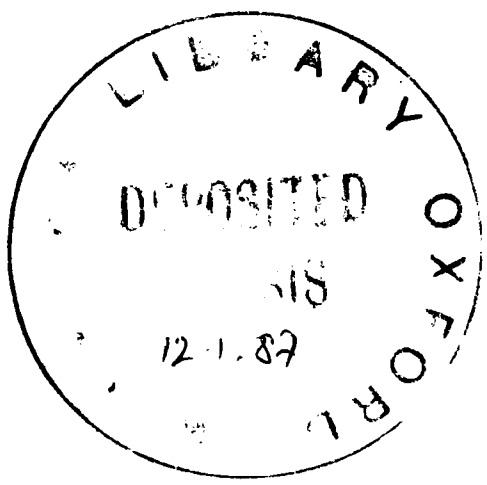
Patterns of resource distribution and exploitation by the red fox (*Vulpes vulpes*) and the Eurasian badger (*Meles meles*): a comparative study.

Heribert Hofer

A thesis submitted for the Degree of Doctor of Philosophy at the University of Oxford

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PATTERNS OF RESOURCE DISPERSION AND EXPLOITATION BY THE RED FOX (Vulpes vulpes) AND THE EURASIAN BADGER (Meles meles): A COMPARATIVE STUDY.

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Thirteen badgers and 20 foxes were radio-tracked in the Wytham Estate, Oxfordshire, between 1981 and 1983. Thirteen badger and 10 fox groups were identified from radio-tracking and bait marking. Badger groups (mean size 1982: 4.45, 1983: 5.82) occupied contiguous territories (size: 22-75 ha) with boundaries marked by latrines. Seasonal variation in marking intensity and choice of marking sites presumably were responses to changing intrusion pressure. Fox groups (mean size: 2.6) occupied stable territories (size: 22-104 ha) with little overlap. Faeces deposition by foxes facilitated territory marking.

Earthworms(Lumbricus terrestris) dominated the diet of badgers (63 % estimated dry weight EDW, faeces), followed by cereals, fruits and other invertebrates. Diet was highly variable between groups and seasons. For foxes, lagomorphs (20 % EDW) and earthworms (33 % EDW) were the most important prey, followed by scavenge and fruits. Variation in diet between groups and seasons was marked in lagomorphs but not earthworms.

Multivariate analyses of habitat parameters revealed a low-dimensional 'resource space' that could be divided into conventional habitat categories. Censuses of prey species indicated that resource presence varied consistently between habitat categories.

Key habitats occurred at fairly constant proportions in territories of both species; their dispersion partly determined the configuration of territory boundaries. The proportions of specific habitats per territory were correlated with the proportions of certain prey items in diets.

Space use by individuals was analysed by spatial autocorrelation methods. Variation in space use by foxes was attributed to variation in resource dispersion. In contrast, individual badgers were similar in their use of space. Here, small-scale heterogeneity in intensity of use may reflect local earthworm availability. In one studied fox group, males and females differed in range use. Individuals in one studied badger group coordinated their use of space probably to minimize foraging interference.

It is suggested that group living in Wytham badgers is a response to defending resources, and a model is proposed to explain how the spatial and social organisation of male and female badgers relate to the characteristics of the resources they require.

To Marion

If you want to get the plain truth

Be not concerned with right and wrong

The conflict between right and wrong

Is the sickness of the mind.

Zen Master Seng-Ts'an

[Raymond M. Smullyan: The tao is silent.

Harper & Row, New York 1977.]

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1. Introduction.

Every animal faces four major tasks:

- avoid being killed or dying
- find something to eat
- find a place to live
- reproduce

The last three tasks deal with resources, ie. the acquisition and exploitation of food, space, and mates. Ever since Crook's (1964) classical study of weaver birds (Ploceinae), ethologists have come to appreciate that three characteristics of resources,

- their occurrence in time and space,
- the predictability of their occurrence,
- their quality,

have a major influence on the way animals organise their lives. Broad interspecific comparisons within major taxa have indicated important trends in the relationship between the social organisation of a species and its feeding ecology, morphological parameters (e.g. body size) and the habitats occupied by that species (Jarman 1974 for antelopes, Clutton-Brock & Harvey 1977 for primates and Bekoff et al 1984 for carnivores). Although the methodology used in these interspecific comparisons are not devoid of criticism (Krebs & Davies 1981, Harvey & Mace 1982), they have been a valuable source of stimulation for many behavioural ecology studies.

Within the carnivores, recent studies have revealed an impressive diversity of

- foraging strategies, ranging from solitary hunting (red fox, Vulpes vulpes, Macdonald 1977a) to highly organised cooperative ventures (e.g. in wild dogs, Lycaon pictus, Frame et al 1979)
- spatial and social systems, ranging from solitary individuals (e.g. bears, Ursus arctos, Craighead 1979) to groups of 80 animals on a territory (spotted hyenas, Crocuta crocuta, Kruuk 1972),
- mating systems, ranging from strict monogamy (golden jackals, Canis aureus, Moehlman 1983), to polygynandry (lions, Panthera leo, Bertram 1975).

A focus of attention has been the relationship between social organisation, in particular the occurrence of group living, foraging strategies, and the dispersion of resources in space and time (Kruuk 1975, Lamprecht 1981, Macdonald 1983a). To date, three classes of benefits derived from group living have been identified for carnivores:

- cooperation in hunting: extension of the dietary spectrum or increase in the efficiency of exploiting resources (e.g. wolf, Canis lupus, Mech 1970)
- cooperation in anti-predator defense: reduction in required vigilance and chance of capture, improvement of foraging rates and chances of escape from a predator (e.g. banded mongoose, Rood 1974)
- cooperation in reproduction: improvement of survival

of cubs due to helpers (e.g. brown hyena, Hyaena brunnea, Owens & Owens 1984)

These benefits explain the occurrence of group living in some, but not all carnivore species. Several species, amongst them the red fox, Vulpes vulpes, the Eurasian badger, Meles meles, and the giant otter, Pteronura brasiliensis, do not fit these explanations, yet have been observed to live in groups (Macdonald 1977a, Kruuk 1978a, Duplaix 1980). Here other explanations are required. Bradbury & Vehrencamp (1976) and Carr & Macdonald (in press) are amongst those who have developed a model, called the Resource Dispersion Hypothesis (RDH), by which specific patterns of the dispersion of resources in time and space may permit the formation of groups, ie. the presence of additional individuals in the range of primary occupants (e.g. a pair), with little or no cost to the primary occupant. Red foxes in the city of Oxford (Macdonald 1981a, Newdick 1983) and badgers in Britain (Kruuk & Parish 1982) have been suggested as candidates for RDH.

Despite the importance of resources, few studies exist that have monitored both the social and spatial organisation of a carnivore population and the dispersion of resources (examples are Hersteinsson & Macdonald 1982 for arctic foxes, Alopex lagopus; Mills 1982 for brown hyaenas, Hyaena brunnea; Doncaster 1985 for urban red foxes). However, this is an essential prerequisite if we want to get beyond broad generalisations, since inter-population comparisons indicate a tremendous variation in the spatial and social organisation within the same species. In red foxes, for instance, range size may vary between 10 hectares (Macdonald, Ball & Hough 1980) in an urban population and 2000 ha in rural populations in Ontario, Canada (Voigt & Macdonald 1985).

This study is an exercise in explaining the spatial and social

organisation of carnivores by the dispersion and availability of resources. Two species, the red fox and the Eurasian badger, were selected as study animals. They were chosen because

- both evade the usual explanations for group living in carnivores,
- previous studies indicate that resources play a vital part in the organisation of their lives,
- both are medium-sized and live in relatively small groups (foxes up to 6, Macdonald 1977a; badgers up to 15 individuals, results of the Annual Badger Census in Wytham, Animal Ecology Research Group, Oxford, unpubl),
- both entertain ranges of a size suitable for a detailed investigation of resource presence,
- both are medium-sized solitary foragers exploiting roughly the same range of prey items.

This thesis is divided into three parts. The first part, Chapters 2 and 3, is dedicated to a detailed description of the characteristics of resources. Here I am concerned with food, and discuss in detail the patterns of dispersion and abundance of different prey items. I considered prey items that were either identified as important in earlier studies of foxes and badgers, or turned up in the analysis of scats of the Wytham populations of both species (see Chapter 4). In the introduction to Chapter 3, the selection of investigated prey items is discussed in more detail. Besides absolute patterns of dispersion and occurrence I was interested in the distribution of prey in relationship to habitats. In Chapter 2, I discuss in detail the definition and relationship between habitats and resources. Here it suffices to mention briefly the reasons that prompted me to include

habitats in an investigation of the relationship between resources and the social and spatial organisation of the predator species:

- previous studies have compared the social organisation of foxes and badgers in relation to habitat types. If different prey show habitat preferences, then habitats may be used as indicators of resource presence. Provided that preferences are consistent between study sites, results of previous studies may be compared with the present study.
- discrete habitat types are a convenient means to structure the range of an individual or a group for large-scale purposes (e.g. in connection with investigations on bovine tuberculosis in badgers or rabies in foxes).
- even within such a small area as my study area, it proved impossible to record quantitatively resource presence over the entire area. Hence, resource presence was investigated in relation to habitat types at specific sampling sites and the results generalized.

The multivariate analyses of records of habitat variables in Chapter 2 show that a carefully designed system of discrete habitat types is sufficient to satisfactorily describe the general (vegetation and prey) structure of the study area as seen from the point of view of foxes and badgers. Hence, the system of discrete habitat types, as recorded in a computerized habitat map, was the reference system with which resource use was compared.

In the second part, Chapters 4 to 6, resource use is described and compared with resource presence (as usually indicated by the habitat map). First, the diet of foxes and badgers in Wytham is analysed in Chapter 4.

Changes over seasons, variation between different group ranges and differences between foxes and badgers are described and discussed. In Chapter 5, I first describe the spatial and social organisation of both species in Wytham and discuss some of their properties, e.g. long-term stability of group ranges and the way ranges are maintained by scent-marking. The spatial system of the predators is then projected onto the habitat map and the relationship between the two levels are discussed. Here my main purpose is to discover the rules along which the considerable intra-population variation in resource use and presence is organised. Chapter 6 complements this discussion by considering the processes that lead from resource presence to resource use: the movements and space utilization by individual foxes and badgers. After a description of the patterns of space utilization, two major aspects are discussed: (i) to what extent can space utilization be explained by resource presence, and (ii) how do members of a group structure their use of space and resources in relation to other members of the group ?

In the third part, Chapter 7, I use the results of the preceding parts to discuss the life history and the observed inter-population variation in the social organisation of badgers. Energetic costs of pregnancy and lactation are shown to be considerable, since females provide most of the parental investment. This places some pressure on the correct timing of major reproductive events in relation to the availability and dispersion of resources. An optimal exploitation of economically defendable resources requires exclusive access to high density resource areas. Under certain circumstances, the presence of several females in a range can be explained as the formation of a coalition to defend the exclusivity of access to high density resource areas. Uncertainty of paternity due to repeated ovulations and delayed implantation in females has profound implications for the way males can hope to maximize reproductive success. Territoriality and the

formation of male groups are discussed as possibilities by which males may attempt to limit other males' access to females and ensure their own reproductive success.

The presence of several males and females in a badger group ('intrasexual coalitions') is subjected to a cost-benefit analysis. The costs and benefits of defending exclusive access to a resource (for males: females, for females: protein-rich food) are analysed as a function of the qualities of the resource (density, availability, renewal, and dispersion) and the population density (intrusion pressure). This yields a model of the social organisation of badgers that accommodates the diverging results of previous studies.

2. Habitat

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2.1.2. Habitat-resources-niche

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2.3.3. Results

2.4. Discussion

2.1 Introduction

Foxes and badgers are surrounded by varying sets of resources as well as other components of the environment. Their activities, ie. their movement patterns, feeding and life histories, are expressions of their relationship with their environment. This relationship is moulded by four main factors:

1. The potential capabilities of the organism as a consequence of its morphological, physiological and behavioural traits
2. The distribution and availability of various resources
3. The influence of other animals (predators, competitors)
4. Environmental (abiotic) factors

In this, and the following chapter, I want to concentrate on the second factor, the distribution and availability of various resources. In the following sections I will define the related concepts of habitat, resources, and niche. I will show that the concept of habitat is useful in a variety of contexts including niche and competition theory and behavioural ecology. Measurement of habitats can indicate the distribution of resources although the relationship between habitats and resources may not necessarily be straightforward. Emphasis is placed on a distinction between various sets of resources as defined by the ability of the animal to use them.

Habitats can be treated as either discrete natural units or as a continuum, a concept related to the gradient concept in plant community ecology (Whittaker 1975). The data sets of sections 2.2 and 2.3 accommodate

both concepts: the habitat map (section 2.2) is an example of discrete habitat types. Its correspondance with the distribution of resources is the subject of Chapter 3. The habitat records (section 2.3) quantify habitat variables and permit the investigation of continuous variation in habitat features. They are analysed by using linear and non-linear methods of multivariate analyses. The analysis demonstrates how habitat parameters can be used in conjunction with indicators of fox and badger presence, and indicates the way habitat parameters can vary in the study area between sites chosen for detailed habitat recording. It also shows the value of habitat characteristics in predicting some of the prey-predator relationships that are the subject of the next chapter.

2.1.1. Some definitions

HABITAT. A survey of the literature dealing with habitat reveals that authors often prefer not to define it at all. A very general definition was provided by Baker (1978) who simply defined habitat as the area that can be used by an animal. Southwood (1981:31) defined habitat as 'the area accessible to the trivial movements of the food harvesting stages' [of any particular animal]. A useful definition of habitat should recognize that habitats contain resources that are important to an animal. Habitats not only contain sets of resources but also competitors, predators, and other elements. However the definition of habitats used in this study centres on the consideration of the resources they contain:

habitat: a spatial unit containing a particular set of resources

Different habitat types can contain the same resources but in different

proportions. The recognition of different spatial units as habitats, ie. the classification of habitats into habitat types depends on the resources considered, but not necessarily on that alone. If habitat is viewed as a continuum of features, any division into types will be arbitrary. Even with continuous variation of habitat parameters, however, it might be sensible to describe discrete types, for at least two reasons. The animal might itself not classify the variation as continuous but as discrete, using a threshold function. Also, two habitat types that show continuous variation of resources with respect to the animal might be very different by some other criterion, e.g. human land use. Thus, there might be some other criteria, perhaps related to the purpose of the study, that make a distinction of habitat types useful even with continuous variation of habitat features. It is important to recognise that definition of habitat and classification of habitats are closely related but not entirely identical processes; the former proceeds in relation to the animal while the latter is a trade-off between the characteristics important to the animal and the purpose of the investigation.

RESOURCES. There are many types of resources and certainly just as many ways of classifying them. Among the commonly recognised types of resources are food (quality, size etc.), space (height in vegetation or other Euclidean distances), physico-chemical characteristics (substrate type) and time (seasonal, diel). Andrewartha & Browning (1961), Andrewartha (1970) and Schoener (1974a) provide good summaries. Classification of an entity as a resource is an essentially animal-oriented process. The reference system is the animal's set of abilities that determine whether it can at least potentially exploit it. The value of the resource might lie anywhere along a gradient between favourable and unfavourable. I distinguish three functional sets of resources (hereafter referred to as SET

1, SET 2, and SET 3):

SET 1: The set of factors out of all those present that constitutes resources as defined by the organism's ability to use them (Hutchinson's fundamental niche).

SET 2: The subset of SET 1 that occurs at the place (habitat) where the organism lives. This might be called the 'local' niche. This subset may or may not include all elements of SET 1.

SET 3: The subset of SET 2 that the organism can actually utilize (Hutchinson's realized niche). This may or may not include all elements of SET 2.

SET 1 resources refer to those resources that are accessible over the entire range of a species. For instance, a fox in Australia will have access to many prey species that do not occur in Europe and a badger living in Finland has a different choice of berries than one in Britain. Any particular individual's range usually covers only part of the species' entire range and therefore has potential access to only a selection of the resources that are part of SET 1: this is the 'local window' to the treasuries of SET 1 and constitutes SET 2. For opportunists, this difference between SET 1 and SET 2 is likely to be great. Now, in a given place (the range of an individual) other factors have an influence on utilization of SET 2 resources. An example is the effect of interference between two conspecifics when they try to hunt the same prey. This is a well known phenomenon in waders (Sutherland & Koene 1982). The first badger might come to a feeding ground with many earthworms accessible on the surface on a mild, humid night in early September. It feeds in the area for about one hour and then leaves. A second badger arrives shortly afterwards

and goes to the same place where earthworms are usually available. On this occasion, however, it will not find a single worm as they have either been caught or disturbed by the first badger. The worms in this particular patch are part of the SET 3 resources of the first, but not of the second badger. Similarly, females might be a resource of value only to sexually mature males, and certain types of food might only be taken if the animal reaches a certain size. Animals might be prevented from exploiting a resource through a lack of training or experience or their state of health: a fox cub has to learn how to catch earthworms (Macdonald (1980)). SET 3 contains all those resources that are accessible and important at a particular moment in time. The relationship between prey abundance and prey availability will be discussed in greater detail in chapter 3.

NICHE. When the concept of the niche was introduced (Grinnell 1917, Elton 1927) it almost immediately came to mean two different things. Grinnell viewed niche as a subdivision of the habitat (Udvardy 1959) and used it to describe the range of environments where a species occurred. This is basically a distributional concept (Whittaker et al. 1973). According to Elton, the niche represented the species' 'role' in the community. Hutchinson (1958) defined niche more formally as a n-dimensional hypervolume where each dimension was equivalent to a natural gradient over which the species can survive and reproduce. Therefore Hutchinson's definition emphasized the concept of fitness while Elton had paid more attention to the trophic relationships within the community. Hutchinson's definition made the application of the niche concept exceedingly difficult in practice but is easy to visualize and thus of great heuristic value. Since then, niche dimensions have been increasingly identified as resource gradients, while the species' tolerance to changes in the physico-chemical environment which dominated early investigations of competition has been

neglected, at least in zoological investigations. The niche of a species is then the combination of the resource utilization patterns over all resource gradients of relevance (Pianka 1981).

2.1.2. Habitat - resources - niche

As can be seen from the previous section, habitat, resources and niche are closely related concepts. I shall now discuss their relationships and then formulate a set of suggestions of how to embark on a habitat description once the purpose of the habitat description has been determined.

2.1.2.1. Identification of resources in different habitats.

Classification of an entity as a resource may not be straightforward as the resource can only be defined with reference to the animal. As Green (1971:543) states in the context of resource dimensions related to the niche of species,

> " One can in theory demonstrate that two species do not occupy the same niche, but one can never demonstrate that they do occupy the same niche as there is always a practical limit to the number of environmental parameters which can be measured."

As one approach to this problem, habitats are classified instead of resources and habitat parameters are recorded to find out how changes in habitat will reflect changes in resource distribution. The great advantage of measuring habitat is that all possible factors relevant to the animal can be included if they have a direct or indirect relationship to the habitat classification criteria. However, as it is an indirect method it will

introduce additional 'noise' because irrelevant factors are entered in the habitat description together with relevant factors. Also, the amount of resource at a particular location will change in time, either because of its own intrinsic dynamics (e.g. cyclicity in the abundance of prey populations) or because the resource is depleted by the organism, competitors, or unfavourable environmental factors such as climate. Thus, habitat can provide only an indication of resource abundance, accounting for some types of variation, but not for others. Note that by measuring habitats as proposed here, only the variation in SET 2 is tackled and that variations in SET 3 are not considered.

We therefore do not necessarily expect a straightforward relationship between habitats and resource distribution and abundance, but an appropriate habitat classification may, nevertheless, mimic important changes from one place to another, if averaged over a period of time.

This approach can be applied for at least three different purposes:

1. When studying animals on a high trophic level such as carnivores or raptors, the number of different resources to be taken into account is considerable and food abundance is difficult to measure. Thus the coarser but more managable approach of measuring habitat might be favoured.

2. To develop a set of parameters that summarises the animal's relationship to its environment in a convenient manner. Here, in contrast to the first point, emphasis is put on parameters that can be conveniently determined but have not necessarily any causal relationship with the animal. For instance, Newton et al. (1977) describe a correlation between sparrowhawk breeding density and soil productivity. If little is known of a species, this approach might be the first step to produce a basis from which the search for the real causes begins.

3. Studies concerned with the assessment of management policies and similar activities ('environmental impact evaluation') have emphasized the

need for classification systems that make it possible to predict changes in the wildlife communities (Macdonald et al. 1981). Here the assumption is that there are relatively few resource gradients for food and breeding requirements on which species can be grouped. The resources vary from habitat to habitat in a manner that is satisfactorily described by presenting different habitat types. Changes in habitat then lead to changes in resource distributions which in turn lead to predictable changes in guild composition and presence (Severinghaus (1981, Short & Burnham 1982). The advantage here is that it might be easier and quicker to agree upon and evaluate habitat types rather than investigate resource distributions in each case.

2.1.2.2. Identification of niche parameters from habitat variables

Although it is acknowledged in the ecological literature that an ultimately satisfactory niche concept has to incorporate reproductive parameters (Pianka 1976, 1981), most present work is concerned with niches as defined by resource utilization patterns. However, due to the above mentioned difficulties of identifying resources as appropriate niche dimensions, habitat variables are measured and possibly combined to construct new axes so that they define the niche of species. This is an important although very practical modification of the Hutchinsonian niche concept. According to MacArthur & Levins (1967) and Levins (1968:48), niche axes with an unambiguous biological meaning which could not be properly measured are replaced by axes that can be measured but have no intrinsic biological meaning. MacArthur and Levins' ideas heralded the use of sophisticated statistical methods to transform biological data to niche axes, if more than one or two factors are to be identified. As subsequent studies showed (e.g. Green 1971, Rotenberry & Wiens 1980), the practical

resolution of MacArthur and Levins' concept has its limitations defined by the way the statistical methods operate. For instance, some techniques tend to separate, others to aggregate species along the new niche axes (see e.g. Williams 1981). An investigator has to be careful as to whether the choice of analytical method is not biased by his view of the species and the community he investigates. The MacArthur-Levins model however has the great advantage that it permits the concept of a habitat continuum, ie. of continuous variation of resources similar to the gradient model of plant communities (Whittaker 1975).

2.1.2.3. Habitat use and bionomic strategies

The two sections that follow both employ habitat rather than the resource as the unit of operation to be considered by the organism. It is assumed that resource spectra are summarized and expressed by habitats and that differences between habitats are indicators of resource changes.

HABITAT SELECTION. This approach views habitats as spatial units each representing different portions of 'environmental' gradients. Animals that occur over a range of habitats in different densities or distribute their activities unevenly between habitats are said to exercise habitat selection. According to Meadows & Campbell (1972:145) this can be defined as:

> "the repertoire of behavioural responses to environmental stimuli by means of which an animal locates its preferred habitat." (Meadows & Campbell 1972:145)

These environmental stimuli comprise resources, lethal conditions etc. Here, spatial units naturally fall into qualitatively different, discrete types called habitats. An individual has to consider the relative pay-offs of each habitat. By choosing to live in one habitat or by allocating time

to different habitats, the individual will also be exposed to the factors influencing the composition of SET 3, the utilizable resources. The spatial distribution of the individuals over the habitats will thus be a result of a trade-off between factors influencing the composition of SET 3 and the payoff each habitat can offer by the sum of the resources it contains.

Interest in habitat selection has increased in recent years as its effects on a variety of population parameters were considered. Schoener (1974b) proposed a series of multiple regression models for competition between species incorporating non-linear relationships, based on the assumption that habitats are merely the 'arena' where competition takes place. His models allowed for varying carrying capacities between habitats. If, however, species evolutionarily diverge in habitat preferences and items in habitats correspond to resource types, instantaneous competition may be quickly reduced and his models inapplicable. Templeton and Rothman (1981) investigated this possibility in a model of genotype specific habitat selection for organisms that are subjected to within-lifetime environmental fluctuations. They demonstrated that the relationship between selection of habitat preference and the genotype's fitness in the particular habitat is complex and sometimes counterintuitive. Hallett and Pimm (1979) developed a method for direct estimation of competition that makes no assumptions about the nature of competition or the amount of resource overlap between species. They noted that structural components of habitats are often found to be correlated with the abundance of species (e.g. Anderson & Shugart 1974, Crowell & Pimm 1976) and suggested a multiple regression model that incorporated habitat variables so that the calculated competition coefficients reflect the effect of each species after the effects of habitat selection have been taken into account. Rosenzweig and co-workers (Rosenzweig 1979, 1981, Pimm & Rosenzweig 1981) investigated the effects of differential habitat use on the fitness of habitat selection strategies

(e.g. habitat specialists vs. generalists) when various costs (e.g. searching cost) are taken into account. Their theory is conceptually related to optimal foraging models with the difference that they consider maximising fitness instead of energy or other foraging units. Finally, Shigesada and Roughgarden (1982) present a model in which they investigate the role of dispersal in relation to population growth and regional population dynamics and show that if they regard the niche axes as habitat axes in space, they can link theories of habitat selection with the theory of local niche partitioning due to MacArthur and Levins (1967) that has been described in section 2.1.2.2.

In essence, habitat selection looks at the whole complex of habitat-resource-niche from a slightly different angle. Habitat is the starting point and the species' response to it, and one species' relation to another, are investigated. Habitats can be arranged along a few dimensions that represent 'quality' gradients. The common use, as a shorthand description, of 'good' and 'bad' habitats is derived from this.

2. BIONOMIC STRATEGIES. Southwood (1977, 1981) suggested a different way of looking at the relationship between habitat and the organisms that live in it. Each organism follows a 'bionomic' strategy that combines reproductive parameters (fecundity etc.) with other life-history traits (longevity, size, range, migration habits). The strategy will evolve to maximise the fitness of the organism in the environment, hence different strategies should suit different environments. Environments or habitats are classified according to the way they have an impact on the bionomic strategy. This is a functional classification that relates

temporal characteristics of habitats:	to	temporal characteristics of organisms:

durational stability,	to	longevity, generation
variation in resource states		time
as expressed through		
variations in carrying capacity		
(SET 2)		
spatial characteristics	to	spatial characteristics
of habitats:		of organisms:
spatial heterogeneity	to	range size and migration
(continuity or patchiness)		habits

Here the emphasis is on evolutionary consequences: habitat selection by the organism will occur as a consequence of its particular bionomic strategy and differential survival in a habitat will select for a certain kind of bionomic strategy in that habitat.

2.1.3. Suggestions

As a summary, habitat description can be designed to satisfy a variety of purposes (cf. Rotenberry 1981). Classification of habitats could

a) reflect changes in resource distribution and abundance;
b) minimize within-guild variation of species present within the same habitat and maximize between-guild variation for different habitats;
c) correlate with or provide niche dimensions;
d) reflect habitat preferences of the organisms;
e) correspond to characteristics of bionomic strategies.

I conclude that it is both interesting and worthwile to do habitat

recording. With regard to the questions of the present study, habitat recording is important for the determination of resource distribution and abundance which can illustrate the niche dimensions of foxes and badgers and provide an explanation for the habitat preferences exhibited by the two species.

I suggest two principles that can aid in the design of habitat recording schemes.

1. The Principle of Adequacy: Describe the habitat by selecting parameters so that you list the habitat factors you think are most relevant to the animal.
2. The Principle of Convenience: Describe the habitat by selecting parameters that most conveniently summarize the patterns of the organism's ecology and behaviour you are interested in.

While it is desirable to record parameters that are of relevance to the animal (adequacy) this is not always feasible, either because it is not clear what is of relevance, or because the relevant parameters are difficult to measure. Selecting parameters that are easy to measure (convenience) offers a solution to this problem. Parameters are then used as indicators of the animal's activities, even though the causal relationships remain open.

Selection of habitat parameters of interest to foxes and badgers is difficult (see section 2.3): some of the factors might be missed altogether, while others cannot be measured although it is known that they are potentially important. For example, determination of the distribution and abundance of small mammals is so draining on manpower and time as to be impractical for many studies of habitat.

2.1.4. The approach

As I wanted to use habitat data for a variety of purposes (listed in sections 2.2 and 2.3) I decided to record habitat data in two different ways (cf. Howard 1981):

1. A habitat map was constructed containing polygonal patches. Each patch was assigned to a particular habitat type. The habitat types were defined after the whole study area had been thoroughly visited; the final classification incorporated the habitat types defined by Newdick (1983). The habitat map corresponds to the concept of recognizable, 'discrete' habitat types and illustrates the application of the Principle of Convenience.

2. A variety of habitat variables were recorded in selected parts of the study area using quadrats with a size of 0.25 ha. The habitat records correspond to the 'continuum' concept: it allows the investigation of continuous variation of habitat parameters and their quantitative relationships. This is particularly useful if habitat parameters are to be employed as niche dimensions. The habitat records are an example of an application of the Principle of Adequacy: it was attempted to record as many relevant parameters as possible while bearing in mind that a compromise had to be found between the desire to record everything of interest and the problems of measurement and the time and manpower available.

In addition, the distribution and abundance of a variety of resources were recorded over large parts of the study area (described in Chapter 3). This was done in an attempt to illuminate how well habitat types (as defined in the habitat map) indicate the distribution of resources.

Details of the construction and layout of the habitat map are described in section 2.2, the habitat records in section 2.3, and the data on resource distribution and abundance are the subject of the next chapter.

2.2. The habitat map

A map of the study area was designed and constructed for six purposes:

1. As a base map to facilitate field work
2. To assess the habitat components of the study area
3. To examine the habitat components of individual and group ranges of foxes and badgers
4. To label all radiotracking data with habitat information to facilitate the examination of habitat use by foxes and badgers
5. To label all other data with any spatial information to facilitate the examination of the distribution and abundance of the respective entities over habitats:
   - fox faeces
   - badger latrines
   - pheasant sightings
   - fox dens, badger setts and rabbit warrens
   - remains of badger interactions (hairs)
   - fox and badger sightings
   - bird remains
6. To facilitate comparisons with the results of Newdick (1983) and Doncaster (1985) on fox movements in Oxford city.

2.2.1. Habitat classification

During summer 1981 the entire study area was thoroughly visited and preliminary habitat information recorded. Land use was then classified into 47 habitat types (Box 1) by expanding Newdick's (1983) classification of fox

Box 1 Classification of habitats for the habitat map.

HAB.NO.	HABITAT NAME	DESCRIPTION
1	Terraced housing.	Rear gardens small, or paved. Front garden reduced or absent.
2	Semi-detached housing.	Typical English garden. Small, usually well tended gardens front and rear.
3	Detached housing.	Large gardens front and rear, often with untended or overgrown areas.
4	Flats.	Blocks of housing surrounded (usually) with lawns. No gardens.
5	Grassland.	Grassland which is uncut, or cut only rarely.
6	Grassley.	Areas of mown grass.
7	Pasture.	Short grassland grazed by animals.
8	Allotments.	Areas divided into small plots for cultivation. Most also have a compost heap.
9	Arable land.	*
10	Scrub.	Woodland with a dense shrub layer, often with bramble.
11	Open woodland.	Woodland with little or no shrub layer.
12	Orchard.	
13	Derelict.	Unused industrial land.
14	Industrial property	Areas of factories (cf no. 18).
15	Market	One area of open market stalls.
16	Hospital.	
17	College.	
18	Commercial property	Shops and offices.
19	**	
20	**	
21	Coniferous woodland.	*
22	Deciduous woodland.	*
23	Farm buildings.	
24	Marsh-land.	
25	Railway.	
26	Major road.	
27	River.	
28	Winter cereals.	
29	Summer cereals.	
30	Root crops.	
31	Rape.	
32	Horticulture.	Cultivation of strawberry, raspberry etc on arable land.
33	Fallow land.	
34	Copse.	Small woodland surrounded by fields.
35	Bracken.	Area with tall 'herbs' dominated by bracken. Usually also contains some bramble and stinging nettles.
36	Hedge.	
37	Deciduous hardwoods	Woodland dominated by deciduous trees with usually rich understorey. Not managed.

Box 1 (Cont.)

38	Deciduous plantations	Woodland dominated by deciduous trees planted since 1945. Usually poor understorey. Trees planted on a more or less regular grid.
39	Beechwood	Plantations consisting solely of beech trees. Usually no understorey.
40	Mixed plantations	Plantations composed of a mixture of deciduous and coniferous trees.
41	Coniferous plantations.	
42	Parkland.	Large gardens dominated by more or less well tended lawns with some trees.
43	Public house.	
44	Riverrine environment with hedges.	Rivers, ditches or ponds surrounded by hedges along the banks.
45	Riverrine environment without h.	Rivers, ditches or ponds with little or no bank vegetation.
46	Sport grounds.	Short grass areas used for recreational purposes, including golf ranges.
47	Various humans.	Picnic sites etc.

* Newdick's categories not used by me for habitat map.
** numbers not used.

habitats, which is used by all members of the Oxford Foxlot (Newdick 1983, Doncaster 1985). The first 27 habitat types are identical with this classification. Some of the habitat categories are not important to my study area, e.g. colleges, or hospitals, but some of the housing types, for instance, occur at the fringe of the study area (Table 2.1). So, while retaining comparability with analyses based on this classification, I elaborated it for use in Wytham. Arable land was split into several categories to permit a more fine-grained analysis of land-use. Rape was included as an arable land category. Woodlands were split into several types based on the type of management corresponding to the plantation types recognized by the Department of Forestry, Oxford (see below). Beechwood was distinguished from other deciduous woodlands in recognition of associated marked vegetational changes and changes in prey abundance, particularly earthworms (see Chapter 3). In contrast to the city, a number of public houses occur at isolated sites within the study area. It was decided that they warranted a separate category as they are potentially good sites for food scraps. On similar grounds, category 46 (sports grounds) was distinguished from category 6 (grass ley) as differential human presence might be of importance in an area that is not as dominated by human presence as is the case with the city. However, the last two criteria had little effect on the overall composition of habitats as can be seen from Table 2.1. Also, for these cases the definition of patch boundaries (see below) would have been unaffected by the assignment to a particular habitat type. For a discussion, and other classification systems, see e.g. Elton and Miller (1954), Short and Burnham (1980), Brown (1980), Armstrong et al. (1981) and Ogle (1981).

Table 2.1. Summary of habitat map.

HAB. NO.	HABITAT TYPE	NUMBER OF PATCHES	AREA (ha)	AVERAGE PATCH SIZE(ha)	PERCENTAGE OF TOTAL AREA
1	Terraced housing.	10	9.48	0.948	0.7
2	Semi-detached h.	7	7.84	1.120	0.5
3	Detached housing	48	6.21	0.129	0.4
4	Flats	-	-	-	-
5	Grassland	39	43.00	1.103	3.0
6	Grassley.	23	35.89	1.560	2.5
7	Pasture.	124	385.36	3.108	26.9
8	Allotments.	15	16.61	1.107	1.2
9	Arable land.	-	-	-	-
10	Scrub.	9	5.27	0.586	0.4
11	Open woodland.	4	2.91	0.728	0.2
12	Orchard.	3	1.09	0.363	0.1
13	Derelict.	4	1.70	0.425	0.1
14	Industrial property	15	14.46	0.964	1.0
15	Market	-	-	-	-
16	Hospital.	-	-	-	-
17	College.	-	-	-	-
18	Commercial property	-	-	-	-
19	**	-	-	-	-
20	**	-	-	-	-
21	Coniferous woodland.	-	-	-	-
22	Deciduous woodland.	-	-	-	-
23	Farm buildings.	20	9.38	0.469	0.7
24	Marsh-land.	49	12.26	0.250	0.9
25	Railway.	-	-	-	-
26	Major road.	6	7.16	1.193	0.5
27	River.	-	-	-	-
28	Winter cereals.	1	4.06	4.060	0.3
29	Summer cereals.	57	368.43	6.464	25.7
30	Root crops.	1	4.27	4.270	0.3
31	Rape.	-	-	-	-
32	Horticulture.	4	6.62	1.655	0.5
33	Fallow land.	4	17.41	4.353	1.2
34	Copse.	1	0.14	0.140	0.0
35	Bracken.	37	24.14	0.652	1.7
36	Hedge.	68	19.09	0.281	1.3
37	Deciduous hardwoods	151	273.54	1.812	19.1
38	Deciduous plantations	28	29.22	1.044	2.0
39	Beechwood	19	15.11	0.795	1.1
40	Mixed plantations	31	36.87	1.189	2.6
41	Coniferous plantations	16	10.26	0.641	0.7
42	Parkland.	27	10.28	0.381	0.7
43	Public house.	3	0.30	0.100	0.0
44	River.env. with hedges	73	24.23	0.332	1.7
45	River.env. without h.	38	11.85	0.312	0.8
46	Sport grounds.	6	15.35	2.558	1.1
47	Various humans.	11	3.92	0.356	0.3
--	all habitats --	952	1433.71	1.340	100.0

2.2.2. Construction of the map

In autumn 1981 and winter 1981/1982 the entire study area was systematically visited using Ordnance Survey maps (scale 1:10000) and the Wytham Woods Atlas (January 1981 version by R.L.Hockin, Department of Forestry, Oxford; scale 1:5000). Location in the study area was facilitated by numerous landmarks and particularly by the orange 100 m grid poles in the woodlands.

A map (scale 1:5000) was constructed by using the Wytham Woods Atlas as a base. The parts of the study area not covered by the Atlas were entered on the map using aerial photographs taken on September 22, 1978 by Hunting Surveys Ltd., Elstree Way, Boreham Wood, Hertfordshire on a scale 1:10000. Slides were used to project the aerial photographs straight onto the map in line with suggestions by Kilford (1979) and Marcot et al. (1981) (see also Fuller (1983). The map was updated with Ordnance Survey maps and field records. Special emphasis was laid on accurate positioning of conspicuous landmarks within large homogeneous areas (e.g. single trees on arable land). Knowledge of their exact coordinates facilitated and improved data recording from such areas. The map was then divided into non-overlapping components called patches. They were marked out using the following criteria.

1. Each patch forms a distinct plot of land and habitat type. Fences, boundary roads or tracks constituted well defined borders. This was usually straightforward and most patch boundaries were thus defined.

2. All boundaries of the compartments recognized by the Forestry Service of Wytham Woods were incorporated. Most compartment boundaries were already 'covered' by the first criterion, but in some cases this meant inclusion of some additional borders. Thus, one compartment might consist of several patches, but one patch would not include sections of more than one compartment.

3. The resulting map was checked against the plantation map of the Department of Forestry, Oxford, to make sure that the boundaries of the areas occupied by the plantation types recognized by the Department of Forestry were included.

4. Minimum size of patches was 30 m by 30 m, to match approximately the accuracy of radio-tracking data.

5. Each patch was delineated with a mininum number of straight lines in order to minimise the memory space required for computer storage.

Criteria 1, 4 and 5 are identical with those of Newdick's (1983) habitat map. The other two criteria were specified to facilitate comparisons with other maps of Wytham Woods. Recognition of compartment boundaries and plantation types is also useful as the management of the woodland and thus potential habitat changes occur in accordance with compartment and plantation boundaries. The map was thus designed to minimize the probability that major habitat changes could occur across patch boundaries during the time of the study. It is easier because of computational considerations to change habitat types or lump patches than it is to modify patch boundaries. During the period of my field work few habitat changes occurred and those were within and not across patch boundaries.

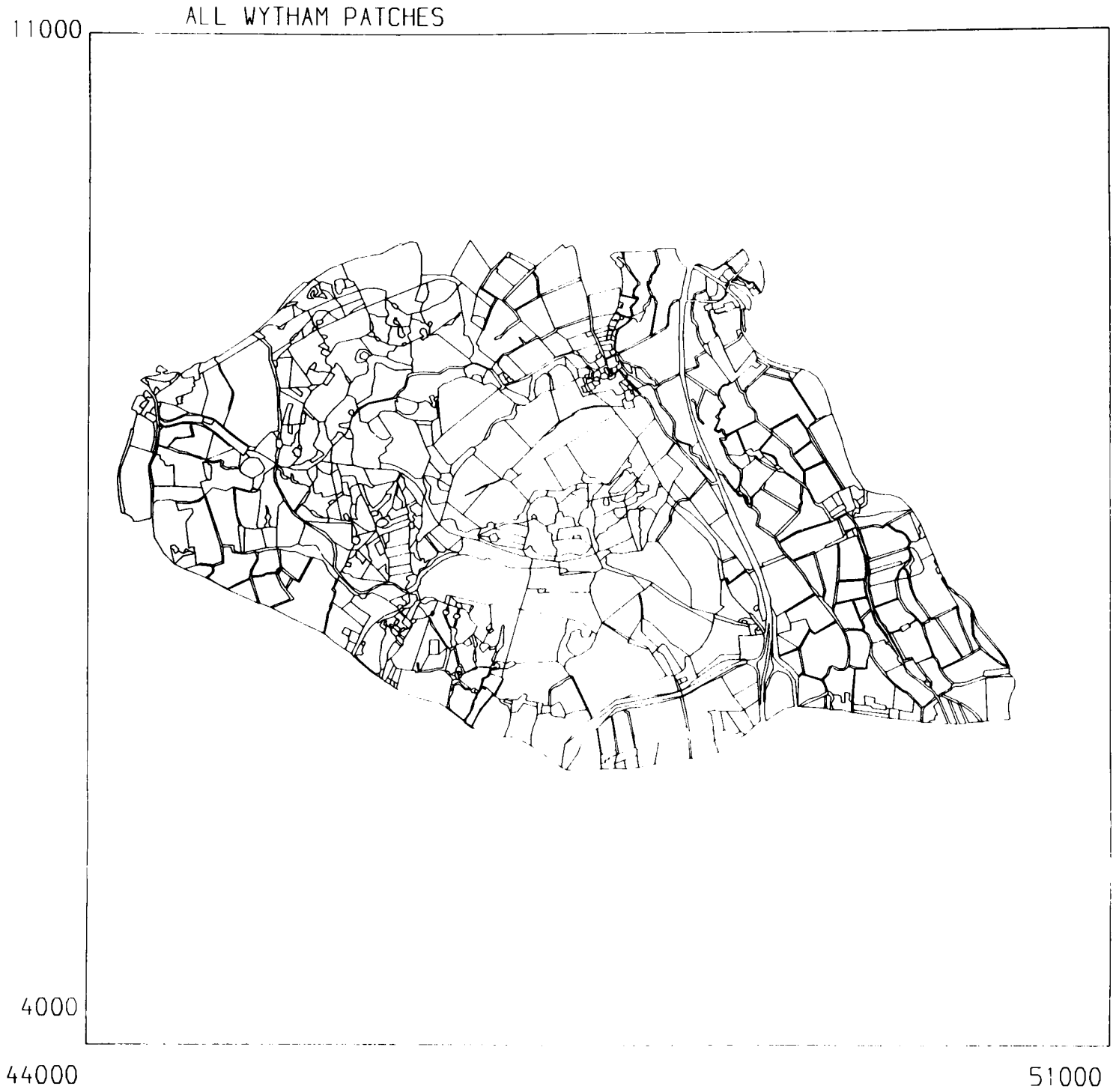
The entire map was then photographically reduced at the photographic laboratory of the Department of Nuclear Physics, Oxford, with a camera that eliminates any distortions resulting from reduction. The map was then digitized and entered into the computer using the same procedure as described by Newdick (1983). The map was checked and corrected using program BODGE and finally assembled with program BUILD (written by M.T. Newdick).

2.2.3. Results

The final map covered the following area (Fig. 2.1): the centre of the map constituted Wytham Woods with Wytham village. To the east, the area covered includes the Western Bypass, and the entire Binsey area between the River Thames, Wolvercote (Godstow Road) and Botley Road. To the south, the Eynsham Road from Botley to the Toll Bridge constituted a very convenient border. To the west and north, the River Thames and the agricultural fields between Wytham Wood and the University Field Station completed the border line. Hereafter, the entire area covered by the map is referred to as the study area. Sections of it are called study sites (e.g. for habitat records).

The map covers altogether 14.3 square kilometres in 952 patches over 34 different habitat types. Program HTOT (written by M.T. Newdick) was used to summarize the components of the habitat map. Results are presented in Table 2.1. Three habitat types dominate the landscape: pasture (124 patches, 26.9% of the area), fields with summer cereals (57 patches, 25.7%) and deciduous hardwoods (151 patches, 19.1%). On average, patches with summer cereals are largest (average size 6.464 ha) and approximately twice the size of pasture patches (average size 3.108 ha) and more than three times the size of deciduous hardwoods patches (average size 1.812 ha). Most other habitat types occur in far smaller patches. Looking at the habitat map in more detail, I tried to gain an impression of 'local' habitat composition. Program NEIGHBOUR was used to create a 'map' containing information on the neighbours of each patch and program PATSUM compiled this information by habitat categories. Each patch was used as a 'window' to the local habitat composition by evaluating the number of neighbouring patches and their habitat types, and an attempt was made to summarize this information in an expression of habitat diversity. Note that habitat diversity refers here to

Fig. 2.1. The computerized habitat map of the study area, with National Grid References (map SP); scale 7 by 7 km. Each area unit represents a habitat patch. The map was produced by program MAPITH, using the GHOST-80 Graphics system.


ALL WYTHAM PATCHES
11000
4000
44000
51000

the presence or absence of habitat types amongst the neighbours of a particular patch, not to any variation within a patch or within a neighbouring patch.

There have been many suggestions of how to measure ecological diversity and a variety of diversity indices have been proposed (e.g. Hill 1973, Heip 1974, & Pielou 1977). Comparison of their performance (Hurlbert 1971, Heip & Engels 1974, May 1975, Pielou 1979, Alatalo 1981, & Kobayashi 1981) has shown that there is no general 'best' index. I decided to use the Dominance Index proposed by Berger and Parker (1970) as it is easy to visualize and calculate, and has been shown to be very robust in many cases (May 1975). The Dominance Index for a given patch is

> the number of patches of the most frequent habitat type amongst the neighbours of the patch divided by the total number of neighbouring patches of the patch

The Dominance Index assumes values in the range between 0 and 1. A small number indicates low dominance of the most frequent habitat type while a value close to 1 indicates high dominance of the most frequent habitat type. A value of 1 indicates perfect dominance: all neighbouring patches are of the same habitat type. In terms of diversity, a high value (high dominance) would indicate good homogeneity or low diversity, and a low value (low dominance diversity) would indicate low homogeneity or high diversity. Results are shown in Table 2.2 and Fig. 2.2. The grand mean of the Dominance Index over all habitats is 0.537. There is, however, considerable, significant scatter between different habitats (Kruskal-Wallis one-way analysis of variance, $H(\text{adjusted}) = 93.28$, $p < 0.001$, $df = 24$). Fig. 2.2a shows that indeed the dominance index decreases and thus diversity increases with the number of different habitat types represented amongst the neighbours (Spearman rank correlation, $rho = -0.717$, $p < 0.001$). The number of neighbouring habitats is correlated with the average patch size (Fig

Table 2.2 Analysis of the properties of patch neighbours summarized by habitat categories. Not occuring habitats are not listed.

Number of patches with at least one neighbour with the same habitat.

