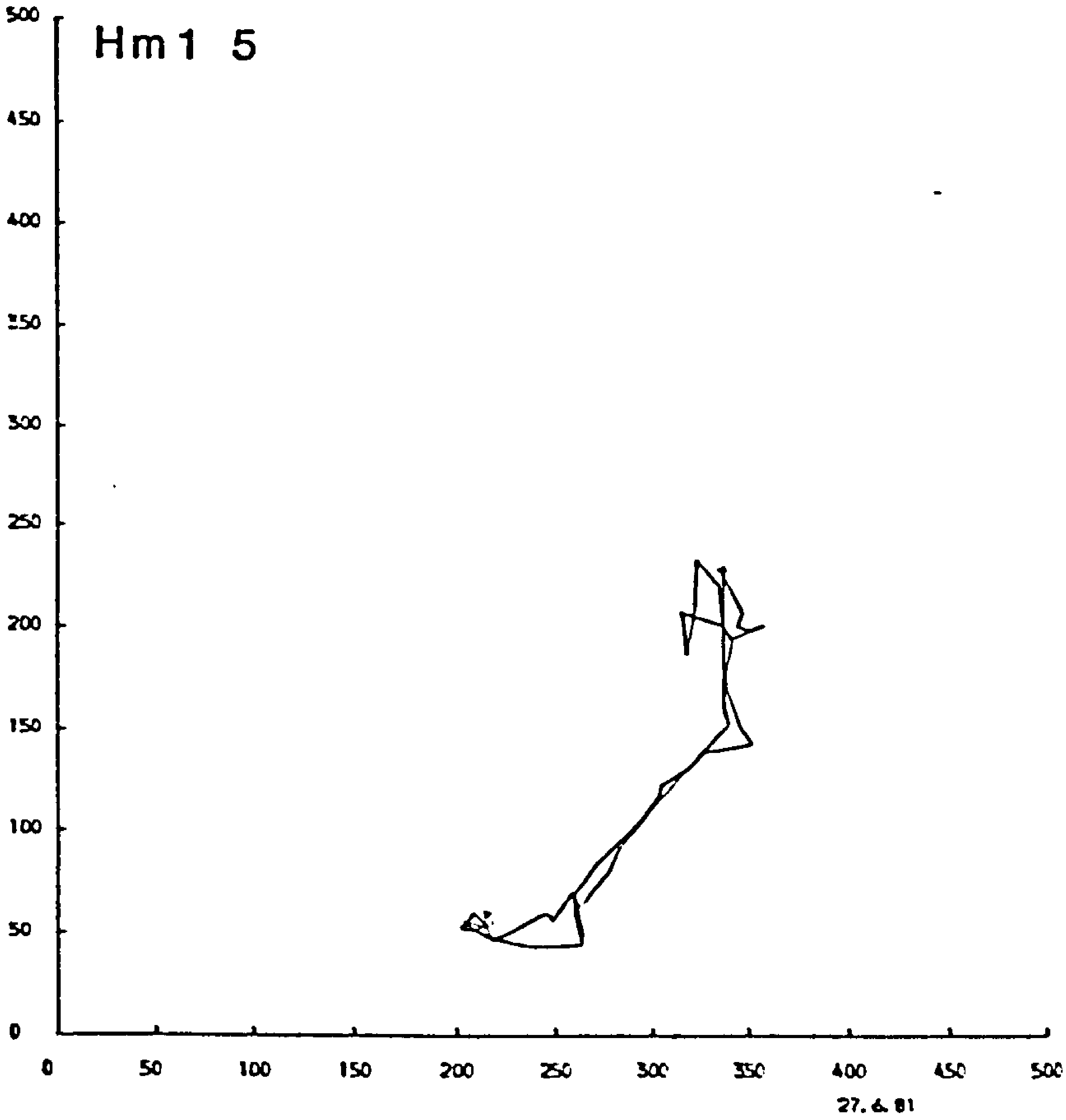