INFORMATION ON CHARACTERISTICS OF NEIGHBOURING PATCHES

HAB. NO.	NO. PAT.	BERGER/PARKER INDEX		NO.NEIGHB. PATCHES		NO.NEIGHB. HABITATS		NO. PATCHES SAME HABIT.		*	HUMAN	PASTURE	ARABLE	WOODL.
		MEAN	S.D.	MEAN	S.D.	MEAN	S.D.	MEAN	S.D.					
1.	10.	0.625	0.69	2.30	2.53	2.10	2.32	0.40	0.81	3.	7.	0.	3.	1.
2.	7.	0.512	0.53	3.00	3.11	2.43	2.49	0.00	0.00	0.	4.	2.	1.	0.
3.	48.	0.578	0.64	2.42	2.75	2.25	2.52	0.25	0.54	11.	24.	21.	4.	12.
5.	39.	0.545	0.61	3.15	3.59	2.36	2.68	0.77	1.25	20.	7.	10.	13.	18.
6.	23.	0.408	0.43	3.87	4.29	3.35	3.63	0.26	0.52	6.	13.	12.	6.	15.
7.	124.	0.472	0.52	4.25	4.71	3.30	3.63	1.02	1.49	71.	40.	73.	28.	45.
8.	15.	0.420	0.50	3.33	3.57	3.20	3.44	0.53	0.83	7.	10.	7.	4.	1.
10.	9.	0.476	0.54	3.11	3.51	2.78	3.07	0.00	0.00	0.	1.	2.	4.	9.
11.	4.	0.313	0.42	2.50	3.04	2.25	2.82	0.00	0.00	0.	1.	3.	1.	2.
12.	3.	0.306	0.31	3.33	3.38	3.33	3.38	0.00	0.00	0.	2.	2.	2.	0.
13.	4.	0.708	0.79	1.75	1.99	1.75	1.99	0.00	0.00	0.	3.	1.	2.	0.
14.	15.	0.422	0.23	3.93	2.15	3.40	1.50	0.27	0.46	4.	7.	6.	2.	4.
23.	20.	0.518	0.58	3.80	4.60	3.05	3.58	0.30	0.56	6.	10.	15.	5.	5.
24.	49.	0.768	0.81	2.37	2.89	1.78	2.08	0.29	0.68	10.	1.	12.	3.	43.
26.	6.	0.464	0.48	5.00	5.23	3.67	3.86	0.33	0.61	2.	6.	2.	3.	2.
28.	1.	0.500	0.00	4.00	0.00	3.00	0.00	0.00	0.00	0.	0.	0.	1.	1.
29.	57.	0.464	0.51	5.04	5.51	3.60	3.93	1.02	1.60	33.	15.	22.	35.	26.
30.	1.	0.571	0.00	7.00	0.00	4.00	0.00	0.00	0.00	0.	1.	1.	1.	0.
32.	4.	0.538	0.63	3.50	3.91	3.00	3.32	2.50	2.81	4.	2.	0.	4.	0.
33.	4.	0.696	0.76	4.00	4.69	2.25	2.58	0.00	0.00	0.	1.	2.	1.	2.
34.	1.	1.000	0.00	1.00	0.00	1.00	0.00	0.00	0.00	0.	0.	0.	1.	0.
35.	37.	0.624	0.68	3.22	3.85	2.27	2.65	0.32	0.71	10.	3.	7.	6.	37.
36.	68.	0.610	0.65	3.22	3.56	2.34	2.57	0.69	1.15	32.	15.	47.	36.	8.
37.	151.	0.509	0.56	5.06	5.71	3.36	3.70	2.19	2.75	127.	23.	48.	42.	133.
38.	28.	0.459	0.51	4.54	5.16	3.32	3.57	1.18	1.58	20.	0.	1.	0.	28.
39.	19.	0.542	0.62	3.42	3.91	2.79	3.10	0.32	0.57	6.	0.	0.	2.	19.
40.	31.	0.533	0.56	4.26	4.56	2.84	3.01	1.35	1.77	22.	0.	1.	1.	31.
41.	16.	0.613	0.65	3.94	4.45	2.63	2.84	0.38	0.63	6.	0.	1.	0.	16.

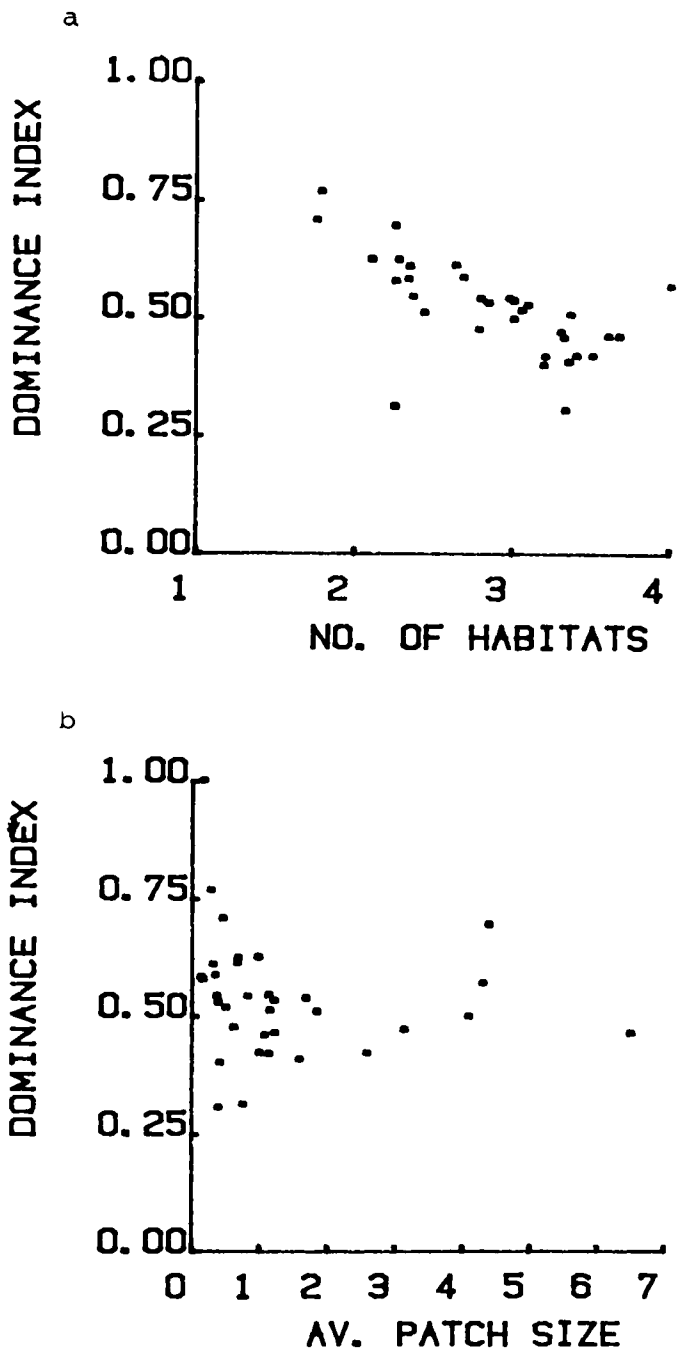
Table 2.2 (Cont.)

41.	16.	0.613	0.65	3.94	4.45	2.63	2.84	0.38	0.63	6.	0.	1.	0.	16.
42.	27.	0.401	0.44	3.52	3.77	3.19	3.36	0.44	0.73	11.	4.	16.	4.	7.
43.	3.	0.583	0.70	2.33	2.79	2.33	2.79	0.00	0.00	0.	2.	1.	0.	1.
44.	73.	0.543	0.59	4.26	4.95	2.97	3.35	0.95	1.45	43.	16.	58.	33.	14.
45.	38.	0.587	0.64	3.76	4.50	2.68	3.03	0.26	0.57	9.	6.	26.	8.	18.
46.	6.	0.421	0.45	4.50	4.87	3.50	3.76	0.00	0.00	0.	3.	3.	1.	0.
47.	11.	0.529	0.25	3.73	1.27	3.09	0.94	0.00	0.00	0.	6.	4.	2.	5.
grand means		0.537	0.13	3.60	1.11	2.80	0.64							

Fig. 2.2. Characteristics of the habitat map, as analysed on a local scale. Each point represents the average value for one habitat.

a. The Berger-Parker Dominance Index (see text) vs. the number of different neighbouring habitats per patch.
b. Dominance Index vs. average patch size.
c. Number of neighbouring patches per patch vs. average patch size.
d. number of different neighbouring habitats vs. average patch size.

Fig. 2.2


a
DOMINANCE INDEX
1.00
0.75
0.50
0.25
0.00
1
2
3
4
NO. OF HABITATS
b
DOMINANCE INDEX
1.00
0.75
0.50
0.25
0.00
0 1 2 3 4 5 6 7
AV. PATCH SIZE
c
NO. OF PATCHES
7
6
5
4
3
2
1
0 1 2 3 4 5 6 7
AV. PATCH SIZE
d
NO. OF HABITATS
4
3
2
1
0 1 2 3 4 5 6 7
AV. PATCH SIZE

2.2d, Spearman rank correlation, rho = 0.549, $p < 0.01$) and so is the number of neighbouring patches (Fig 2.2c, Spearman rank correlation, rho = 0.652, $p < 0.001$). However, the dominance index does not show a systematic relationship with average patch size (Fig. 2.2b).

The average number of neighbouring patches is 3.6 and the average number of neighbouring habitats somewhat lower, 2.8. As can be seen from Table 2.2, there is considerable variation between habitats.

As can be seen from Table 2.2, some habitats occur as isolated spots; they are always surrounded by different habitats. These isolated patches include semi-detached housing, scrub, open woodlands, orchards, derelict land, fallow land, public houses, sports grounds and various human-related habitats (this list excludes all habitats that occur only once). The highest number of neighbouring patches with the same habitat occurs amongst deciduous hardwood patches where about 40% of the neighbours (2.19 out of 5.06) belong to the same habitat type. (There is also one site in the Binsey area where horticultural patches are located next to each other, where 2.5 out of 3.5 neighbours are of the same habitat type). In contrast, these figures are 24% for pasture (1.02 out of 4.25) and 20% for summer cereals (1.02 out of 5.04). With regard to the number of patches that have at least one neighbour with the same habitat type, again deciduous hardwood patches

show the highest proportion (127 out of 151 (= 84%) have at least one neighbour that is again a deciduous hardwood patch). The same figures for pasture and summer cereals are 71 out of 124 (= 57%) and 33 out of 57 (= 58%). However, the figures for deciduous hardwoods, pasture, and summer cereals are not quite comparable as, for example, two pasture fields merely separated by a hedge (habitat 36) are not included in this list. In this context the fact that a fox or a badger passing from one patch of pasture or summer cereals to the next also crossed a hedge might be inconsequential, so for comparison the analysis for pasture and arable fields was repeated while excluding hedgerows. The following categories of first order and second order neighbours were distinguished:

- patches with at least one hedge but no other patch of the same habitat type
- patches with at least one hedge and at least one other patch of the same habitat type

In both cases another patch of the same habitat type could have followed the hedge (second order neighbour with same habitat type). This patch was counted only if it bordered against the hedge but was not contiguous with the patch in question (in some cases, a patch would start as a first order neighbour and then change into a second order neighbour as a hedge pushed in between the original patch and the neighbouring patch). Results are presented in Table 2.3. In an additional 16 cases for pasture and 10 cases for summer cereals there was at least one second order neighbour of the same habitat type separated by a hedge from the origin patch and the origin patch had no first order neighbour of the same habitat type. The corrected figures for pasture are then 87 cases out of 124 (= 70%) and 43 cases out of 57 for summer cereals (= 75%) with at least one neighbouring patch of the same habitat type. For both pasture and summer cereals with hedges there was no dependence of the occurrence of first order

Table 2.3 Numbers of first and second order neighbour patches of the same habitat type for origin patches with hedges surrounding them for pasture and summer cereals.

(a) pasture

	ORIGIN PATCH WITH AT LEAST ONE HEDGE AS A NEIGHBOUR		
	plus first order neighbours of same habitat type	without first order neighbours w.s.h.t.	sum
with second order neighbour of s.h.t.	19	16	35
without second order neighbour of s.h.t.	9	3	12
sum	28	19	47

χ^2 = 1.59, df = 1; not significant

(b) summer cereals

	ORIGIN PATCH WITH AT LEAST ONE HEDGE AS A NEIGHBOUR		
	plus first order n. of same hab. type	without f.o.n.o.s. h.t.	sum
with second order neighbour of s.h.t.	8	10	18
without second order neighbour of s.h.t.	5	5	10
sum	13	15	28

χ^2 = 0.07, d.f. = 1; n.s.

neighbours and second order neighbours with the same habitat type (pasture: χ^2= 1.59, ns; summer cereals: χ^2= 0.07, ns; Table 2.3). Thus, hedges aside, a fox or a badger leaving a patch in deciduous hardwoods is slightly more likely to enter another patch of the same habitat than if it was on pasture or in summer cereal fields.

The last four columns of Table 2.2 list the total number of neighbouring patches belonging to four coarse super-types, called HUMAN or human-dominated, PASTURE, ARABLE LAND and WOODLAND. These supertypes served to investigate specific patterns but were not intended to summarize exhaustively all habitat types represented in the habitat map. Habitat types were assigned as follows:

HUMAN	categories	1,2,3,4,14,23,25,26,43,47
PASTURE	categories	6,7
ARABLE LAND	categories	28,29,30,32,33
WOODLAND	categories	34,37,38,39,40,41

Looking at the three biggest habitat types, pasture, summer cereals and deciduous hardwoods, it can be seen that they are most commonly next to patches from the same super-type (pasture: 73, summer cereals: 35, deciduous hardwoods: 133). Hedges (category 36) occur more frequently next to PASTURE than to any kind of ARABLE LAND (47:36). Only a few of the deciduous hardwood patches have contact with any human-dominated habitat types and none of the other recognised woodland types (categories 38-41) have. Farms (category 23) are most often surrounded by PASTURE (15) than anything else while the number of ARABLE FIELD and WOODLAND next to them is equal (5:5). Some of the industrial properties are next to WOODLAND (4). Both mown (category 6) and unmown grasslands (category 5) are most frequently next to WOODLAND while the number of human-dominated patches next to mown grasslands is nearly twice as high as the number next to unmown grasslands (13:7). Both rivers with and without hedges on their banks are usually next to

PASTURE followed by woodlands (58:14 and 26:18).

2.3. The habitat records

The habitat map provided a classification of habitats which is easy to use and sufficiently standardized to facilitate application in other areas. However, it does not provide any ordinal quantification of habitat characteristics. As briefly mentioned in section 2.1.4, quantification of habitat features permits the evaluation of continuous variation in a way similar to the gradient concept of plant communities (Whittaker (1975)). Within my study area, continuous variation is most likely to occur in areas which are least affected by human influence. Variation on farm land is controlled by the farmer. Thus, habitat quantification should be most fruitful where the scope for variation is least self-evident. In Wytham this would be all the areas that fall inside the main woodland boundary.

Selection of habitat variables is a difficult process. On the one hand, all variables that have any importance for foxes and badgers according to the literature should be considered in order to include the maximum number of resource related parameters; on the other hand there is a practical limit as to what can be achieved (see Principles of Adequacy & Convenience, section 2.1.3). I decided to record parameters that were of a more general nature, such as selected vegetational and structural features, in addition to resource parameters that can be included in a habitat recording scheme. No parameters on rodent abundance were included as there is no variable according to the literature that could be easily measured and be a reliable indicator. Also, no attempt was made to measure the abundance of earthworms, another very important prey type for both foxes and badgers (see Chapter 4). Instead, I decided to dedicate a special study to the investigation of abiotic and biotic factors as possible indicators of

earthworm abundance (see Chapter 3). Some of the variables concerning vegetation and structural features were those recorded during the forestry census (see below) whereas others were ones that I judged to be sufficiently general to have wide applicability (Box 3 provides a list and definitions of the variables finally selected). The resource variables finally selected were easy to record, although their quality as indicators for resource presence varies. For instance, three parameters were selected to indicate the status of rabbit holes and badger and fox earths. For foxes and badgers the parameters are direct indicators of the abundance of a resource. Trout and Tittensor (1983) showed that there was a correlation of 0.557 between number of rabbit holes and abundance of adults, whereas adult abundance and number of sites where faecal pellets were found are correlated at 0.739. However, numbers of adults seen itself proved to be an unreliable indicator of abundance due to the uncontrolled affect of disturbance prior to the count.

In this study, bird remains almost exclusively consisted of remains of wood pigeons. The relationship between number of bird remains found and bird abundance is unknown, but probably the location of pigeon remains indicate suitable catching sites (ie. availability) rather than local variation in pigeon abundance. Pheasants sighted is likely to be a reliable indicator of pheasant abundance since pheasants tend to seek shelter in underground cover during day (see Chapter 3). Their escape tactic in winter relies heavily on camouflage and they fly off only if they are approached to less than two meters. It is difficult to assess human disturbance. One possible way is the recording of the frequency at which human beings occur in a particular area and their activities there (summarised on a 6-value scale defined in Box 3). Together with selected parameters on fox and badger presence the whole set of parameters should give an adequate picture of the habitat structure and a more tolerably reliable account of resource

BOX 2 Variables and scoring methods for habitat census 1974.

VEGETATION Cover

(1) Top cover: above 2.5 meters
(2) Middle cover: 0.5 - 2.5 meters
(3) Bottom cover: 0 - 0.5 meters

measured on a percent scale and entered to the nearest 5 percent.

Ecosigs

(4)	Rubus fruticosus	bramble*
(5)	Pteridium aquilinum	bracken
(6)	Chamaenerion angustifolium	fireweed
(7)	Endymion non-scriptus	bluebell
(8)	Urtica dioica	stinging nettle
(9)	Mercurialis perennis	dog's mercury

* the aggregate

measured on a 0 to 5 scale (see text).

OTHER DATA

(10) Slope
(11) Water presence
(12) mean pH

see text for quantification procedures.

presence.

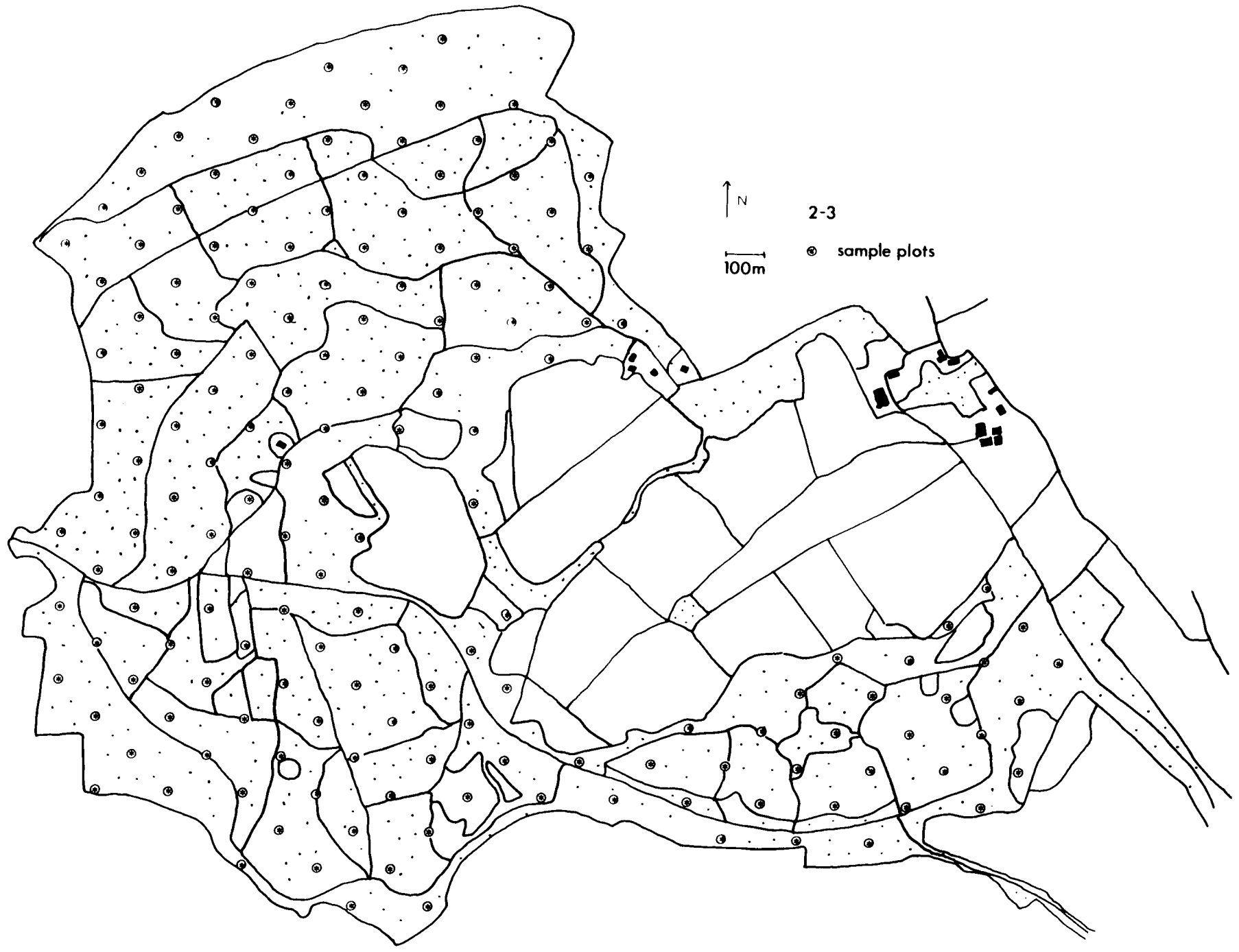
Two data sets are used to evaluate habitat patterns. The first was kindly provided by Dr. H.C. Dawkins, Department of Forestry, Oxford (see Box 2). The second constitutes my own records. The two data sets were recorded for different purposes. Dr. Dawkins designed his sampling scheme as a part of a long-term surveillance system for British woodlands (Dawkins & Field 1977, 1978). His records are exclusively from woodland areas and concentrate on aspects relevant to trees. They are, however, so comprehensive that they can be easily used for other purposes. Dr. Dawkins' data (hereafter referred to as forestry data) do not cover potential fox and badger resources or signs of fox and badger presence, so I had to do additional habitat recording that would provide such information.

2.3.1. Methods: Forestry Data.

Statistical considerations for the two habitat sampling schemes are discussed in detail in Appendix 1. Collection of the forestry data is described by Dawkins and Field (1977, 1978). The following section summarises the procedure they adopted, emphasising those data I extracted from their set (Box 2).

The forestry data from Wytham were collected throughout summer 1974, the soil samples taken mostly in summer 1976. A quadrat of 10 by 10 meters was placed at a distance of 14.142 meter at an angle of 45^{o} northeast from the nearest 100 m intersection point. The position of quadrats of two rows were alternating; in the same row, the distance from one quadrat to the next was 200 m. 164 quadrats were recorded, placed over the entire wood but excluding Bean Wood (Fig 2.3). Variables measured included structural features, e.g. coverage at different height classes, monitoring of important species (ecosigs), number, species and various measurements of trees, all

Fig. 2.3. The central area of the study area with the locations of the sample plots of the Forestry habitat data (regularly dispersed on a 200 m lattice). Woodland stippled, agricultural areas blank, human settlements black. Woodland segmented into the compartments recognized by the Dept of Forestry, Oxford.


N
2-3
100m
sample plots

plant species occurring in the plot, special features, slope, aspect, water, composition of ground cover, pH of three soil depths and data on soil chemistry (anorganic and organic compounds etc.). From these data I compiled the information on coverage, all six ecosig species, slope, water and the mean of all three pH values (Box 2). They were recorded by the following procedures:

1. Coverage was measured for three height levels, bottom cover (0 - 0.5 m), middle cover (0.5 - 2.5 m) and top cover (above 2.5 m), along an imaginary line from the southwest to the northeast corner of the plot. All living material contributed to the value estimated by eye and entered to the nearest 5 percent.

2. The presence of 6 species of ecological significance (ecosigs) was measured by estimating the percentage ground cover over the whole plot from living specimen rooted within the plot. A 0 to 5 scale was used with cover values defined as

0 - absent 1 - up to 5 % cover 2 - 5-25 % cover

3 - 25-50 % cover 4 - 50-75 % cover 5 - over 75 % cover

3. Slope was measured using a relaskop as the greatest overall net slope and entered to the nearest percent as an integer number.

4. Water presence or absence was measured on a 0 to 5 scale:

0 nil

1 some on surface, probably temporary

2 ditch or holes liable to fill

3 small stream or large ditch with water

4 larger stream (never encountered)

5 pond or river (never encountered)

5. Soil pH was calculated using an average of 12 soil samples taken from 3 different depths (0-10 cm, 10-20 cm, 20-30 cm) at four different positions within the plot. Soil samples were taken mostly in 1976.

BOX 3 Variables and scoring methods for habitat census 1982.

VEGETATION

Cover / Eco-sigs / Vege-tation types

1) Top cover — in definition and scoring
2) Middle cover — scale identical with
3) Bottom cover — forestry records.
4) Bramble — (as for cover, but scoring
5) Bracken — (scale 0 to 5, indicating
6) Stinging N. — (increasing abundance)
7) Marsh — area with swampy ground and long reed
8) Grassland — long grass; no human interference
9) Pasture — short grass, regularly grazed
10) Grassley — long grass; regularly mowed
11) Arable land — wheat fields
12) Coniferous — coniferous trees

measured on a 0 to 5 scale identical with the scale used for ecosigs.

STRUCTURE

13) Structural density: density of physical elements, such as plants,wooden pieces, rocks, houses etc on a scale representing relative ease of access by humans
- 0 - no elements present above ground (pasture etc)
- 1 - as in grasslands with some shrubs or in open woodlands with no understorey and widely dispersed trees; straight walking possible
- 2 - woodland with little understorey and trees closer; some detours in walking necessary
- 3 - woodland with some understorey and dense stands of large trees;walking is slow and path has to be selected with care
- 4 - thicket:dense stands of trees with dense understorey and dense shrub and scrub layer; walking difficult and crawling often necessary
- 5 - as in 4 but even worse; not accessible for humans; attempts to cross require considerable support by tools (some areas in Bean Wood)

14)Human Presence/Disturbance: scored on 0 to 5 scale
- 0 - no human disturbance (never scored)
- 1 - researchers and gamekeeper
- 2 - forestry service
- 3 - agricultural; walkers along tracks
- 4 - road
- 5 - human settlements

RESOURCES, FOX AND BADGER INDICATORS

15) number of rabbits seen
16) number of places where rabbit pellets were found
17) number of pheasants sighted
18) number of bird remains found (i.e. bundle of feathers)
19) number of earths found
20) total number of holes whether active or inactive
21) number of recently used holes (fresh digging etc.)
22) number of fox faeces found
23) number of foxes seen
24) number of badger latrines found
25) total number of pits found (see Chapter 4.3)
26) number of pits with fresh droppings

2.3.2. Methods: fox and badger habitats

Data were recorded on variables of four different classes (Box 3): vegetation data, structural data, data on resource presence and data related to fox and badger presence. Altogether 26 variables were measured. Data were recorded by a two-man team (myself and a visiting biologist, Jose Colon) between January 26th and February 16th 1982. Two areas were covered: the Marley Wood/Pasticks area and the Bean Wood/Hill End Camp area. The exact location of the plots is presented in Fig. 2.4. A total of 232 and 209 plots were visited in Marley and HEC area respectively. In practice, we went to a 100 m intersection of the National Grid System marked by an orange pole and recorded the four plots next to it (ie. northeast, southeast, southwest and northwest); the 'central area' was located within the 'base area' by walking a fixed number of steps from the 'pole' corner of the base area (point of origin) using a compass to keep the direction constant. Before commencing the habitat recording we had determined our step size (average length per step) in trial runs and found it highly constant for both of us. Results for such runs are shown for one of us in Table 2.4. We also trained our ability to follow a straight line through woodland in several trials. During the habitat recording the person standing at the point of origin continuously checked the progress of the person walking, correcting if necessary. Under extreme conditions (thickets, marshland) this had to be repeated until we were sure that the central area was satisfactorily located. As a result of our training prior to the actual recording we feel confident about our method but do not recommend it for applications involving distances much larger than those which we used (ca. 40 m). Within the central area, cover values, structural density, and ecosigs were assessed. First, a score for each of the two halves of the

Fig. 2.4. Central and southern parts of the study area (computerized habitat map), with the two habitat record areas represented by dotted lines: top area is MARLEY, bottom area is HILL END CAMP.

Fig. 2.4

HABITAT RECORD AREAS



Table 2.4 Constancy of step size for 7 trial walks through woodland.

TRIAL WALK NO.	DISTANCE [m]	NUMBER OF STEPS	STEPS/METER
1	300	407	1.36
2	222	288	1.3
3	222	259	1.2
4	177	226	1.27
5	100	142	1.42
6	100	133	1.33
7	94	112	1.2

MEAN = 1.297 steps/meter equivalent to 0.77 meter/step
S.D. = 0.075 or 5.8%

quadrat was estimated and from that the final score for the total central area determined. Next, a zigzag course was walked on a circle approximately half way between the border of the base area and the central area. This was done with one person standing in the central area and checking the progress of the person walking the zigzag course. We attempted to cover the entire area between the central area and the border of the base area as comprehensively as possible and much time was spent to achieve this. Thus, the remaining variables (vegetation types, resource and fox & badger indicators) were assessed for the entire base area.

2.3.3. Results

I shall first present a short summary of the raw habitat data and then proceed with their analysis.

Table 2.5 presents a summary of the forestry data with the number of plots that had scores greater than zero. Most of the 162 plots considered had top, middle and bottom canopies greater than zero indicating a varied and complex structure. Amongst the six ecosig species, bramble was most widely spread and occurred in ca 85% of all plots. Fireweed was nearly as widespread as bramble, while stinging nettles and bluebells occurred less frequently. Most plots did not have any indication of water on the surface (only 8 plots) and are situated on some kind of slope, corresponding to the two-hill layout of Wytham Woods.

Table 2.6 lists the results for the 1982 habitat census for each of the two study sites separately and combined. Marley Area is mostly dominated by woodland; 212 out of 232 plots are situated inside the woodland boundary. Hill End Camp/Bean Wood Area however includes both woodland (Bean Wood) and the pastures and grasslands around the camp. This is reflected by the high number of plots with some proportion of pasture and grassley. Other main

Table 2.5. Number of sample plots with values greater than zero for each habitat variable measured during forestry census, summer 1974.

NUMBER	VARIABLE	NO. OF PLOTS
1	Top cover	155
2	Middle cover	148
3	Bottom cover	161
4	Bramble	141
5	Bracken	98
6	Fireweed	136
7	Bluebell	38
8	Stinging nettle	61
9	Dog's mercury	119
10	Slope	151
11	Water	8
12	Mean pH	162

total number of plots recorded : 164 plots
number of plots used in all analyses: 162 plots

2 plots excluded from all analyses as no pH value available

Table 2.6 Number of sample plots with values greater than zero for each habitat variable measured in 1982.

NUMBER	VARIABLE	NUMBER OF SAMPLE PLOTS IN MARLEY AREA	H.E.CAMP AREA	TOTAL AREA
1	Top cover	202	61	263
2	Middle cover	200	59	259
3	Bottom cover	198	200	398
4	Marsh	12	9	21
5	Grassland	29	16	45
6	Grassley	8	35	43
7	Pasture	2	78	80
8	Arable Land	12	41	53
9	Coniferous W.	57	0	57
10	Struct.Density	197	62	259
11	Bramble	119	37	156
12	Bracken	60	0	60
13	Sting. Nettles	43	1	44
14	Rabbits seen	5	1	6
15	Rabbit pellets	84	32	116
16	Pheasants	11	3	14
17	Feathers	14	1	15
18	Number of earths	39	22	61
19	All holes	39	22	61
20	Active holes	23	11	34
21	Latrines	14	0	14
22	All pits	14	0	14
23	Active pits	9	0	9
24	Foxes seen	1	0	1
25	Fox faeces	62	10	72
26	Human disturbance	223	209	432
total no. of plots consid.		226	209	435
total no. of plots record.		232	209	441

6 PLOTS in Marley Area were excluded from all analyses as the data for resource and fox/badger presence are missing.

differences between the two study sites are the absence of any kind of coniferous woodland and bracken and badger latrines from Hill End Camp. Only at one place were bird remains found and the number of fox faeces found in the sample plots declined from 62 (Marley) to 10 (HEC). Some variables had only rare positive entries: during the entire three weeks of habitat recording, only one fox was sighted in Marley and altogether five rabbits were seen at both study sites.

The data were used to run standardized principal components analyses (PCA) and detrended correspondance analysis (DCA) (see Appendix 2 for a detailed discussion of statistical methods and interpretation of the results). The PCA (R-mode) were run using the GENSTAT statistical package available on the University's VAX 11/780 computer, with correlation matrix option. This transforms the raw data scores to units of deviation from the mean of each variable scaled to units of variance, resulting in a correlation matrix of variables. This is called a standardized PCA and comparative studies have shown that this type of PCA is generally superior to other PCA options (see Appendix 2). The output consists of a correlation table which shows the correlation of each of the original variables with the new axes (thus indicating the relative contribution of each original variable to the new axes, the principal components), the scores of each sample on the new components and a plot of the samples on selected axes.

DCA was run using program CP40 (DECORANA) of the Cornell Ecology Programs series which was obtained by the Oxford University Computing Sevice and implemented on the University's VAX. Program CONVERT was written to transform the original habitat data into a format suitable for input to DECORANA. Program CONVERT also allowed the elimination of specific variables and/or samples from the data set and automatically excluded all samples that had not a single positive entry for any of the remaining variables, as DECORANA does not permit either samples or variables that have

Table 2.7. Summary of Principal Components Analyses (PCA) and Detrended Correspondance Analyses (DCA) runs of the 1974 and 1982 habitat data.

RUN NO.	TYPE	DATA SET	VARIABLE SET	NO. VAR.	NO. SAMP.	EIGENVALUES FIRST	SECOND	THIRD	FOURTH
1	PCA	For.	environm.	3	162	1.104	0.977	0.919	-
2	PCA	For.	vegetation	9	162	2.146	1.663	1.256	0.913
3	PCA	For.	veget. + env.	10	162	2.186	1.746	1.461	1.112
4	PCA	For.	select.veget.	6	162	1.921	1.309	0.930	0.858
5	DCA	For.	select.veget.	6	162	0.133	0.077	0.052	0.033
6	DCA	For.	vegetation	9	162	0.128	0.075	0.061	0.039
7	DCA	Marl.	select.veget.	6	* 212	0.322	0.105	0.081	0.041
8	DCA	Marl.	vegetation	10	* 212	0.348	0.202	0.111	0.082
9	DCA	Marl.	vegetation	13	226	0.737	0.393	0.253	0.120
10	DCA	Both	resources	6	149	0.855	0.143	0.050	0.021
11	DCA	Marl.	predator/prey	6	132	0.581	0.259	0.179	0.074
12	DCA	HEC	predator/prey	6	50	0.871	0.401	0.144	0.040
13	DCA	Both	predator/prey	9	183	0.837	0.652	0.241	0.101
14	DCA	Marl.	resour.+veget.	19	226	0.725	0.315	0.240	0.152
15	DCA	HEC	resour.+veget.	15	207	0.820	0.429	0.188	0.142
16	DCA	Both	resour.+veget.	19	433	0.793	0.334	0.247	0.197
17	DCA	Marl.	all variables	20	226	0.538	0.260	0.210	0.164
18	DCA	HEC	all variables	16	209	0.613	0.333	0.209	0.085
19	DCA	Both	all variables	23	435	0.564	0.275	0.226	0.190

* Run 7 & 8 excludes all plots that were outside the woodland boundary by more than 50 % of their area.

not a single positive entry. As a result, different DCA runs operated on a different number of samples. Only in Runs 7 and 8 were plots excluded specifically, in all other cases the number of samples for each run is simply the number of samples that had at least one positive entry for the variables considered.

Altogether 19 ordinations were run (Table 2.7). 4 PCA and 2 DCA were run on forestry data and the remaining 13 on my own data set. Table 2.7 indicates in a shortlist the types of variables selected for each run, the actual number of variables considered, the number of samples considered (ie. with positive entries) and the first four eigenvalues of each analysis. In PCA, eigenvalues are produced by the eigenanalysis of the transformed samples-by-variables matrix (into either a variance-covariance or correlation matrix) and indicate the variance accounted for by the relevant principal component. In recipropcal averaging and DCA, the eigenvalues indicate the amount of contraction in the variable scores achieved by the ordination. The axes are then ordered according to their eigenvalues so that the first component or the first DCA axis has the highest eigenvalue, ie accounting for the highest amount of variance. Thus, a high value indicates a lot of variation accounted for. The eigenvalues of PCA and DCA are not directly compatible in their absolute values (cf. RUN 4 (PCA) and 5 (DCA) and RUN 2 (PCA) and RUN 6 (DCA) on identical data sets for both ordination methods), but what is of interest are the differences in eigenvalues of the first few axes: if the first axis has a high eigenvalue and the following axes very low values in relation to the first (see e.g. RUN 10), most of the variation in the data is summarized in one dimension by the first axis while the following dimensions contribute relatively little. However, if the converse is true, the second, third etc. axis might be important for the understanding of the variation in the data.

Results of the 19 runs are presented in Table 2.8 (PCA correlation

Table 2.8 Correlation of original variables with principal components for RUNS 1 to 4 (cf text and Table 2.6).

RUN 1: environmental variables only.

	PC 1	PC 2	PC 3
Slope	0.6624	0.0056	0.7491
Water	-0.5263	0.7151	0.4601
Mean pH	-0.5331	-0.6990	0.4766

RUN 2: vegetation variables only.

	PC 1	PC 2	PC 3	PC 4
Top cover	0.4463	-0.1770	0.1692	0.1650
Middle cover	-0.3754	0.1473	-0.0787	-0.0756
Bottom cover	-0.3265	-0.5036	0.1611	-0.3580
Bramble	-0.2409	-0.1031	0.7001	-0.2470
Bracken	-0.5645	-0.0192	-0.0294	0.1697
Fireweed	0.0941	-0.6149	-0.2210	-0.0060
Bluebell	-0.3848	0.1530	-0.1153	0.5021
Stinging nettle	0.0458	-0.2486	0.4666	0.6882
Dog's mercury	-0.1331	-0.4680	-0.4103	0.1529

RUN 3: vegetation and environmental variables.

	PC 1	PC 2	PC 3	PC 4
Top cover	-0.4105	0.0106	-0.3147	0.0451
Middle cover	0.3699	0.0713	0.1512	-0.0600
Bottom cover	0.2750	-0.5120	-0.0968	0.3202
Bramble	0.2618	-0.0144	-0.4076	0.5391
Bracken	0.5543	-0.0830	-0.0105	-0.1745
Fireweed	-0.1675	-0.6274	-0.0130	-0.1083
Bluebell	0.3979	0.1055	0.0530	-0.2242
Stinging nettle	-0.0097	-0.0669	-0.5990	-0.1083
Dog's mercury	0.1128	-0.4249	0.0057	-0.3231
Slope	-0.0365	-0.1550	-0.3123	-0.2711
Water	0.0959	0.0209	0.0317	0.5108
Mean pH	-0.1831	-0.3336	0.4921	0.2413

RUN 4: selected vegetation variables.

	PC 1	PC 2	PC 3	PC 4
Top cover	0.4614	0.3363	0.4621	0.2725
Middle cover	-0.3969	-0.2869	0.6943	0.0521
Bottom cover	-0.4307	0.3729	-0.4595	0.2569
Bramble	-0.3295	0.5503	0.2389	0.4469
Bracken	-0.5789	-0.1060	0.1035	-0.2893
Stinging nettle	0.0193	0.5929	0.1596	-0.7574

matrices) and Figs. 2.5 to 2.19 (DCA runs; the number of the run is identical with the second digit of the figure number to facilitate comparison of figures and RUN numbers as listed in Table 2.7). Ordinations were run for two main purposes: comparison of ordination techniques and analysis of the variation of habitat parameters in the two habitat censuses.

COMPARISON OF ORDINATIONS. RUNS 4 and 5 and RUNS 2 and 6 used vegetation variables to compare the two ordination techniques. In RUNS 2 and 6 all vegetation variables were used while in RUNS 4 and 5 only those for which I had data from my own recordings (RUN 7 uses DCA to ordinate these). A comparison of Fig. 2.5 and Table 2.8 shows that for RUNS 4 and 5 both ordinations are similar in that they group MID COVER, BOT COVER and BRAMBLE together on the first axis (ie. the correlation coefficients are similar) placing BRACKEN a little aside at one end and TOP COVER and STINGING NETTLES at the other end. The exact positions of the variables differ, however. On the second axis, DCA groups BOT COVER, BRAMBLE and BRACKEN closely together while there is no such clustering evident in the PCA. With the exception of BOT COVER, PC 3 corresponds far better to DCA axis 2, suggesting that PC 2 might perhaps be a quadratic distortion of PC 1. A similar outcome, although less clearly, is shown by RUNS 2 and 6 (Table 2.8 and Fig 2.6), supporting the superiority of DCA over PCA. Inspection of the actual correlation values in RUNS 2 and 4 reveals that the first component (PC 1) has a positive correlation only with TOP COVER, no correlation with STINGING NETTLES and FIREWEED, but otherwise is negatively correlated with the remaining variables. I interpret this as being primarily due to a light gradient. RUN 1 shows that for the forestry data, SLOPE and WATER are, not unexpectedly, negatively correlated. According to PC 2 (RUN 1), increased presence of water corresponds to a more acidic soil. This however is based on only 8 plots with water present (Table 2.5) while

FIG 2.5 *DCA OF FORESTRY DATA: COVER AND SELECTED ECOSIGS ONLY*

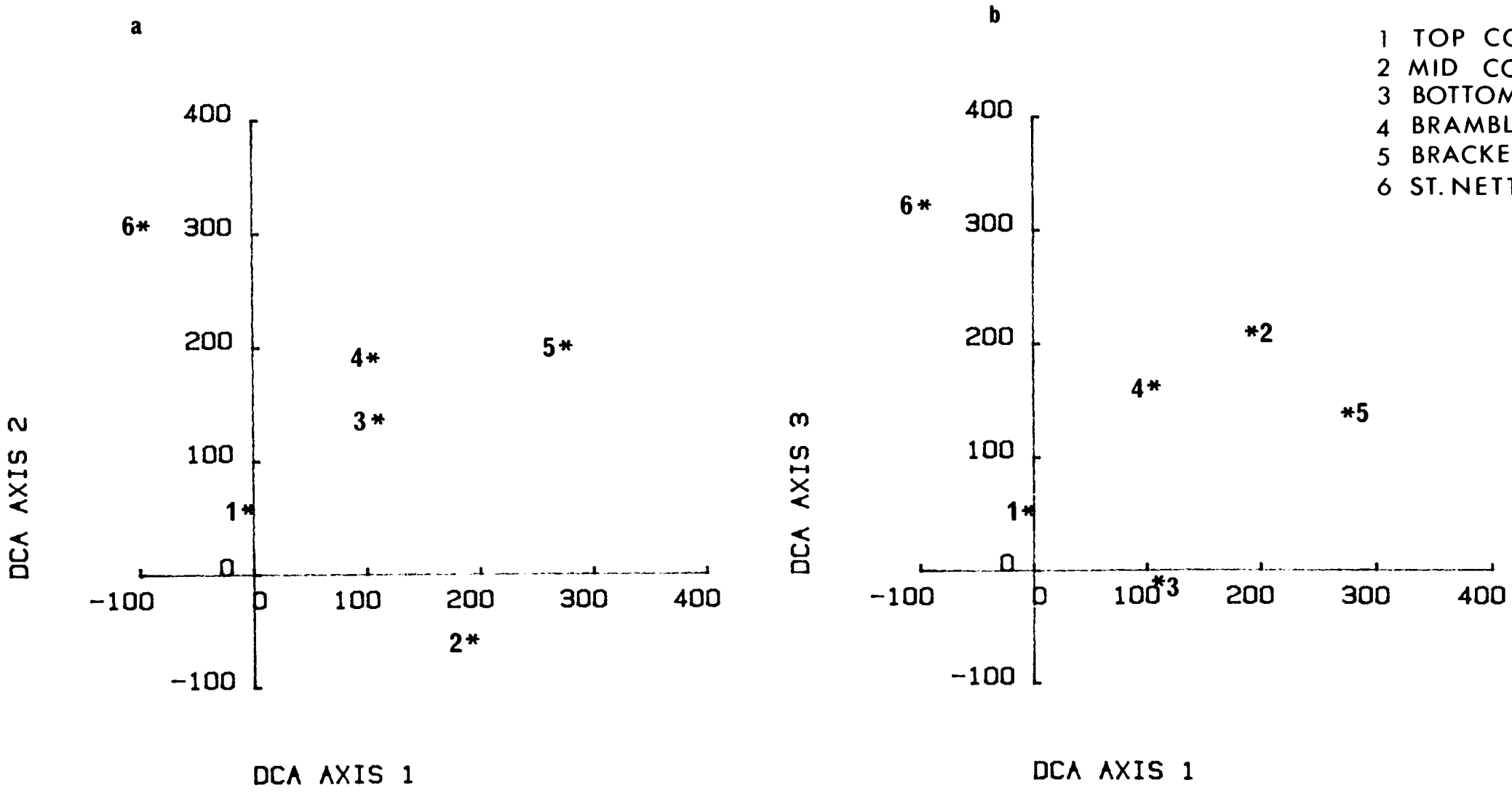


FIG 2.6 *DCA OF FORESTRY DATA: COVER AND ALL ECOSIGS ONLY*

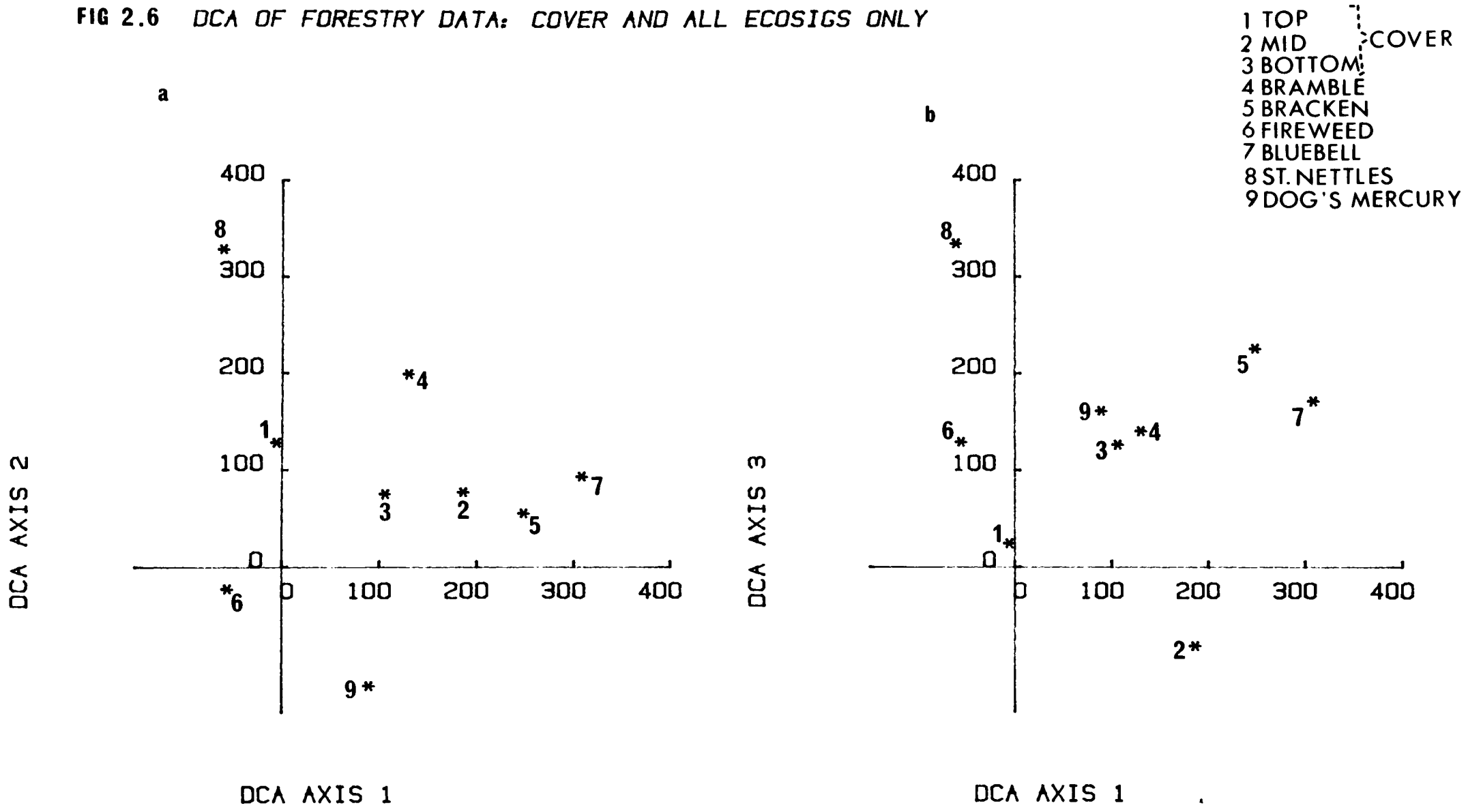
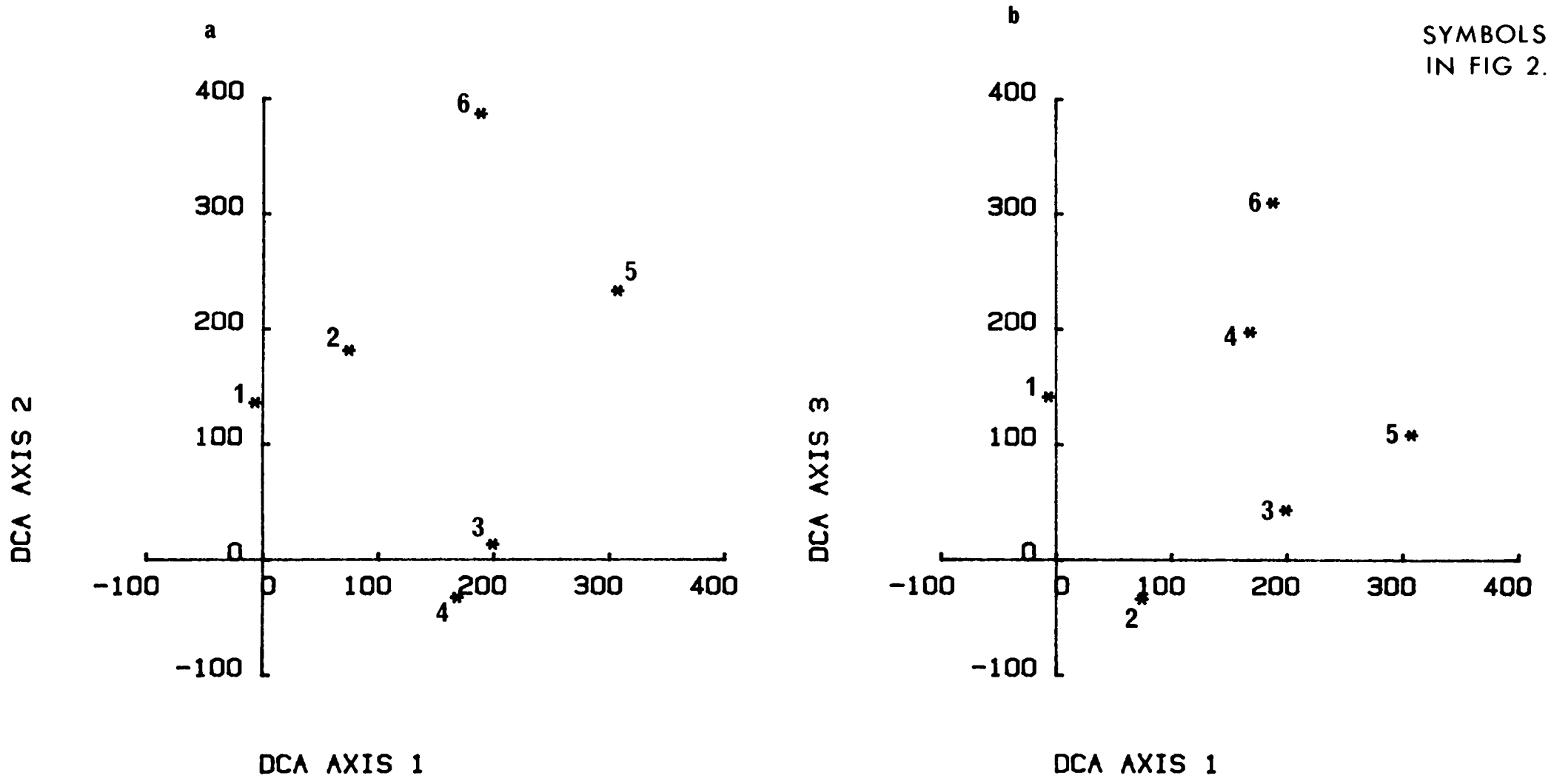


FIG 2.7 *DCA OF MARLEY AREA (DATA FROM 1982): SELECTED VEGETATION VARIABLES ONLY FROM WOODLAND PLOTS*



the pH can range from 4.1 to 8.7 in areas without apparent presence of water and thus should not be taken too importantly. If all environmental parameters and vegetation features are ordinated together, the correlations of the vegetation variables are reversed in sign but not very much in value (PC 1 of RUN 3). If, however, only pH is added to the vegetation variables, the signs of the correlations correspond to the other PCA runs.

In summary, DCA and PCA yield similar results for the first axis or component while DCA avoids quadratic distortions and is more reliable in accounting for the underlying variation in the higher axes. The vegetation exhibits a clear pattern, with most of the vegetation variables negatively correlated to top cover. Slope and water have some influence on the sign of the correlation of the variables with the PC 1 while consideration of pH confirms the pattern established by the vegetation variables alone.

COMPARISON OF FORESTRY CENSUS AND 1982 CENSUS. A comparison of the forestry data and my own records is interesting for several reasons. First of all it permits me to establish how much basic vegetational features correspond at different times of year (forestry census: summer; 1982 census:winter), and if such a correlation can be established, does an increase in detailed information reveal any additional information on the composition of the habitat (the forestry data covered 0.5% of their study area while my vegetation data cover 1% of my study site which is only part of the forestry's total study area)?

RUNS 5 and 7 are DCA ordinations for the same variables recorded during the forestry and the 1982 census. I excluded all samples drawn from plots of which more than 50% lay outside the woodland boundary. The results are presented in Fig. 2.5 and Fig. 2.7. As can be seen from Table 2.7, the ordination of the winter data (RUN 7) is more powerful than for the summer data (RUN 5) (eigenvalue for the first axis: winter 0.322, summer 0.133).

The reduced vegetation makes different habitats appear more clearcut and shifts emphasis towards trees and shrubs that are less reduced in presence than herbs. However, the structure remains in general the same: DCA axis 1 is very similar for both studies: TOP COVER is separated from a cluster comprising MID COVER, BOT COVER and BRAMBLE while BRACKEN is set apart. The only difference concerns STINGING NETTLES, which is an annual plant and whose distribution in winter is probably not representative of its summer distribution. The second axis reveals the differences between seasons: MID COVER is closer to TOP COVER in winter than in summer and MID COVER and BOT COVER/BRAMBLE exchanged their relative positions. In summary, both censuses reveal the same dominating feature on the first axis while seasons are distinguished on the second axis.

ANALYSIS OF 1982 CENSUS. In the following I will discuss the variation amongst the various components of the habitats at both study sites of the 1982 census. I will first continue the description of the vegetational features of Marley (RUNS 8 and 9), then look at the resource parameters alone (RUN 10), add predator parameters to the resources (RUNS 11 to 13), and finally look at the combination of vegetation and resource parameters (RUNS 14 to 16) and all parameters together (RUNS 17 to 19).

In general, variables were first selected according to whether they fitted into the category in question. Program CONVERT indicated then, which variables did not have enough positive entries. As a general rule, variables with positive entries in less than 5% of the cases were excluded (unless stated otherwise), even if they might have been appropriate for the particular run in question. Thus, it is possible that runs of the same kind can have different sets of variables as indicated in Table 2.6 (e.g. RUNS 14 and 15).

RUN 8 ordinates all vegetation variables present in the woodland plots (Fig 2.8). Five groups emerge: CONIFEROUS WOODLAND, STRUCTURAL DENSITY/TOP COVER/MID COVER, MARSHLAND, BOT COVER/BRAMBLE, and GRASSLAND/BRACKEN/STINGING NETTLES. If the remaining Marley plots are added (RUN 9, Fig 2.9), including the rarely occuring types GRASSLEY and PASTURE, the vegetation ordination is completely dominated by the three added variables (Fig. 2.9a, variables 6,7, and 8) and the woodland patterns are deferred to the third axis: compare the arrangement of variables that occur both in Fig. 2.8 and Fig. 2.9b along the third DCA axis! On the first axis of RUN 9, this is due to the fact that ARABLE LAND is very different from everything else which compresses the other variables into a tight cluster. The second axis demonstrates the tendency of reciprocal averaging and DCA to place rare variables at the opposite end of the spectrum, deferring the remaining variation to the third axis. Note that the increased number of variables in RUN 8 results in a slight increase of the eigenvalue of the first axis compared with RUN 7 but a doubling of the eigenvalue of the second axis, indicating that the 6 variables of RUN 7 present only part of the total vegetation variation.

RUN 10 (Fig. 2.10) looks specifically at all the resource dimensions, combining data from both study sites. FEATHERS (ie. bird remains) and PHEASANTS are placed at the two ends of the spectrum. This might be partly due to the already mentioned tendency of correspondence analysis to place rare variables at opposite ends. Fig. 2.11b and Fig. 2.13b show, however, that there must also be some other factors accounting for the difference. All except one of the bird remains found were wood pigeons, the one exception was a pheasant. Fig. 2.10 shows also a separation of MOS EARTHS from RABBIT PELLETS and a more pronounced separation of MOS ACT. HOLES from RABBIT PELLETS, implying that the number of rabbit pellets is a less

FIG 2.8 *DCA OF MARLEY AREA (DATA FROM 1982): VEGETATION VARIABLES ONLY FROM WOODLAND PLOTS*

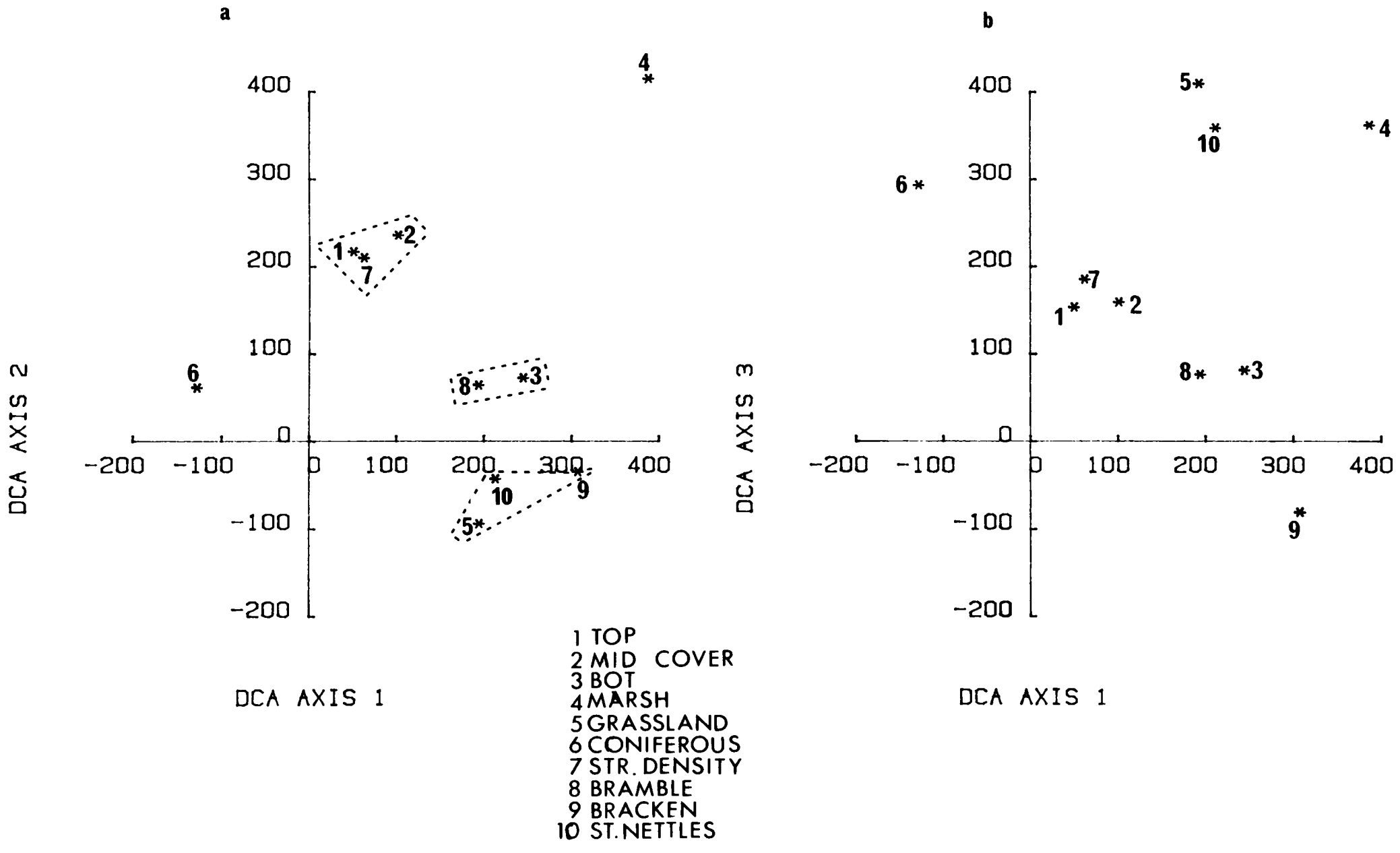


FIG 2.9 *DCA OF MARLEY AREA (DATA FROM 1982), VEGETATION VARIABLES ONLY*

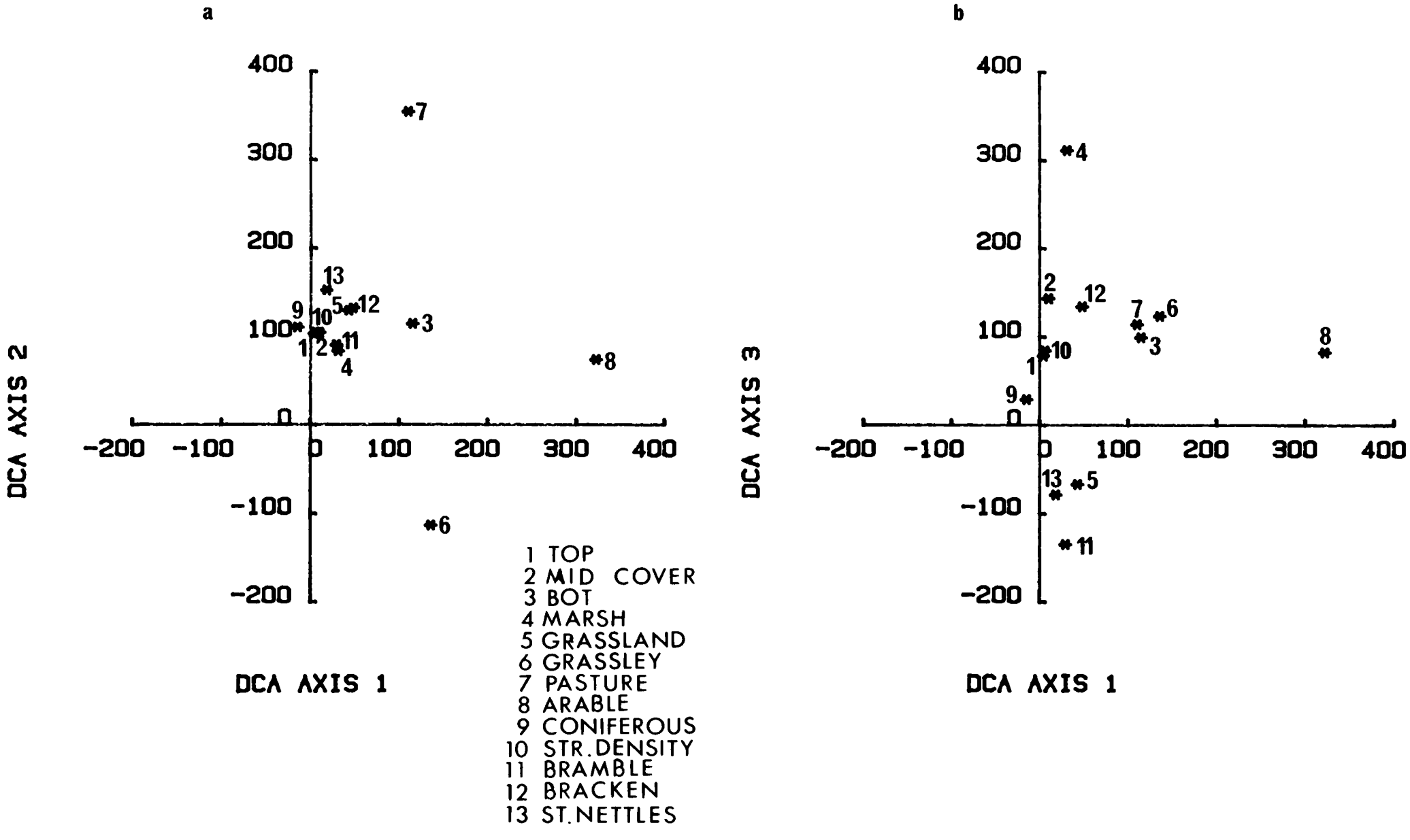
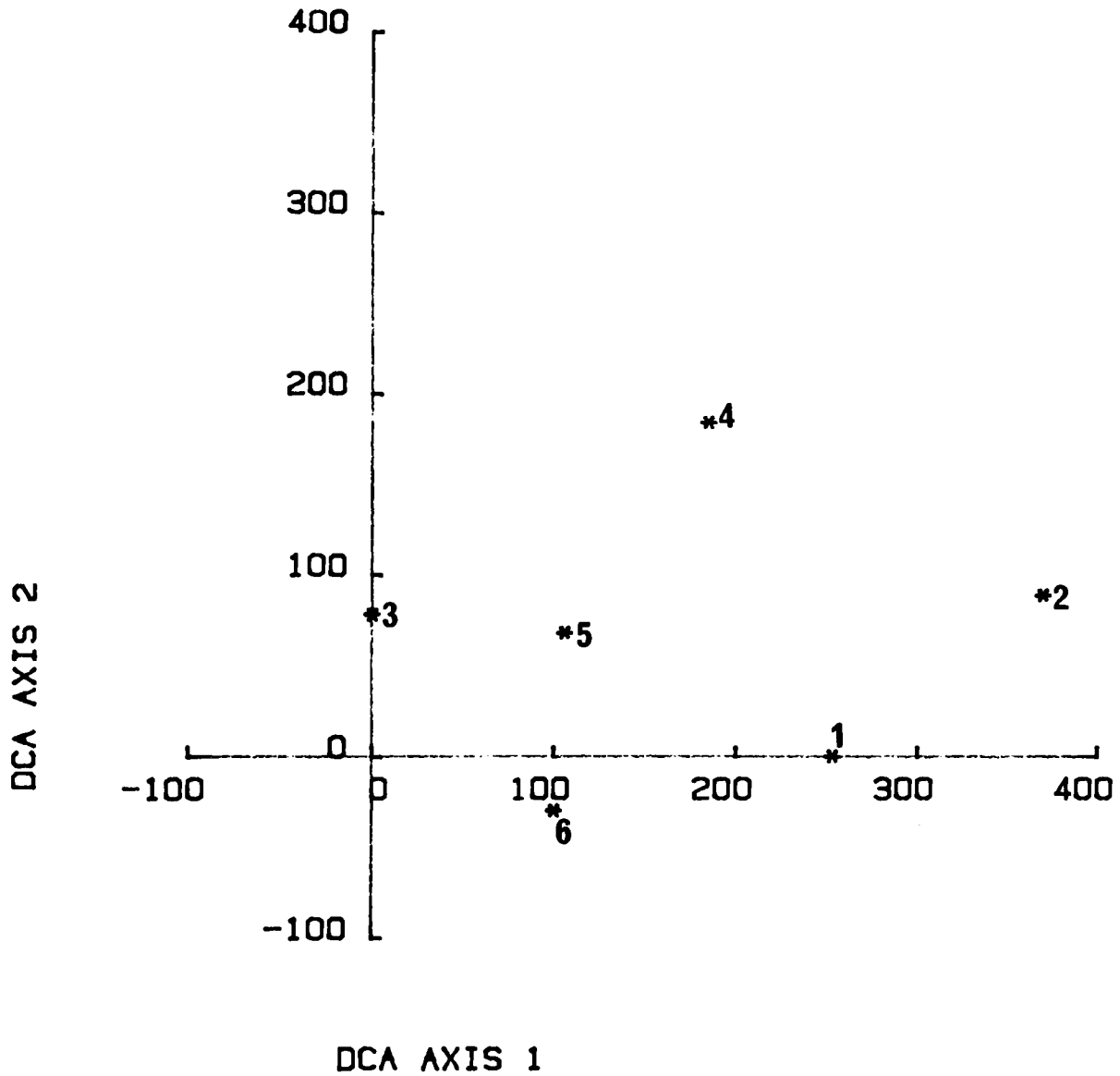


FIG 2.10 *DCA OF ALL WYTHAM DATA (1982): RESOURCE VARIABLES ONLY*



1 RABBIT PELLETS
2 PHEASANTS
3 FEATHERS
4 NOS EARTHS
5 NOS HOLES
6 NOS ACT. HOLES

reliable indicator for adjacent active holes than for earths in general and that rabbits might drop their pellets at some distance from active holes in a habitat different from that where the hole can be found. In fact, many places with rabbit pellets are at a distance of 50 to 100 m from an active hole and thus likely to fall into a different habitat. It might frequently occur that fresh rabbit pellets are placed more closely and indiscriminantly to old, unused holes (explaining the chosen correspondence of DCA scores). This would have important implications for a fox assessing rabbit activity and distribution from the occurrence of rabbit pellets.

If predator parameters are added to resource parameters (RUNS 11 to 13, Fig. 2.11 to 2.13), some interesting new patterns appear. LATRINES (definition see Box 3) is separated from the other parameters on the first two axes if both study areas are combined (Fig. 2.13) and more pronounced on the third axis for Marley only (Fig. 2.11). FOX FAECES appears as part of the central cloud, if both sites are combined (Fig. 2.13) but is placed at the end of the spectrum on axes 2 and 3 for Hill End Camp (Fig. 2.12), axis 2 and 3, and axis 2 of Marley (Fig. 2.11). FOX FAECES and NOS EARTHS are close for both sites combined (Fig. 2.13) similar to either Marley or Hill End Camp alone - but FOX FAECES and NOS HOLES/NOS ACT. HOLES are at a greater distance, similar to RABBIT PELLETS. In general, FOX FAECES appear to correspond fairly closely to parameters of prey activity (PHEASANTS and RABBIT PELLETS). FOX FAECES appear relatively close to RABBIT PELLETS if both sites are combined, and also in each study site. PHEASANTS and FOX FAECES are close on most axes except axis of RUN 13, and axes 1 and 3 of RUN 11. A general result of RUNS 11 to 13 is that they have high eigenvalues (Table 2.6) but a less clear clustering than in the vegetation ordinations. Thus, amongst the vegetation parameters are several correlated parameters which express a very similar type of variation, while each predator/prey variable is more distinct. This result makes intuitive sense.

FIG 2.11 *DCA OF MARLEY AREA (DATA FROM 1982): PREDATOR/PREY VARIABLES ONLY*

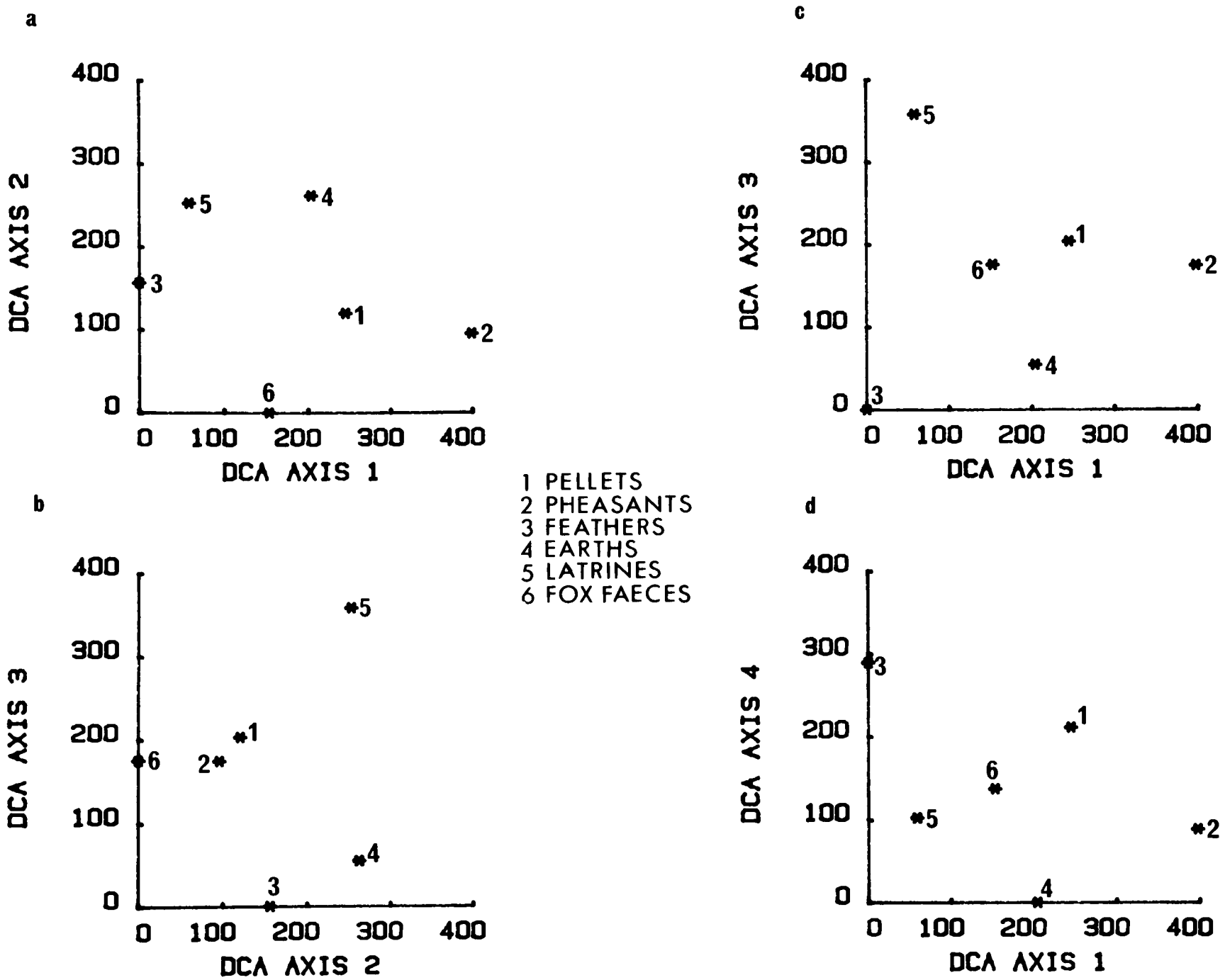


FIG 2.12 DCA OF HILL END CAMP & BEAN WOOD AREA (DATA FROM 1982): PREDATOR/PREY VARIABLES ONLY

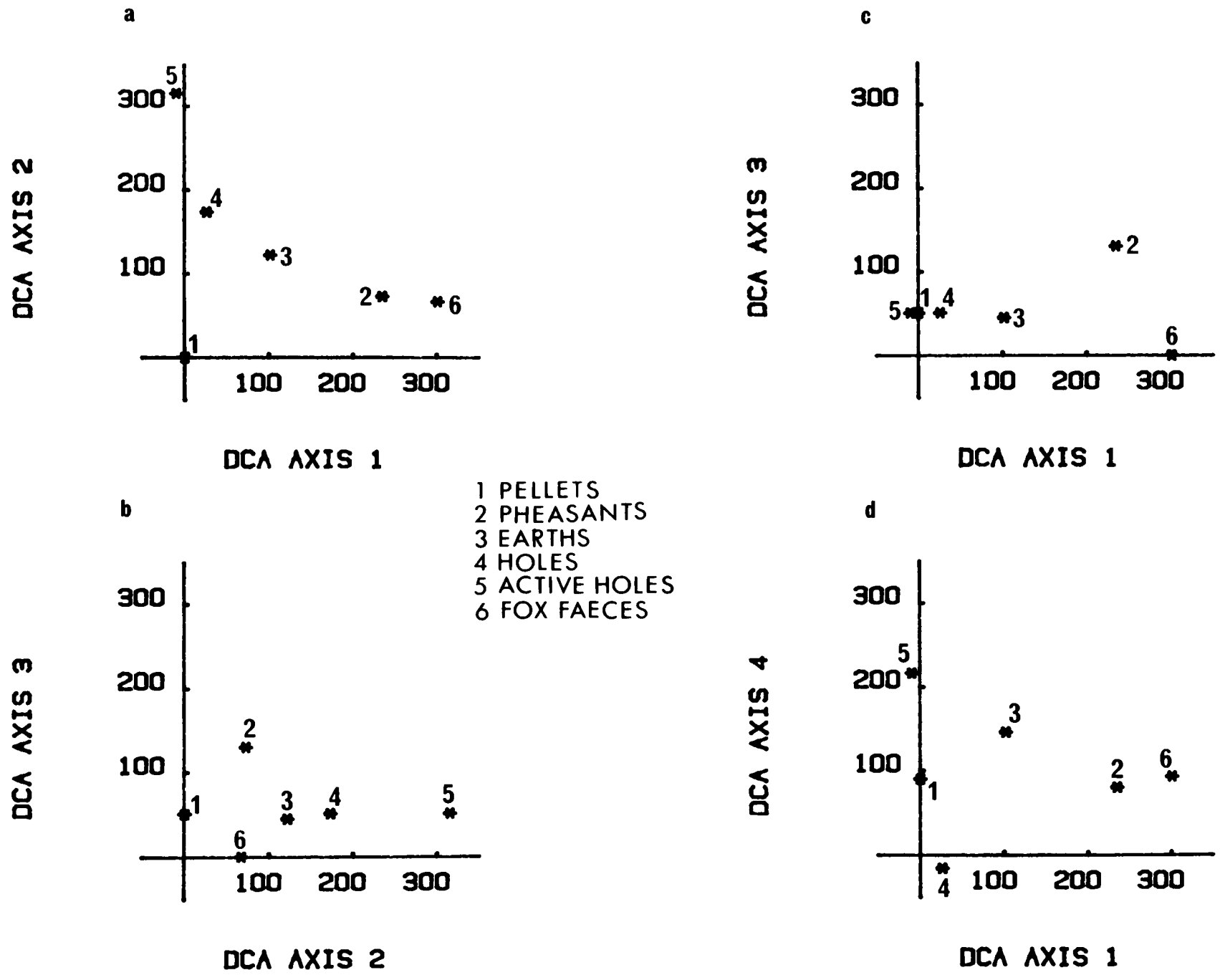
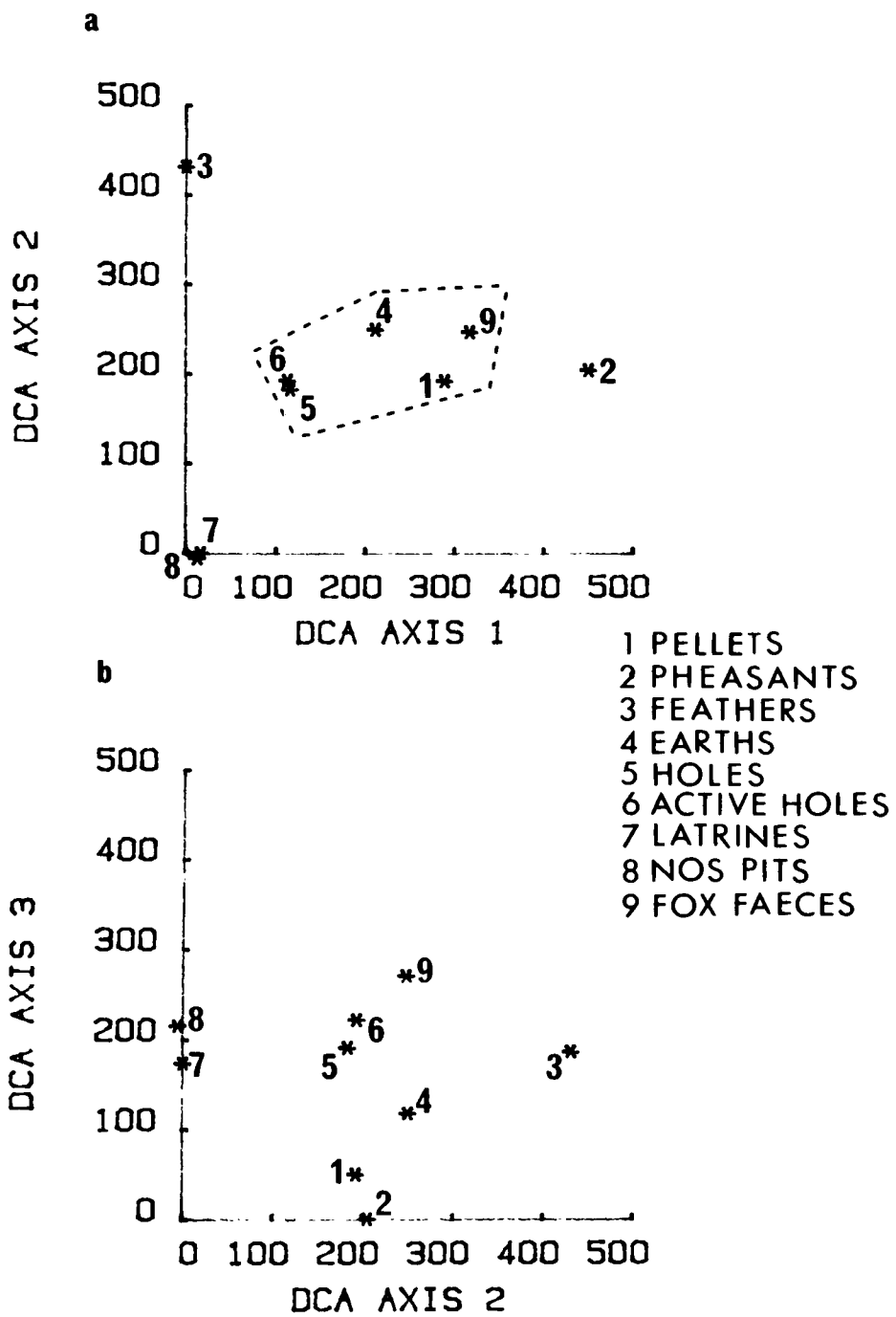


FIG 2.13 *DCA OF ALL WYTHAM DATA (1982): PREDATOR/PREY VARIABLES ONLY*

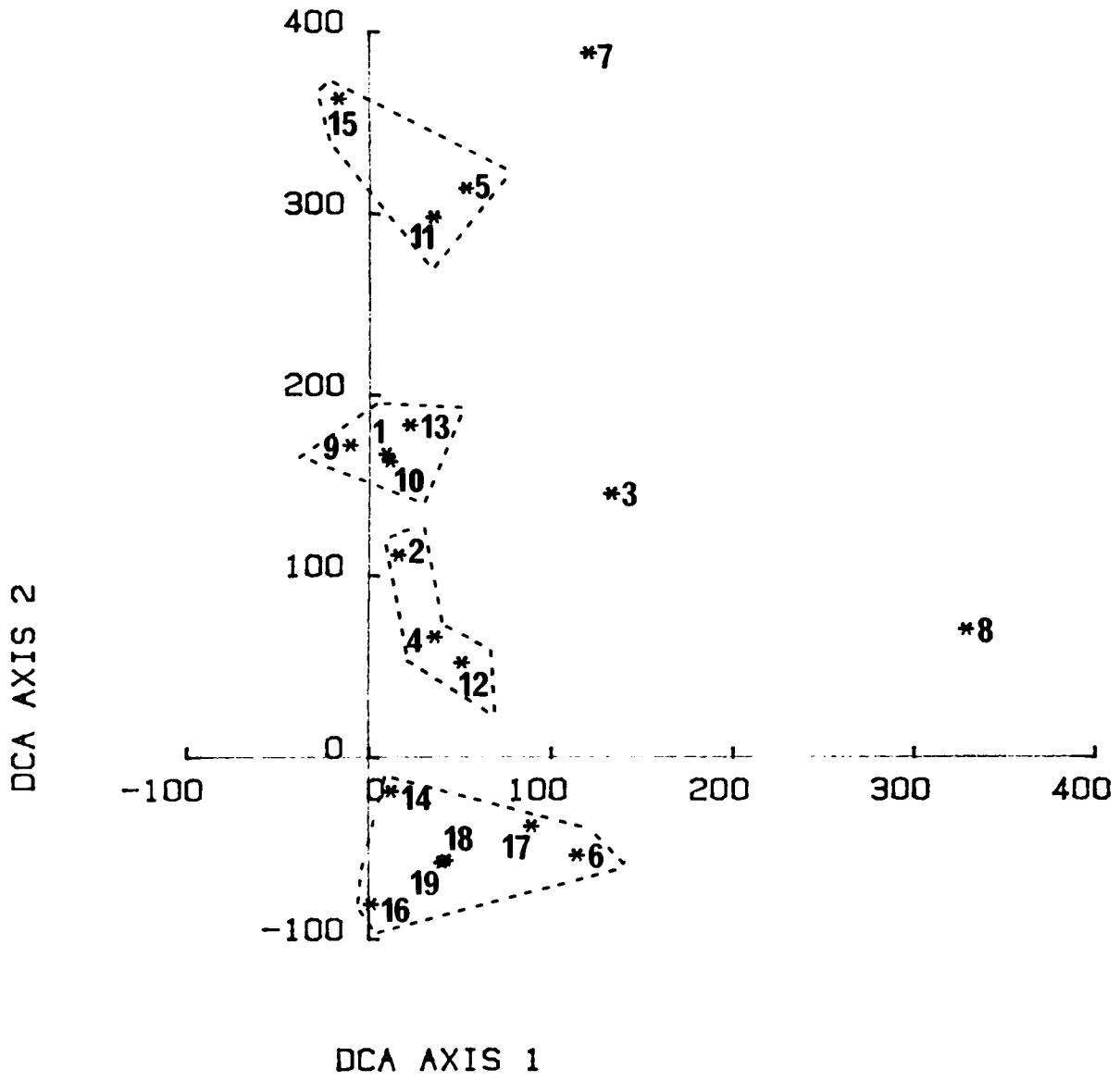


RUNS 14 to 16 provide ordinations of resource and vegetation parameters together. If both study areas are taken together (Fig. 2.16) the first DCA axis expresses a gradient of coverage or structural density (or light penetrability) ranging from very open areas (ARABLE and PASTURE) over GRASSLEY and long GRASSLAND to the densest type, CONIFEROUS WOODLAND. Along this axis the resource parameters are concentrated in one block at a position of medium density corresponding to the zone from GRASSLEY to BRACKEN. Within this zone of medium density the second axis distinguishes the vegetation parameters (the clusters with variables 4, 5, 11 to 13 and 1, 2, 10) from the resource parameters. This demonstrates that resource parameters show a kind of variation which is not completely minimised in vegetation features. This makes intuitive sense; Chapter 3 will deal in detail with the environmental prerequisitves of certain resources.

Within the block of resource parameters (variables 6, 4 to 19 of Fig. 2.16) NOS EARTHS is more oriented towards the side of open, low structural density while RABBIT PELLETS and NOS ACTIVE HOLES covary with denser vegetation and NOS HOLES assumes a position between NOS EARTHS and NOS ACTIVE HOLES. This trend may be explained by vegetational changes which leave the old, unused earths (included in NOS EARTHS and NOS HOLES but not in NOS ACTIVE HOLES) in the open; they may have in fact been left in favour of sites in a better cover. Earths in areas with denser cover have a higher number of holes and thus NOS HOLES is placed between NOS ACTIVE HOLES and NOS EARTHS. The 'density value' of NOS ACTIVE HOLES and RABBIT PELLETS corresponds to the value of MARSH (variable 4 in Fig. 2.16) and is slightly less than BRACKEN or STINGING NETTLES (variables 12 and 13), while PHEASANTS and FEATHERS correspond to GRASSLAND and GRASSLEY, respectively.

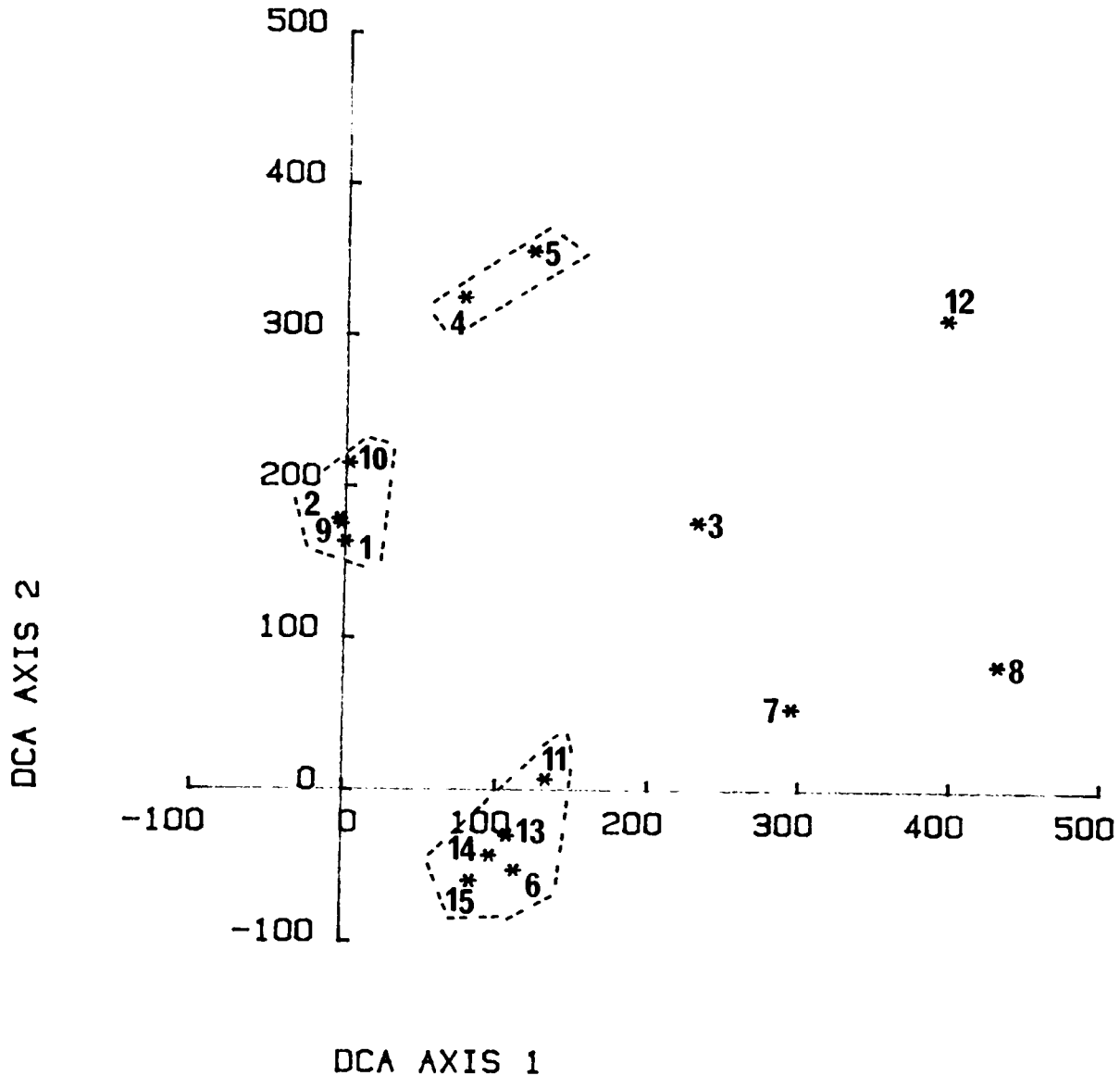
The picture for Marley (Fig. 2.14) and Hill End Camp (HEC, Fig. 2.15) shows some interesting deviations from the pattern for the entire set of data (Fig. 2.16). The interpretation of the first DCA axis remains the

FIG 2.14 *DCA OF MARLEY AREA (DATA FROM 1982): RESOURCE AND VEGETATION VARIABLES ONLY*



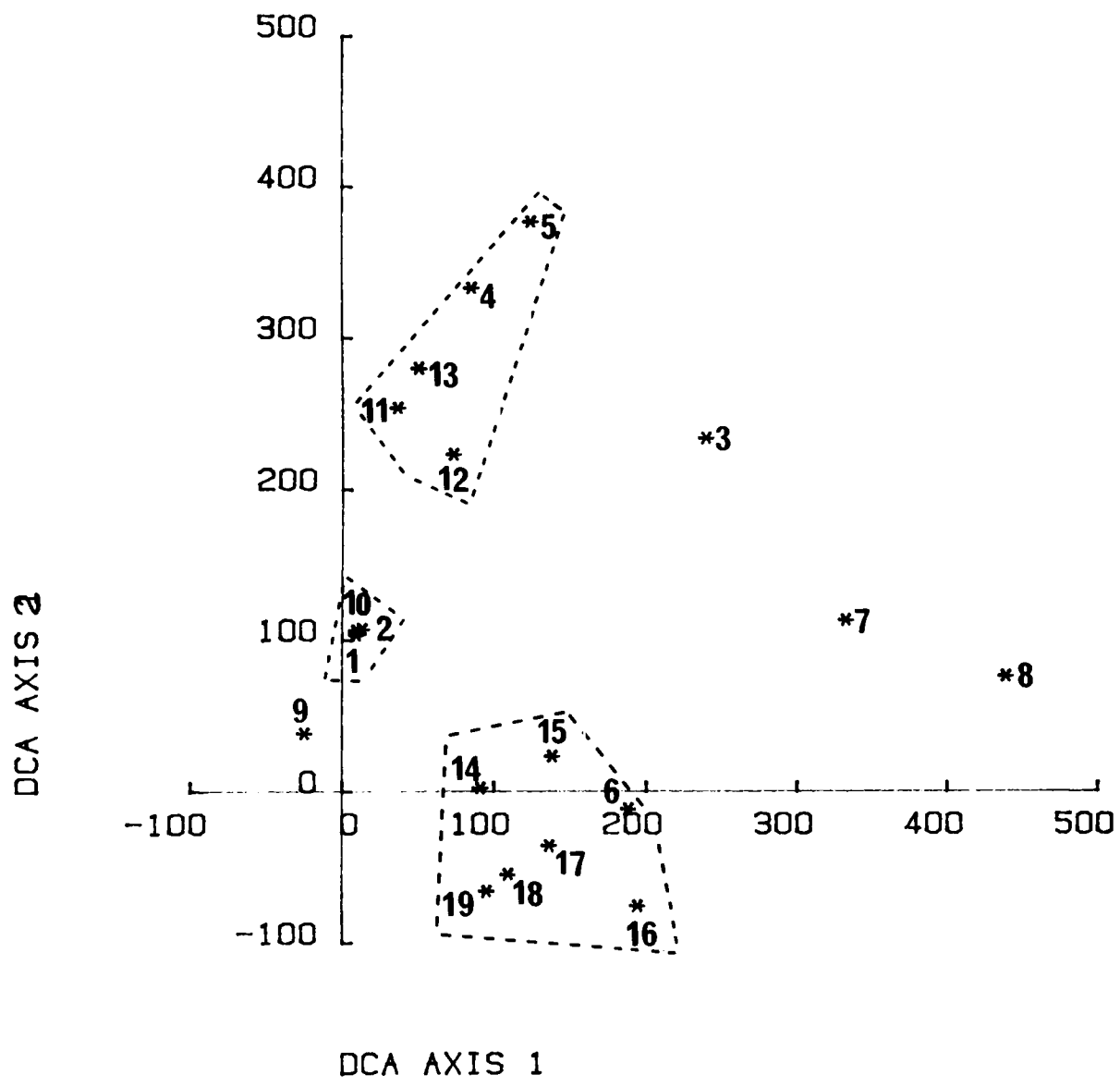
1	TOP COVER
2	MID COVER
3	BOTTOM COVER
4	MARSH
5	GRASSLAND
6	GRASSLEY
7	PASTURE
8	ARABLE LAND
9	CONIFEROUS W.
10	STRUCT. DENSITY
11	BRAMBLE
12	BRACKEN
13	STING. NETTLES
14	RABBIT PELLETS
15	PHEASANTS
16	FEATHERS
17	NOS EARTHS
18	NOS HOLES
19	NOS ACT. HOLES

FIG 2.15 *DCA OF H. E. C. & BEAN WOOD AREA (1982): RESOURCE AND VEGETATION VARIABLES ONLY*



1	TOP COVER
2	MIDDLE COVER
3	BOTTOM COVER
4	MARSH
5	GRASSLAND
6	GRASSLEY
7	PASTURE
8	ARABLE LAND
9	STRUCT. DENSITY
10	BRAMBLE
11	RABBIT PELLETS
12	PHEASANTS
13	NOS EARTHS
14	NOS HOLES
15	NOS ACT. HOLES

FIG 2.16 *DCA OF ALL WYTHAM DATA (1982): RESOURCE AND VEGETATION VARIABLES ONLY*

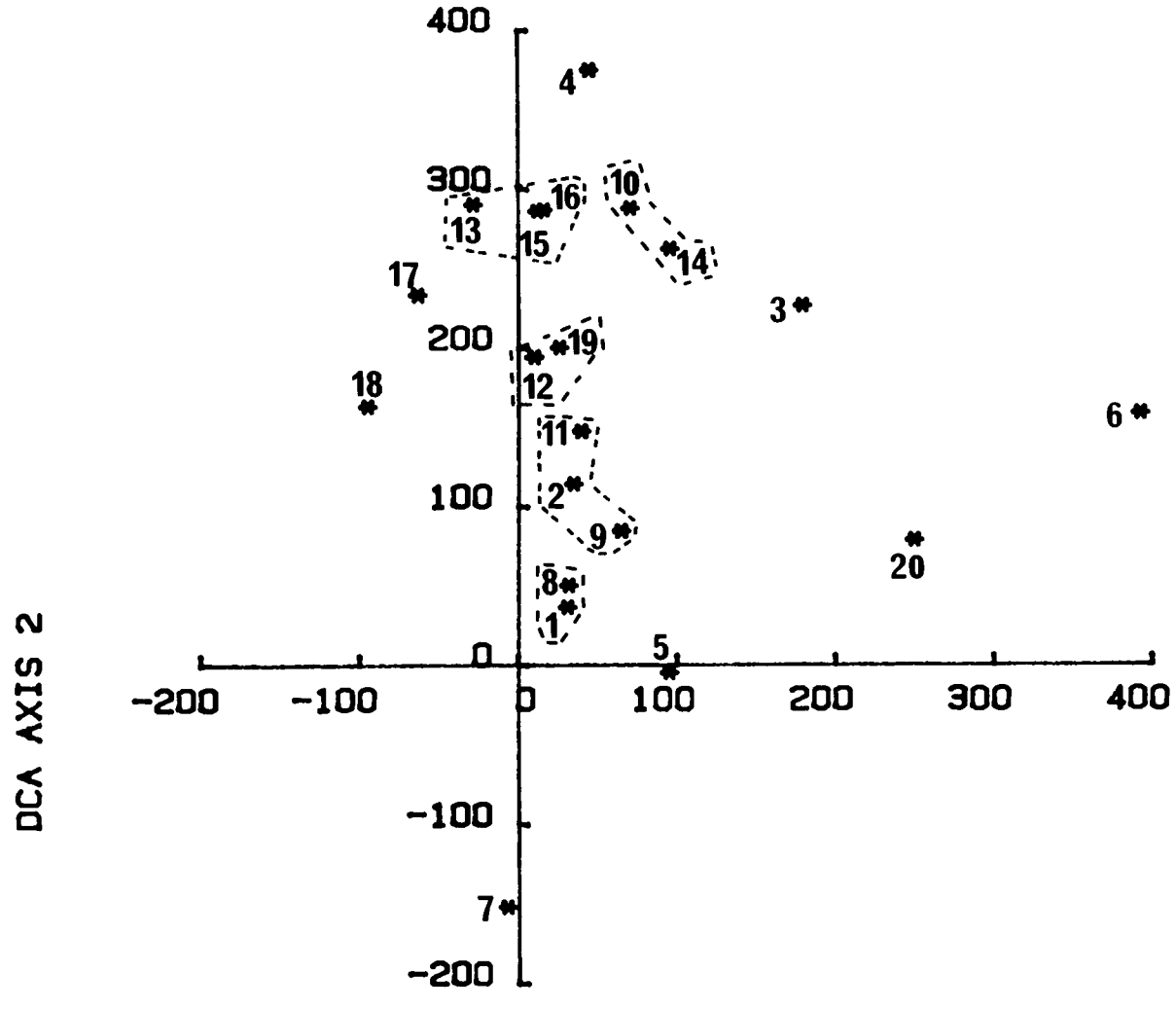


1	TOP COVER
2	MID COVER
3	BOTTOM COVER
4	MARSH
5	GRASSLAND
6	GRASSLEY
7	PASTURE
8	ARABLE LAND
9	CONIFEROUS W.
10	STRUCT. DENSITY
11	BRAMBLE
12	BRACKEN
13	STING. NETTLES
14	RABBIT PELLETS
15	PHEASANTS
16	FEATHERS
17	NOS EARTHS
18	NOS HOLES
19	NOS ACT. HOLES

same: a gradient from open areas with low structural density to areas with high density and low light penetrability. Both Marley and HEC show the same arrangement of variables along the first DCA axis, corresponding to the result for the entire data set, with three exceptions. For both the total area and HEC, BRAMBLE shows a lower score (ie. higher density) than MARSH while in Marley MARSH and BRAMBLE have the same score along this gradient. Also in Marley, PASTURE coincides with BOTTOM COVER and GRASSLEY while it is well separated from both in HEC and the total area. PHEASANTS, in the total area with a DCA axis 1 score equivalent to GRASSLAND, changes in Marley to denser cover (CONIFEROUS WOODLAND) but in HEC to the opposite side, the very open areas (DCA axis 1 score between the scores of PASTURE and ARABLE). Despite these radical changes between study sites along the first DCA axis, the position of PHEASANTS on the second axis remains remarkably constant: for both HEC and Marley, it is close to GRASSLAND. In addition, in Marley it is also close to BRAMBLE while in HEC it is also close to MARSH. This corresponds to the original data set and my subjective impression very closely: the pheasants in the HEC area were seen in the grassland near to the marsh and arable fields while in Marley they were usually found in patches of thick bramble understorey or grassy rides in mixed plantations. This is a very good example for the utility of multivariate techniques such as DCA: the techniques provide general trends underlying the variation in habitat structure but they also identify important associations of variables amongst the entire set of possible associations and they do it in an objective and reproducable manner.