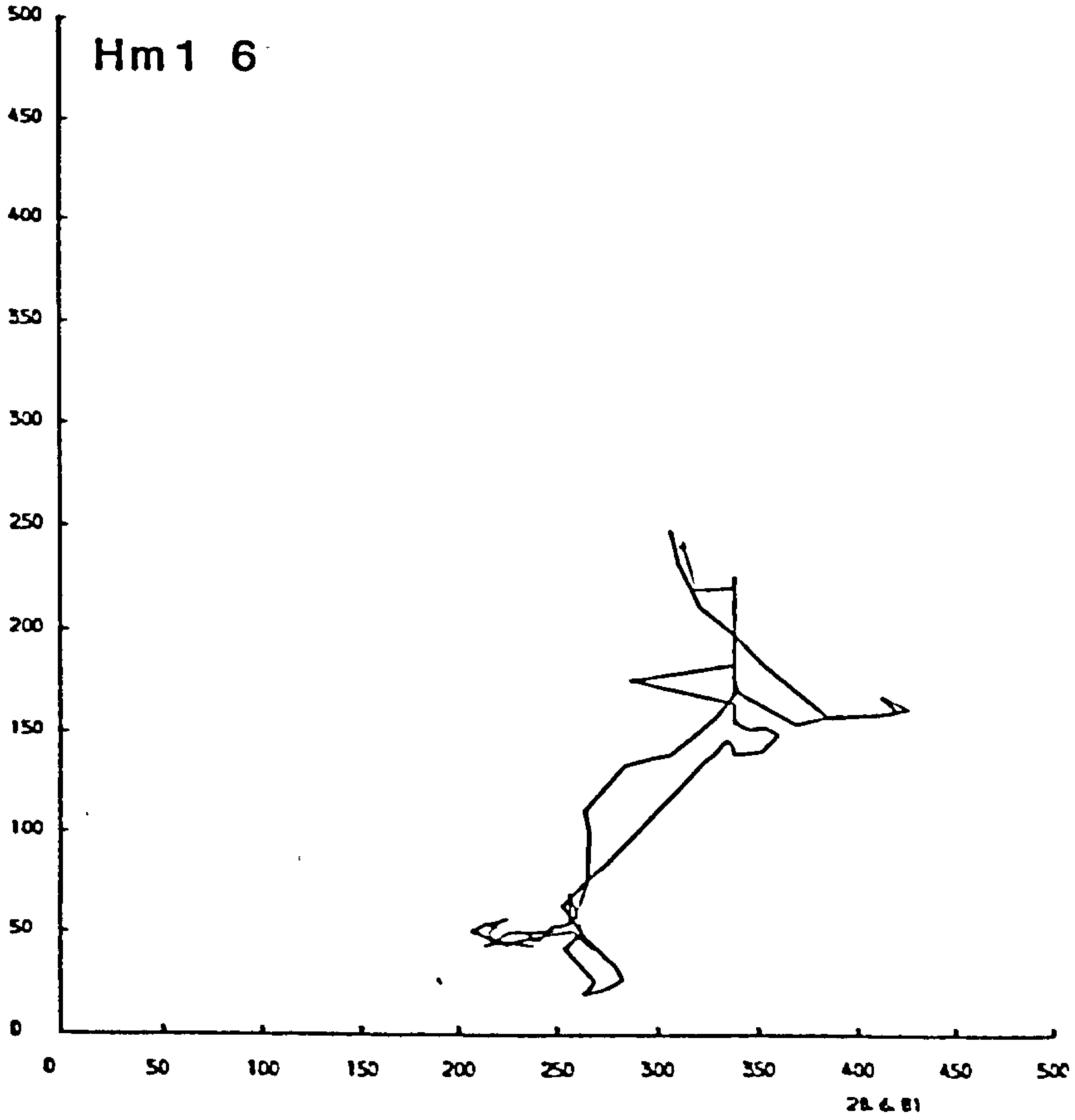

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