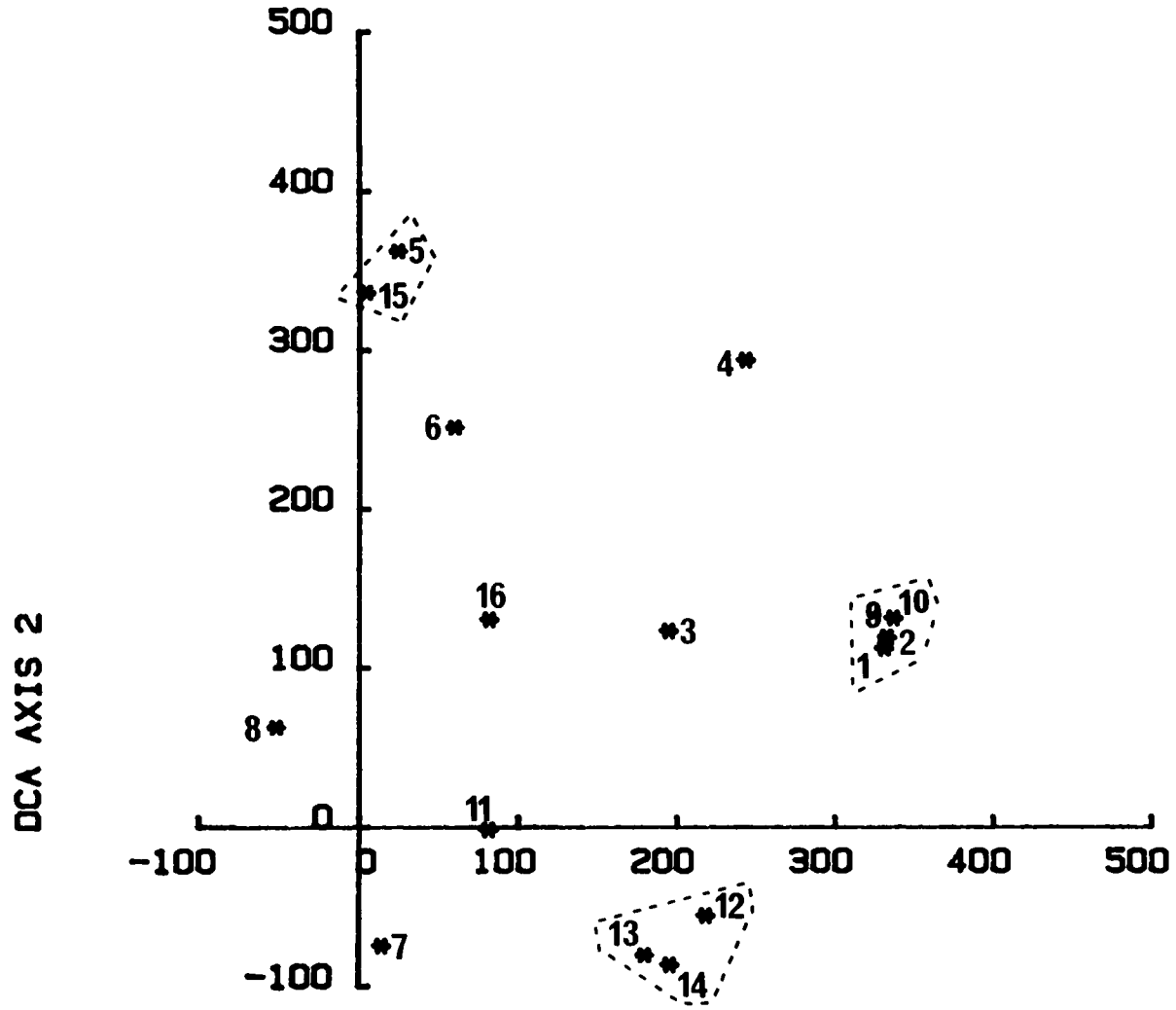
Finally, RUNS 17 to 19 were run to look at the composite effect of all parameters. For all three sets of data (Marley, Fig. 2.17; HEC, Fig. 2.18; total area, Fig. 2.19) the interpretation of the first and most important DCA axis remains the same in comparison with earlier ordinations (in particular RUNS 14 to 16). A gradient of structural density and cover

FIG 2.17 *DCA OF MARLEY AREA (DATA FROM 1982)*



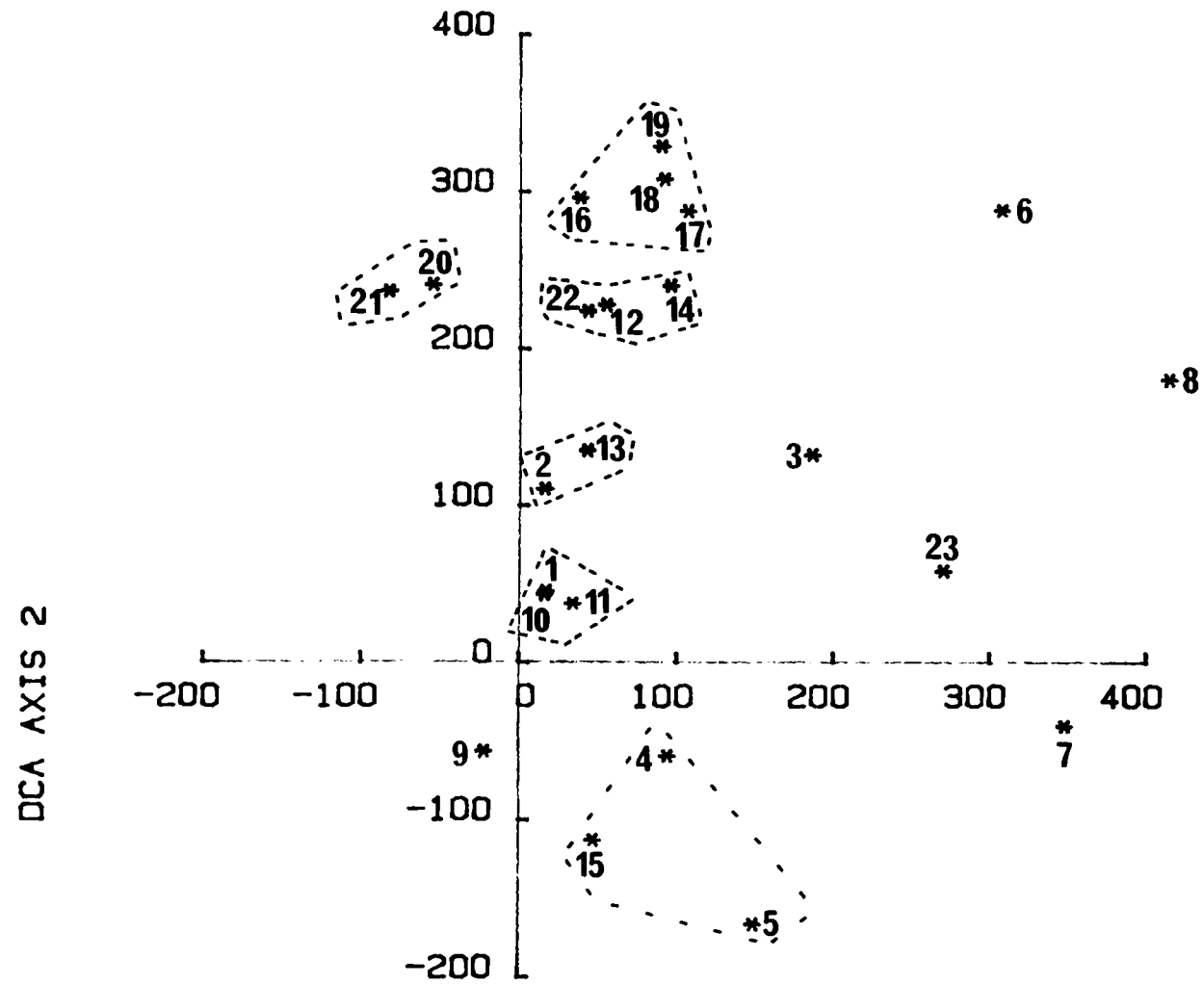
1	TOP COVER
2	MID COVER
3	BOT COVER
4	MARSH
5	GRASSLAND
6	ARABLE LAND
7	CONIFEROUS W.
8	STRUCT. DENSITY
9	BRAMBLE
10	BRACKEN
11	STING. NETTLES
12	RABBIT PELLETS
13	FEATHERS
14	NOS EARTHS
15	NOS HOLES
16	NOS ACT. HOLES
17	LATRINES
18	NOS PITS
19	FOX FAECES
20	HUMAN DIST.

FIG 2.18 *DCA OF HILL END CAMP & BEAN WOOD AREA (DATA FROM 1982)*



1 TOP COVER
2 MID COVER
3 BOT COVER
4 MARSH
5 GRASSLAND
6 GRASSLEY
7 PASTURE
8 ARABLE LAND
9 STRUCT. DENSITY
10 BRAMBLE
11 RABBIT PELLETS
12 NDS EARTHS
13 NOS HOLES
14 NDS ACT. HOLES
15 FOX FAECES
16 HUMAN DIST.

FIG 2.19 *DCA OF ALL WYTHAM DATA (1982): ALL VARIABLES*



1	TOP COVER
2	MIDDLE COVER
3	BOTTOM COVER
4	MARSH
5	GRASSLAND
6	GRASSLEY
7	PASTURE
8	ARABLE LAND
9	CONIFEROUS W.
10	STRUCT. DENSITY
11	BRAMBLE
12	BRACKEN
13	STING. NETTLES
14	RABBIT PELLETS
15	PHEASANTS
16	FEATHERS
17	NOS EARTHS
18	NOS HOLES
19	NOS ACT. HOLES
20	LATRINES
21	NOS PITS
22	FOX FAECES
23	HUMAN DIST.

ranges from open areas with little cover and high light penetrability to areas with dense cover and low light penetrability. The second DCA axis separates the three groups of variables (vegetation, resource, predators). In Marley and in the whole area, the inclusion of fox, badger, and human presence (variables 17 to 20) separates RABBIT PELLETS from the other resource variables and increases the distance between NOS EARTHS and NOS HOLES/NOS ACTIVE HOLES. Badger LATRINES and NOS PITS (definitions in Box 3) are grouped together with FOX FAECES and RABBIT PELLETS. LATRINES and NOS PITS are associated with densest cover; they surpass even CONIFEROUS WOODLAND. In HEC, FOX FAECES is placed between GRASSLAND and PASTURE and therefore in more open cover than in Marley (here between MARSH and MID COVER). For all three data sets HUMAN DISTURBANCE assumes a position in fairly open ground.

The inclusion of the additional 'predator' variables results in a considerable stretching of the first DCA axis for Marley, a moderate stretching for the total area and a contraction for HEC relative to the corresponding RUNS 14 to 16 with only vegetation and resource variables. All eigenvalues of the first DCA axis of RUNS 17 to 19 decreased relative to RUNS 14 to 16, ie. DCA axis 1 of RUNS 17 to 19 accounted for less of the variance than did the DCA axis 1 for RUNS 14 to 16. Thus, the effect of the inclusion seems to be an increase in variation space and the result a less clear cut, higher dimensional structure. This impression is enhanced by a comparison of the eigenvalues of RUN 10 (resource variables only for the total area) and RUN 13 (resources and predator variables for the total area). In RUN 10, the first DCA axis accounts for most of the variance since the eigenvalues of the higher axes are very low (Table 2.7). In contrast in RUN 13, the second and the third eigenvalues are much higher than the second eigenvalue of RUN 10 (0.652 and 0.241 against 0.143). The ordinations including vegetation and resource parameters only (RUNS 14 to

16) seem to me the most successful and useful ordinations indicating a low-dimensional habitat structure and a clear and straightforward interpretation of the ordination axes. Despite the field impression of apparent complexity and seemingly endless changes in vegetation patterns it is reassuring and interesting to note that most of this variation can be arranged in a low-dimensional structure. This is also remarkable from another point of view: with a low-dimensional structure, habitat selection by foxes and badgers and related adaptation processes can more easily be envisaged and analysed.

2.4 Discussion

In the following section I want to discuss the relationship of the two approaches to habitat recording and classification, namely the discrete habitat types of the habitat map (section 2.2) and the continuous habitat structure as revealed by the habitat records (section 2.3), and relate this to the overall aims of this study.

The identification and classification of areas as discrete habitats is based on the personal decision of the researcher and thus neither necessarily undisputed nor entirely reproducable, but of great utility for further analysis under a broad perspective. A summary of the environment in a certain area as a discrete habitat has a filtering effect on continous small scale variations which are neglected ('flocked out'); only the broad lines of structural variation permit. An appropriate system of discrete habitats is equivalent to an efficient filter that is arranged on the right scale of variation, considers the correct habitat parameters (ie. the parameters responsible for the important variation) and yields habitat types that are actually different from each other! Since habitat was defined in relation to the animal's requirements and potential resources (section 2.1), there is the possiblity (and the hope) that foxes and badgers might view

their environment through a filter corresponding in its effects to my habitat categorization. Obviously, if the habitat categories do not correspond to the categories as seen through the animal's filter, little can be said about 'habitat' utilization by animals, as the results would be based on an artificial and inadequate system. Thus it should be a central point in any investigation of carnivore behavioural ecology based on habitats to find a procedure which describes how well the chosen habitat categorization corresponds to the habitat structure as perceived by the animals. As far as I am aware, this is the first study in carnivore ecology to combine two different approaches to habitat description and show how a system of discrete habitat types can be compared with the continuous variation of 'actual' habitat structure as represented by a sample of continuously varying habitat parameters, so that an estimate of the adequacy and efficiency of the habitat categorization is possible.

For this comparison the following procedure was adopted: Program HABCOORD placed a systematic grid of five equidistant points over each recording unit of the habitat records (the 'basal area' or by 50 by 50 m cell). Programe SRCH2HAB then evaluated the patch number and habitat type (from the habitat map) for each grid point. Program HABSEL compared the habitat types of all five grid points in each cell and selected only those cells with all gridpoints having the same habitat type. Thus, only homogeneous cells as defined by the system of the habitat map were admitted for further analysis. Program HABDECO took each of these homogeneous cells and tagged it with its scores on the four DCA axes of the RUNS 17 to 19. In Marley, only three habitat types, bracken, deciduous hardwoods, and mixed plantations had big enough sample sizes (ie. a sufficient number of homogeneous cells) to be useful for a statistical analysis (Table 2.9). In Hill End Camp (HEC) five variables satisfied this condition (grassley, pasture, summer cereals, deciduous hardwoods, sportsgrounds, Table 2.10) and

Table 2.9 Kruskal-Wallis one-way analysis of variance on differences between different habitat types (as defined according to habitat map categories) on their DCA scores (of the habitat records) of RUN 14. Each admitted sample is a 50 m^2 basal area which is completely covered by one habitat type.

Part I: Marley

Habitat types: Bracken, deciduous woodland, mixed plantations.

a) Kruskal-Wallis test (n = 119, df = 2)

DCA axis	H (adjusted)	significance
one	30.13	0.001
two	54.14	0.001
three	3.417	ns
four	12.81	0.005

b) Multiple comparison tests

DCA axis	Habitat with high score	Habitat with low score	actual value	critical value	signi-ficance
one	deciduous	bracken	17.3	24.92	ns
	bracken	mixed pl.	20.8	25.92	ns
	deciduous	mixed pl.	38.1	11.87	<0.001
two	bracken	deciduous	38.8	21.27	<0.001
	bracken	mixed pl.	83.3	22.13	<0.001
	deciduous	mixed pl.	44.5	10.13	<0.001
four	deciduous	bracken	10.1	26.73	ns
	bracken	mixed pl.	14.8	27.81	ns
	deciduous	mixed pl.	24.9	12.73	<0.001

Table 2.10 Kruskal-Wallis one-way analysis of variance on differences between habitat types (as defined according to habitat map categories) on their DCA scores (of the habitat records) of RUN 18. Each admitted sample is a 50 sqm basal area which is completely covered by one habitat type.

Part II: Hill End Camp

Habitat types: Grassley, pasture, summer cereals, deciduous woodland, sports grounds.

a) Kruskal-Wallis test (n = 112, df = 4)

DCA axis	H (adjusted)	significance
one	87.33	<0.001
two	67.91	<0.001
three	47.98	<0.001
four	32.24	<0.001

b) Multiple comparison tests (only pairs with significant differences)

DCA axis	Habitat with high score	Habitat with low score	actual value	critical value	significance
one	grassley	cereals	42.4	11.43	<0.001
	deciduous	grassley	38.1	10.17	<0.001
	pasture	cereals	33.3	8.59	<0.001
	deciduous	pasture	47.2	6.82	<0.001
	sports g.	pasture	13.7	13.15	<0.05
	deciduous	cereals	80.5	8.48	<0.001
	sports g.	cereals	47.0	14.09	<0.001
	deciduous	sports g.	33.5	13.08	<0.001
two	cereals	grassley	15.7	15.36	<0.05
	deciduous	grassley	50.5	13.66	<0.001
	sports g.	grassley	48.6	20.37	<0.001
	cereals	pasture	21.3	11.53	<0.001
	deciduous	pasture	56.1	9.15	<0.001
	sports g.	pasture	54.2	17.66	<0.001
	deciduous	cereals	34.8	21.39	<0.001
	sports g.	cereals	32.9	18.92	<0.005
three	grassley	deciduous	38.6	16.6	<0.001
	grassley	sports g.	54.4	24.74	<0.001
	pasture	cereals	21.0	14.01	<0.005
	pasture	deciduous	44.9	11.12	<0.001
	pasture	sports g.	60.7	21.45	<0.001
	cereals	deciduous	23.9	13.84	<0.005
	cereals	sports g.	39.7	22.98	<0.001
four	grassley	cereals	42.9	20.82	<0.001
	grassley	deciduous	30.5	18.52	<0.002
	pasture	cereals	43.2	15.63	<0.001
	pasture	deciduous	30.8	12.41	<0.001
	sports g.	cereals	33.5	25.64	<0.02

Table 2.11 Kruskal-Wallis one-way analysis of variance on differences between habitat types (as defined according to habitat map categories) on their DCA scores (of the habitat records) of RUN 19. Each admitted sample is a 50 sqm basal area which is completely covered by one habitat type.

Part III: Total area

Habitat types: Grassley, pasture, summer cereals, bracken, deciduous woodland, mixed plantations, sports grounds

a) Kruskal-Wallis test (n = 237, df = 6)

DCA axis	H (adjusted)	significance
one	175.8	<0.000
two	59.8	<0.001
three	87.5	<0.001
four	96.4	<0.001

b) Multiple comparison tests (only significant pairs)

DCA axis	Habitat with high score	Habitat with low score	actual value	critical value	signi-- ficance
one	cereals	grassley	50.0	25.42	<0.001
	grassley	bracken	79.2	34.94	<0.001
	grassley	deciduous	83.0	21.71	<0.001
	grassley	mixed	138.3	23.72	<0.001
	cereals	pasture	35.4	18.36	<0.001
	pasture	bracken	93.8	30.19	<0.001
	pasture	deciduous	97.6	12.73	<0.001
	pasture	mixed	152.9	15.91	<0.001
	cereals	bracken	129.2	31.71	<0.001
	cereals	deciduous	133.0	16.00	<0.001
	cereals	mixed	188.3	18.63	<0.001
	cereals	sports g.	51.6	31.71	<0.002
	bracken	mixed	59.1	30.36	<0.001
	sports g.	bracken	77.6	39.75	<0.001
	deciduous	mixed	55.3	13.12	<0.001
	sports g.	deciduous	81.4	28.82	<0.001
	sports g.	mixed	136.7	30.36	<0.001

Table 2.11 (Cont.)

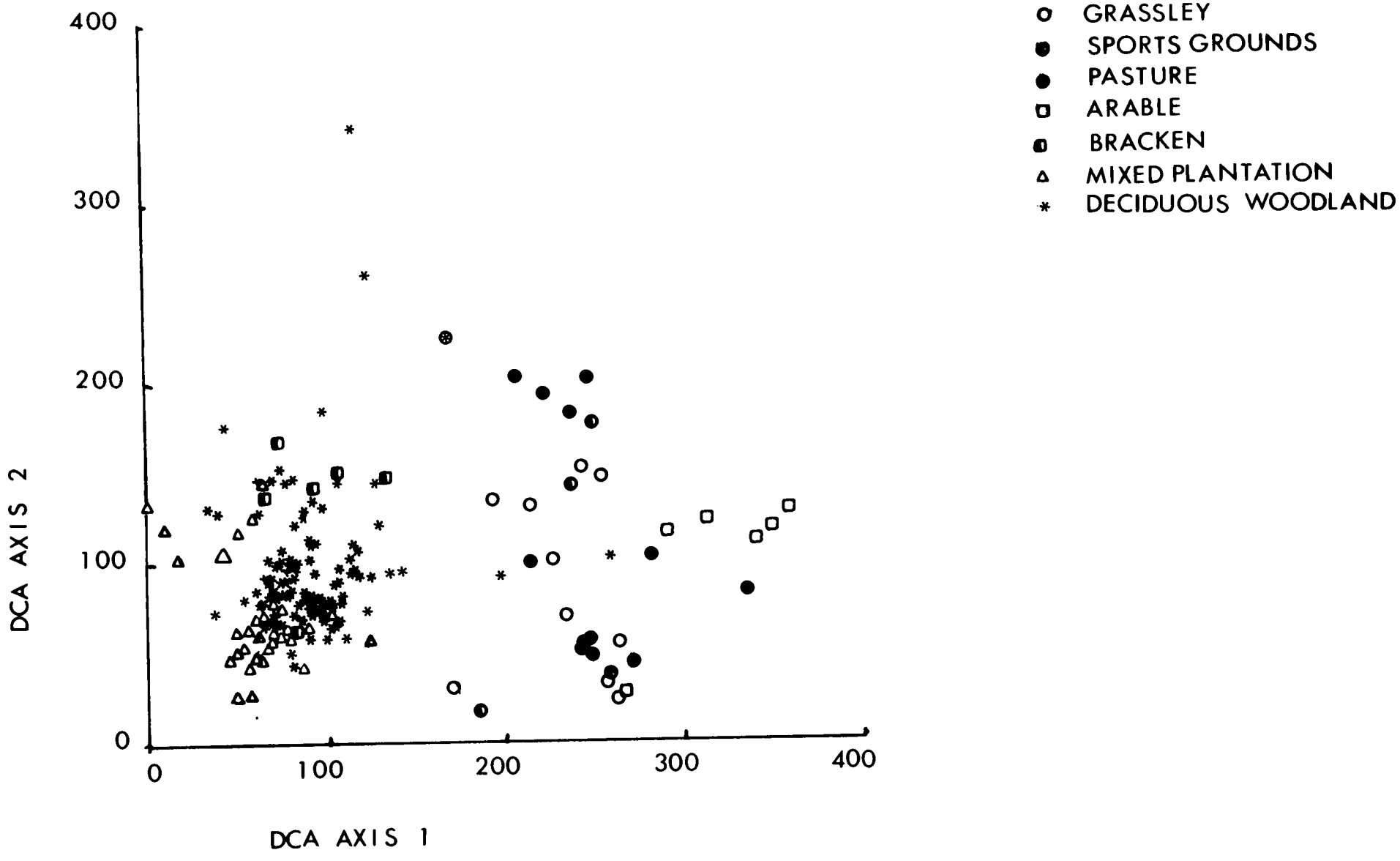
DCA axis	Habitat with high score	Habitat with low score	actual value	critical value	signi-ficance
two	cereals	grassley	71.7	43.52	<0.002
	bracken	grassley	81.0	59.81	<0.01
	sports g.	grassley	79.0	59.81	<0.01
	cereals	pasture	107.6	31.42	<0.001
	bracken	pasture	116.9	51.68	<0.001
	deciduous	pasture	55.3	21.99	<0.001
	sports g.	pasture	114.9	51.68	<0.001
	cereals	deciduous	52.3	27.39	<0.001
	cereals	mixed	97.1	31.89	<0.001
	bracken	deciduous	61.6	49.33	<0.02
	bracken	mixed	106.4	51.97	<0.001
	deciduous	mixed	44.8	22.46	<0.001
	sports g.	deciduous	59.6	49.33	<0.02
	sports g.	mixed	104.4	51.97	<0.001
three	pasture	grassley	37.4	36.87	<0.05
	cereals	grassley	50.6	39.88	<0.02
	grassley	mixed	78.6	37.21	<0.001
	grassley	sports g.	81.0	54.81	<0.005
	pasture	deciduous	63.3	19.97	<0.001
	pasture	mixed	116.0	24.96	<0.001
	pasture	sports g.	118.4	47.36	<0.001
	cereals	deciduous	76.5	25.1	<0.001
	cereals	mixed	129.2	29.23	<0.001
	cereals	sports g.	131.6	49.74	<0.001
	bracken	deciduous	70.5	45.21	<0.005
	bracken	mixed	123.2	47.62	<0.001
	bracken	sports g.	125.6	62.35	<0.001
	deciduous	mixed	52.7	20.58	<0.001
	deciduous	sports g.	55.1	45.21	<0.02
four	cereals	grassley	66.5	38.36	<0.001
	grassley	deciduous	57.5	32.99	<0.001
	grassley	sports g.	102.2	53.09	<0.001
	cereals	pasture	57.5	27.89	<0.001
	pasture	bracken	52.9	45.88	<0.05
	pasture	deciduous	66.5	19.34	<0.001
	pasture	sports g.	111.2	45.88	<0.001
	cereals	bracken	110.4	48.18	<0.001
	cereals	deciduous	124.0	24.31	<0.001
	cereals	mixed	51.8	28.31	<0.001
	cereals	sports g.	168.7	48.18	<0.001
	mixed	bracken	58.6	46.13	<0.02
	mixed	deciduous	72.2	19.94	<0.001
	deciduous	sports g.	44.7	43.79	<0.05
	mixed	sports g.	116.9	46.13	<0.001

for the total area, seven habitat types were available (all HEC types plus bracken and mixed plantations, Table 2.11). Differences between the DCA scores were investigated for each axis by computing a Kruskal-Wallis one-way analysis of variance using the MINITAB statistical package available on the university's VAX-11/780. The same statistics could not be used on the original variables or a combination of them as some of them are correlated with each other and therefore not statistically independent.

There was only one case, the third DCA axis of Marley (Table 2.9a), where no significant differences in the DCA scores of different habitat types were found. In all other cases the Kruskal-Wallis test is highly significant which indicates at least a well spaced variation of DCA scores among the habitat types. In Fig. 2.20 each cell is plotted according to its score for DCA axes 1 and 2 from RUN 19; cells of different habitat types were marked with different symbols. Particularly conspicuous is the cluster formed by deciduous hardwoods cells which is close to but still separated from the cluster formed by mixed plantation cells.

For each data set (Marley, HEC, total area), a posteriori multiple comparison tests were conducted which allow the identification of all those pairs of habitat types which are significantly different from each other while keeping the level of significance (the likelihood of a type I error) over all comparisons constant. (More detailed remarks on this type of multiple comparison tests can be found in section 4.2.3). In general, the proportion of 'significant pairs', ie. the relative number of pairs where the habitat types show a difference which cannot be accounted for by chance alone, is high for HEC (between 50% (DCA axis 4) and 80% (DCA axes 1 & 2), Table 2.10b) while only one of three pairs were significant on DCA axes 1 & 3 in Marley. This is probably mainly a problem of sample size, since there were only 6 homogenous cells for bracken, and thus large variation. As a closer inspection of Tables 2.10b and 2.11b shows, even such 'closely

Fig. 2.20 Distinction of conventional habitat categories, as defined by the computerized habitat map, by the habitat records, as represented by the DCA axes 1 and 2. Each symbol represents one 50 by 50 m cell exclusively covered by one conventional habitat category.


400
300
200
100
0
0
100
200
300
400
DCA AXIS 2
DCA AXIS 1
GRASSLEY
SPORTS GROUNDS
PASTURE
ARABLE
BRACKEN
MIXED PLANTATION
DECIDUOUS WOODLAND

related' habitats as grassley, pasture and sports grounds are significantly different on many DCA axes.

As may be recalled from section 2.3.5., the first axis of the DCA ordinations was interpreted as a gradient of structural density and light penetrability ranging from open areas with high penetrability to areas packed with dense vegetation and low light penetrability while the second axis distinguished resource variables from predator and vegetation variables. While some of the closely related habitats (e.g. bracken and deciduous woodland; grassley, pasture and sports grounds) are indistinguishable on the first DCA axis in all three data sets, most of them are separated on the second, the resource axis, although the habitat parameters chosen certainly did not consider all important resources (section 2.3.1). This most encouraging result is further corroborated by the detailed investigations reported in Chapter 3, where, for instance, a significant difference in earthworm abundance and biomass could be shown between deciduous hardwoods and mixed plantations, or where bracken showed a higher index of rabbit activity than decidious woodland. Other studies indicate that a distinction of habitat types might be justified even if the resource presence is similar as for grassley and pasture but the resource availability changes due to differential hunting success of the predator changes. A case in point is the reduced hunting success of badgers foraging for earthworms in long grass habitat (grassland, Kruuk et al. (1979)).

In summary, the apparent complexity of Wytham Woods' biotic structure can be summarised as a low-dimensional habitat space and is adequately represented by the system of discrete habitat types developed in section 2.2. The foregoing analysis demonstrates that a definition of habitats as units of resources is not only useful in theory but also feasible in practice. In the following chapter the abundance of selected resources is investigated in more detail and the present discussion of resources that are

part of SET 2 (the local window to the fundamental niche, section 2.1.1.) extended to a detailed consideration of the relationship of resource abundance, resource availability, and the foraging techniques of foxes and badgers which together determine the composition of SET 3.

3. Resources

3.1. Introduction

3.2. Earthworms (Lumbricidae)

3.2.1. Introduction

3.2.2. Methods

3.2.3. Results of present study

3.2.4. Discussion

3.3. Pheasant (Phasianus colchicus)

3.3.1. Introduction

3.3.2. Pheasant census and observations

3.4. Wood pigeon (Columba palumbus)

3.4.1. Introduction

3.4.2. Observations on wood pigeons and pigeon remains

3.5. Lagomorphs

3.5.1. Introduction

3.5.2. The rabbit population in Wytham Woods

.1. Methods

.2. Results

.3. Discussion

3.6. Rodents

3.6.1. Ecology of voles and mice

3.6.2. Antipredator tactics and defense

3.6.3. Predator foraging

3.6.4. The rodent populations in Wytham

3.7. Discussion

3.7.1. Comparison of prey characteristics

3.7.2. Foraging tactics of predators in relation to the energy obtained from different prey.

3. Resources.

3.1. Introduction.

In this chapter I shall present information on the abundance of resources and relate them to the foraging techniques of foxes and badgers. There are two main aims:

1. to explore further the extent to which habitats can be predictors of resource abundance;
2. to investigate the conditions by which a resource that is present (and thus an element of SET 2, the local niche (section 2.1.1.)) also becomes available to the predators (and thus an element of SET 3, the realized niche).

The results should answer the question of what food availability a badger or a fox might 'expect' in given habitats and thus may explain patterns of use in habitat and prey selection by foxes and badgers. The aim is to interpret the predator's movements through different habitats.

In the previous chapter it was shown that the discrete habitat types of the habitat map correspond well to the actual, continuous habitat variation. It is therefore legitimate to restrict the following discussion of resource abundance and availability to habitats as defined by the habitat map.
The difference between food abundance and availability is critical (section 2.1.2). Natural selection could favour traits that minimize the time a prey individual spends in states where it is available to predators. This in turn would require the predators to be efficient in the detection of available prey and favour the development of searching strategies designed to optimize a resource yield function such as maximization of net energy intake or minimization of time spent foraging resulting in a selection of prey types

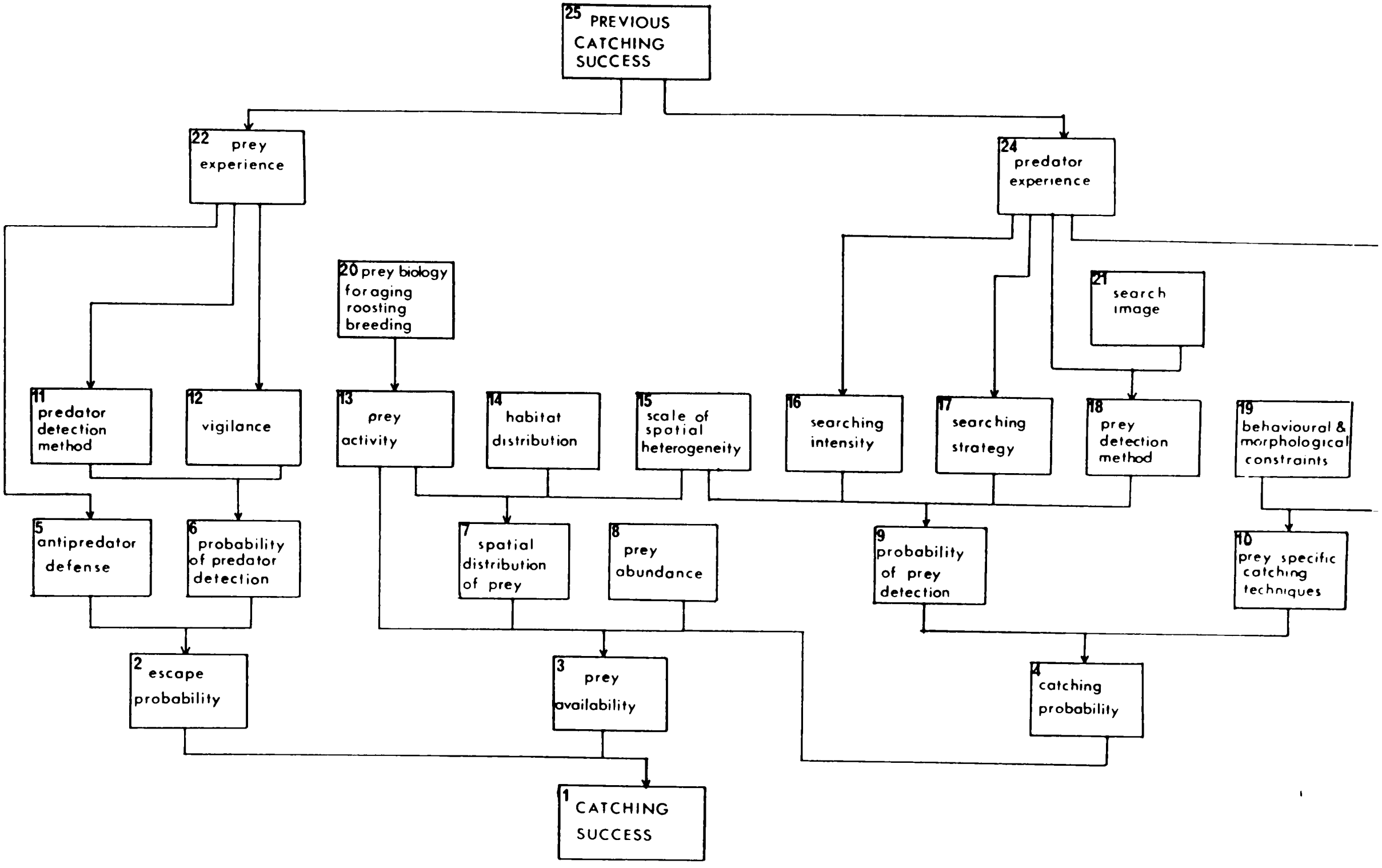
by the predators. In sections 3.2. to 3.6. I shall discuss the mechanisms and factors that determine the likely foraging success of foxes and badgers for a given prey in a given area, while section 3.7. will discuss the decision of what a predator should do in order to maximize fitness, ie. e.g. how much time it should spend foraging for a particular type of prey. Fig. 3.1. depicts a general model for the factors that influence the capture success of a predator. The model was designed with reference to carnivore behaviour and ecology. These factors will be shown to be of importance for certain prey but they do not represent an exhaustive list. For instance, a model for predators in lacustrine ecosystems would place more emphasis on the sensory limitations of the predator and the effects of prey body size (e.g. gape-limited predators) and reduce the importance of small scale habitat heterogeneity and prey experience (Zaret (1980)). In the model, ecological circumstances are underrepresented on the understanding that the importance of various factors may change if ecological circumstances (habitat, weather) change. Factors 14 and 15 are examples of such an influence.

In the following accounts of five selected prey I will list the aspects of prey biology and behaviour along with the predators' foraging techniques pertinent to the proposed scheme. Earthworms, rabbits, rodents, pheasants, and wood pigeons were selected for detailed accounts because

- they are important elements of the diet of one or both predator species as shown in Chapter 4 (earthworms, rabbits, rodents);
- there is a strong scientific and public interest in the corresponding predator/prey relationship (pheasants);
- previous accounts of prey and predator biology do not satisfactorily explain how foxes in Wytham Woods are

Fig. 3.1. General model of the factors that may influence the capture success of a (terrestrial carnivore) predator. This model serves as background for the description of the prey characteristics and predator foraging tactics in the remainder of Chapter 3. As an example consider foxes as predators and earthworms as prey. Numbers denote boxes of the figure.

Capture success[1] of foxes is a function of worm availability[3] and escape probability[2] of worms. This in turn depends on the probability of fox detection[6] and the antipredator defense[5] of worms which consists of withdrawing into the burrow, or, if already seized by a fox, by extending the posterior chaetae into the soil and expanding the posterior segments. Probability of fox detection[6] depends on, perhaps, vigilance[12] and the detection method[11]. For worms, it is not known whether vigilance is important; it may, however, be important for birds. Worms react to vibrational and tactile stimuli, causing them to disappear into the burrows[11]. Worms are probably little influenced by experience[22] but this may be of importance to wood pigeons. To minimize the escape probability of worms, a fox should walk slowly with a 'light step'[11] and seize its prey quickly[5].
Prey availability is a function of prey presence and dispersion[7,8], its activity[13] and the catching probability[4].
Prey dispersion is a function of the dispersion of high quality habitats[14,15] (section 3.2). Earthworms are stationary; their activity[13] is concentrated on the surroundings of each individual's burrow. Worms in quiescence[20] are deep down their burrow and hence virtually inaccessible[3]; the same is usually true of birds roosting on top of trees.
The capture probability[4] of a fox depends on the probability of worm detection[9] and the catching technique[10]. Foxes catch worms by plunging their head onto the ground and pulling the worm out of the burrow with a quick sideward sweep of the head. Young foxes have to learn[23,24] this. Due to their smaller and weaker paws[19], foxes are less inclined than badgers to dig up worms in firm but promising soils. Foxes detect[18] worms by acoustic cues from the noise caused by the surfacing activities of the worm, perhaps using some kind of search image[21]. Due to the irregular distribution[15] of worms, foxes walk in different modes through a patch[17] and spend different amounts of time in them[16].


25 PREVIOUS CATCHING SUCCESS
22 prey experience
24 predator experience
20 prey biology foraging roosting breeding
21 search image
11 predator detection method
12 vigilance
13 prey activity
14 habitat distribution
15 scale of spatial heterogeneity
16 searching intensity
17 searching strategy
18 prey detection method
19 behavioural & morphological constraints
5 antipredator defense
6 probability of predator detection
7 spatial distribution of prey
8 prey abundance
9 probability of prey detection
10 prey specific catching techniques
2 escape probability
3 prey availability
4 catching probability
1 CATCHING SUCCESS

successful predators on this prey.

3.2. EARTHWORMS (LUMBRICIDAE)

Among the 27 lumbricid species recorded for Britain (Gerard (1964)) only two, Lumbricus terrestris and Lumbricus rubellus, are shown to be utilized by badgers and foxes, according to scat analyses and feeding observations (Kruuk (1978a), Kruuk & Parish (1981, 1982), Macdonald (1980, 1984)). L. terrestris far outweighs L. rubellus in importance so that L. rubellus is only exploited in the absence of L. terrestris as demonstrated in wetlands and moorlands in Scotland (Kruuk et al, references above). I therefore restrict my discussion to L. terrestris. All future references to earthworms, or worms, unless otherwise stated, are intended to refer to L. terrestris only.

3.2.1. INTRODUCTION.

ACTIVITIES. Earthworms live in burrows, often descending to a depth of one to two meters (Edwards & Lofty (1977)). They have a natural life expectancy of one to two years but have been observed to live for several years in the laboratory. They primarily feed on leaf litter, but also consume considerable quantities of other organic matter and soil. They forage by surfacing from their burrow, searching the surrounding area for leaves, which they collect and return to their burrows. Their burrows are sealed with a leaf or small piles of stones ('worm cairns'). They do not feed on the surface but hoard leaves down their burrows.

L. terrestris shows preference for certain types of litter. Food selection experiments (e.g. Satchell & Lowe (1967)) demonstrated that leaves of different plant species, particularly trees, differ in their palatability

to worms. Palatability is important as it determines the food supply actually available to earthworms which in turn influences worm densities and biomass (Edwards & Lofty (1977)). Palatability seems to be influenced by a variety of factors including the chemical compositiion of the leaves, particularly the presence of secondary compounds such as phenols and condensed tannins. These are found for example in the leaves of larch, spruce, oak and beech (comparatively unpalatable to earthworms) and are absent in dog's mercury, nettles, elderberry ash and wych elm (Brown et al. (1963)). Reynolds and Jordan (1975) suggested a leaf palatability scale (with particular reference to North American earthworms) with

Robinia ›› Alnus = Populus › Prunus = Salix = Ulmus =
Acer = Liriodendron › Fraxinus = Tilia = Gleditsia =
Betula › Quercus = Fagus › conifers

These results suggest that worms show both relative preference (for e.g. sycamore (Acer) and ash (Fraxinus)) and relative avoidance (conifers, oak (Quercus), beech (Fagus)) of certain species (Satchell & Lowe (1967)).

L. terrestris has a clear seasonal pattern of activity mainly influenced by climatic factors (Rundgren (1977), Satchell (1967)). For southern Sweden, Nordstrom (1975) and Rundgren (1977) reported that worm activity is greatest from late March to mid-December, as long as soil temperatures are higher than 0^{o} C. In Britain, the same activity pattern can be observed (Satchell (1967)). During periods of adverse conditions such as frost or prolonged periods of drought, worms can enter a latent phase (diapause) and are then found at greater depths in the soil.

L. terrestris shows a negative phototaxis to strong light and a positive phototaxis to dim light (Satchell (1967), Edwards & Lofty (1977)), restricting surface feeding to the hours of dusk and darkness.

Consequently, most surfacing activity has been found to occur between 6 pm and midnight (Baldwin (1917)), and extending to 6 am (Edwards & Lofty (1977:138)). Otherwise, L. terrestris is known to be able to tolerate a wide range of environmental conditions: it survives a wide range of pH values (pH 3.7 to 7.5, Edwards & Lofty (1977)), can survive severe desiccation (up to 70 % loss of water) and live submerged under water for many days (Roots (1956)). However, L. terrestris generally increases in abundance with increasing pH value, is never actually found in flooded soils or in soils with a pH of less than 4.1 and after prolonged rains surfaces frequently and for extended periods of time (Edwards & Lofty (1977)).

General motor activity and particularly surfacing has been shown to be influenced by a variety of factors. Kollmannsperger (1955) reported an optimum soil temperature of 10.5^{o} C. Satchell (1967), in experiments conducted at Rothamsted Field Station, found surfacing to be positively correlated with rainfall in the previous four days, soil temperature and air temperature. Nights most suitable for earthworm activity were those with grass-air temperatures above 2^{o} C, soil temperatures around 10.5^{o} C and when there had been some rain in the previous four days. Gerard (1967) investigated the effects of soil moisture and temperature on the activity and depth distribution of several species of earthworms in pasture. He found that L. terrestris was never quiescent, but occurred significantly deeper in experimental dry soils than in experimental wet soils, thereby suggesting increased surfacing activity under wet conditions. On a lawn Kruuk (1978a) found a significant correlation of the number of worms with the amount of rainfall during the previous 24 hours. Macdonald (1980) in a study of fox predation on L. terrestris obtained a best fit of earthworm activity with climatic factors in a multiple regression equation that included relative humidity, amount of rainfall, time since last rainfall and departure from the optimal temperature. He and Kruuk (1978a) also

emphasized the importance of wind as a negative influence on surfacing activity promoting an exponential decrease of relative air humidity with increasing windspeed (see Kruuk (1978a)). The possibility remains that if food supply for worms is low or it is dry for some time, worms might surface more frequently than expected (Satchell (1967)).

Worms show habitat preferences related to food preferences and soil conditions. Abundance figures have been reported from a variety of countries for different habitat types and soils (see e.g. summary in Edwards & Lofty (1977)). They show that L. terrestris varies considerably in abundance and biomass both between and within habitats. Amongst the factors that influence worm abundance within habitats are soil moisture (Vernon et al.(1981)), soil type (Cuendet (1984)), soil depth (Phillipson et al. (1976)), and management history (Edwards & Lofty (1982a, 1982b), Andersen (1980), Edwards & Lofty (1977)). When comparing the suitability of different habitats for earthworms, important additional factors include plant composition and pH (bearing an influence on light intensity, humidity, and evaporation), soil temperature and food supply (Bocock et al. (1977), Bocock & Adamson (1982), Nicholson & Owen (1982), Standen (1979)). In an attempt to evaluate these factors and their interrelations, Reynolds & Jordan (1975) proposed a general model of earthworm activity and abundance.

Data on the distribution, abundance and biomass of L. terrestris in different habitats in Wytham Woods are available from 4 studies:

1971 - 1973	beechwood at Brogden's Belt; Phillipson et al. (1976, 1978)
1974 - 1975	a variety of habitats, mostly in the Marley - Jew's Harp area; Kruuk (1978a)
1981	three different types of woodland, around Nealing's Copse and The Chalet; Cuendet (1984)

1982 a variety of habitats (Fig. 3.9), along the Singing Way and at Rough Common; this study.

Table 3.1 presents summaries of the densities and biomass obtained by the four studies. The results of Phillipson et al. (1978) are the value for beechwood on rendzina listed under Cuendet (1984) in Table 3.1. Note that my data differ from those of the other studies (but see discussion below) in that I explicitly identified only adult Lumbricus and large immatures (> 70 mm) that are easily distinguished from the closely related L. rubellus (Gerard (1964), G. Cuendet, pers. comm.), but did not make an attempt to identify smaller juveniles as this is a difficult and time consuming task (all smaller juveniles were assigned to the category OTHER JUVENILES). This is not likely to have caused any serious error in the estimation of worm biomass, although the number of L. terrestris will certainly be smaller than expected from the results of other studies. As Table 3.3 confirms, OTHER JUVENILES represent only 20.35 % of the total biomass while constituting the bulk (64.67%) of the number of individuals collected. Adult and large juvenile L. terrestris are few in number (together 18.1 %) but contribute most to the overall biomass (71.2 %). With these restrictions in mind, Table 3.1 shows that worms were most abundant in deciduous woodlands and pasture, less in arable land and least in plantations. For other habitats, Standen (1979) and Kruuk and Parish (1981, 1982) showed that L. terrestris occurs rarely or not all in wetlands and moorlands while Raw (1962) and Raw and Lofty (1959) found high populations in orchards.

ANTIPREDATOR DEFENSE AND TACTICS. L. terrestris possesses senses for chemical, visual, vibrational, tactile and other types of stimuli. Strong vibrations e.g. caused by somebody walking quickly over the ground will cause the worms to disappear. When touched, worms will retract back into

Table 3.1 L. terrestris numbers and biomass in different habitats, mostly sampled with formalin extraction method, in different areas of Wytham. Results from four studies. Data are standard errors except for data from Cuendet (1984) which are 95% confidence intervals. Data from the literature are: data from Table 1, Kruuk (1978a), habitats tentatively placed under the most likely soil categories as no information from the original paper available (see section 3.2.4); May + October average from Table 8, Cuendet (1984). Cuendet's value for beechwood on rendzina was derived from Phillipson et al (1978; see section 3.2.4). My data are estimated numbers (see text). Biomass for Kruuk's data were calculated using his average value of 4.27g for a L.terrestris. Approximate S.U. were obtained for these biomass calculations by multiplying them with 4.27 as well.

VEGETAT.	SOIL	KRUUK (1978a)	N	CUENDET (1984)	N	THIS STUDY	N
a) densities (m^{-2})							
Beechw.	clay	-		0.0	10	-	
Beechw.	rendz.	-		14.4± 6.8	10	-	
Decid.	clay ?	18.92±1.9	41	36.1± 7.5	10	15.80±3.7	8
Decid.	rendz.	?		43.9±10.8	10	24.93±3.0	8
Plant.	clay	-		-		12.70±3.6	8
Plant.	rendz.	4.16±1.4	13	-		4.79±2.2	8
Arable	clay ?	11.30±2.9	11	-		23.02±7.4	8
Pasture	clay ?	22.73±1.9	29	-		21.09±7.2	4
Grassl.	rendz.	-		-		7.85±2.3	8
b) biomass (g fresh weight m^{-2})							
Beechw.	clay	-		0.0		-	
Beechw.	rendz.	-		24.7±16.4	10	(-	
Decid.	clay	80.8± 8.2	41	74.8±29.7	10	84.3±19.4	28
Decid.	rendz.	?		71.5±30.5	10	83.1±14.5	8
Plcnt.	clay	-		-		38.1±13.0	8
Plant.	rendz.	17.7± 6.1	13	-		17.5±10.5	8
Arable	clay?	48.2±12.2	11	-		83.0±25.1	8
Pasture	clay?	97.1± 8.2	29	-		77.3±10.5	6
Grassl.	rendz.	-		-		23.0± 5.9	8

their burrows. The strength of their reaction depends on how much they are protruding from their burrow. If most of the body is below the soil surface, the worm will withdraw only slightly, away from the immediate vicinity of the stimulus (Edwards & Lofty (1977)). However, if the worm has partly left the burrow it will actively resist any attempt to pull it out by extending their posterior chatae into the soil and expanding their posterior segments. It is then virtually impossible to pull them out, and if grasped strongly enough, the worms frequently break into two parts (Edwards & Lofty (1977), pers. obs.). If worms have been subjected to adverse stimuli or treatment, they will withdraw deeply into their burrow and not reappear for some time.

PREDATOR FORAGING. Earthworms are a comparatively stationary prey and thus an excellent subject for the study of predator foraging tactics. Kruuk (1978a), and Kruuk et al. (1979) have published detailed accounts on the foraging behaviour and efficiency of badgers and Macdonald (1980) described the foraging behaviour of foxes in relation to earthworms. Studies on earthworm foraging by other species are available, e.g. the pioneering studies of Smith (1974a, 1974b) on European blackbirds (Turdus merula), and studies on the black-headed gull (Larus ridibundus, Cuendet (1983)).

In a patch of high worm densities, both badgers and foxes wander slowly in a highly convoluted path, head close to the ground. Under conditions of intermediate or low worm densities, foxes tend to follow a less convoluted path and visit a larger area over the same time (Macdonald (1980a)). The badger seems to locate the worms primarily by olfactory clues, keeping its head close to the ground. When a worm is located, it lowers its head to the ground, and pulls the worm out of its burrow by a quick upward movement of its head while holding the worm between its incisors. Foxes while foraging for worms listen for any audible sign of worm surfacing activity.

When a worm is located the fox pauses, apparently to determine its precise position, and then plunges its head onto the ground pulling the worm out of its burrow with a quick sideways sweep of its head. Capture rates appear to be similar for both species under the same conditions (Macdonald (1977a, 1980)). Foxes might, however, use badgers as a clue to sites with high worm densities, particularly under bad 'worming' conditions (Macdonald (1980a)). There is some evidence that badgers forage 'optimally' (at least if defined by the marginal value theorem (Charnov (1976)), leaving a particular site if the capture rate drops below an average rate for several sites (Kruuk (1978a)). Some foxes, however, if living in groups with more than 2 members, tend to leave a patch too late with respect to optimality considerations. As Macdonald (1980a) suggests this should be seen in connection with the social organization of the foxes with subdominant animals deliberately 'overfishing' the worm patches as they are prevented from access to preferred feeding sites by the dominant animals in the group.

3.2.2. METHODS.

I have collected data with a view to answering three questions about worm ecology:

(1) how do worm densities and biomasses vary between habitats ?

(2) what factors could be used by foxes and badgers to locate patches with high worm densities and/or biomasses ?

(3) could an animal familiar with its range predict microclimatic patterns important in determining worm surfacing activity ?

Earthworm samples were collected in July 1982 by the formalin

extraction method (Raw (1959)). The relative merits of different sampling methods have been discussed by several authors (e.g. Satchell (1969, 1971)) and the formalin extraction method has been found to yield similar or slightly worse results in comparison with other methods for most worm species but superior results for deep burrowing species such as L. terrestris. The efficiency of formalin sampling has been shown to be closely related to the factors affecting motor activity of earthworms. Lakhani and Satchell (1970) determined that soil temperature and soil moisture are the two main factors affecting the efficiency of formalin sampling and they developed an equation for deriving corrected population estimates from samples with conditions deviating from optimal conditions as determined in experiments (soil temperature of 10.6° and soil moisture of 10 %). Optimal conditons are most likely to be encountered in spring or in autumn. Using Lakhani and Satchell's correction equation (equation (1); see below) it should be possible, however, to obtain results comparable to other studies from other times of the year. The advantage of a summer sample extracted with formalin lies in the fact that only the active part of the population is collected which is the only one of interest to foxes and badgers! Thus, summer sampling can provide two measures of earthworm populations: using the correction factor, the 'true' population density can be estimated while the actual numbers collected provide an index of the density of the active and, for foxes and badgers, potentially accessible population. Results from summer should be of particular interest as this must be a 'bottleneck' period of worm availability to foxes and badgers.

Samples were collected from 5 different habitats (as recognized by the habitat map classification, section 2.2 and Box 1): deciduous woodland, mixed coniferous/deciduous plantations, summer cereals (arable land), pasture, and long grassland. I also attempted to sample different soil types and selected within two habitats (deciduous woodland and mixed

mixed plantations) two sites, each on a different soil type (clay and rendzina, Fig. 3.9).

In a given habitat, a site of approximately 30 m by 30 m was randomly chosen. At each site, 8 sample plots (except 6 on pasture) were evenly spread over the site subject to the local topography (e.g. large surfacing tree roots were avoided). According to Satchell (1971) 8 plots should yield a population estimate with an error of ca 10%. As the results indicate, my density and biomass estimates (Table 3.1) were similar to the results of other studies, but with larger standard errors due to the small sample sizes.

Slopes were avoided to keep the formalin solution confined to the defined sample area. At each sample plot an aluminium frame of size 0.55 m by 0.55 m was pressed firmly into the ground and everything loose including the grass layer on pasture removed from the soil surface, thus exposing the bare soil. Soil temperature, air temperature and vegetation parameters were measured (Box 4) and a soil sample was taken with a corer (diameter 3 cm) from approximately 10 cm depth. The soil sample was stored in airtight plastic bags and processed within 24 hours (see below).

The vegetation parameters measured included cover values of 6 height classes and the amount of litter present within the frame as assessed on a scale of 0 to 4 (Box 4). These parameters were selected as being likely to affect the food supply of worms and/or influence the microclimatic conditions at the site.

Next, a watering can was used to spread the formalin solution evenly over the area surrounded by the frame. Several applications were made, each separated by several minutes. Most of the worms did not react to the first application but came out of their burrows immediately after the second. I continued to apply the solution until either the soil was waterlogged or no worm had surfaced for two consecutive applications. I considered it more

BOX4: Vegetation and soil parameters measured during earthworm samling.

a) VEGETATION

Coverage in each of 6 height classes were recorded on a scale of 0 to 6:

0 -	none		
1 -	0 - 1%	4 -	25 - 30%
2 -	1 - 5%	5 -	50 - 75%
3 -	5 - 25%	6 -	› 75%

Height classes were defined as follows:

TOPTREE - large mature trees of at least 6 to 10 m height (large oak and beech and sycamore trees).
SECTREE - smaller trees either not yet fully grown or not growing any larger. Examples are larch, spruce and beech and oak trees in plantations.
SHRUB - shrubs and large woody plants of the hazelnut or elderberry type; also small hawthorns in plantations.
TALLHERB - large non-woody, herbaceous plants such as bracken, large bramble aggregates or tall grasses.
LOWHERB - small herbaceous plants, e.g. dog's mercury, bluebell etc.
BOTCOVER - vegetation covering the immediate soil surface. Mainly mosses.

b) LITTER

The amount of litter was assessed on a 0 to 4 scale:

0 - no litter present
1 - litter present, but loosely scattered
2 - litter densely scattered
3 - litter present as a thin, continuous surface
4 - litter present in several layers

c) SOIL PARAMETERS

A soil sample was taken close to the frame with a corer (diameter 3 cm) from a depth of 10 cm and placed in air-tight plastic bags. Samples were processed within 24 hours to determine SOIL MOISTURE and pH.

A 15 g sample was taken and oven dried at 105 C until successive weighings indicated a weight change of less than 2 mg. SOIL MOISTURE is then the difference between the wet weight and dry weight expressed as a percentge of the wet weight (see Allen et al. (1974)).

pH was measured electrometrically using a standard Pye pH meter.

important to collect all worms willing to surface rather than to confine myself to a strictly standardized treatment. Usually this required 4 to 5 applications using a total of 20 to 25 litres. Worms were collected as soon as they surfaced and stored in 4% formalin solution (Satchell (1971)).

Earthworms were identified using external characteristics following the keys provided by Gerard (1964). They were classified into the categories juveniles or adults according to the presence or absence of a clitellum and identified as L. terrestris or other. No attempt was made to distinguish between L. terrestris and other species if the specimen was less than 70 mm long. Each specimen was weighed and its length measured.

Population figures were estimated using the correction equation from Lakhani and satchell (1970):

$$\text{est. pop.} = \text{obs. pop.} * e^{[0.0075\ (\text{temperature} - 10.6)^2]} * e^{[-0.0214\ (\text{moisture} - 40)]} \qquad (1)$$

Total dry weight was calculated using the conversion formula by Phillipson et al. (1978, July value):

$$\text{total dry weight} = 0.1927\ \text{preserved weight} \qquad (2)$$

This formula is nearly identical with a formula derived from Satchell (1971, eqn. (3)) and Lakhani and Satchell (1970, eqn. (4)):

$$\text{total dry weight} = \text{fresh weight (biomass)} / 6.37$$

$$\text{including guts} = 0.1912\ \text{preserved weight} \qquad (4)$$

I selected Phillipson's et al. formula as it was established using

Wytham worms. Biomass was calculated as fresh weight at sampling time using the conversion factor provided by Satchell (1971) (eqn (3). Energy equivalents were calculated using the conversion factors from Phillipson et al. (1978):

energy equiv. = 17.209 kJ g^{-1} total dry weight (5a)
immatures (July) including guts

energy equiv. = 16.649 kJ g^{-1} total dry weight (5b)
adults (July) including guts

Program WORMFOR utilized the conversion factors listed in eqns (1) to (5) and provided a summary for each sample plot for six dependent earthworm variables

(1) observed population density [individuals m^{-2}]
(2) estimated population density [individuals m^{-2}]
(3) observed biomass [g m^{-2}]
(4) estimated biomass [g m^{-2}]
(5) observed energy equivalents [kJ m^{-2}]
(6) estimated energy equivalents [kJ m^{-2}]

Statistical analysis was performed using the statistical package MINITAB available on the University's VAX and the Dept. of Zoology's PDP-11.

Soil samples were processed following the procedures recommended by Allen et al. (174) for determining fresh soil moisture and pH. Large roots and stones were removed from the soil and a 15 g sample oven dried at 105 °C until successive weighings indicated a weight change of less than 2 mg. pH was measured using a standard pH meter. All samples were processed at the

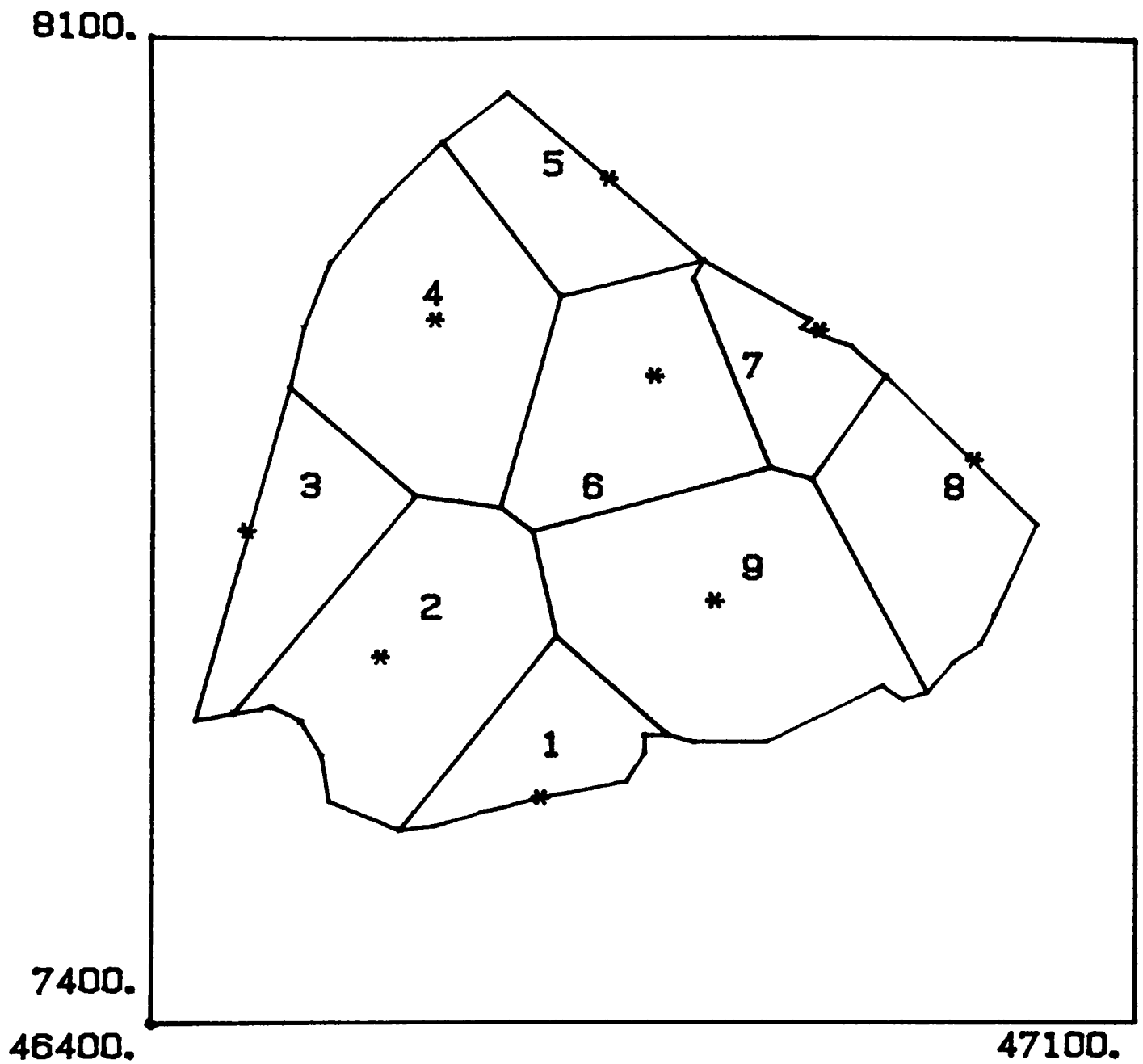
University Field Station in Wytham.

The western half of Wytham Park was selected as an area of pasture suitable for microclimatic measurements. The area consists of three fields separated by fences and is regularly grazed by cattle. It is shaped like a shallow valley and surrounded on three sides by woodland and bordered on the fourth side by pastures, arable fields and a small piece of woodland known as Wormstall Duck Pond. A spring originates in the southwestern upper half and runs northeast towards Wormstall Duck Pond along the bottom of the valley between moderate to steep slopes.

Measurement of microclimatic variables and obsevations on earthworm activity were conducted by N. Wadham (1984). Data were collected in spring on 9 mights between 29th March 1983 and 9th April 1983 and in autumn on 6 hights between 15th September 1983 and 21st September 1983. Measurement points for the microclimatic measurements were selected to gather information about changes in wind exposure and soil temperature. Points 3,4,5 and 1,9,8 were symmetrically arranged about the valley midline to accommodate changes in exposure as predicted by the prevailing wind direction (Fig. 3.2): points 1 and 3 lie in the shadow of the wood, points 4 and 9 lie on exposed areas in the centre of two fields and points 5 and 8 lie on the North east boundary directly exposed to the wind. Points 2,6, and 7 lie along the base of the valley with predicted reduced wind exposure. At dusk, each point was visited sequentially from 1 to 9. At each measurement point, soil temperature was recorded using two thermistor probes. The data value for the point was taken as the mean of both observations. Wind speed was recorded using a hand held anemometer as the average speed over one minute.

In addition, the entire area was split into sections (strata) which were thought to reflect possible changes in worm abundance (Fig. 3.3) according to changes in water content, slope and litter presence. Sections

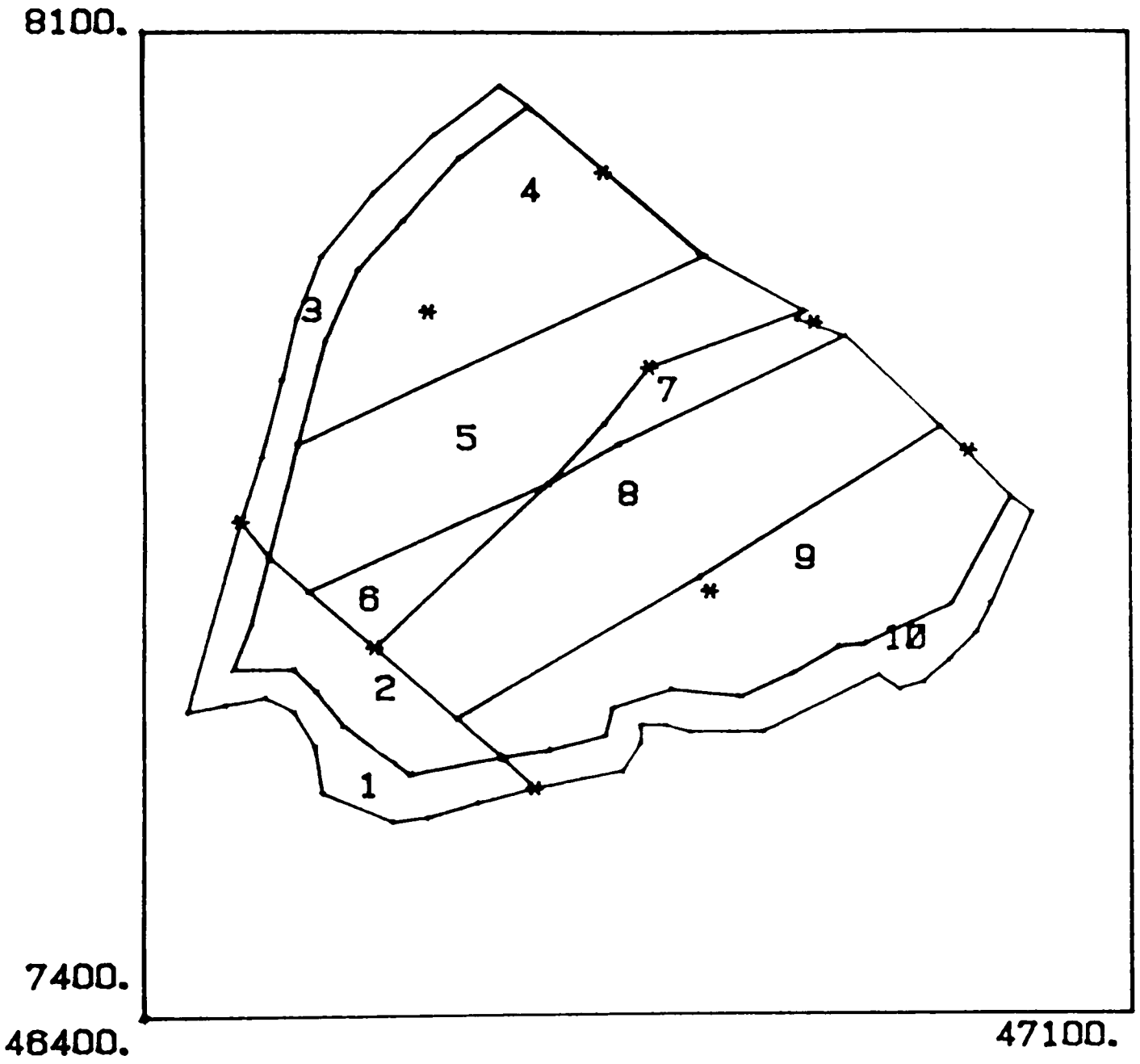
CLIMATIC ZONES WYTHAM PARK



1 - 9 NUMBER OF CLIMATIC ZONE

STARS SITES OF MICRO - CLIMATIC MEASUREMENTS

EARTHWORM STRATA WYTHAM PARK



1 - 10 NUMBER OF EARTHWORM STRATUM

STARS SITES OF MICRO - CLIMATIC MEASUREMENTS

1,3, and 10 run parallel to the woodland boundary reflecting increased litter presence and reduced wind. Sections 6 and 7 are at the bottom of the valley with 7 being considerably wetter than 6 due to the flooding of the area next to the ditch. Sections 2,4,5,8, and 9 reflected different degrees of slope with its possible consequences for water levels, humidity etc. (Reynolds & Jordan (1975)) and take into account possible differences between fields due to differential grazing by the cattle. Section 2 had the steepest slope, followed by 5 and 8 while 4 and 9 had only a slight slope. Several fixed transects were walked through each section to record worm surfacing activity, using a torch fitted with a red light. Worms were counted on several occasions, but only on the first night was an appreciable amount of surfacing observed. Thus we confirmed that earthworms occurred but were not able to obtain reliable quantitative results. Data were analysed using MINITAB statistical package.

3.2.3. RESULTS OF PRESENT STUDY.

Altogether 684 worms were collected from 54 plots. Table 3.2 shows the distribution of numbers and average weights over different habitats and Table 3.3 summarizes data on length and weights. Other juveniles comprised the bulk of the earthworms sampled in terms of numbers (64.67 %) but constituted only 20.35 % of the total preserved weight biomass. L. terrestris constituted only a small fraction of the numbers (18.1 %) but the bulk of the weight (70.18 %). On average, an adult L. terrestris weighed 6.75 g (preserved weight (PW); n=38) while the large immature L. terrestris weighed 2.48 g PW (n=86) yielding an overall average figure of 3.79 g PW. Adults of other species weighed on average 0.438 g PW (n=117) and juveniles 0.252 g PW (n=443), with an overall average of 0.291 g PW (n=560).

The average weight of L. terrestris adults and juveniles varies

Table 3.2 Numbers and weights of earthworms collected in different habitats, July 1982.

a) numbers.

VEGETATION	SOIL	TOTAL	LUMBRICUS			OTHERS		
			TOTAL	ADULT	JUVEN	TOTAL	ADULT	JUVEN
Deciduous	clay	200	24	12	12	176	36	140
Deciduous	rendz.	174	37	9	28	137	22	115
Plantation	clay	63	17	4	13	46	7	39
Plantat.	rendz.	118	8	1	7	110	21	89
Pasture	clay	31	13	7	6	18	10	8
Grassland	rendz.	38	11	3	8	27	9	18
Arable	clay	60	14	2	12	46	12	34
-- all sites --		684	124	38	86	560	117	443

b) weights (g preserved weight; L. terrestris only).

VEGETATION	SOIL	ALL		ADULTS		JUVENILES	
		MEAN	S.D.	MEAN	S.D.	MEAN	S.D.
Deciduous	clay	4.5	2.77	6.85	1.24	2.17	1.61
Deciduous	rendz.	2.80	1.87	5.40	1.53	1.96	0.99
Plantation	clay	2.49	2.30	5.96	2.46	1.42	0.55
Plantat.	rendz.	3.09	1.78	6.75	0	2.57	1.07
Pasture	clay	3.02	1.36	4.02	0.76	1.86	0.83
Grassland	rendz.	2.37	1.71	4.63	0.72	1.53	1.02
Arable	clay	2.96	0.53	3.59	0.18	2.86	0.50

c) one-way analyses of variance on weight differences between habitats.

HABITAT LEVELS	EARTHWORM AGE CATEG.	D.F.	F	SIGNIFICANCE
all 4 woodland vegetation/soil categories	all	3 & 82	3.71	$p < 0.025$
all 7 habitats	all	6 & 117	2.67	$p < 0.025$
all 4 woodland vegetation/soil categories	juveniles	3 & 56	1.99	n.s.
all 7 habitats	juveniles	6 & 79	2.98	$p < 0.025$

no ANOVAR was computed for adults as sample sizes were too small (see under a)).

Table 3.3 Summary of weights and lengths of earthworms collected in Wytham Woods, July 1982.
Weights in section a and c are preserved weights, in section b fresh weight at time of sampling (L. terrestris).
Units: weights in g, lengths in mm.

a)

	ALL WORMS LENGTH	ALL WORMS PRES. WEIGHT	ALL LUMBR. LENGTH	ALL LUMBR. PRES. WEIGHT	ALL OTHERS LENGTH	ALL OTHERS PRES. WEIGHT
N	684	684	124	124	560	560
MEAN	70.4	0.801	122.8	3.11	58.9	0.291
MEDIAN	61.0	0.260	119.0	2.49	54.0	0.200
STDEV	36.2	1.432	33.4	2.07	24.8	0.346
SEMEAN	1.4	0.055	3.0	0.19	1.0	0.015

b)

	ALL LUMBR. BIOMASS	LUMBR. ADULTS BIOMASS	LUMBR. JUVEN. BIOMASS
N	124	38	86
MEAN	3.79	6.75	2.48
MEDIAN	3.03	6.28	2.18
STDEV	2.52	2.07	1.30
SEMEAN	0.23	0.34	0.14

c)

	LUMBR. ADULTS LENGTH	LUMBR. ADULTS WEIGHT	LUMBR. JUVEN. LENGTH	LUMBR. JUVEN. WEIGHT	OTHERS ADULTS LENGTH	OTHERS ADULTS WEIGHT	OTHERS JUVEN. LENGTH	OTHERS JUVEN. WEIGHT
N	38	38	86	86	117	117	443	443
MEAN	158.0	5.54	107.2	2.03	67.7	0.438	56.6	0.252
MEDIAN	162.0	5.16	105.0	1.79	56.0	0.220	52.0	0.200
STDEV	29.0	1.70	21.3	1.06	30.7	0.581	22.4	0.236
SEMEAN	4.7	0.28	2.3	0.11	2.8	0.054	1.1	0.011
%TOTAL WEIGHT		38.36	-	31.82	-	9.34	-	20.35
%TOTAL NUMBERS		5.55	-	12.55	-	17.08	-	64.67

considerably between habitats (Table 3.2). The mean weight of adults over all four woodland sites is significantly larger than the mean of the exposed habitats (arable, pasture and grassland; t-test, two-tailed, t = 5.53, p=0.000). Several one-way analyses of variance show significant differences of mean weights for different habitats and worm categories (Table 3.2c).

Table 3.4 presents the results of the calculations performed by program WORMFOR. As a comparison of the 'observed' against 'estimated' columns shows, Lakhani & Satchell's (1970) formula (eqn (1)) yields estimated population densities of up to four times higher than the observed density. However, the correction factor varies considerably between habitats and is far higher in exposed habitats (pasture and arable land) than in woodland.

Statistical analyses were then performed to obtain answers to the following questions:

1. Are there differences between habitats of L. terrestris densities, biomass and energy equivalents ?
2. Which habitats differ significantly ?
3. Are there differences between soil types in L. terrestris densities?
4. How do soil type and habitat type affect worm densities, biomass and energy equivalents ?
5. Do L. terrestris densities, biomass and energy equivalents show any relationship to vegetation and soil parameters ?
6. What is the relationship between these parameters and the earthworm variables ?
7. What is the pattern of microclimate over one habitat ? How could this pattern affect the foraging efforts of badgers and foxes. ?

Table 3.4 *L. terrestris* densities, weights, and energy equivalents in different habitats, July 1982. Densities are in individuals m^{-2}, weights are g fresh weight m^{-2}, and energy equivalents are in kJ m^{-2}. All values ± standard errors.
R: factor derived from eqn (1) that, if multiplied with observed values, yields estimated values. Indicates the extent to which sampling conditions deviated from the optimum.

VEGETATION	SOIL	DENSITY		WEIGHTS		ENERGY EQUIVALENTS		R
		OBSERVED	ESTIMATED	OBSERVED	ESTIMATED	OBSERVED	ESTIMATED	
Deciduous	BOTH	12.6±1.6	20.4±3.7	53.3±8.3	83.7±11.7	142.1±21.9	223.3±31.0	
Deciduous	clay	9.9±2.3	15.8±3.7	54.4±13.5	84.3±19.4	144.6±35.9	223.7±51.5	1.596
Deciduous	rend.	15.3±1.9	24.9±3.0	52.1±10.5	83.1±14.5	139.7±27.9	222.8±38.3	1.627
Plantat.	BOTH	5.2±1.3	8.7±2.3	16.9±5.4	27.8±8.5	45.7±14.5	74.6±22.6	
Plantat.	clay	7.0±2.0	12.7±3.6	21.3±7.5	38.1±13.0	57.0±19.9	101.9±34.4	1.814
Plantat.	rend.	3.3±1.7	4.8±2.2	12.5±8.0	17.5±10.5	33.6±21.5	47.3±28.3	1.455
Pasture	clay	7.2±2.3	21.1±7.2	26.4±8.4	77.3±25.7	70.1±22.1	205.6±67.9	2.931
Grassland	rend.	4.5±1.4	7.8±2.3	13.1±3.4	23.0±5.9	35.2± 9,1	61.6±15.8	1.733
Arable	clay	5.8±2.0	23.0±7.4	20.9±6.3	83.0±25.1	56.5±17.0	224.8±68.2	3.966

DENSITIES, BIOMASS AND ENERGY EQUIVALENTS. Each of the six dependent variables (estimated and observed densities, biomasses, and energy equivalents) were investigated on differences between the studied habitats using a Kruskal-Wallis one-way analysis of variance after initial checks with an Fmax-test (Sokal & Rohlf (1981)) showed that variances were too uneven to guarantee homogeneity of variance between groups for most analyses. Results are presented in Table 3.5a. There is a significant difference in all dependent variables considered. Multiple comparison tests were then performed to detect pairs of habitats that differed significantly in their earthworm content (Conover (1980:231)). Results are shown in Table 3.5b. A comparison of the observed and estimated categories shows that the Lakhani and Satchell correction factor reduces the 'observed' significant differences between deciduous woodland and arable land and creates 'estimated' significant differences between arable and plantations. Plantations show the lowest values, always significantly different from deciduous woodland. With respect to earthworm densities this result justifies, in retrospect, the distinction between different types of woodland in the habitat map classification (chapter 2.2).

Deciduous woodland is also significantly different from long grassland which has low values comparable to plantations. 'Estimated' pasture does not differ from plantation for worm densities, but does for estimated biomasses and energy equivalents. The average worm biomass derived from data given in Table 3.4 is in pasture 3.66 g, in plantation 3.20 g. As Table 3.2a reveals this is due to a different age structure in the population: pasture was the only habitat with more adults than juveniles while many juveniles but very few adults were collected in the plantations. Thus, if climatic conditions are favourable and the surfacing worm population resembles the estimated population, foxes and badgers foraging in pasture encounter not only overall higher biomasses per patch but also on

Table 3.5 Kruskal-Wallis one-way analysis of variance on differences between habitats. Dependent variables are the 1982 results from Table 3.4.

a) Results of the Kruskal-Wallis test.

DEPENDENT VARIABLE	H	H ADJUSTED FOR TIES	PROBAB. LEVEL
Density observed	13.05	13.45	< 0.05
Density estimated	12.30	12.44	< 0.05
Biomass observed	15.20	15.37	< 0.005
Biomass estimated	15.46	15.63	< 0.005
Energy equiv. obs.	15.36	15.53	< 0.005
Energy equiv. est.	15.58	15.75	< 0.005

b) A posteriori multiple comparison tests to identify significant differences between pairs of habitats.
Only pairs with significantly different population means are listed.

DEPENDENT VARIABLE	HABITAT HIGH MEAN	HABITAT LOW MEAN	TEST VALUE	CRITICAL VALUE	SIGNI-FICANCE
Density obs.	Deciduous	Plantation	17.5	10.3	< 0.001
	Deciduous	Grassland	18.6	12.6	< 0.005
	Decidous	Arable	15.5	12.6	< 0.02
Density est.	Deciduous	Plantation	15.9	10.3	< 0.005
	Deciduous	Grassland	17.0	12.6	< 0.01
	Arable	Plantation	12.61	12.6	< 0.05
Biomass obs.	Deciduous	Plantation	19.5	10.3	< 0.001
	Deciduous	Grassland	19.7	12.6	< 0.005
	Deciduous	Arable	15.1	12.6	< 0.02
Biomass est.	Deciduous	Plantation	18.9	10.3	< 0.001
	Deciduous	Grassland	17.8	12.6	< 0.01
	Pasture	Plantation	14.3	13.95	< 0.05
	Arable	Plantation	15.2	12.6	< 0.02
Energy eq. obs.	Deciduous	Plantation	19.6	10.3	< 0.001
	Deciduous	Grassland	20.0	12.6	< 0.002
	Deciduous	Arable	15.2	12.6	< 0.02
Energy eq. est.	Deciduous	Plantation	18.9	10.3	< 0.001
	Deciduous	Grassland	17.9	12.6	< 0.01
	Pasture	Plantation	14.3	13.95	< 0.05
	Arable	Plantation	15.3	12.6	< 0.02

average heavier individuals.

Within deciduous woodland and plantation, the two sample sites representing different soil types were compared using t -tests (all data were normally distributed according to the Shapiro-Wilk test for normality as implemented on MINITAB (Ryan et al (1982))). None of them proved to be significant. To further investigate possible effects of soil type, a two-way analysis of variance was run after establishing that homogeneity of variance held for these data. Densities, biomasses and energy equivalents were compared for deciduous woodland on clay and rendzina and mixed plantation on clay and rendzina. Soil type proved to be of no importance in any of the cases (Table 3.6). For densities, however, soil accounted for a significant amount of variance after the variation due to habitat had been considered. The effects of soil turn out to be different for the two habitats (Table 3.4): all dependent variables increase from deciduous woodland on clay to deciduous woodland on rendzina while the opposite trend is found in plantations.

VEGETATION AND SOIL PARAMETERS. The correlations of the vegetation (6 cover values and litter, Box 4) and the two soil parameters (soil moisture and pH) with observed and estimated earthworm variables are presented in Table 3.7. If all sample plots are considered together (Table 3.7a), three variables (definitions see Box 4) emerge that are significant: top tree cover (tree canopy) and bottom cover are both positively correlated with all earthworm variables except estimated densities while secondary tree cover is negatively correlated. The positive correlations with canopy and bottom cover are easily understood as a function of providing shade, reducing wind, litter and increased levels of humidity (moss). It is less clear what kind of negative influence could be exerted by secondary tree cover. Note that this correlation is found only in deciduous woodland (Table 3.7b) and not in

Table 3.6 Two-way analysis of variance on the 1982 *L. terrestris* results from Table 3.4. Habitats considered are DECIDUOUS and PLANTATION on different soil types. Factors are habitat and soil type.

DEPENDENT VARIABLE	EFFECT OF HABITAT		EFFECT OF SOIL		INTERACTION	
	F	p	F	p	F	p
Density obs.	14.05	< 0.01	0.17	n.s.	5.25	< 0.05
Density estim.	13.21	< 0.01	0.04	n.s.	7.08	< 0.025
Biomass obs.	12.82	< 0.01	0.30	n.s.	0.10	n.s.
Biomass estim.	14.40	< 0.01	0.55	n.s.	0.44	n.s.
Energy eq. obs.	12.82	< 0.01	0.27	n.s.	0.11	n.s.
Energy eq. est.	14.48	< 0.01	0.51	n.s.	0.47	n.s.

Table 3.7 Spearman rank correlation of 1982 *L. terrestris* results with vegetation and soil variables. Only significant correlations are listed. probability levels: * $p < 0.05$; ** $p < 0.01$

a) Correlation over all habitats together (n=54).

	TOPTREE	SECTREE	BOTCOVER
Density observed	0.328 *		0.384 **
Density estimated			
Biomass observed	0.420 **		0.407 **
Biomass estimated	0.289 *	−0.352 *	0.273 *
Energy equiv. obs.	0.422 **		0.409 **
Energy equiv. est.	0.287 *	−0.353 *	0.273 *

b) correlation within habitats.

	DECIDUOUS WOODLAND (n=16)			PLANTAT. (n=8)	GRASSL. (n=8)
	TOPTREE	SECTREE	PH	PH	TALLHERB
Density obs.	−0.566 *		0.631 *	−0.577 *	
Density estim.	−0.595 *		0.625 *	−0.583 *	0.739 *
Biomass obs.		−0.588 *			
Biomass estim.		−0.628 *			
Energy equiv.obs.		−0.585 *			
Energy equiv.est.		−0.626 *			

plantations.

In no case does litter show a correlation with earthworm variables. This is presumably due to the fact that the litter available at this time of the year is dominated by less palatable species (oak, beech etc.). As Table 3.7b also indicates, pH could be responsible for the opposing tendencies observed earlier for deciduous woodland and plantations: presence of earthworms increases with pH in deciduous woodland (from clay to rendzina) and decreases for plantations (from rendzina to clay).

In grassland, tall herb cover shows a strong correlation to earthworm presence. This might be due to the fact that dense long grass reduces wind and thus increases humidity while also providing more organic material. This, however, could only be partially exploited by badgers or foxes as the capture success of badgers decreases with sward length (Kruuk et al. (1979)) and a similar effect could be expected for foxes. Macdonald (1980) suggested that foxes skirted the edge of long grass patches to get the best compromise.

All factors were then combined in a multiple regression equation to detect possible interaction effects between variables. The first multiple regression considered all 54 plots and all parameters. The results were unsatisfactory: Table 3.8 demonstrates that only a small fraction of the variation is accounted for; in two cases the regression is not significant and none of the multiple regression coefficients is significantly different from zero except soil moisture for observed biomasses and energy equivalents. If anything, this again emphasises the paramount importance of water relations to earthworms. I then decided to investigate whether any relationship between earthworm abundance parameters and environmental variables existed within given habitats. Due to small sample sizes, regressions were only run on the deciduous woodland and plantation plots (both n=16). None of the regressions for plantations, nor for deciduous

Table 3.8 Multiple regression analysis on 1982 L. terrestris results. Predictor variables are vegetation and soil variables. Multiple regression for all plots on all predictor variables (df: regression 9, residuals 35).

DEPENDENT VARIABLE	R-SQUARED ADJUSTED FOR D.F.	F-RATIO OF ANOVAR	p
Density observed	0.166	1.97	n.s.
Density estimated	0.066	1.35	n.s.
Biomass observed	0.342	3.54	< 0.01
Biomass estimated	0.199	2.22	< 0.05
Energy equiv. obs.	0.341	3.52	< 0.01
Energy equiv. est.	0.197	2.20	< 0.05

t - ratio test on difference of coefficients from 0 : only MOISTURE significantly different at $p < 0.05$ for the two regressions with BIOMASS OBS. and ENERGY EQUIV. OBS.

BIOMASS OBS. = - 5.5 + 3.63 LITTER + 0.81 TOPTREE
- 5.90 SECTREE - 3.01 SHRUB - 2.13 TALLHERB
+ 0.68 LOWHERB + 6.36 BOTOMCOV
+ 2.34 MOISTURE - 2.85 PH

EN.EQUIV. OBS = - 16.9 + 9.7 LITTER + 2.06 TOPTREE - 15.6 SECTREE - 7.7 SHRUB - 5.71 TALLHERB + 1.8 LOWHERB + 17.1 BOTOMCOV + 6.25 MOISTURE - 7.3 PH

woodland showed any significant results. I therefore decided to select only those vegetation parameters that had previously shown a significant correlation with the dependent variables (Table 3.7b). The resulting multiple regression was significant for the two measures of density (Table 3.9) which were the only ones with non-significant regressions when all habitats were pooled (Table 3.8). The two regressions for observed and estimated densities showed different sets of coefficients to be significant and thus perhaps distinguish between seasonal effects (effects on motor activity) and long term effects (general level of population density). This still does not explain why secondary tree cover should have a negative effect on earthworm presence.

To summarize the results of this section, there seems to be little gained from using cover or litter as an indicator of earthworm presence at this time of the year (summer). Highest 'active' (observed) densities are found in deciduous woodland while few worms were present in exposed habitats. Higher 'active' biomasses are generally found in wetter soils. Sites with large trees or well developed bottom cover (moss) which again are dependent on a wet soil are favourable for worms. The results emphasize the dominating role of humidity and soil water content for earthworm numbers at a time when their food supply is restricted.

MICROCLIMATE. The third question concerns earthworm surfacing activity in relation to microclimatic pattern. The investigation was designed to see whether microclimatic conditions over a relatively uniform habitat showed any kind of consistency that could be useful in predicting surfacing activity.

During both periods of recording little precipitation fell and most nights were dry. Soil temperatures in spring were well below, and in autumn well above the optimum temperature of 10.5^{o} C. There were persistent

Table 3.9 Multiple regression analysis on L. terrestris results. Predictor variables are selected vegetation and soil variables.

a) Multiple regression for Deciduous plots only on the three predictor variables TOPTREE, SECTREE, and pH which correlated significantly at least once with any of the dependent variables (cf. Table 3.7). df: regression 3, residuals 12, n=16 .