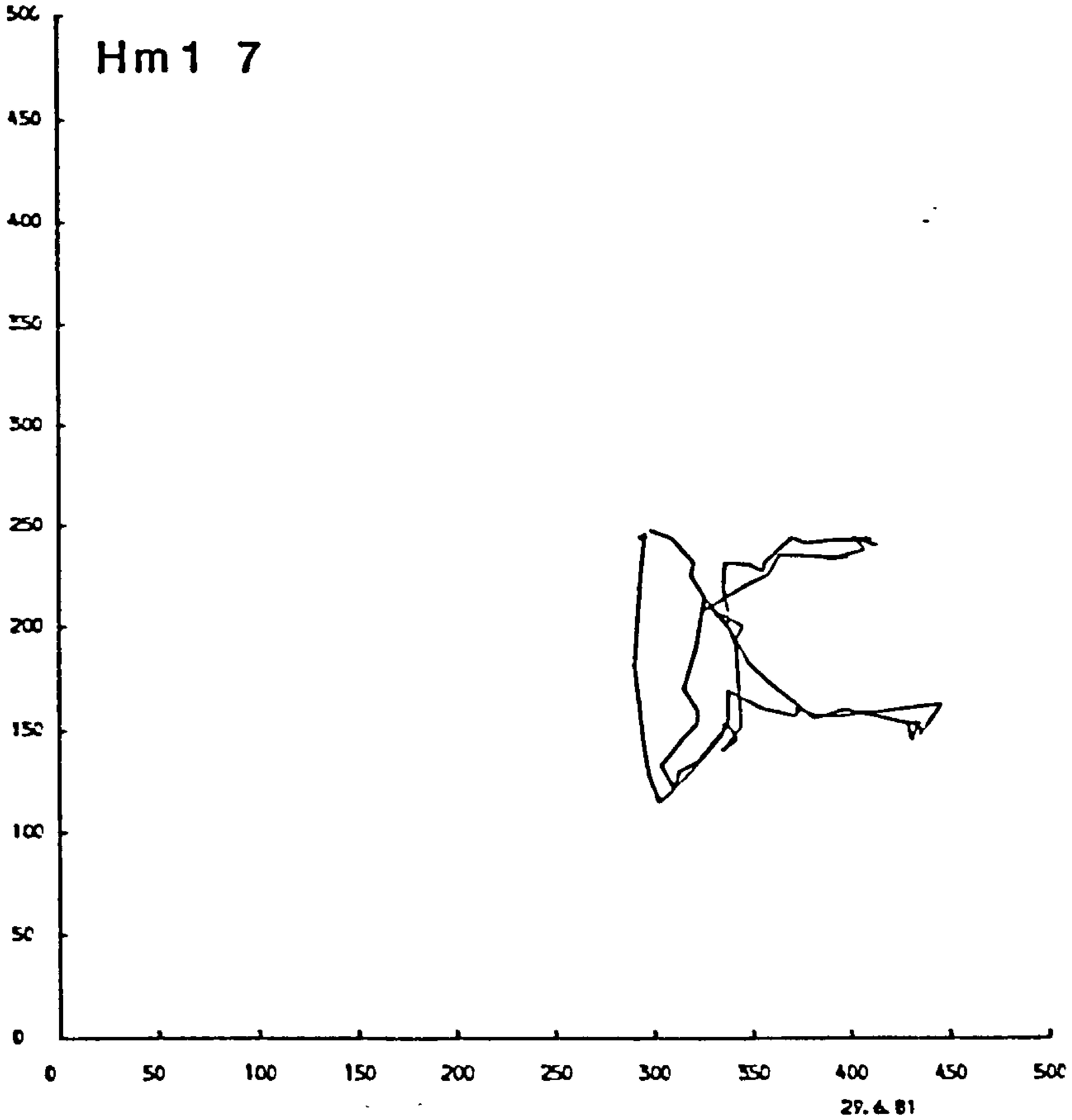