DEPENDENT VARIABLE	R-SQUARED ADJUSTED FOR D.F.	F-RATIO OF ANOVAR	p
Density observed	0.554	7.204	< 0.01
Density estimated	0.557	7.277	< 0.01
Biomass observed	0.233	2.520	n.s.
Biomass estimated	0.302	3.163	n.s.
Energy equiv. obs.	0.235	2.535	n.s.
Energy equiv est.	0.306	3.200	n.s.

b) t - ratio test on difference of coefficients from 0.

DEPENDENT VARIABLE	INTERCEPT	TOPTREE	SECTREE	PH
Density observed	n.s.	n.s.	< 0.05	< 0.05
Density estimated	n.s.	< 0.05	n.s.	< 0.05

c) equations:

DENSITY OBS. = 13.6 - 2.84 TOPTREE - 1.31 SECTREE + 2.35 PH
DENSITY EST. = 25.4 - 5.06 TOPTREE - 2.02 SECTREE + 3.64 PH

differences in soil temperature between 6.4^{o} C and 8.1^{o} C for spring and 12.7^{o} C and 14.5^{o} C in autumn. A one-way analysis of variance yielded significant differences between sites for soil temperature in spring ($F=3.53$, $n=81$, df.= 8 and 72, $p<0.005$) but not in autumn and not for wind speed in either recording period. However, the pattern of variation between sites compared between the two seasons is the same ($\chi^2 = 0.83$ for soil temperature and 1.92 for wind speed, n.s.), as illustrated by Fig. 3.4.

Table 3.10 presents a matrix of Spearman rank correlations between the sites for both variables for each period. Position 5 does not correlate in wind speed (spring) with any of the points on the same side, nor with any of the points in the bottom of the valley, but it correlates with positions 8 and 9 on the other side. The exposed positions 5, 8, and 9 correlate well with each other but poorly with other positions. Position 4 is a unique place which correlates well with both the group of positions 5, 8, 9 and with the positions 1, 2, and 3. An exception to this is the non-correlation with position 6 which, although geographically close, is placed in a different topographical situation. Soil temperature in spring demonstrates a strong group of positions on the side of the Wormstall Duck Pond (5 - 9) while there is no correlation between 1 to 3. This situation changes in autumn where there is little correlation in soil temperature between sites 5 to 9 and the fewer sites correlate than in spring. However, position 2 is still correlated with position 6 for wind speed.

Figure 3.5 shows how the territorial boundary between the Jew's Harp badger Clan and the Sunday's Hill badger Clan (based on radiotracking results) partitions the valley. Thus it may be of little importance that conditions on one side of the valley (e.g. position 5) can be predicted from the other side (e.g. position 9) while it is more relevant for the local badgers that there is some correlation within the sites at the southwest end of the valley (positions 1 to 3) but less correlation with the more distant

Table 3.10 Spearman rank correlation of soil temperature and wind speed for Wytham Park. Correlations between all measurement points.
Only significant correlations listed.
* p < 0.05; ** p < 0.01.

a) WIND SPEED IN SPRING 1983

	1	2	3	4	5	6	7	8
2	1.00**							
3	0.70 *	0.70 *						
4	0.72 *	0.72 *	0.74 *					
5								
6	0.90**	0.90**						
7	1.00**	1.00**		0.71 *		0.92**		
8				0.89**	0.74 *			
9				0.92**	0.69 *			0.85**

b) TEMPERATURE IN SPRING 1983

	1	2	3	4	5	6	7	8
2								
3		0.77 *						
4								
5		0.70 *	0.91**					
6				0.70 *	0.81 *			
7					0.73 *	0.92**		
8				0.70 *	0.69 *	0.88**	0.72 *	
9			0.73 *	0.75 *	0.81 *	0.95**	0.85**	0.85**

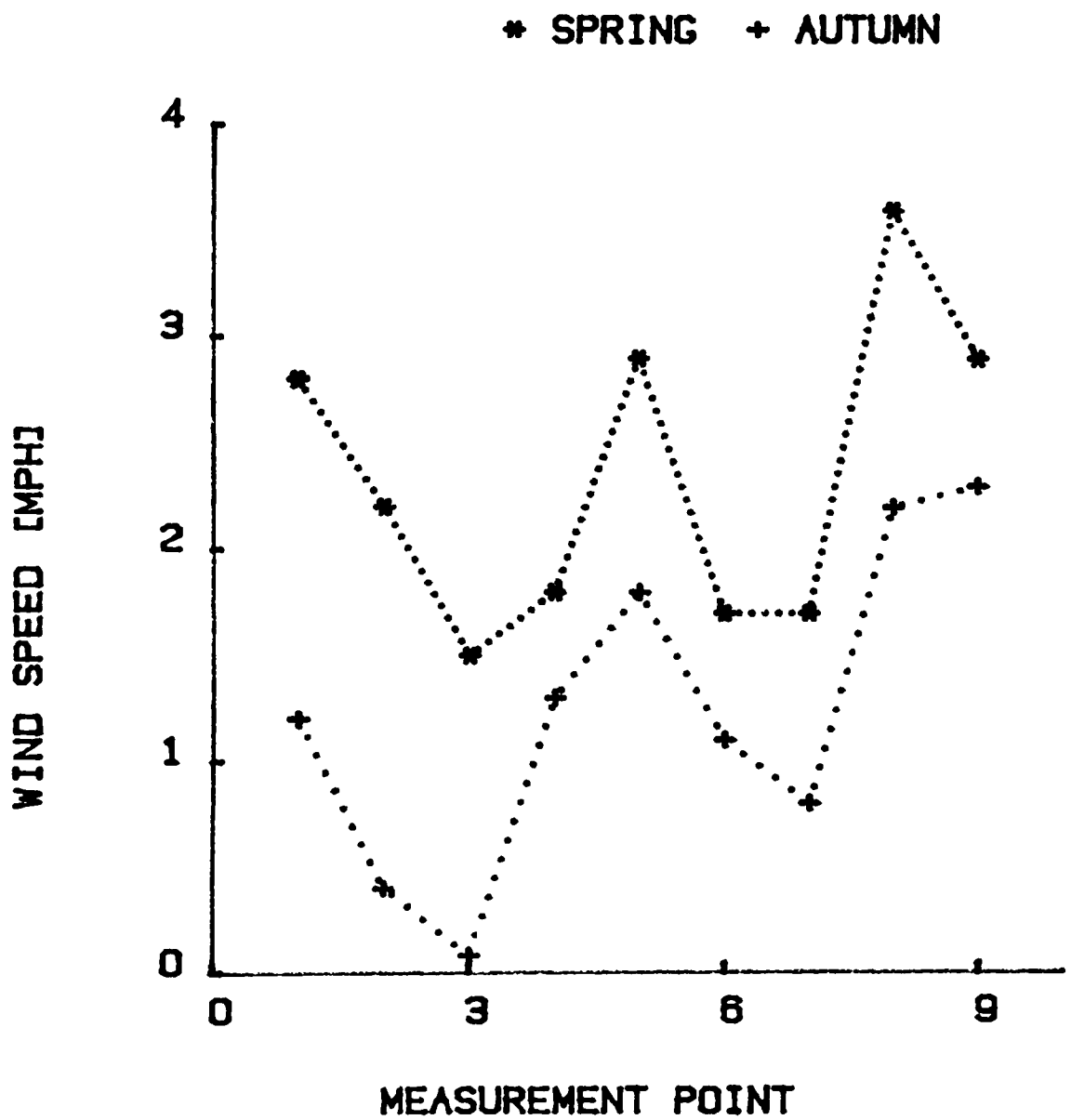
c) TEMPERATURE IN AUTUMN 1983

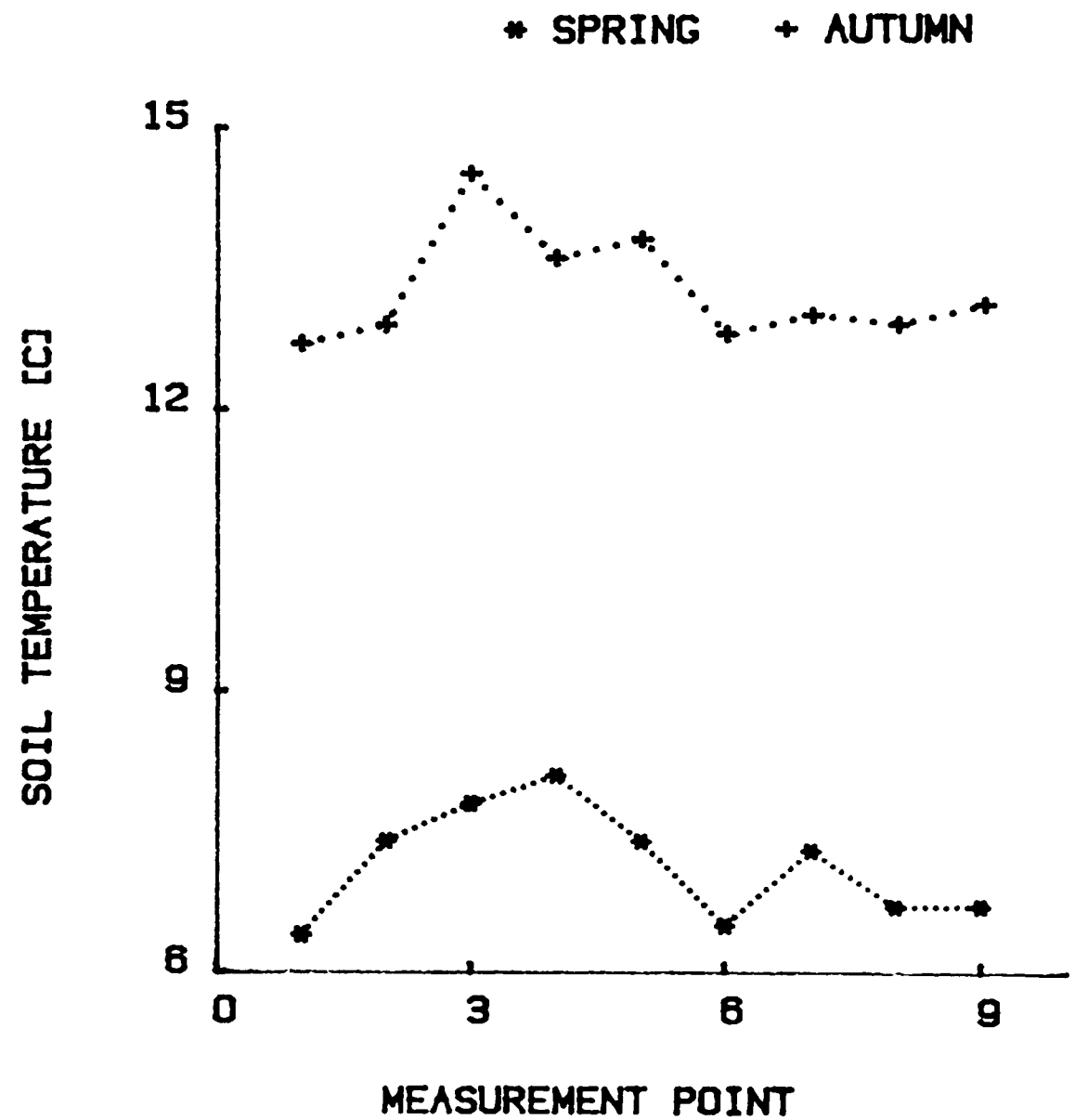
	1	2	3	4	5	6	7	8
2								
3								
4			0.96**					
5								
6	0.93 *							
7								
8						0.8 *		
9			0.97**	0.89 *				

d) WIND SPEED IN AUTUMN 1983

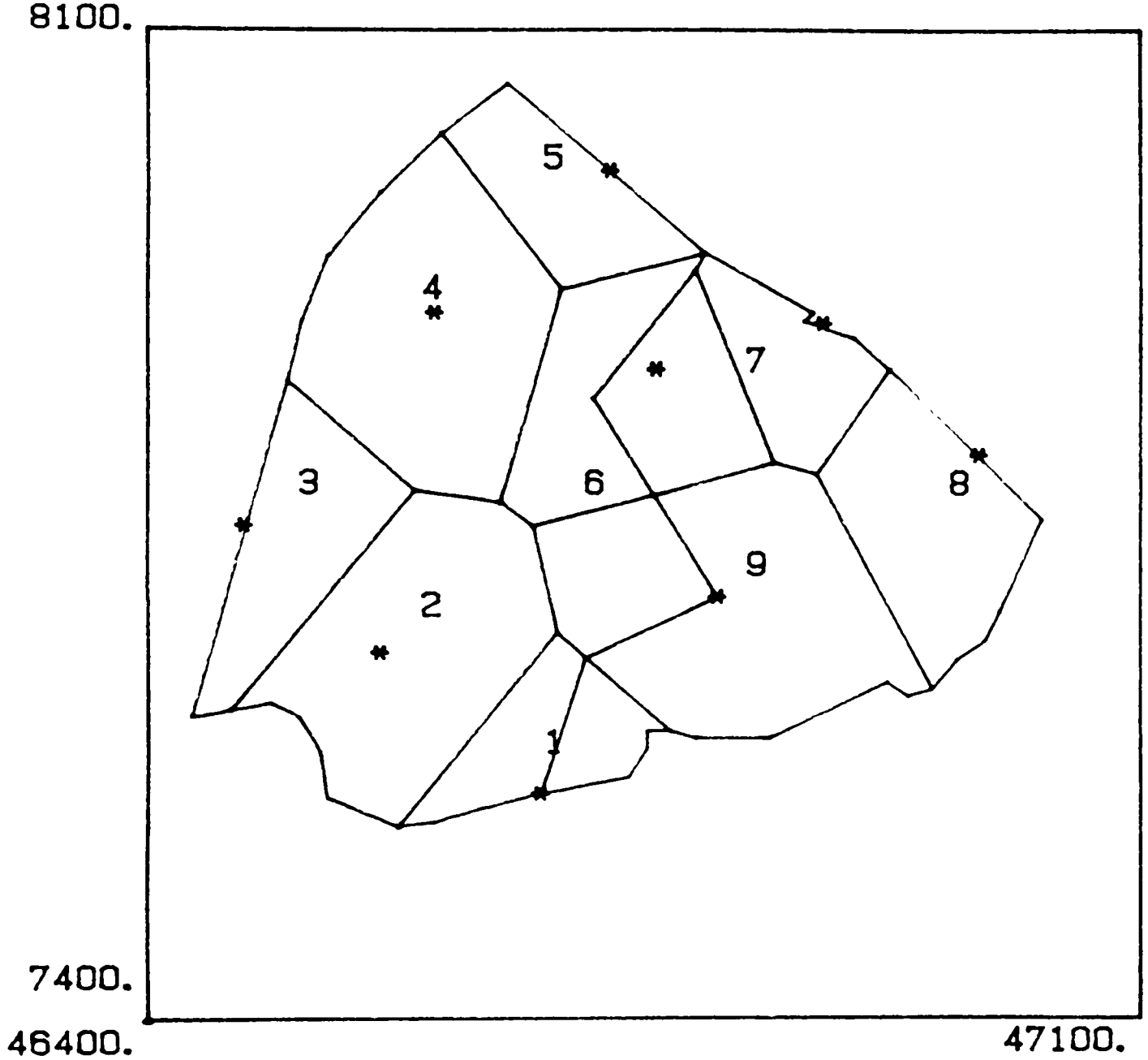
	1	2	3	4	5	6	7	8
2								
3								
4								
5		0.86 *						
6		0.87 *						
7								
8								
9								0.87*

MICROCLIMATE IN WYTHAM PARK (SPRING AND AUTUMN 1983)





CLIMATIC ZONES IN WYTHAM PARK



STARS - MEASUREMENT POINTS
NUMBERS - ZONE NUMBERS

BADGER TERRITORY BORDER
RUNS THROUGH ZONES
1, 9 AND 6

sites towards Wormstall Duck Pond. The observed differences in soil temperature and wind speed between sites were similar in their distribution, indicating an element of temporal stability while on the other hand the degree of correlation between sites changed between the seasons. There are at least two simple, and even complementary strategies which could efficiently exploit these correlations. The first strategy would utilize the correlations between the type of weather and the status of the earthworm populations found at a particular site while a second strategy would use the correlation amongst several sites. Thus, a badger (or a fox) would make a decision according to the rule

A: if humidity and wind is such and such then go to site(s) X/Y/Z;
B: if site X is fruitful then try also sites Y and Z but avoid sites A and B etc.

The two rules could also be combined:

C: if humidity and wind is such and such try first site X, not Y; and depending on the result, continue either to sites A,B, .. or to sites C,D, .. but not to both.

It is difficult to decide which one of the rules promises to be most successful, as this depends on the number of different climatic conditions recognised by the animal (rule A) or the number of patches that are used as 'first' patch (rule B), ie. patches that serve as indicators for the profitability of other patches. However, it seems likely that the utilization of all the information available (rule C) may improve the foraging success relative to rules A and B. Whether certain patches are constantly visited as 'first' patches and how an individual moves through a

given night is the subject of Chapter 6.

3.2.4. DISCUSSION.

EARTHWORM SAMPLING DESIGN AND IDENTIFICATION PROCEDURE. A comparison of my results with Kruuk (1978a) and Cuendet (1984) shows general agreement (Table 3.1). Kruuk (1978) showed significant differences between woodland and plantation and no differences between deciduous woodland and pasture. His results for arable land correspond to my observed populations while they differ for the estimated populations by a factor of two. However, some caution is needed when comparing his results with those of other studies. Unlike Cuendet (1984), Phillipson et al. (1978) or the present study, he did not distinguish between different soil types and as he did not give a precise reference for the locations of his sampling plots they can only be tentatively placed (as in Table 3.1) according to the dominating soil characteristics of the area he mentioned ('Marley-Jews Harp' area). It is likely that he sampled from sites on both soil types since his density estimate for deciduous woodland lies between my density estimates for clay and rendzina (Table 2.4).

Kruuk (1978a) does not describe in detail how he identified the worms in his samples but he essentially followed a procedure similar to mine (Kruuk, pers. comm. 13.10.1984). Cuendet (1984) used a different sampling design (systematic placement of sample points along a linear transect; handsorting of the top 25 cm of the soil plus formalin sampling), and identified all specimens down to species level, resulting in similar biomass estimates but different density estimates, up to twice as high as the results presented here or those of Kruuk (Table 3.1). His value for beechwood on rendzina was derived from Phillipson's et al. (1978) original data (where sample sites were distributed on a stratified random basis) by placing a linear transect

over their sampling area and selecting the 10 nearest plots from their original May/June and October/November samples. The average of Phillipson's et al. (1978) original results for the two periods is 11.27 L. terrestris m^{-2} as compared to 14.4 m^{-2} as derived by Cuendet. This shows that even different sampling regimes yield approximately similar results.

VARIATIONS IN BODY WEIGHT. Kruuk's worm biomasses were calculated using an average weight of 4.27 g for all habitats. This value is slightly less than Cuendet's (1984) mean fresh body weight for adults, ranging from 4.291 g in beech/rendzina woodland to 4.545 g in non-beech/rendzina and 4.665 g in non-beech/clay, and more than my mean fresh weight value of 3.79 g for adults and juveniles combined (adults separately: 6.75 g; juveniles: 2.48 g; Table 3.3). Unfortunately, Kruuk does not indicate how many juveniles and adults were represented in the sample of 41 L. terrestris from which he derived his mean value, so any interpretations of the differences have to remain speculative. Whatever the explanation, these differences obviously affect the biomass calculations, as can be seen in Table 3.1. While Kruuk's and my density estimates for pasture are very close (22.73 ind m^{-2} vs. 21.09 ind m^{-2}, a difference of 7.7 %), his biomass estimate (97.1 g m^{-2}) is 25.6% larger than mine (77.3 g m^{-2}).

Kruuk (1978a) did not examine whether body weight varied between habitats. Cuendet (1984) did not find significant differences of adult mean fresh body weights for L. terrestris between the woodland types he considered. In the present study, differences in juvenile mean body weight were not significant for the woodland sites, but became significant when all habitats were considered. Although small sample sizes prevent any firm conclusions for adults, inspection of Table 3.2b reveals differences between the woodland sites, but more pronounced differences between woodland and open habitats, resulting in overall significant differences for both the 4

woodland sites and all 7 habitats if both juveniles and adults are considered together. Table 12 of Cuendet (1984) indicates a noticable decline of mean adult fresh body weight from May (non-beech/clay: 6.05 g; non-beech/rendzina: 5.095 g) to October (n-b/c:4.288 g; n-b/r: 4.380 g). A possible explanation for this result could be a change in the age structure of the populations with the majority of adults in autumn being freshly matured ex-juveniles. If this change takes place during summer, habitat differences in mean adult and overall body weight between habitats could reflect differential progress in the transformation of the populations, in which case Cuendet's findings and the results of the present study would not be incompatible.

EFFECTS OF SOIL AND LITTER. Both Cuendet (1984) and the present study found differences between habitats to be more important than between soil categories. However, there were some important effects of soil type, once the variance due to habitat differences was considered. Thus, the results of these two studies urge any future investigations to consider both habitat and soil type and to account for this in sampling design and subsequent analysis.

Rendzina contains a high content of carbonate which provides a pH near neutrality independent of the type of litter. This allows soil microorganisms to break down the polyphenolic substances of the beech leaves, thus improving the palatability of beech litter. In the clay, without the buffering effect of carbonates, the soil is acidic and induces reduced microbial activity which leaves the litter unpalatable for a long time, severely restricting the amount of food available (Cuendet (1984)).

The results of the present study do not show any significant relationship between the amount of litter present and L. terrestris populations. Litter was assessed on a 0 to 4 scale and this might have been

too crude to give reliable results. Furthermore, the litter that was still present in July could be litter of less or not preferred species and thus was of little or no importance to the worms. To investigate this possiblity, Cuendet (1984) recorded quantitatively the species composition and the total amount of the litter present at his study sites. The input of litter at the beginning of the litter 'year' in November was comparable for the two non-beech woodlands (440 g m^{-2} on clay; 400 g m^{-2} on rendzina) and beech on rendzina (411 g m^{-2}). Beechwood on clay had 1597 g m^{-2} (factor of 4). By June, non-beech on rendzina was reduced to 82 g m^{-2}, non-beech/clay to 137 g m^{-2} and beechwood on rendzina to 220 g m^{-2} while beechwood on clay had 1443 g m^{-2} of litter present (factor of approximately 10).

The importance of litter as food for earthworms is mainly expressed by the litter species composition as indicated by the type of habitat. This determines how much food is available, no matter what amount of overall litter is present. Preferred litter vanishes rapidly while less preferred litter declines only slowly and seems to be accumulating from year to year as expressed by the high values of beechwood on clay at both sampling occasions.

HABITAT DIFFERENCES AND FORAGING STRATEGIES OF FOXES AND BADGERS. The results of the present study reveal differences in earthworm populations between habitats with consequences for the foraging activity of foxes and badgers. As the large differences between estimated and observed population levels (Table 3.4) indicate, only a fraction of the earthworm population is active in July and this fraction declines from open (exposed) habitats such as arable land and pasture or grassland to woodland. While it is true that plantations contain only low densities, they might be of increased interest to foxes or badgers, if for some reason they are not able to use the much more preferable deciduous woodland. This could be especially the case for

young and subordinate animals that might be prevented from access to more profitable sites by dominant individuals or for a range which does not happen to encompass any deciduous patches. If climatic conditions are unfavourable (e.g. in periods of dryness), plantations would still be more humid and thus favour the surfacing activity of worms. An additional source of attraction at all times of the year may be the grassy rides that often separate patches of woodland from each other, as they probably contain a locally more abundant population of worms.

Nothing is known of whether profitability of worms is similar for different worm weight or length categories. Thompson and Barnard (1984) have shown that the profitability of earthworms eaten by plovers and lapwings decreases sharply with increasing worm length. Such a drastic effect might not necessarily be expected for badgers or foxes. However, badgers sometimes manage to secure only parts of a large worm (Kruuk (1978a), pers. obs.), indicating that the optimal size as expressed by the profitability might not necessarily correspond to the maximum size available. A habitat such as plantation on rendzina, while generally unfavourable because of the low worm densities, might be of increasing interest as it contains larger than average juveniles (which might be close to the optimal size; Table 3.2b) if unsuitable weather conditions or other reasons prevent successful foraging in more exposed habitats. This, together with the aforementioned reasons, could explain, why Kruuk (1978a) found that badgers in Wytham spent a large amount of their time (27 %) in plantations. Kruuk does not indicate from which season his activity estimates were compiled, but the increased use of plantations by the badgers of his study during dry spells of weather seems to support the view expressed above.

MICROCLIMATE. As Kruuk (1978a) noted, large microclimatic differences exist

between different sites within the same habitat, even if they are quite close to each other. In the present study, an attempt was made to see how much microclimatic variables vary and whether this variation had any predictable spatial or temporal components. Patterns of spatial stability were found while changes occurred between seasons. Thus, an animal with memory should be able to predict climatic conditions over its range (at least within certain habitats) but it would also need to occasionally update its knowledge of the climatic conditions at different sites. As described in section 3.2.3., there are at least three simple strategies conceivable that can efficiently exploit these regularities of micro-climatic conditions.

3.3 PHEASANT (Phasianus colchicus).

Three game bird species occur in Wytham, the pheasant (Phasianus colchicus), the partridge (Perdix perdix) and the woodcock (Scolopax rusticola). There are comparatively few woodcocks in Wytham: during the habitat census in January and February 1982 only three individuals were encountered. Partridges can be regularly seen on the grassy rides and major tracks. Middleton (1935) and others have described the impact of fox predation on partridge populations, particularly during the breeding season. However, I did not find a single partridge remain killed by foxes in Wytham and no attempt was made to sample systematic information on their distribution. Thus, the rest of this section is restricted to a description of the predator/prey relationship between foxes and badgers and pheasants.

3.3.1 INTRODUCTION

ACTIVITIES. Pheasants are gamebirds with a complex mating system,

territories and little dispersal (Ridley (1983)). Males establish territories from their second year onwards, on average less than 400 m away from their birthplace. The spatial distribution of pheasants is fairly stable. Males winter close to their territories (on average at a distance of ca 150 m) and defend subsequent territories close to last year's ones (on average at a distance of ca 70 m). Female wintering grounds were on average ca 200 m away from last year's nesting grounds and the subsequent nesting site was on average ca 170 m away from last year's (Ridley (1983)). Pheasants stay in small groups during the winter (average group size 3.14), but if there is little shelter available, up to 20 birds may be found in one group. During winter, pheasants use three types of cover (Gates & Hale (1974)): roosting cover for nighttime use, loafing cover used between daytime periods of feeding activity, and emergency cover after snowfall. Preferred wintering habitats were wetland shrubs and scrubs in east-central Wisconsin (Gates & Hale (1974)), and mixed woodland in Ridley's study, ie. mixed plantations of dense thickets of fir, pine, beech, sycamore and cherry about 8 m in height with little ground vegetation. However, if there is little cover available, pheasants may roost on the ground. In March territories are established between males trying to monopolize areas used by females for foraging. Females are recruited in small groups (harems) to male territories and their home range is mostly confined to the male's territory. The harem members are accompanied by the resident male while feeding, but females sometimes leave his territory, particularly in cover, and they nest outside the territory.

Pheasants show habitat preferences for feeding grounds, territories and nesting cover. Results for habitat preferences in territories are shown for two british studies (Lachlan & Bray (1976), Ridley (1983)) in Table 3.11. In Ridley's study, territories were always established along edges of cover and open areas; only open grounds more than 150 m away from cover and mixed

Table 3.11 Habitat composition of male pheasant territories in two British studies. Source: Lachlan & Bray (1976) and Ridley (1983).

1) Percentage composition of the habitat of three types of areas (Lachlan & Bray (1976))

HABITAT TYPE	15 COCK PHEASANT TERRITORIES	14 SAMPLED AREAS NOT OCCUPIED	WHOLE STUDY AREA
woodland without shrub layer	2.9 ± 4.7	–	1.2
shrub layer under woodland	25.3 ± 14.9	–	19.9
shrub without woodland canopy	17.1 ± 12.8	2.0 ± 1.4	8.4
tall herb	2.2 ± 3.2	–	0.9
open field	51.5 ± 19.0	98.0 ± 1.4	68.6
buildings	1.0 ± 1.4	–	1.0

2) Distribution and size of territories along habitat edges. (Ridley (1983)).

HABITAT EDGE	NUMBER OF TERRITORIES	MEAN AREA
woodland edges	15	2.16 ± 0.59 ha
hedgerows	4	1.90 ± 0.36 ha
clearings	4	1.62 ± 0.25 ha
Length of cover edge	89 m to 648 m	
Average territory size	2.0 ha	

woodland areas more than 50 m away from open ground remained undefended by the 10th of April each year. Not all of the available habitat was used. In Lachlan's and Bray's study shrub layer, with or without additional woodland cover, and open fields were the dominating habitat features. Nesting areas were, in Ridley's study, primarily scrub and immature hawthorn plantations and deciduous woodland (beech and ash plantations with an understorey of bramble, stinging nettles and various grasses). Pheasants prefer to feed in the open on fields, grasslands, rides, and clearings, changing to deciduous woodlands in autumn.

PREDATION AND ANTIPREDATOR TACTICS. Goshawks and foxes predominate amongst natural predators (Kenward (1977), Kenward et al. (1981), Dumke and Pils (1973), Macdonald (1979), Gill (1979)). Pheasants, particularly the females, are well camouflaged. In Sweden, however, they seem to prefer escaping to cover over relying on camouflage, at least against goshawk predation (Kenward et al. (1981)). In a detailed study of the mortality of radiotagged pheasants in a preserve in Wisconsin with only 6% of the area covered by woodland, mammals killed 38% and raptors 28% of the radiotagged females when predation was implicated as a cause of mortality (Dumke & Pils (1973)). Foxes accounted for a loss of 251 of a total population of 859 hens. Dumke and Pils (1973) concluded that the scarcity of cover and subsequent roosting on the ground made pheasants particularly vulnerable to mammalian predation.

Fox predation on hens nesting in early summer has frequently been described as the main cause of casualties during the breeding season (Gill (1979)). On an estate with pheasant rearing the time of the annual pheasant release coincided with a peak of fox predation on pheasants (Macdonald (1979)). Foxes have been implicated in reducing the game bag on shooting estates, suggesting to some people that fox predation limits pheasant

numbers (see Gill (1979)). Experiments in areas with and without human fox control did not show, however, an increase in game bag due to the control of predators (Macdonald (1979)), Trautman et al. (1974)), although game bag increased in areas where the fox population was decimated by rabies epidemics (Jensen (1970), Spittler (1974)).

In summary, fox predation is successful 1) if there is little cover available to pheasants, either through lack of suitable habitat or during winter, when there is generally less cover available than during the vegetative period; 2) on breeding hens sitting on their nests; 3) on unexperienced young birds particularly if they had been reared in captivity.

The only detailed investigation on predation on pheasants by badgers is Anderson's (1954) study on the diet of the Danish badger. Only one pheasant hen and one cock pheasant (believed to be scavenged) were found in stomach samples but 27% of the stomach samples (n = 103) between middle of May and middle of July contained bird eggs with a large proportion of pheasant and partridge eggs. Thus, it seems likely that predation on adults is negligible and nests are taken opportunistically if encountered.

3.3.2 PHEASANT CENSUS AND OBSERVATIONS

I tried to establish a picture of the pheasant populations in my study area primarily by determining where pheasants occurred and how their behaviour compared to the habits as reported by Ridley (1983) and Lachlan and Bray (1976). I collected bird remains and pheasant sightings incidently throughout the period between January and end of May in 1983 and systematically during the habitat census in Marley Wood in January/February 1982 and during the periods of 'latrine walking' in March and April 1982 and 1983.

Territorial males generally showed a very small flight distance,

particularly when approached by car. In January and February, pheasants were sometimes observed to settle on their roosts in big groups, usually in old, well grown hawthorn thickets. On one occasion (12th February 1983), I counted at least 24 pheasants roosting together at a height of 4 m in a hawthorn thicket at the very northeastern tip of Marley Plantation, a place LIO (male fox from Marley) used to visit regularly at dawn and dusk.

On 107 occasions altogether 140 pheasants were counted in both years. In the majority of cases (90 out of 107) only one pheasant was observed, on 14 occasions two pheasants were seen, on two occasions four pheasants and once, already mentioned, 24 individuals were counted. Of the 107 sightings 89 were defined as unique observations, ie. the sightings were at least 100 meters apart from each other within the same year. Particularly during spring, male pheasants were repeatedly seen at exactly the same location (see Fig. 3.6). These unique sightings were investigated for possible habitat preferences related to their cover value. Due to small sample sizes, habitats were summarized under seven categories:

HUMAN	Habitats 1,2,3,4,14,23,25,26,43,47 (definition Box 1)
GRASSLAND	Habitats 5,6,7,46
ARABLE	Habitats 9,28,29,30,31,32,33
SPECIAL AGRICULTURE	8,12,13,42
OTHER	Habitats 24,27,45
WOODLAND	Habitats 11,21,22,34,37,38,39,40,41
SHRUB	Habitats 10,35,36,44

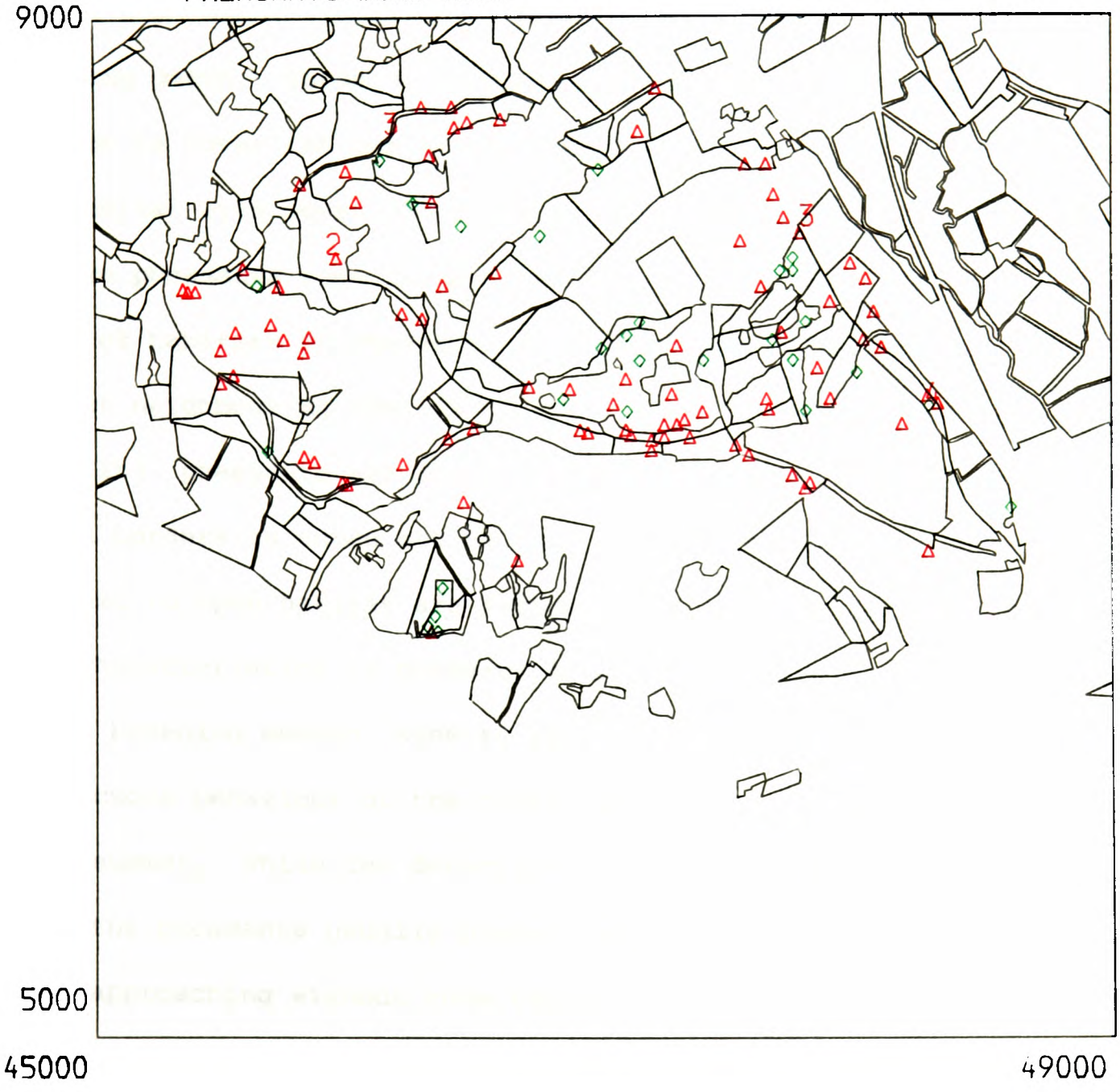
These categories were then classified as 'open' (HUMAN, GRASSLAND, ARABLE, SPECIAL AGRICULTURE, OTHER) and 'cover' habitats (WOODLAND, SHRUB). Program SRCH2P was run to identify patch and habitat number for each pheasant sighting. The modified data were then submitted to program BORDER.

Fig. 3.6. Census data of bird populations projected onto the computerized habitat map. Habitats plotted are habitats 7, pasture, and 37, deciduous woodland.

Red triangles: pheasant sightings; results combined from 1982 and 1983. A red number indicates more than one sighting at a site.

Green diamonds: feather remains (24 wood pigeons, 4 other birds); data combined from 1982 and 1983.

PHEASANTS/BIRD REM.



This program calculates for a given point the shortest distance to the border of its patch, the coordinate of the intersection of the shortest distance with the patch border and identifies the number and habitat type of the neighbouring patch at the point of intersection. Thus, program BORDER identifies the nearest neighbouring patch for any given coordinate within a patch. The P-STAT statistical package, available on the university's VAX-11/780, was used to evaluate the association of the habitat type of each patch with a pheasant sighting with the habitat type of the nearest neighbouring patch. Table 3.12a presents the results. Pheasants were mostly seen in cover (66 out of 89 cases) and were also most likely next to another habitat with cover (53 cases). Only in 12.4% of the cases (11 out of 89) were pheasants seen in open habitats next to open habitats. The selection of habitats by pheasants is independent from the cover value of the nearest neighbouring habitat ($p = 0.4$, n.s.). Looking at the distances (Table 3.12b), pheasants are at a similar actual and proportional distance from patch borders in three out of four cases. Only pheasants in open habitat next to open habitat are further away from the patch border.

The characteristics of pheasant ecology and behaviour, particularly during the breeding season, seem to facilitate their detection; especially the conspicuous behaviour of the cocks patrolling their territory in spring and early summer. While the detection probability may be very high in open habitats, the pheasants usually place themselves so that there is little chance of approaching without them taking notice. Due to the small tendency of pheasants to disperse within and between years foxes could certainly assess the current status of the population within their range and predict future developments to some extent.

Table 3.12 Distribution of pheasant sightings over 'open' and 'cover' habitats in relation to the habitat type of the nearest neighbouring patch.
'Open' habitats were all habitats classified as HUMAN, GRASSLAND, ARABLE, SPECIAL AGRICULTURE, OTHER (see text). 'Cover' habitats were all habitats classified as WOODLAND or SHRUB.
Proportional distance is distance to the nearest neighbouring patch in relation to the longest distance to a neighbouring patch from the position of the pheasant.
Cell contents are a) cell counts, and expected values, b) two measures of distance :1) absolute distance to the nearest neighbouring patch; 2) proportional distance.

a) Frequencies

	NEIGHBOURING HABITAT		
HABITAT	open	cover	ROW TOTALS
open	11	12	23
	9.3	13.7	
cover	25	41	66
	26.7	39.3	
TOTAL N	36	53	89
MEAN	18.583	14.396	

CHI SQUARE = 0.7006 (PR=0.403)
WORST EXPECTED VALUE = 9.3034
D.F. = 1.0000

b) Absolute and proportional distances

	NEIGHBOURING HABITAT			
HABITAT	open	cover	MEAN (absol.)	MEAN (Proport.)
open	24.909	15.333	19.913	
	0.383	0.243	0.310	
cover	15.800	14.122	14.758	
	0.124	0.180	0.159	
MEAN (absolute)	18.583	14.396	16.090	
MEAN (proport.)	0.203	0.195	0.198	

3.4. WOODPIGEON. (COLUMBA PALUMBUS)

3.4.1 Introduction

ACTIVITIES. Wood pigeons are gregarious throughout the winter, feeding in compact flocks, often with up to 100 individuals, on fields on various crops and seeds (Murton (1965)). Roosting is nocturnal and communal, though gregarious tendencies are much less pronounced in breeding birds. Wood pigeons roost mainly in tall trees, particularly conifers and deciduous trees using firm leafy branches at a height of 6 to 15 m (M.Wilson, in press). In February and March territory formation takes place with males moving to the middle tree canopy from which they give territorial calls before roosting with the other birds, slowly extending their territorial activities until they roost in their own territories. The midday period spent on feeding decreases until July when nearly all time is spent in the territory (Murton & Isaacson (1962)). Breeding takes places throughout the summer until September. The most preferred breeding habitats are coniferous woodland (Murton (1958): on average 5.6 nests/acre), hedgerows (4.4 nests/acre) and deciduous woodland (1.5 nests/acre). Wood pigeons have several feeding grounds that are used very regularly. Both entire flocks and individual pigeons revisit the same places again and again.

PREDATION AND ANTIPREDATOR TACTICS. Wood pigeons fall prey to a variety of predators. Tomialojc (1979) listed more than 20 predator species and concluded that nest-site selection and other aspects of wood pigeon biology evolved under predation pressure. Goshawks and crows are important avian predators while martens and cats are important mammalian predators. Kenward (1978a, 1978b) investigated the reaction of wood pigeons to human disturbance and goshawk predation. Goshawk attacks on pigeons feeding on

brassica fields were more successful in the hour before sunset than in the previous four hours, and single birds and small flocks suffered a higher predation rate than flocks with more than 10 wood pigeons. He suggested that increased group size resulted in an increased vigilance and attributed the higher capture success before sunset to increased vulnerability of pigeons because of pre-roost crop-filling. Wood pigeons quickly resettled on the fields whether they were disturbed by humans, traffic, or goshawks.

Neither badgers nor foxes are mentioned as predators in Murton's (1965) monograph on the wood pigeon. Tomialojc (1979) and Rzebik-Kowalska (1972) list the fox as a predator on adults. Badgers are not mentioned in either of the sources. There seem to be few opportunities for foxes to catch pigeons if their roosting, breeding or flock feeding habits are considered. However, remains of wood pigeons eaten by foxes can be regularly found in Wytham. How is this possible?

3.4.2. OBSERVATIONS ON WOOD PIGEONS AND WOOD PIGEON REMAINS

Almost all of 28 collected bird remains were wood pigeons, except one black bird, one marsh tit, and two pheasants. Fig. 3.6 shows the spatial distribution of 28 bird remains that were left by foxes (birds taken by foxes can be easily distinguished from birds taken by sparrowhawks as sparrowhawks pluck the feathers neatly, while foxes simply bite them off). A more detailed analysis of the habitats where remains of wood pigeons were found is presented in Table 3.13. Results were obtained by running programs SRCH2F and BORDER and submitting the data to P-STAT in a way similar to the analysis of the pheasant data. The results are not straightforward to interpret as the places where the prey remains were found may not be identical with the place of capture. Remains were found well inside patches within mixed plantations but close to the patch border of pasture and summer

Table 3.13 Distribution of bird, particularly wood pigeon remains left by foxes over different habitats. Definitions of 'open' and 'cover' habitat as in Table 3.12. Cell contents: b) cell counts and expected frequencies; c) absolute and proportional distances.

a) Habitats where bird remains were found.

Habitat type	mean shortest distance to nearest neighbouring patch (in meters)	S.D.	sample size
pasture	16.11	25.6	3
scrub	23.33	0.0	1
marshland	9.22	0.0	1
summer cereals	15.57	22.1	2
bracken	0.00	0.0	2
deciduous hardw.	9.67	13.8	14
mixed plantations	36.92	42.8	4
riverrine with hedges	5.21	0.0	1

b) Frequency of occurrence of wood pigeon remains in open and cover habitats

	NEIGHBOURING HABITAT		
HABITAT	Open	Cover	ROW TOTAL
Open	2	5	7
	2	5	
Cover	5	12	17
	5	12	
TOTAL	7	17	24

Yates chi square test = 0.19, n.s.

c) Absolute (metres) and proportional distances of places (where wood pigeon remains were found) to nearest neighbouring patch

	NEIGHBOURING HABITAT		
HABITAT	Open	Cover	ROW MEAN
Open	18.0	10.6	12.7
	0.06	0.246	0.193
Cover	4.0	21.4	16.3
	0.024	0.338	0.246
COLUMN MEAN	8.0	18.2	15.3
	0.034	0.311	0.230

cereals. As Fig. 3.6 indicates, the remains found in open habitats are close to woody habitats and most of the prey remains found in deciduous woodland are fairly close to areas with open habitats; in particular, those that were found in cover next to open habitats are nearly on the border of the patch (Table 3.13c). This is an interesting contrast to the sightings of pheasants (Table 3.12b) where sightings in cover habitat were at an equal distance from open and from cover habitat. No dependence was found for the type of habitat where remains were found and the habitat of the nearest neighbouring patch (Table 3.13b).

Foxes might be able to opportunistically catch some pigeons while they feed on fields. Kenward (1978b:282) showed in an analysis of the spatial distribution of pigeons feeding on a brassica field that some pigeons were quite close to the surrounding hedges that could provide the necessary cover for a stalking fox. However, I believe that the majority of the pigeons are actually caught by foxes in the woodland (Table 3.13a). Many wood pigeons are shot on the farms that are next to the study area. Not all of these may be killed. David Macdonald and I once found a pigeon injured with gunshot which would have been an easy victim for foxes. Also, wood pigeons can be observed regularly in the woodland. Table 3.14 presents a list of wood pigeon sightings in Marley Wood and Marley Plantation for a 10-day period in April 1984 (data kindly provided by Marion East). The pigeons were not specifically searched for and most of the data were collected by approaching the pigeons by car. Regular visits to bathing, drinking or feeding sites seem to be common and thus should be predictable for foxes as well.

3.5. LAGOMORPHS

As there are practically no brown hares (Lepus europaeus) present in Wytham, I restrict my account of lagomorphs to a description of rabbit

Table 3.14 Wood pigeon sightings between 6th and 16th April 1984.
Observations restricted to Marley Wood and Marley Plantation.
* indicates place with more than one sighting.

DATE	TIME	GRP. SIZE		COORDIN.	LOCALITY DESCRIPT.	ACTIVITY	APPROACH	REACTION	FLIGHT DIST.
840406	0900	1		47740800	next to footpath in undergrowth	?	by foot	take off	25 m
	1100	1		47500745	on track junction	?	by foot	take off	125 m
	1200	1		47700770	on wide green ride	?	by foot	take off	50 m
840407	0900	1	*	48060774	on track junction	feeding	by car	take off	-
	1032	2		48390695	on track on a slope	feeding	by car	take off	-
	1059	1		48530712	in cover 10m off a foot path	feeding	by foot	take off	-
	1230	2	*	48060774	on track junction	feed.?	by car	take off	-
840408	0845	4	*	48350744	side of main track in dog's mercury cover	?	by car	take off	50 m
840410	0800	1	*	47890806	edge of woodland	feeding	by car	did not move	
	1300	2	*	48350744	in grass verge	?	by car	take off	6 m
	1301	3	*	48170763	on side of track	?	by car	take off	50 m
	1302	2	*	48060774	on track junction	bathing	by car	take off	150 m
840411	0800	1	*	48060774	on track junction	feed.?	by car	take off	10 m
840412	0930	3	*	48170763	on verge of track	?	by car	take off	50 m
	0930	1	*	48350774	on verge of track	feeding	by car	take off	100 m
	1330	2		48230760	grass verge of track	feeding	by car	take off	-
	1332	3	*	47890806	edge of woodland	?	by car	take off	-
	1800	3		48310749	at edge of track	?	by car	take off	-
840413	0800	1		48010778	at edge of track	?	by car	take off	50 m
	0810	3		48620701	in undergrowth close to edge of woodland	feed.?	by foot	take off	60 m
	1200	2	*	47860801	edge of woodland	?	by car	take off	-
	1430	1		48400706	edge of track	?	by car	take off	-
	1432	2		48380717	edge of track	?	by car	take off	-
840414	0800	2		48360729	edge of track	?	by car	take off	-
	0805	4	*	47890806	edge of woodland	drinking	by car	take off	-
	1200	2	*	47860801	edge of woodland	?	by car	take off	-
840416	0800	1		48560688	edge of woodland	?	by car	take off	-

presence (Oryctolagus cuniculus). My account of rabbit ecology and behaviour follows Lloyd (1977) unless other sources are cited. A general monograph on rabbits was written by Thompson and Worden (1956).