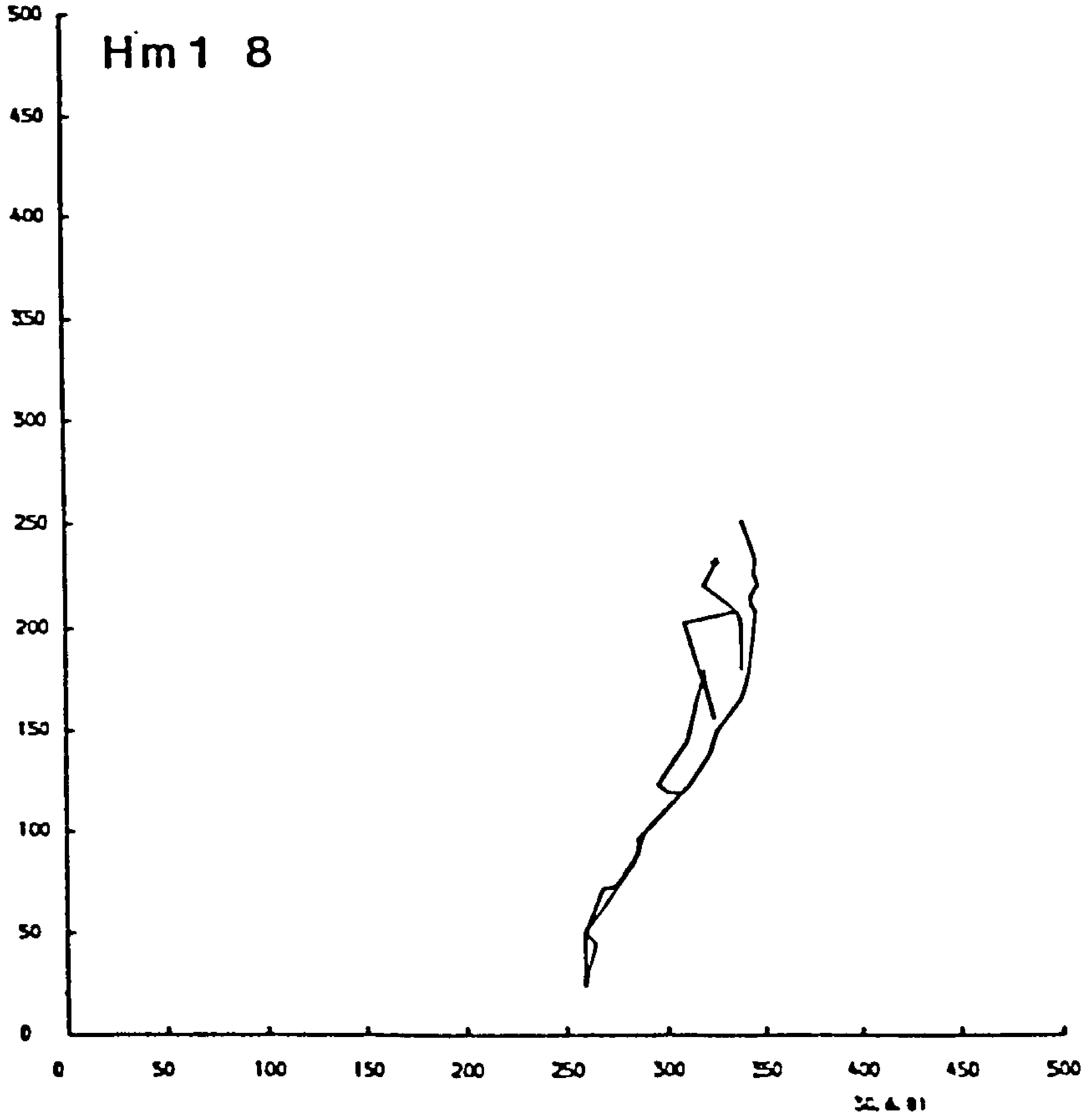