3.5.1. Introduction

ACTIVITIES. Rabbits are small herbivores, reaching a size of up to 40 cm (length) and an adult weight between 1.2 and 2 kg with pregnant females reaching up to 2.2 kg. Rabbits are usually crepuscular and nocturnal but may also become diurnal if undisturbed. Rabbits occupy special burrows called warrens (systems of interconnecting tunnels with multiple entrances) which are necessary for breeding (Garson (1981), Cowan, pers. comm.). Warrens may also be used as a daytime refuge, although in a study using radiotracked individuals, Wheeler et al. (1981) showed that most rabbits prefer to stay above ground in cover during the day. Severe adverse weather causes only a slight increase in the proportion of rabbits taking refuge in a warren while an increase in population density reduces the proportion of rabbits staying in warrens considerably (relegation effect; Gibb (1981)). Dominant individuals keep their offspring in the main warren but subordinate and satellite females may have to dig special breeding stops or occasionally keep nests above ground in dense cover. Times of "emergence" at dusk or at night can be variable, even if ground predators are absent. Activity depends on intensity of moonlight and cloud cover; rabbits tend to be more timid in strong moonlight.

Rabbits use runs to and from feeding areas. Erect grasses are most preferred but rabbits are also attracted by cereal fields, pastures and roots. Most preferred habitats are therefore areas of relatively short grass which are in close proximity to some kind of refuge (warrens or cover vegetation). At high population densities rabbits increase the amount of

time spent on feeding during night and day and eventually sacrifice their morning rest period. The amount of available feed in the vicinity of the warren is quickly reduced and they have to go further away in order to obtain sufficient food.

ANTIPREDATOR TACTICS. Rabbits play a major role as a keystone prey species in temperate, particularly meditterranean-type ecosystems (Delibes & Hiraldo (1981), Wagner (1981)). An efficient communal alarm system serves to warn all group members of the approaching danger. Alarm is signalled visually by an erect posture and flashing of the tail during high speed running, and acoustically by thumping with the hind legs above and below ground. Rabbits are fast runners that change flight direction rapidly several times in an escape sequence. They usually move less than 200 metres away from cover and prefer to be active when visibility is low. There is the suggestion that synchrony of estrus and births may be an adaptation to "swamp" predators with a flood of young (Garson (1981)). Diseases, particularly coccidiosis and myxomatosis, reduce the rabbits' alertness (pers. obs.). As a result, some predators like the imperial eagle (Aquila adalberti) showed an increase in rabbit consumption (Delibes & Hidalgo (1981)), after myxomatosis was introduced.

PREDATOR FORAGING. Both foxes and badgers are known to take rabbits. European badgers have been characterized as 'croppers' rather than hunters since they mostly dig out nests with young rabbits but seldom attempt to hunt adults (Neal (1977), Delibes & Hidalgo(1981)), in contrast to the North American badger (Taxidea taxus) where rabbits may be a staple part of the diet (Neal (1977), Lindzey (1971), Long & Killingley (1983)). Nests are located by scent or hearing and dug out vertically rather than by opening up a tunnel (Neal (1977)).

Foxes hunt adults and young, usually above ground although they might endeavour to try and sneak into a rabbit warren if the entrance is large enough. There is some evidence that fox predation on rabbit nests is related to edaphic conditions: in an Australian study, predation was heavy on stony soils (Myers & Parker (1965)). Foxes use a variety of tactics to catch rabbits above ground. They usually stalk them if the habitat is suitable, or they hide and wait close to warrens, or they chase them in the open. In the latter case they are only successful if the rabbit is somehow not capable of maintaining full escape speed (in case of disease etc.) or if it detected the fox too late. Similarly, North american red foxes stalk cottontail rabbits (Sylvilagus spec.) but are outrun by them in the open, even in snow (Scott (1943)).

3.5.2. The rabbit population in Wytham Woods

3.5.2.1. Methods

The following methods were used:

1. Identification of rabbit warrens.

2. Notes of rabbit signs. During the 1982 habitat census the number of sites with rabbit pellets in each 'basal' area (see section 2.3) was recorded. This parameter is a reliable indicator of rabbit distribution and abundance and has been used for some time (Taylor (1956), Lloyd (1977), Oosterveld (1983), Trout & Tittensor (1983)). During the habitat census, patches with rabbit hair were also frequently noted. According to Trout and Tittensor (1983) the correlation of adult abundance and number of hair sites along habitat boundaries is moderate (0.425). Since such sites were

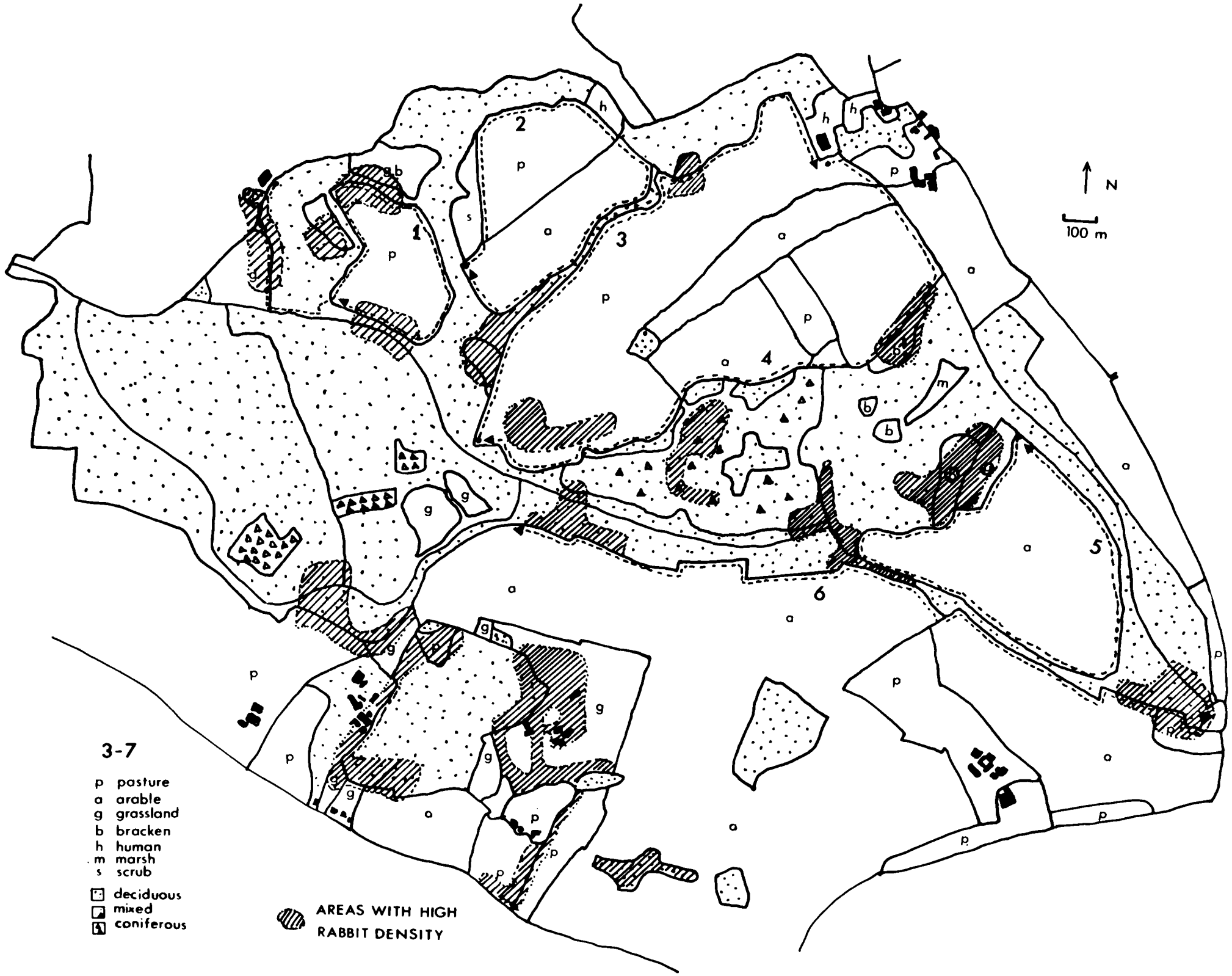
recorded regularly only during part of the habitat census, it was not possible to evaluate them quantitatively. However, the results gave the distinct qualitative impression that rabbits occurred regularly in dense woodland areas, perhaps to a greater extent than would be expected from the literature.

3. Records of rabbit sightings. Wherever a rabbit was seen, the place, habitat, number, time and special conditions were recorded. This information was used to compile Fig. 3.7 where the major areas of rabbit occurrence together with a coarse habitat map are presented.

4. Transect walks. After some exploratory attempts in autumn 1982, several transects along habitat boundaries were designed according to the system introduced by Trout and Tittensor (1983) for the MAFF rabbit survey and adapted to the local circumstances. In principle their results should be comparable with my study.

Six transects were designed along habitat boundaries, ie. usually boundaries between so-called open and cover habitats (e.g. woodland and pasture). Transects were walked between March 24 and March 31, 1983, by Christa Helmer. Three parameters were recorded: number of rabbits seen, number of rabbit warrens encountered, and number of places with rabbit pellets. If possible, a strip of 10 meter width was searched for any signs of rabbits. Only rabbits that stayed in the vicinity of the transect route were counted. In practice this turned out to be no problem, since the rabbits seen were close to the habitat boundary. All six transects were walked at least twice: the first time only rabbits were counted, while on the second round the number of rabbit pellet places and the number of warrens were counted. Transects were walked at dusk as initial trials showed a much reduced number to be present at dawn. Since all transects were walked

Fig. 3.7. Map of the central part of the study area, with the distribution of main habitat categories, buildings (black) and track roads. Areas with high rabbit abundance shaded. Dotted lines represent rabbit transects; number of transect and direction of walking indicated.


N
100 m
1
2
3
4
5
6
3-7
p pasture
a arable
g grassland
b bracken
h human
m marsh
s scrub
deciduous
mixed
coniferous
AREAS WITH HIGH
RABBIT DENSITY

within a week, time differences between different subpopulations are probably negligible.

3.5.2.2. Results

A qualitative summary on the distribution of rabbits in Wytham is presented in Fig. 3.7. Major habitats are illustrated together with areas of high rabbit density. Emphasis was placed on a correct outline of habitat boundaries close to the major rabbit areas while such a detailed split up of habitats was not done in areas where rabbits occurred only at low densities (e.g. Radbrook Common Area). Also shown are the routes of the six transects (numbered 1 to 6) and the direction of transect walking. Although rabbits occur at low densities more or less everywhere in Wytham Woods, there are areas of peak abundance with a corresponding increase in warren density (Fig. 3.8). Many areas of peak abundance combine open and cover habitats but some are almost exclusively restricted to woody areas (e.g. one area close to the Pasticks). This may be partly due to tradition: before 1960 the areas around the Pasticks (which are today mixed plantations) consisted of arable land and pasture fields, surrounded by small strips of woodland, ideal for rabbits. Although there is little known about rabbit dispersal, it seems that a warren is passed from one female group to the next generation female group (probably close kin) (Garson (1981)). Rabbits may simply have stayed there, despite the habitat changes. It is likely that the grassy rides in this area are very important to the rabbits; they were seen to feed there at any time of the night or day.

In Fig. 3.8 all rabbit warrens in the area, whether active or inactive, are plotted on a habitat map showing pasture (habitat 7), long grassland (habitat 5), grass ley (habitat 6), marsh (habitat 24) and bracken (habitat 35), facilitating a comparison with the areas of rabbit peak abundance in

Fig. 3.8. Rabbit warrens (red stars) projected onto the computerized habitat map. Habitats plotted are habitats 7, pasture, 36, hedge, and 44, riverrine environment with hedge.

RABBIT WARRENS



Fig 3.7. A more quantitative evaluation of the habitats in which rabbit warrens occur is presented in Table 3.15. The number of rabbit warrens per habitat were also evaluated with respect to the nearest neighbouring habitat, using program BORDER (see sections 3.3 and 3.4). The majority of warrens can be found in woodland (57%), followed by grassland (26%), shrub (13%), arable land (3.5%) and human (0.6%), altogether a total of 170 warrens, a significant deviation from an expected random distribution (χ^2 = 16.88, df =6, p<0.01). The habitat where a warren is found is not independent from its nearest neighbouring habitat (χ = 40.805, p<0.001). Could this mean that the rabbits select a place not just considering the requirements of a warren but also its position to the feeding grounds?

The most frequent nearest neighbouring habitat is again woodland (38%). Warrens were numerous only in three habitat super-types (grassland, woodland, shrub) while they are placed next to a host of different neighbours (human, grassland, arable land, woodland, shrub, other). A closer look at the deviations of observed from expected cell counts reveals some interesting patterns: given that a warren is in grassland, it is more frequently than expected next to some kind of woodland. Given that a warren occurs in woodland, it is more likely to be next to woodland again while less likely than expected to any other habitat super-type. Given that a warren occurs in shrub, it is more likely to be next to some kind of grassland or arable land while less likely to be next to woodland or shrub. This pattern seems to be best compatible with Wheeler's et al. (1981) observation that rabbits tend to spend the day above ground. A warren in the open, but close to cover could facilitate a mother's visits.In the case of warrens sited in shrub it may be more important to be close to feeding grounds, since both scrub and hedges provide a very dense understorey.

Table 3.16 presents a brief summary of the six transects. Their length varied between 1.95 and 2.55 km. According to Trout and Tittensor's (1983)

Table 3.15 Distribution of rabbit warrens over habitats (as defined on the habitat map), summarised under super-types (definition see below).

HUMAN: habitats 1,2,3,4,14,23,25,26,43,47
GRASSLAND: habitats 5,6,7,46
ARABLE: habitats 9,28,29,30,31,32,33
WOODLAND: habitats 11,21,22,34,37,38,39,40,41
SHRUB: habitats 10,35,36,44
OTHER: habitats 24,27,45

The first numbers in the table are observed, the second expected counts.*

		Habitat of the nearest neighbour patch						
		Human	Grassland	Arable	Woodland	Shrub	Other	Sum
Habitat of the patch with warren	Grassland	4 1.62	8 6.75	3 4.86	13 22.94	10 5.67	6 2.16	44
	Woodland	2 3.57	9 14.88	10 10.71	64 50.58	10 12.5	2 4.76	97
	Shrub	0 0.81	8 3.37	5 2.43	8 11.47	1 2.83	0 1.08	22
Sum		6	25	18	85	21	8	163

$\chi^2 = 40.81$, $p < 0.001$ (df = 1)

* 7 warrens are not considered since they occur somewhere along the border of the habitat map

Table 3.16 Summary data on transects of rabbit and rabbit signs counts

	Transect number					
	1	2	3	4	5	6
Length (meters)	2280	1960	1945	2295	2550	2480
Number of 75 m-sections	30	26	26	31	34	33
Number of rabbits seen	9	0	3	6	3	1
Number of rabbit warrens	1	2	0	1	2	1
Number of rabbit pellet pl.	26	2	10	19	19	43
Density of rab. per 75 m section	0.29	0	0.12	0.19	0.09	0.03
Density of rabbit pellets/section	0.86	0. 08	0.39	0.61	0.56	1.30

design, each transect was subdivided into 75 m sections and all subsequent densities refer to a unit length of 75 m. The number of rabbits seen was small on most transects, and it was highly variable. For instance, a second walk along Transect 1 yielded only two sightings.

The number of rabbit pellet places was judged to be the most reliable indicator of rabbit presence. As Table 3.15 shows, densities of rabbits seen and densities of pellet places do not covary very well (Spearman's rank correlation, rho = 0.37, n.s.). In Table 3.17 a more detailed compilation of pellet place densities in relation to the habitat types along the transect is pesented. I distinguished between the habitat type, on which side the transect was walked ("inside" habitat) and the habitat on the other side of the boundary ("outside" habitat). Along each transect, one element represented a distance over which the inside and outside habitat do not change. The length of each habitat type was computed by adding the length of all elements where the given habitat type was present, independent of possible habitat changes on the other side of the habitat boundary. The densities are the mean of the counts of all elements with a given habitat present.

In general, pellet places were clumped along the transect, not regularly distributed over the entire length. The highest densities were found on transect sections with bracken as outside habitat (densities of 3 and 5 pellet places per 75 m), also one section with pasture on the inside (5 pellet places per 75 m). This section is a short section and was immediately next to Botley Lodge at the very southeast of the wood. Since high density sections seemed to be very short, I investigated the possibility that the length of a section belonging to the same habitat type (either as inside or as outside habitat) exerts an influence on pellet place densities. There is a weak negative correlation (Spearman rank correlation, rho = −0.29, n.s.), if all elements (defined as sharing the same inside and

Table 3.17 Density of rabbit pellet places along habitat boundaries. Lengths (L) of habitat boundary unit sections are 75 m, densities (D) per unit section. "Inside habitats" are the habitats on the side where the transect was walked, "outside habitats" are the habitats on the other side of the habitat boundary.
PASTURE = habitat 7; ARABLE = habitat 29; GRASSLAND = habitat 5; BRACKEN = habitat 35; SCRUB = habitats 10, 36, 44; WOODLAND = habitat 37; HUMAN = habitats 3, 23, 26.

	Transect number											
	1		2		3		4		5		6	
	L	D	L	D	L	D	L	D	L	D	L	D
Inside:												
WOODLAND	5.78	0.96	–	–	–	–	–	–	–	–	–	–
PASTURE	21.84	0.76	12.55	0.00	25.63	0.39	12.10	0.41	–	–	2.0	5.0
GRASSLAND	2.55	1.62	–	–	–	–	–	–	–	–	–	–
ARABLE	–		13.60	0.22	–	–	18.50	0.76	34.00	0.56	31.0	1.07
Outside:												
WOODLAND	30.17	0.86	17.60	0.17	16.00	0.25	21.90	0.41	27.00	0.33	33.0	1.30
SCRUB	–	–	4.25	0.00	5.00	1.00	4.70	0.00	5.0	0.80	–	–
BRACKEN	–	–	–	–	–	–	2.00	5.00	2.00	3.00	–	–
HUMAN	–	–	3.30	0.00	4.63	0.00	2.00	0.00	–	–	–	
–												

outside habitat, not listed in Table 3.16) are considered. Looking at the relationship of element length and pellet place density within an inside or outside habitat type, I found a highly significant positive correlation of element length for "outside" woodland and pellet place density (Spearman rank correlation, rho = 0.886, $p<0.01$), ie. the longer a strip of woodland as outside habitat the higher the density of pellets.

If different habitats are compared, the following results were obtained: no significant differences in pellet place densities were found between pasture and arable as inside habitats (Mann-Whitney U-test, n = 4 (ie. excluding the high density element of pasture of Transect 6), M = 4, U = 15, n.s.; n = 5 (including ..), m = 4, U = 24, n.s.), nor was there a difference between outside habitats (exact Kruskal-Wallis one-way analysis of variance on woodland, scrub, and bracken, n = 12 (n = 16, n2 = 4, n3 = 2), H (adjusted) = 4.921, df = 2, n.s.). However, the sample sizes are very small and thus the results should be interpreted with caution. To investigate the relationship of woodland as outside habitat with neighbouring outside habitats and inside habitats more closely, the two following comparisons were made:

1. Mann-Whitney U-test on differences between sections with bracken and woodland as outside habitat, with inside habitat only arable land: this difference was significant (U = 19, n = 2, m = 8, $p<0.025$). Although again based on a small sample size, this result is particularly valuable, since it justifies the differentiation of bracken and deciduous woodland as separate habitats. We shall later see that at least one radiotracked fox spent a lot of time in one of the bracken areas close to the boundary to arable land.
2. Mann-Whitney U-test on differences between section with pasture and arable land as inside habitat, with woodland as outside habitat in all cases: there were no significant differences (U = 48, n = 6, m = 8, n.s.).

Thus it seems that rabbits tend to visit pasture and arable land to similar extents, at least those sections which are close to woodland.

To summarize, the results from the transects, the density of pellet places (and thus presumably the amount of rabbit activity and the number of rabbits) varies between different types of "cover" habitat (such as bracken and woodland) but does not seem to vary significantly between different types of open habitats (such as pasture and summer cereals). If a fox can include long strips of woodland next to some open habitat in its home range it can expect a higher activity (expressed as higher density of pellet places) of rabbits along the habitat boundary. The majority of rabbit warrens lies inside woodland.

Signs of fox predation on rabbits were occasionally found but successful captures were observed only twice. On the first occasion, a radiotracked vixen (PINTOOTH) was observed through an image intensifier from the Eynsham road on November 1st, 1981, between 4.32 and 4.40 a.m. She came out of a hedge onto a pasture and started to move slowly as if foraging for earthworms. At the same time several rabbits sat or foraged approximately 150 m away on the same field of pasture. After several minutes of similar, slow movements in the direction of the rabbits, Pintooth suddenly started a high-speed sprint and covered at least 50 metres within 2 or 3 seconds. Most rabbits saw the fox in time and vanished into the nearby hedge except one, apparently younger individual which sat closest to the fox and was caught. On another occasion (25.11.83, 11.30 a.m.), Marion East watched an untagged fox moving into dense scrub at the south west of Marley plantation where she shortly before had also seen several rabbits. Within a minute, several loud screams could be heard and the fox left the scrub again, this time an obviously freshly killed rabbit in its mouth.

3.5.2.3. Discussion

Although my data on rabbit occurrence in Wytham are limited, some interesting results were found in comparison with the literature. Lloyd (1977) described the ideal habitat of rabbits as a fairly small area of short grass close to some cover. While this kind of habitat is certainly also favoured by Wytham rabbits, their flexibility and perhaps their ability to utilize a wide range of resources allow them to occur in other kinds of habitats where short grass may be a minor element; even areas of mixed plantations seem to support a viable population. Moreover, the majority of warrens were found in woodland (mostly deciduous woodland) and most warrens were again next to some kind of woodland habitat. The important implications for a fox or badger searching for rabbits or rabbit nests are to spend some time looking at woodland, at habitat boundaries from open to cover habitat and at typical feeding grounds such as short or long grass areas. Surprisingly, bracken was identified as a habitat with high rabbit presence (expressed as a high density of rabbit pellet places). Another interesting result was the increase of pellet place density (and thus presumably rabbit activity) with the length of the woodland strip along a habitat boundary with woodland and some type of open habitat. I judged my own data to be insufficient to explore how well the density of pellet places reflects actual rabbit activity or rabbit abundance. However, Trout and Tittensor (1983) found a high correlation of the number of adults counted with the number of dropping places and urine patches (0.729) in a study designed similar as mine and other studies, particularly Taylor (1956) and Oosterveld (1983), identified pellet place densities as a reliable indicator of rabbit abundance.

3.6. Rodents

Seven species of rodents were found in food remains left by foxes and badgers in Wytham Woods (section 4.2):

field vole	Microtus agrestis
bank vole	Clethrionomys glareolus
wood mouse	Apodemus sylvaticus
house mouse	Mus musculus
common doormouse	Muscardinus avellanarius
common rat	Rattus norvegicus
grey squirrel	Sciurus carolinensis

Of these species, I am going to look at the first three, which have been subjects of many studies in Wytham (and elsewhere) since the late 1940's (e.g Miller (1955, 1958), Kikkawa (1964), Watts (1968, 1969, 1970), Evans (1973), Flowerdew (1972), Southern (1970, 1979a), Southern & Lowe (1968, 1982)) which are still continued (the project of the Animal Ecology Research Group of the Department of Zoology, Oxford; Fenn (unpubl.)). The following sections summarize these and other studies and are updated by the most recent unpublished results.

3.6.1. Ecology of voles and wood mice

All three species are of small size, with a length of approximately 10 cm (excluding the tail) and weights of between 15 and 40 grams. The wood mouse is clearly distinguished from the two voles by its large ears and the long tail and its smaller size. Table 3.18 surveys the main ecological features of the three species. Although any of the three species may

overlap with others in habitat use, different habitat selection criteria and food requirements usually cause them to be well separated from each other. In all three species reproduction starts in spring and continues throughout summer until it ceases in autumn unless food supply and mild weather permit the animals to breed through the winter. Populations develop in a cyclic or non-cyclic manner, with occasional outbreaks of plagues, particularly in the field vole, and subsequent breakdowns of the populations (Southern (1979b)).

3.6.2. Antipredator tactics and defence

All three species of rodents are prey to many predators (see Flowerdew (1979a, 1979b), Evans (1979)), both avian and mammalian species. As a result, the antipredator strategies may be general. It is not known whether any of these species have a communal alarm system. Their escape probability may more depend on the chance of the predator locating them rather than their active escape efforts (e.g. Dickman & Doncaster (1984)). For instance, Skoog (1970) suggested that the preference Swedish badgers showed for Microtus relative to Clethrionomys or Apodemus may simply be related to the fact that the badgers spend most of their time in fields where the runways of the field vole are superficial and clearly exposed and where nests can be dug out easily while in the woodland, mice paths may not be found so easily and digging may be hampered by tree roots. Also, Southern and Lowe (1968) found tawny owls (Strix aluco)) to prefer wood mice to bank voles and could relate this to the increased presence of wood mice in open parts of the woodland.

3.6.3. Predator foraging

Both badgers and foxes are known to take all three species of rodents

(Neal (1977), Macdonald (1977)). Badgers tend to dig up the runways until they reach a rodent nest and take the adults and young. They usually do not attempt the capture of free-running adults; wood mice are too agile for them (Neal (1977)).

Foxes prefer field voles relative to bank voles and wood mice (Macdonald (1977)). Foxes usually use a hunting technique described as a pounce (Smith (1944), Dekker (1983)). Burrows or actively used runways are identified by scent. The fox then typically pauses until it locates the prey by acoustic cues followed by a big jump which may cover up to 4.5 meters. The fox then quickly seizes the prey and chews it a couple of times to kill it. Sometimes foxes simply stamp on mice or voles without leaving the ground with their hindpaws. If a fox missed its prey it starts to dig with quickly alternating front feet until it captures its prey. Despite the frequent observations of these hunting techniques, no systematic study exists which shows whether catching success may be influenced by vegetation height, soil type or similar factors. It is conceivable that dense grassland makes it more difficult for foxes to dig out their prey quickly enough if they missed it and it may increase the probability of missing the prey altogether.

3.6.4. The rodent populations in Wytham

Information from several other studies relating to minimum and maximum densities is summarized in Table 3.19. The highest density was calculated for Microtus with 49.5 individuals per hectare or 1 individual per 200 m^2. Godfrey's study (1955) shows that local variation in the development of different subpopulations can be considerable. The most recent trapping efforts at Rough Common and Sunday's Hill also show variation between study sites (S. Fenn, pers. comm.).

Table 3.19 Summary of density estimates and numbers captured of rodent studies in Wytham

a) Minimum and maximum density estimates

Species	Area	Season	Parameter	Density	Reference
Microt.	Rough Common	Autumn	Max. dens.	49.5	Chitty et al. (1968)
Clethr.	Great Wood	Autumn	Max. dens.	39.5	Southern (1970)
Apod.	Great Wood	Autumn	Min.-max. d.	12-20	Southern (1970)
Cl+Apod.	Marley Wood	Autumn	Min.-max. d.	21-39	Flowerdew (1972)

b) Trapping results by Godfrey (1955) at two rough grassland areas (number of individuals caught at each trapping site)

Year	Month	Rough Common	The Dell
1950	May	7	12
	August	21	29
1951	May	16	36
	August	100	9
1952	May	35	3
	August	11	-

In spring 1982, I put out Longworth traps on five grids on rough grasslands at various parts of the Wood in order to compare these grassland areas with each other and with woodland areas trapped elsewhere in Wytham Woods (Southern's study). Fig. 3.9 indicates the places of the five grids while Table 3.20 summarizes the characteristics of the grid and the trapping results. Very few voles were caught (Table 3.20). The extension of the trapping session to six rounds (one round every morning and afternoon) did not yield any improvements in numbers. Presumably the severe winter 1981/82 had catastrophic effects on the vole populations. The results of my trapping are consistent with Susan Fenn's trapping at Rough Common and Sundays Hill and the trapping in woodland (by Ken Marsland, continuation of H.N. Southern's study). Since the maintenance of five grids with a total of 238 traps meant too much effort in the long run, I decided to abandon trapping and took Ken Marsland's data as a crude approximation to the recent development of all three species in Wytham Woods.

Fig. 3.10 presents the last 11 years of these data together with the results up to December 1983. Of particular interest is the development between 1981 and 1983. Population levels break down completely after the very severe winter 1981/82. Both Apodemus and Clethrionomys populations quickly recover towards winter 1982 reaching long-term average values. Apodemus numbers increase even further but also drop quickly towards the end of 1983 while Clethrionomys seems to be then very stable. The Microtus populations recovered similarly to average values (S. Fenn, pers. comm.).

3.7 Discussion

In my discussion of resources I shall concentrate on two related aspects: a comparison of prey characteristics and the expected foraging tactics of a predator in relation to the energy obtained from different

Table 3.20 Rodent trapping in Wytham Woods spring (April) 1982.

a) Description of trapping sites. All trapping grids were placed in rough grasslands. Distance from trapping point to trapping point = 13 meters.

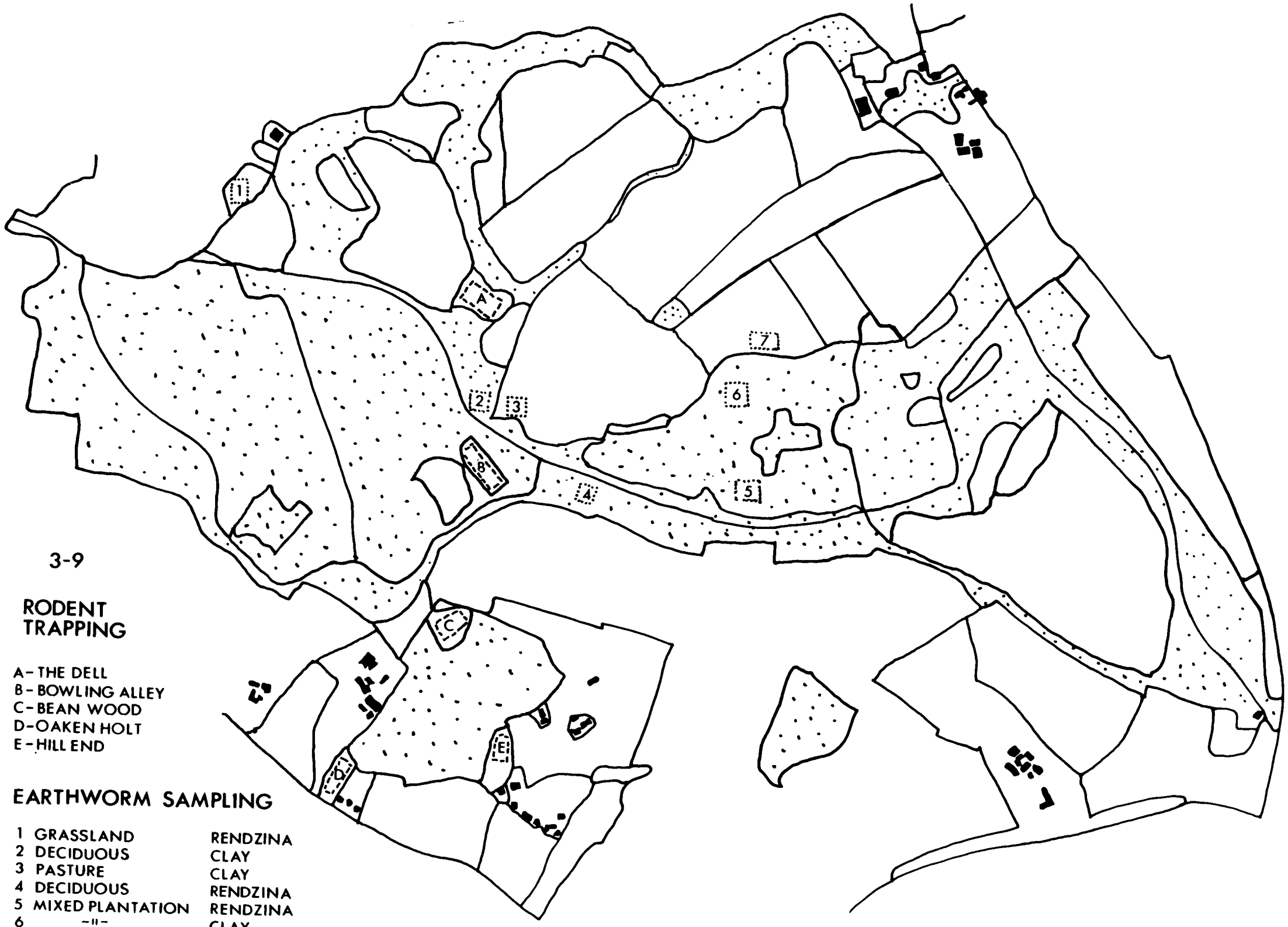
Grid number	Grid name	Number of stations	Size (ha)	Number of traps
A	The Dell	5 x 7 = 35	0.4056	70
B	Bowling alley	3 x 7 = 21	0.2028	42
C	Bean Wood	3 x 5 = 15	0.1352	30
D	Oaken Holt	3 x 8 = 24	0.2366	48
E	Hill End	3 x 8 = 24	0.2366	48

b) Trapping results. One night prebaited with oats before the traps were set for the first time. Caught animals were identified, aged, weighed and fur clipped for individual identification.
A = adult; J = juvenile; ( ) = marked animal recaught

		Trapping round						
Grid no.	Species	1 31.3. morn.	2 31.3. aft.	3 1.4. morn.	4 1.4. aft.	5 2.4. morn.	6 2.4. aft.	Sum
A	Microtus	0	2A 1J	0	0	0	0	3
	Clethrio.	2A	0	0	0	0	0	2
B	Microtus	0	0	0	0	0	0	0
	Clethrio.	1A	0	1A	0	(2)1A	(2)1A	4
C	Microtus	0	0	0	0	0	0	0
	Clethrio.	0	0	0	0	0	0	0
D	Microtus	2A 1J	1J	1A	0	(1J)	0	5
	Clethrio.	0	0	2A	1J	1A 1J	0	5
E	Microtus	0	0	0	0	0	0	0
	Clethrio.	0	0	0	0	0	0	0

Total Microtus: 8; total Clethrionomys: 11

Fig. 3.9. Map of the central part of the study area. Main woodland and field boundaries as in Fig. 3.7. Human buildings black, sampling sites for rodent trapping and earthworm sampling indicated.



3-9

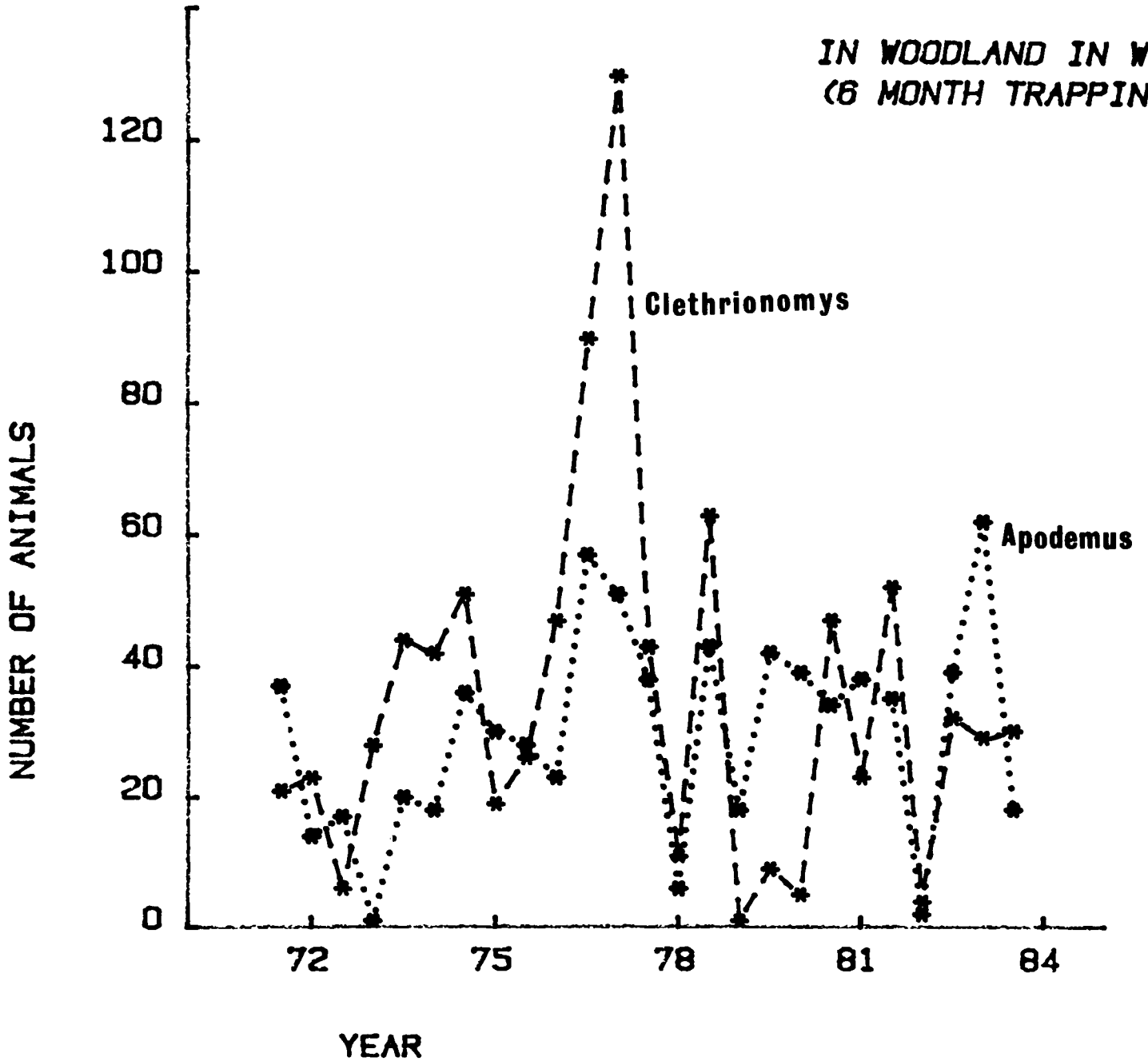
RODENT TRAPPING

A - THE DELL
B - BOWLING ALLEY
C - BEAN WOOD
D - OAKEN HOLT
E - HILL END

EARTHWORM SAMPLING

1	GRASSLAND	RENDZINA
2	DECIDUOUS	CLAY
3	PASTURE	CLAY
4	DECIDUOUS	RENDZINA
5	MIXED PLANTATION	RENDZINA
6	-"-	CLAY
7	ARABLE	CLAY

NUMBERS OF APODEMUS SYLVATICUS AND CLETHRIONOMYS GLAREOLUS
IN WOODLAND IN WYTHAM
(6 MONTH TRAPPING)



prey. The discussion not only considers resources as presented in the previous sections 3.2 to 3.6 but also includes other resources such a invertebrates (excluding earthworms), scavenge, fruits, and cereals. For convenience, these items are all included in the term 'prey'.

3.7.1. Comparison of prey characteristics

Table 3.21 summarizes some of the features of different prey types relevant to movement and foraging decisions of predators. Obviously, for a predator to utilize the full spectrum of prey types necessitates keeping track of many different things! In Table 3.21, prey were allocated to four classes, arranged according to ascending size. As prey items increase in size from tiny to medium-sized (class I to IV), they not only increase in energy contents but also in effort required to capture them, and difficulty in monitoring their abundance, while at the same time decreasing in density.

Common to all prey items is a fairly stable and predictable distribution across habitats, usually both on a long-term as well as short-term basis. A fox will find pheasants in the same copse year after year, earthworms are invariable at higher densities in deciduous woodlands than in plantations and the locations of rabbit warrens are longstanding and conspicuous. However, the predator's knowledge of resource distribution and availability patterns will never be perfect, lagging behind recent changes and bedevilled by chance events.

3.7.2. Foraging tactics of predators in relation to the energy obtained from different prey.

As illustrated in Table 3.21, different kinds of prey pose different problems to the predator, but also promise different yields. While the

Table 3.21 A comparison of selected characteristics of fox and badger prey.

	Class I: Inanimate			Class II: Invertebrates	
	Fruits	Cereals	Scavenge	Earthworms	Others
1. Predictability of spatial distribution over habitats	very high	very high	high	high	high
2. predictability of spatial distribution within habitats	high	very high	varying	low	low
3. predictability of abundance patterns & population development	high but very seasonal	high but very seasonal	varying	high	varying,often strongly seasonal
4. predictability of availability	very much dependent on abundance	identical with abundance	identical with abundance	rather complicated & low (microclimate)	much dependent on abundance
5. Density per ha (literature & estimates)	> 10000	> 10000	?	> 10000	> 1000
6. Home Range and Movement patterns	-	-	-	small; basically stationary	small; in restricted areas
7. Locomotory abilities	-	-	-	slow moving except for quick retreat	ground:slow air: flight through vibrations
8. Antipredator detection	-	-	-		restricted; a variety of means
9. Antipredator defense	-	-	-	retreat into burrow	move fast; fly; distaste ful (mimicry)
10. Capture success of predator (%)	100	100	100	?80 - 100	?50 - 100
11. How does experience help the predator ?	-	-	where to expect it	reliability of predicting availability increases; efficient capture	where to look in which season for what
12. Main problem faced by predator	(seasonal changes in) ABUNDANCE			(complicated patterns of) AVAILABILITY	
13. Energy content per item (kJ/item)	ca 0.02 blackberries	?	?	10.137	3.53 beetles
14. Reference for 13.	Sorensen 1981			Box 5	Randolph et al 1976

	Class III: Small vertebrates		Class IV: Medium-sized vertebrates		
	Rodents	Passerines	Wood pigeons	Pheasants	Rabbits
1. Predictability of spatial distribution over habitats	fairly good	varying	fairly good	fairly good	fairly good
2. predictability of spatial distribution within habitats	low	very low	low	low;except for males during breeding season	varying
3. predictability of abundance patterns & population development	varying; seasonal	varying; seasonal	good	good	good; seasonal
4. predictability of availability	low	low	low; high abundance often means low availability (roost)	low	changes with season (cover etc)
5. Density per ha (literature & estimates)	12 - 74	ca 5 - 50	? (low)	< 1 - 5	up to 100
6. Home Range and Movement patterns	small; seasonal migrations possible	small (territories) to large (flocks)	larger areas; irregular	small; little migration from year to year	medium; regular
7. Locomotory abilities	very mobile	very mobile;flight	very mobile;flight	very mobile; flight	very mobile & fast
8. Antipredator detection	scent and acoustics (?)	vigilance alarm calls	vigilance alarm calls	vigilance alarm calls	vigilance alarm calls
9. Antipredator defense	avoidance of areas with predator scent;locomotion	flight; mobbing	large groups; flight; high roosting sites	cryptic colouring (females); flight high roosting sites	fast movements;escape to burrows
10. Capture success of predator (%)	low to medium	low	low	low	low to medium
11. How does experience help the predator ?	where & when to look; timing of pounce	where & when to look; how to stalk; where to find nests	how to stalk ?	where to find breeding hens; how to stalk them	how to stalk; how to capture
12. Main problem faced by predator	DETECTION		DETECTION AVOIDANCE		
13. Energy content per item (kJ/item)	ca 117	ca 88	ca 2926	ca 7315	10693
14. Reference for 13.	5.6 kcal/dry weight conversion factor (Slobodkin 1962); conversion factor of 0.25 dry weight/wet weight (estimate)				Box 5
	ca 20 g body wt (Corbet & Southern 1977)	ca 15 g body wt	ca 500 g body wt Scherner 1980	ca 1250 g body wt Glutz 1973	

detailed investigation of prey biology in sections 3.2 to 3.6 emphasized the complexity of interactions betwen prey and predator, I will now concentrate on one salient aspect of prey choice, the energy yield per individual in relation to the hunting effort required. Using earthworms (low energy yield and hunting effort per individual) and rabbits (high energy yield and hunting effort per individual) as examples, I shall demonstrate how prey choice should vary in relation to changes in population characteristics of the prey populations, if the possibility of simultaneous encounters of more than one prey type is considered. Under these circumstances, no ranking of food types based solely on 'intrinsic' properties of the food items is possible. Instead, if the density, spatial distribution, age structure or other factors contributing to a change in prey availability are considered, the ranking of food types may change (Engen & Stenseth 1984a, 1984b).

If a predator encounters more than one prey type simultaneously, as may be quite common in nature, it can choose between 'doing nothing', pursuing prey type I' or 'pursuing prey type II'. Since most predators can only handle one prey item at a time, all other prey except the one being hunted has a chance to escape. In such a situation a predator should always select the prey type that maximizes.

$$G_i - k_L T_i \qquad (1)$$

where

G_i energy of prey item i

T_i hunting time of prey item i (ie. time needed to stalk, capture and handle)

k_L maximum obtainable energy/time over a long period

(Engen & Stenseth 1984a). In the case of a two-prey system where:

prey type I large prey that is time consuming to hunt

prey type II smaller prey that is quickly hunted

a predator should always choose prey type I, the large prey, if

$$k_L < k_o \qquad (2)$$

with

$$k_o = (G_1 - G_2)/(T_1 - T_2)$$

and type II, if

$$k_L > k_o$$

(Engen & Stenseth 1984a). Obviously, the long-term expected maximum energy/time is a function of the density and thus the encounter rate of the different kinds of prey. For instance, if density of prey type I increases greatly (the large prey), then the long-term expected maximum energy/time would rise. If, as a result, k_L becomes larger than k_o we would expect the predator to switch from prey type I to prey type II (see eqn (3)). Thus, an increase in the abundance or density of a prey type could mean a reduction in its proportion of the predators diet! This surprising prediction has been termed 'self-reduction' by Engen & Stenseth (1984a, 1984b) and demonstrates that the right prey choice may be far from obvious.

Using rabbits as an example for prey type I, earthworms as an example for prey type II, I shall show how the fox's choice (ie. ranking of food types) may be expected to vary as a result of the variation in energy per time unit obtained from the prey types. Since the value for energy includes both successful and unsuccessful hunts, energy gain will be a function of capture success (itself a complex function of prey and predator biology). Hunting time can similarly be expected to vary considerably, depending on the method of hunting (stalking or ambush predation) and environmental features (vegetation etc.). Population dynamics are also important, since a change in age ratio during the reproductive season will reduce the average weight and thus energy obtained from an average prey individual, all else

being equal. In a simple model, capture success (of rabbits), hunting time and changes in age ratio in the rabbit population have been considered as variables, to answer three questions:

1. Are there conditions under which the energy per unit hunting time obtained from rabbits drops below a threshold so that foxes should prefer earthworms?

2. When should we expect a change in food preferences to occur in relation to the population development of rabbits?

3. Can we find any evidence from the Wytham population that changes in food preferences occur, as for instance described by the phenomen of 'self-reduction'?

The precise conditions for self-reduction to be possible are:

1. Energy G_1 obtained from rabbits is higher than the energy G_2 obtained from earthworms.

2. Hunting time T_1 for rabbits is higher than for earthworms (T_2), so that yield per unit time (G/T) is less for rabbits than for worms ($G_1/T_1 < G_2/T_2$).