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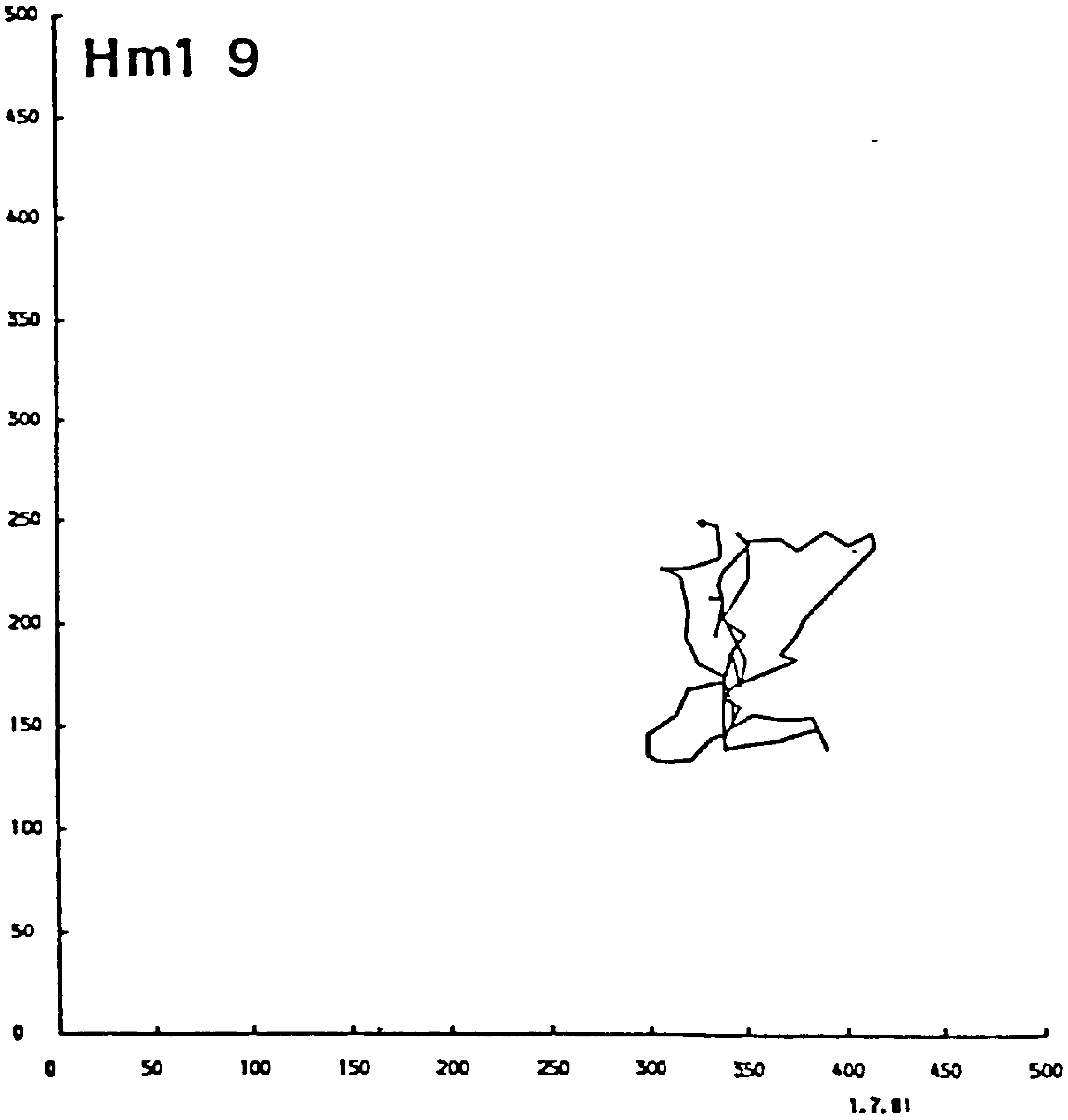

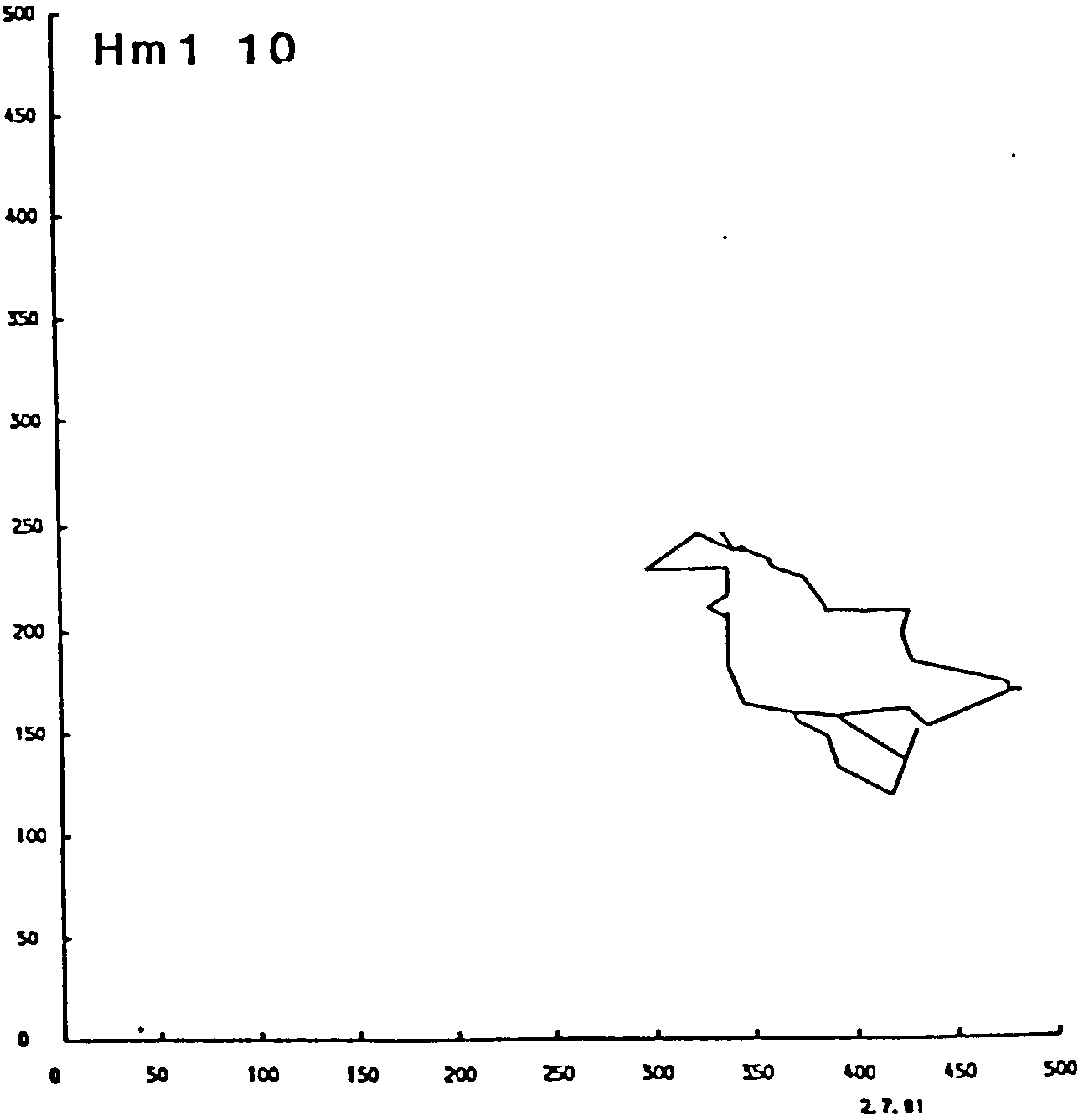

search path	Fm1	Hm1	Fm2
1	0.030	0.016	1.671
2	0.072	0.418	-
3	0.471	1.110	-
4	2.950	1.923	-
5	1.403	4.681*	-
6	0.108	0.426	-
7	1.862	0.327	-
8	0.200	1.007	-
9	0.072	3.414	-
10	-	0.328	-

Table A1 Chi^2 values of move-length sequence for search paths of three male cats. Critical value 3.840, $p < 0.05$

search path	Fm1	Hm1	Fm2
1	2.540	0.000	0.011
2	1.627	0.155	-
3	2.397	0.044	-
4	4.741*	1.340	-
5	0.021	1.521	-
6	0.200	0.095	-
7	2.891	0.313	-
8	0.247	0.000	-
9	0.955	6.107*	-
10	-	0.446	-

Table A2 Chi^2 values of turn-angle sequence for search paths of three male cats. Critical value 3.840, $p < 0.05$

search path	Fm1	Hm1	Fm2
1	0.938	0.917	0.034
2	0.460	0.246	-
3	0.320	1.157	-
4	0.017	0.430	-
5	1.392	0.058	-
6	0.000	1.191	-
7	0.033	0.019	-
8	0.062	2.261	-
9	0.040	0.026	-
10	-	0.065	-

Table A3 Chi^2 values of move-length sequence for search paths of three male cats. Critical value 3.840, $p < 0.05$

search path	Fm1	Hm1	Fm2
1	0.156	0.917	1.671
2	0.000	0.246	-
3	0.951	1.157	-
4	0.000	0.430	-
5	0.124	0.058	-
6	0.112	1.191	-
7	0.009	0.019	-
8	0.000	2.261	-
9	0.000	0.026	-
10	-	0.065	-

Table A4 Chi^2 values of turn-angle vs move-length sequence for the search paths of three male cats. Critical value 3.840, $p < 0.05$

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