In Box 5 I have summarized the parameter values and the equations incorporating the effects of capture probability and hunting time on energy yield per unit hunting time; Fig. 3.11 is a plot of the results. Energy contents per individual show a thousand fold difference between rabbit and earthworm. However, differences in energy yield per unit hunting time are smaller. Since earthworms are caught at a high rate and eaten quickly, the potential for ingestion of earthworms is considerable. For rabbit hunting, neither a reduction in capture success from intermediate to low levels nor an increase in hunting time from intermediate to high values have drastic effect. With the parameter values used, improvements in hunting time are rewarded more than improvements in capture success. This favours a predator that stalks rather than sits and waits for the rabbit to approach its hiding place. On this basis the observed tactic of rabbits disturbed by a fox

Box 5. Calculation of energy gain per unit hunting time.

For rabbits, energy gain per unit hunting time G_i/T_i was calculated as a function of capture probability CP and hunting time T_i, since they are expected to vary widely. For earthworms, the two parameters are assumed to be constant.

Energy gain G_i = Energy per animal x Catching Probability CP

Energy (p.a.) = $C \times f_1 \times W \times f_2$; with

- C caloric value per gram dry weight
- f_1 conversion factor dry weight/wet weight
- w body mass in gram (ie. wet weight)
- f_2 conversion factor kcal to kJ = 4.18

	Rabbit	Earthworm
C	5.685 kcal g^{-1} (European hare, Myrcha 1968)	17.037 kJ g^{-1} (from section 3.2 adjusted for age ratio; Table 3.2a)
f_1	0.3 (Golley et al. 1965)	0.157 (section 3.2)
W	1500 g (taken as typical, range 1200-2000 g, Lloyd 1977)	3.79 g (Table 3.2)
Energy	10693.35 kJ per adult	10.137 kJ per average individual encountered
CP	varies from 0.05 to 5	0.95 (estimate)
G_i	varies	9.123 kJ
T_i	varies from 5 to 30 min	0.49 min (average) 0.25 min (good)
G_i/T_i	varies	18.611 kJ min^{-1} (average) 36.492 kJ min^{-1} (good c.)

vanishing into their warrens for half an hour (Macdonald, 1977) appears to be an efficient one.

In Fig. 3.11, the dotted line numbered 1 indicates the level of expected earthworm energy gain (36.492 kJ min^{-1}) under good hunting conditions. If a fox hunts rabbits in circumstances below this line, conditions 1 and 2 are fulfilled, and - from the theory - a change in food preferences becomes likely. Note, however, that a switch in prey choice is only likely to occur, if k_L becomes larger than k_o (eqn (2) and (3)), ie. the abundance of rabbits increases. We shall therefore examine the changes that are likely to happen during the reproductive season of the rabbits, ie. a time when population density of rabbits increases and the age ratio in the population changes.

During the breeding season from January to June, more and more juvenile rabbits join the adult population so that the expected energy gain from an <u>average</u> individual captured will become reduced. Generally,

$$\text{energy} = p_a E_a + p_j E_j \qquad (4)$$

with

p_a, p_j proportions of adults and juveniles in the diet

E_a, E_j energy from adults and juveniles, respectively

Assuming that the energy content of juveniles does not differ from that of adults per gram body mass, and setting g as the ratio of average gain expected at time t_2 (rabbit population consisting of adults and juveniles, ie. during breeding season) in relation to previous gain at time t_1 (adults only, ie. during winter before breeding season),

$$g = (p_a E_a + b\, p_j\, Ea)/Ea \qquad (5)$$

with $E_j = b\, E_a$ and b = ratio of juveile to adult body weight

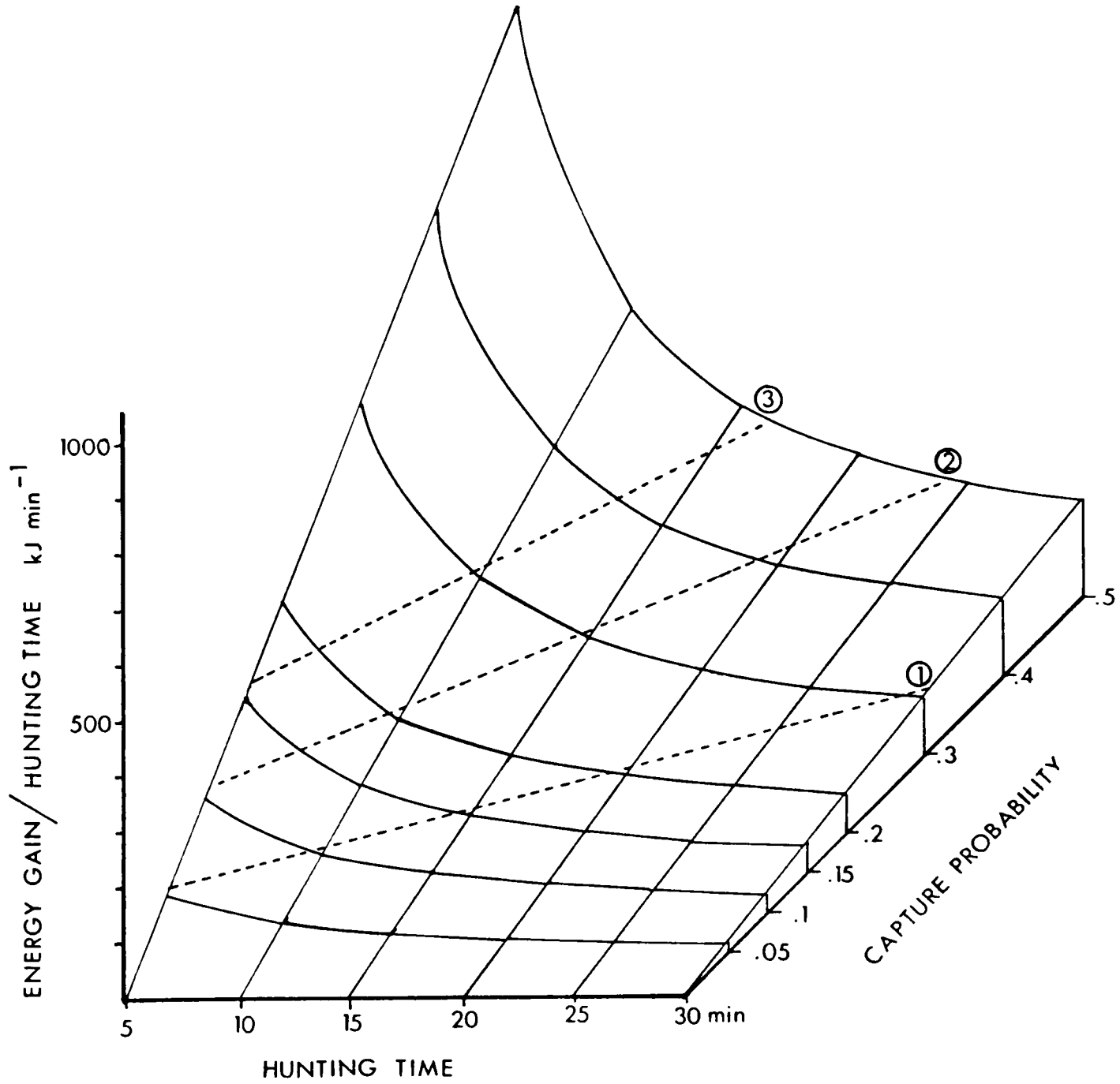
or

$$g = p_a + b\, p_j \qquad (6)$$

If juveniles are assigned a quarter of the body weight of adults (b = 0.25)

Fig. 3.11. Model of energy gain per unit hunting time for foxes hunting rabbits as a function of hunting time and capture probability. Calculations according to the formulae presented in Box 5.
Lines 1–3: Lines of equal energy gain for foxes hunting rabbits or hunting earthworms.

Line 1: foxes hunting adult rabbits only.
2: foxes hunting adults and juveniles in proportion 1:2.
3: foxes hunting adults and juveniles in proportion 1:9.


ENERGY GAIN / HUNTING TIME kJ min⁻¹
1000
500
5
10
15
20
25
30 min
HUNTING TIME
③
②
①
.5
.4
.3
.2
.15
.1
.05
CAPTURE PROBABILITY

$$g = pa + 0.25\ p_j$$

Thus g will be 1 if only adults are present; g will decrease to 0.5 at an age ratio of 1 adult:2 juveniles, further decrease to 0.325 at a ratio of 1:9 and reach its minimum value of 0.25 if only juveniles are present. Reducing the energy gain by the factor g is equivalent to increasing the threshold level where condition 2 begins to hold, ie. multiplying the expected energy gain from earthworms by 1/g. For the age ratios 1:2 and 1:9 the corresponding threshold values are 77.042 kJ min^{-1} and 118.526 kJ min^{-1}. These are represented in Fig. 3.11 by the dotted lines 2 and 3. With an increase in the ratio of juveniles:adults (corresponding to an increase in overall population density) a fox is therefore more likely to find itself in a situation when it should switch from rabbits to earthworms, provided it has the chance to encounter both prey types simultaneously.

There are two factors that may modify the true energy yield per unit hunting time to make it different from the average expected yield, ie. the yield as expected from the change in age ratio as described above. Both factors derive from juvenile stupidity; they are improved capture success (relative to capture success of adults), leading to a higher energy gain per gram body mass from juveniles than the energy gain obtained from adults, and reduced hunting time and effort that should tempt foxes to take disproportionately many young and so create a ratio of juveniles to adults in the diet of the predator that is higher than the population ratio. In the latter case, a reduced energy gain (relative to the average expected gain) would result. Both factors may in the end cancel each other out, but data are not available to test this.

The probability of switching from rabbits to earthworms increases towards the end of the breeding season, when the age ratio changes in favour of juveniles and the overall population density of rabbits increases. This is a time (April and May) when conditions for foraging for earthworms have

improved and are at their optimum, suggesting that the figures for energy yield from earthworms per unit hunting time calculated in Box 5 are conservative estimates. Under these simple, but not implausible conditions, I would therefore expect fox home ranges with high rabbit densities to be likely to exhibit self-reduction in their diet from winter (beginning of rabbit breeding season) to spring (end of breeding season), despite an increase in the simple abundance of rabbits if rabbits and earthworms occur in the same habitats. Two confounding conditions may render it difficult to show self-reduction in practice. Social hierarchies within fox groups can have an influence on the range of prey a subordinate fox is able to use (Macdonald 1980), and large differences in experience and traditions between individuals and/or groups may further modify the actual thresholds for prey switching. Profound differences in hunting traditions between groups have been shown e.g. in wolves (Mech 1970, Mech pers. comm.). Nevertheless, anticipating the results of the analysis of the diet (Chater 4) and fox home ranges (Chapter 5), there is some evidence that self-reduction occurs in some ranges in Wytham: in two fox ranges with high rabbit densities (ranges 6 and 7), a significant reduction in the proportion of rabbit in the diet was found from winter to spring, when rabbit numbers were nevertheless known to increase. In contrast, neighbouring range 5, with lower rabbit densities than range 6 or 7, increased the proportion of rabbits in its diet - in that case rabbit population densities may not have been sufficiently high to force the foxes of range 5 to reduce their amount of rabbit hunting! An alternative explanation would be that in range 5 the possibility of <u>simultaneous</u> encounters of rabbits and earthworms is reduced, since the rabbits seem to occur more in wooded areas while earthworms are present on pasture. In ranges 6 and 7, both rabbits and earthworms are present on pasture and also deciduous woodland.

4. Diet

4.1 Introduction

4.2 Fox diet

4.2.1 Methods of sampling

4.2.2. Methods of analysis

4.2.3. Results

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.2. Temporal variation in the diet

.3. Variation in the diet of different ranges

.1. General diet composition of ranges

.2. Seasonal variation in the diet or ranges

4.2.4. Fox diet: summary

4.2.5 Comparison with other studies

4.3 Badger diet

4.3.1 Methods of sampling

4.3.2. Methods of analysis

4.3.3. Results

.1. General composition of the diet

.2. Temporal variation in the diet

.3. Variation in the diet of different ranges

.1. General composition of the diet

.2. Temporal variation in the diet

.4. Comparison of border and non-border latrines

4.3.4. Badger diet: summary

4.3.5. Comparison with other studies

4.4 Comparison of fox and badger diet

4.1 Introduction

In this chapter I turn my attention to one aspect of resource utilization: the diets of the fox and badger populations in Wytham. In the previous chapters, the analyses of the habitat composition, the prey populations and the foraging techniques of foxes and badgers indicated where the prey can be found and how its availability varies. The processes underlying prey selection together with the predator's foraging efficiency determine the portion of the available prey which is used. The diets of the two predator species are the result of this process.

The diets of foxes and badgers have been widely studied, partly because this is one of the few aspects of their behavioual ecology that can be studied easily. However, as Macdonald (1977a) stressed, many studies have only limited usefulness since the diversity of methods used precludes detailed comparisons. A comprehensive list of European studies of the diet of the red fox is provided by Jensen & Sequiera (1978) while information on the diet of European badgers is presented by Andersen (1954), Skoog (1970), and Kruuk and Parish (1981).

In this study it was important to adopt a method of analysis that disclosed the details of each species' diet, and did so in a way which thereafter facilitated comparison between them. Ideally, the method should also maximise the opportunities for comparison with other studies. The analysis of dried remains of undigested food items in faeces proved to be such a method. Several measures of the importance of each prey type in the diet were investigated and simultaneous use of estimated dry weight and frequency of occurrence were found - in line with other Oxford studies (Macdonald (1977a,b), Newdick (1983), Doncaster (1985)) - to provide the best compromise between a maximum of quantitative information, a minimum of

cumulative systematic error and the potential comparability between species and reproducability in other studies. Estimated dry weight of each digested food type was used as a measure of its contribution to the diet, annually and seasonally for each species (sections 4.2 and 4.3). In addition, the diets of animals within ranges for which there were sufficient sample sizes were investigated.

A computer program incorporating a filtering procedure (Appendix 3) was used to avoid ambiguities when each faeces was assigned to a range. The different patterns of faeces deposition by foxes and badgers necessitated different filtering procedures for each species. In the case of badgers, samples collected from sites on the border of neighbouring badger ranges ("border-latrines") were excluded from analyses of the diet within individual ranges. For foxes, there was some overlap between neigbouring ranges, so that all droppings collected in the overlap zones were excluded from analyses of the diet within each range. These filtering procedures reduced some sample sizes, but enhanced the value of the results by reducing "noise" in the data. My analyses of the diet composition of badgers and foxes in group ranges involved both spatial and temporal trends, and thus yielded a very detailed picture of variation of the diet of the two predator populations.

Several methods have been used to study the diet of foxes and badgers (see Newdick (1983)):

1. Collection of food items around dens
2. Following tracks
3. Analysis of stomach contents
4. Analysis of droppings
5. Direct observation

In this study several methods were tried, the principal one being the

analysis of undigested food remains in faeces. In addition, prey remains (mainly those of birds) were collected whenever encountered (see Chapter 3). This proved to be very unsatisfactory since the sample size was small (28 bird remains collected between 1981 and 1983). Direct observations on feeding habits of marked and unmarked foxes and badgers were made whenever possible. They were also used to evaluate predation techniques (Chapter 3) and to analyse patterns of activity and habitat use (Chapter 6). For instance, chance observations confirmed that foxes were hunting during the day; on one occasion an adult fox was seen to take a rabbit at 11 a.m. in Marley Plantation (at the southeast corner of the wood). On another occasion a male fox was seen to return to its den with a freshly killed male pheasant at 11.30 a.m. and feed the prey to its vixen and the cubs.

I decided to concentrate upon collecting and analysing droppings because this

- was easy, quick and therefore efficient;
- disturbs the study populations comparatively little, with the possible exception of disrupting scent-marking (Macdonald, 1980);
- allows repeated sampling of the output of the same individuals (in contrast to the analysis of stomach contents);
- provides a standardized approach to allow a comparison of the diet of both species.

4.2. Fox diet

4.2.1. Methods of sampling

A total of 2030 fox droppings were collected over the entire study area

between April 1981 and October 1983; (data for April, May and June 1981 were kindly provided by D.W. Macdonald). As it was impossible to search all parts of the study area with the same intensity, a 'core' area was defined which was visited regularly (sometimes daily, but at least once every 14 days, Fig. 3.9).

Table 4.1 records the sample sizes for each month, summarized over the three years, for each season over the entire study area, together with the grand totals for all recognized fox ranges and seasonal totals for ranges with a reasonable sample size (ie. the five ranges which were later investigated in detail and SURPRISE's range (No. 8, Swinford Lodge)). The uneven temporal distribution of sampling effort is partly due to reduced sampling effort due to restrictive weather conditions e.g. snowfall in December, and partly due to restrictions on my daylight activities imposed by the necessity of tracking by night.

Identification of fox droppings in the field proved to be easy (see Newdick (1983)). Badger droppings could also readily be identified (Kruuk (1978b)): they are usually much larger than fox faeces, have a characteristic texture and odour and are usually deposited at specially prepared sites (latrines). In the three field seasons of the study I found badger faeces outside latrines on only two occasions but both droppings were readily identifiable as badger faeces because of their size, and texture.

On collection, each fox dropping was placed in an envelope and the following details recorded:

1. Date
2. Map coordinates
3. Information on the details of location:
    .1. Presence or absence of a path
    .2. Presence or absence of a junction of paths
    .3. Presence or absence of a conspicuous object

Table 4.1 Numbers of fox droppings collected. Data from all years (1981-1983) are combined

a) Sample sizes for different months

January	84	
February	218	
March	354	
April	321	
May	45	
June	87	
July	191	
August	281	
September	192	
October	151	
November	97	
December	5	TOTAL: 2026

b) sample sizes for different seasons

season 1 (December to February)	307	
season 2 (March to May)	720	
season 3 (June to August)	559	
season 4 (September to November)	440	TOTAL: 2026

c) sample sizes for different ranges

Range number	Name	Number of droppings	
1	Home Farm	80	
2	Churchgrove	10	
3	Great Wood	16	
4	Tilbury	8	
5	Woodend	145	
6	Singing Way	573	
7	Hill End Camp (HEC)	153	
8	Swindon Lodge	70	
9	Binsey	2	
10	Marley Wood	138	TOTAL: 1195

d) sample sizes for selected ranges for each season

Range	Name	Season 1	Season 2	Season 3	Season 4	Total
1	Home Farm	10	22	25	23	80
5	Woodend	7	86	21	31	145
6	Singing Way	113	175	191	94	573
7	HEC	17	53	45	38	153
8	Swindon	2	15	6	47	70
11	Marley	24	91	9	54	138
		173	440	297	287	1159

.4. Nature of the conspicuous object, if present

4. Smell (codes: 0 - none; 1 - weak; 2 - medium; 3 - strong)

5. Age (codes: 1 - within the last two nights; 2 - older than the last two nights but within the last week; 3 - older than a week)

A path was defined as a visible break in the vegetation with signs of animal tracks. Any man-made track was also regarded as a path. Age was estimated on the basis of appearance and accounting for prevailing weather conditions. For experienced field workers the coding was straightforward in the field. In trials, two independent collectors were highly consistent in assigning the same age and odour classes to given droppings. The envelopes were oven dried at 50° and stored prior to analysis.

4.2.2 Methods of analysis

In principle, the analysis of the faecal contents followed the procedure described by Macdonald (1977a) and Newdick (1983):

Each fresh dropping was weighed and then crumbled into a petri dish where its composition was examined under a binocular microscope. The prey remains were separated into categories and the percentage of the total volume comprised of each category was estimated by eye. As most faeces consisted of only two or three types of prey remains, the error associated with the estimation by eye is probably low. Also, Macdonald & Dickman (unpubl.) have recently shown that results from this relatively quick method do not differ from those of tedious wet sieve techniques. The analysis of the faeces was performed by David Macdonald in order to keep the systematic error of faeces analysis constant and reduce error variation between different Foxlot studies to a minimum.

The major prey types were categorized as follows (definitions from Newdick (1983)):

1. Small mammals (e.g. rodents, insectivores) Tightly packed tufts of brown hairs which can be distinguished from the longer brindled guard hairs of lagomorphs or their pale, woolly underfur. The size of bone chips and presence of teeth also aided diagnosis. The species were identified by examining the hairs microscopically according to the keys provided by Day (1966) and Debrot (1982).

2. Invertebrates Fragments of exoskeleton of, for example, beetle elytra or caterpillar remains, were easily identifiable, as were fragments of snail shell. Chaetae of earthworms were recorded separately.

3. Fruits Pips of soft fruit, plum stones and pieces of integument could be identified, often associated with a characteristically hard, dark, and often aerated matrix. Whenever possible the fruit type was identified and recorded using an extensive collection of samples of different types of fruits and berries.

4. Birds Traces of feathers, especially quills, usually accompanied by a grey flaky matrix. They were identified to the level of order under microscopic examination of the spicule patterns.

5. Lagomorph see small mammals

6. Scavenge This faecal material consisted of a homogeneous matrix and was often accompanied by non-food items such as plastic, string, or elastic bands. Newdick (1983) performed baiting experiments which showed that food of human origin invariably appeared as this type of uniform matrix.

7. Soil Soil was almost invariably accompanied by chaetae of earthworms and is taken as an indicator of their representation in the diet. Macdonald (1977a, 1980[a]) showed that this is a justifiable assumption.

8. Grass Indigestable grass fragments could be clearly identified.

9. Domestic shock Fur tufts of the unusual colours of 'exotic' breeds.

10. Others Any items that could not be placed in the other categories. This included e.g. the remains of deer, cow pats and various other prey types the precise identity of which were recorded separtely under a section "curiosities".

11. Cereals These were barely digested and clearly identifiable.

12. Tree fruits Readily distinguishable from all other types.

All data were allotted codes and subsequently transferred to the university's VAX-11/780 computer. Several programs were written in order to check the data for inconsistencies and errors and to add necessary information: Program WYFPROG checked double and erroneous labelling of faeces, program TINPUT inserted dates, program WINPUT inserted weights and program CINPUT inserted coordinates of the location of the dropping into the file with the results of the scat analysis. Each weight, date and map coordinate was labelled with its dropping reference number. Program HAIR finally inserted the identity of small mammal, fruit and bird species, checked the data for detectable typing errors and reformatted the data for further analysis. Statistical analysis was performed with procedures ('macros') which I wrote for the MINITAB statistical package available on the VAX.

From the raw data, five measures of diet were computed using a variety of techniques and correction factors. These are:

1. Frequency of occurrence: This is the number of occurrences of a prey category found in the droppings and usually expressed as a percentage of the total number of droppings. As it disregards any quantitative information on the bulk of the remains in the dropping, it is inadequate alone as a measure of the relative importance of prey categories. Rather it indicates the

degree of regularity with which each prey category is consumed.

2. Estimated volume This is the percent volume of each prey category in each dropping, as estimated by eye. Prey items that are many times larger than the average size of a dropping, e.g. rabbits, occupy most of a faeces while prey items such as beetles occupy only a fraction of the dropping. Together, the frequency of occurrence of the prey items and its estimated volume provide information on the relative contribution of each prey category to the total diet (see Fig. 4.3).

3. Estimated dry weight Here, each percent volume is multiplied by the dry weight of each dropping. This gives a measure where the estimated volume (measure 2) is corrected by the dry weight of each dropping. This estimation of dry weight of undigested food remains assumes equal density of each food category in the faeces.

4. Estimated fresh weight Using Lockie's (1959) and Macdonald's (1977a) correction factors for different digestibilities of different prey items, the fresh weight of prey eaten can be derived from the estimated dry weight of undigested remains in the faeces. This measure seems to come close to an ecologically useful quantification of diet. However, the undoubted errors associated with the correction factors are not precisely known.

5. Calorific value By applying another set of correction factors (from Macdonald (1977a)) the calorific intake from each food types can be calculated from the estimated fresh weight.

Each of the measures suffer from some bias; the ecologically most useful measures also suffer from the most multiplicative effects of several potential sources of errors. As a compromise I decided, in line with previous studies (Macdonald (1977a), Newdick (1983)), to use estimated dry weight as a basis for most of my analyses. This measure is easy to compute and well suited for comparisons between populations or with other species.

Most important, since there are no correction factors for digestibility or calorific intake available for badgers, estimated dry weight is the most sophisticated measure available for the comparative aspect of this study.

4.2.3. Results

4.2.3.1. General composition of the diet

The diets of Wytham's foxes as calculated according to each of the five measures are presented in Table 4.2 and Fig. 4.1. Some interesting trends emerge from a comparison of the different measures. A group of seven prey categories dominate the diet while the remaining five contribute only a very small proportion to the total diet. Amongst the seven important prey types, both earthworms and invertebrates occur frequently but in terms of mass or volume contribute much less. This is particularly striking for invertebrates. The importance of earthworms is drastically reduced when digestibilty and calorific intake are taken into account. In terms of fresh weight or calorific intake, the two most important prey types are lagomorphs (ie. mostly rabbits as there were practically no hares present in the study area) and scavenge followed by birds and fruits. Interestingly, small mammals contribute only little to the overall diet.

The relationship between frequency of occurrence and relative amount present in a particular dropping is shown in Fig. 4.2 and 4.3. In Fig. 4.2 estimated percent dry weight is plotted against frequency of occurrence with the dotted line representing equal proportion of estimated dry weight and frequency of occurrence. Most food types are below the line and thus overrepresented, if only frequency of occurrence is considered, with invertebrates showing an extreme deviation. Thus, invertebrates are regularly consumed but contribute little to the total amount of food

Table 4.2 The diet of Wytham's foxes, estimated by five measures. The percentage values are the percentage contribution of each prey category to the overall result

FREQUENCY: number of occurrences of a prey category
EST. VOLUME: mean of estimated percent volume share of each prey category in each dropping
EST. DRY WEIGHT: mean of (EST. volume/100 * weight of each dropping)
FRESH WEIGHT: mean of (EST. DRY WEIGHT * correction factor)
CALORIES: mean of 9FRESH WEIGHT * correction factor)

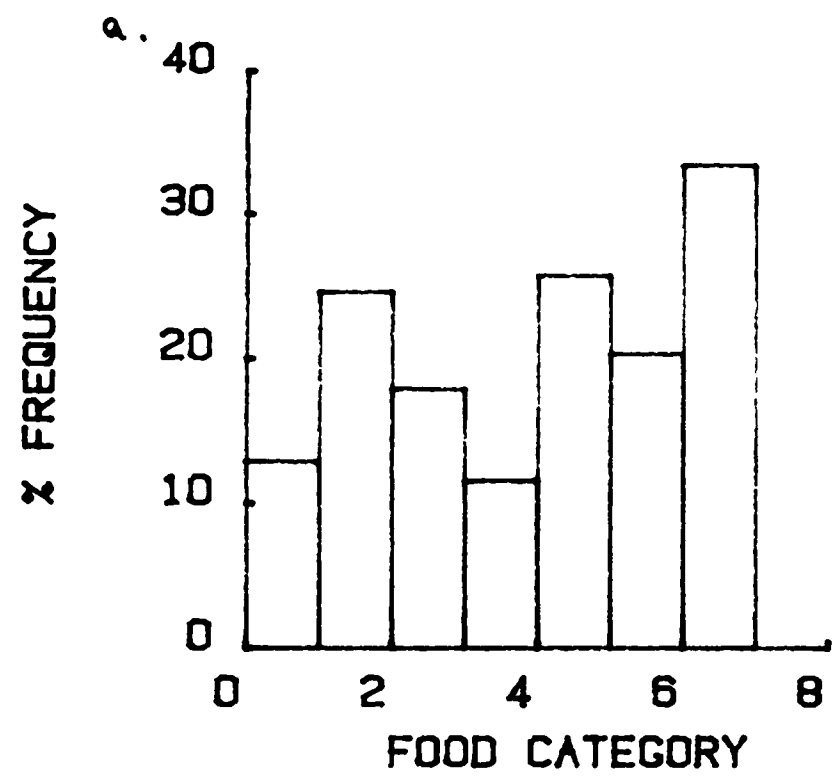
	% freq.	% est. vol.	% est. dry wt.	% fresh weight	% cals
Small mammals	12.81	7.84	5.41	4.35	5.40
Invertebrates	24.58	2.04	1.52	0.78	1.47
Fruit	17.88	13.58	11.99	20.73	9.84
Birds	11.53	6.88	6.31	9.84	11.73
Lagomorph	25.76	23.66	19.78	29.38	35.01
Scavenge	20.34	16.01	17.68	25.83	30.77
Earthworms	33.45	24.33	33.14	8.07	4.86
Grass	1.53	1.28	0.92		
Domestic	0.10	0.04	0.08		
Other *	2.96	2.51	1.74		
Cereals	2.36	1.74	1.39		
Tree fruit	0.25	0.08	0.06		

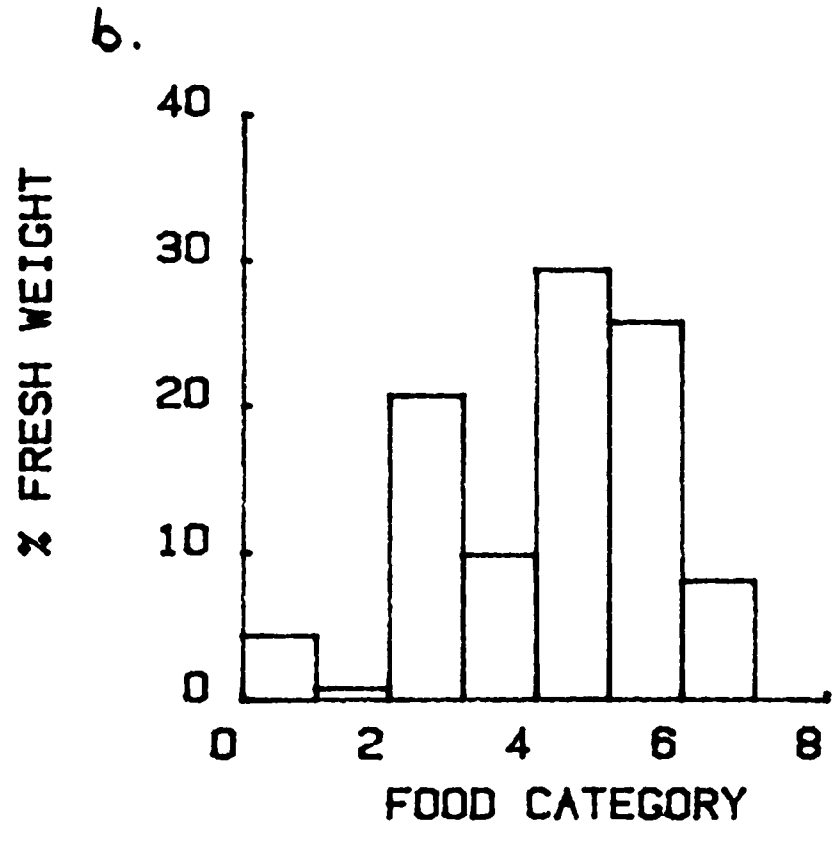
Fig. 4.1. The diet of Wytham's foxes, as measured by four different categories:

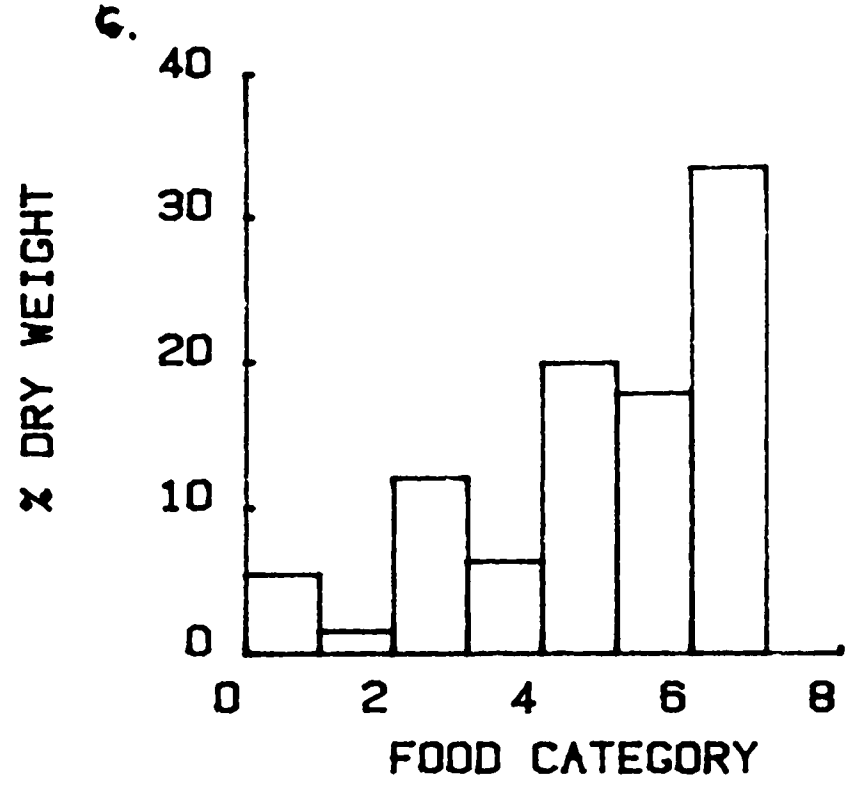
a. per cent frequency
b. per cent fresh weight
c. per cent dry weight
d. per cent calories

Measures are explained in more detail in the text and in Table 4.2. Food categories are (in brackets typical abbreviations in the following figures):

1 - small mammals	SM
2 - other invertebrates	INV
3 - fruits	FR
4 - birds	BD
5 - lagomorphs	LAG
6 - scavenge	SCA
7 - earthworms	EW


a.
% FREQUENCY
40
30
20
10
0
0
2
4
6
8
FOOD CATEGORY


b.
% FRESH WEIGHT
40
30
20
10
0
0
2
4
6
8
FOOD CATEGORY


c.
% DRY WEIGHT
40
30
20
10
0
0
2
4
6
8
FOOD CATEGORY

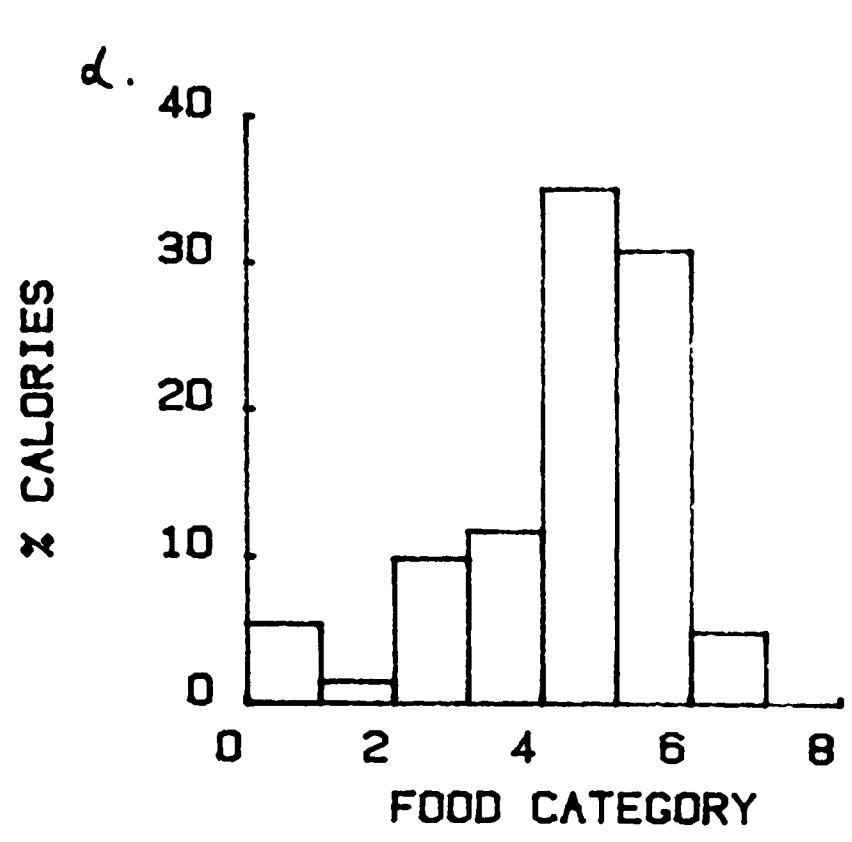
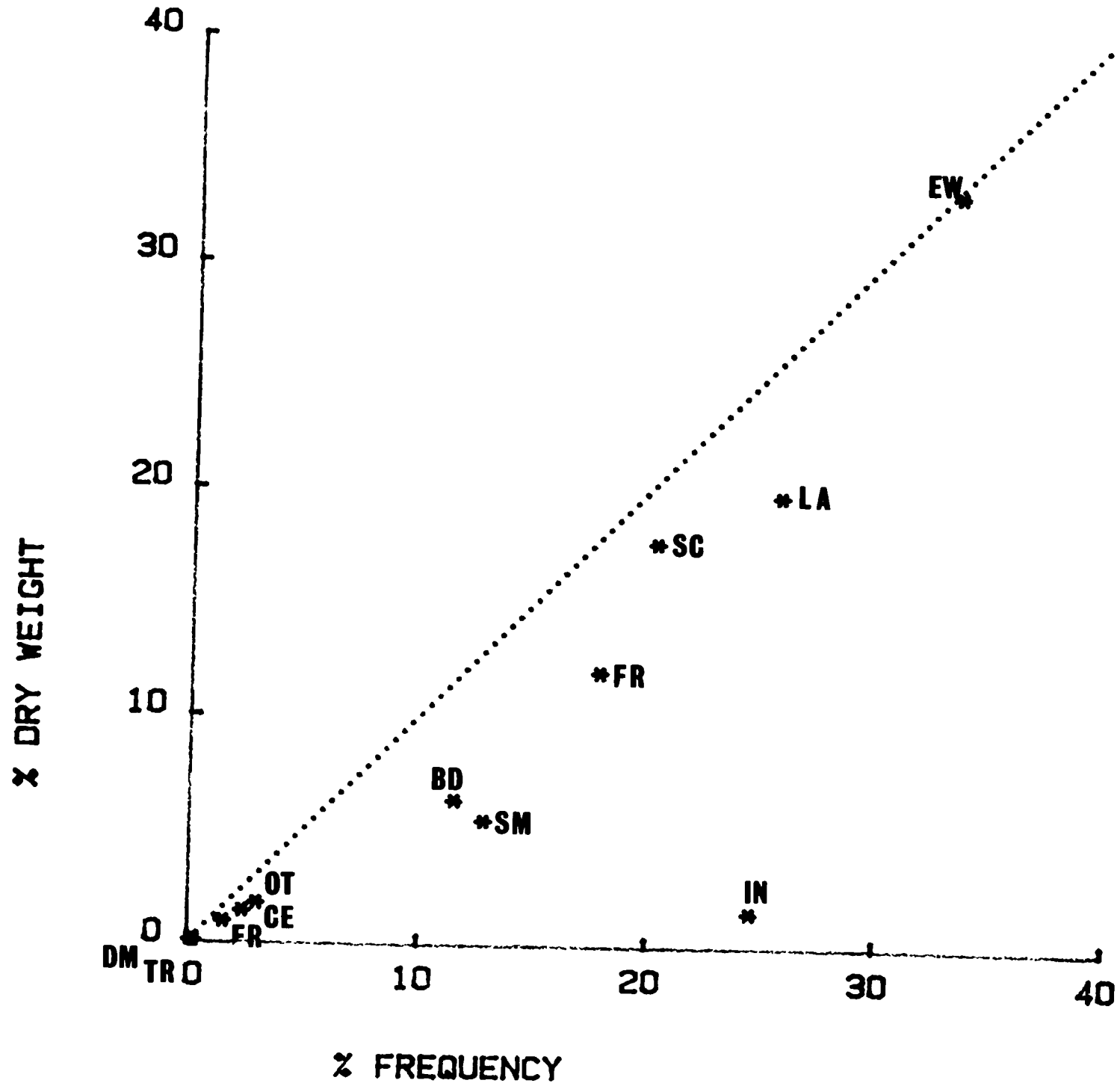

d.
% CALORIES
40
30
20
10
0
0
2
4
6
8
FOOD CATEGORY

Fig. 4.2. Plot of estimated dry weight against frequency of occurrence of all prey categories. All fox faeces considered. If the two measures are equal, then all points should fall on the line. The results indicate that many prey items are comparatively often present but do not contribute much to the overall diet.

Abbreviations:

SM	small mammals
IN	other invertebrates
FR	fruits
BD	birds
LA	lagomorphs
SC	scavenge
EW	earthworms
GR	grass
DM	domestic animals
OT	others
CE	cereals
TR	tree fruits

4-2


40
30
20
10
0
% DRY WEIGHT
EW
LA
SC
FR
BD
SM
OT
CE
FR
IN
DM
TR
O
10
20
30
40
% FREQUENCY

consumed.

In Fig. 4.3 percent estimated volume is plotted against percent frequency of occurrence. Here percent estimated volume refers to the mean values of only those droppings that contained something of the prey type in question. For instance, of all fox droppings that contained any lagomorph remains, the mean percent volume estimated by eye was 92%, ie. on average a dropping that contained at least some parts of lagomorph, contained nearly exclusively lagomorphs! The dotted lines indicate the proportion of the total diet if percent estimated volume as a proportion is multiplied by the relative frequency of occurrence; these plots give an impression of the importance of each prey category. Only two categories, lagomorphs and earthworms constitute more than 20% of the total diet (note that in Fig. 4.3 correction factors for dropping weight or digestibility are not applied). Fruits and scavenge constitute between 10 and 20% and small mammals and birds less than 10% each.

The results indicate the versatility of the fox population to utilize different prey types with the effect that none of the prey categories totally dominates the diet.

In the following sections I shall show how the importance of prey categories changes seasonally and differs between neighbouring ranges with respect to the seven most important food types (small mammals, invertebrates, fruits, birds, lagomorphs, scavenge, and earthworms). In general each food type is treated in the text and in the tables in the same sequence illustrated in Table 4.2.

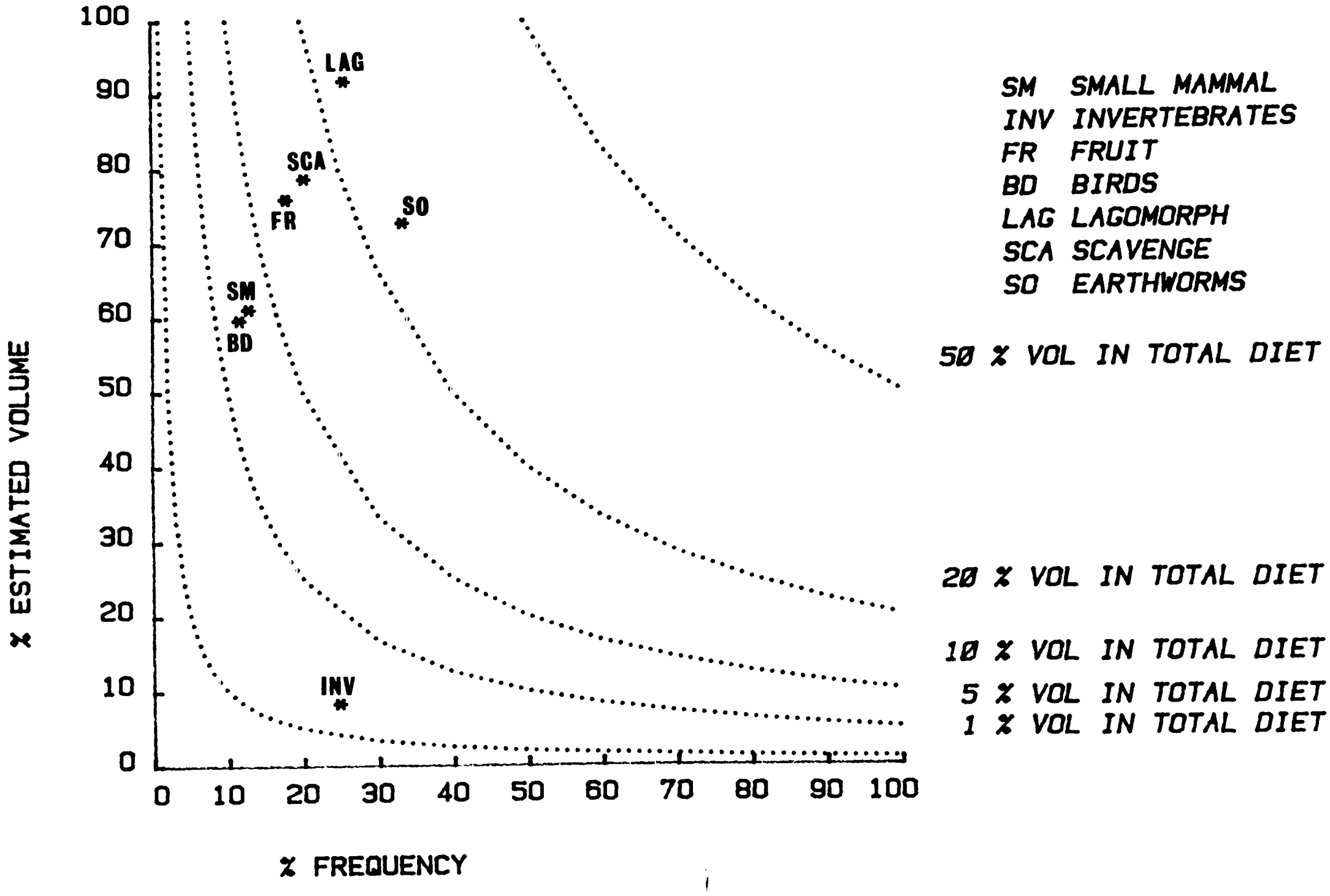
4.2.3.2 Temporal variation in the diet

In Fig. 4.4 the relative contributions of the seven most important prey types are illustrated for each season (as defined in Table 4.1). As in Fig.

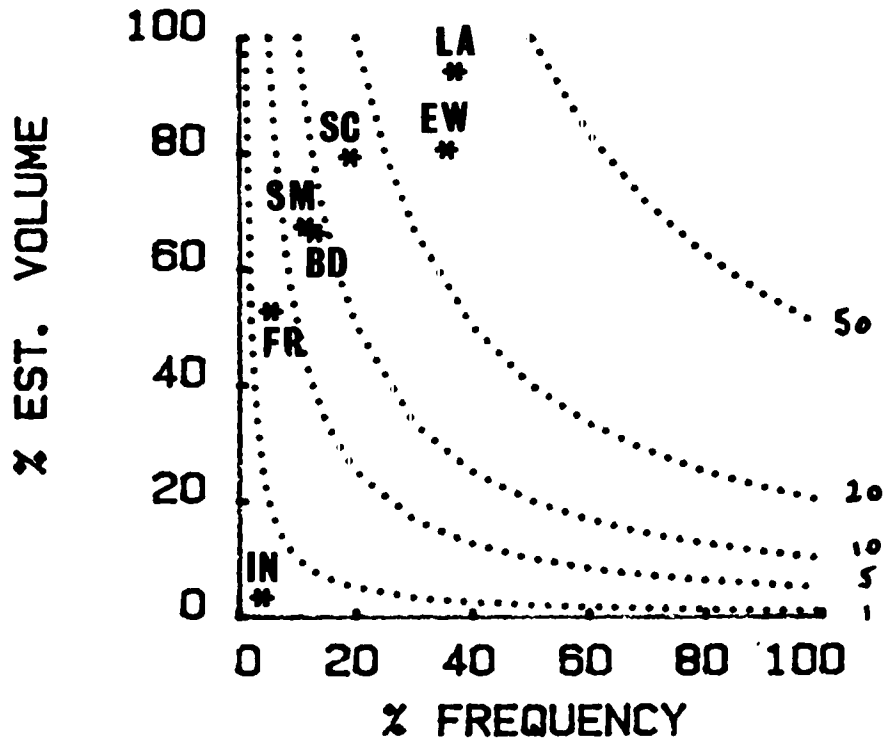
Fig. 4.3. Average percent volume per faeces of each prey category vs. frequency of occurrence, a so-called 'Kruuk-plot'. All fox faeces.

Fig. 4.4. Similar plots (and identical symbols) as in Fig. 4.3., but each season plotted separately.

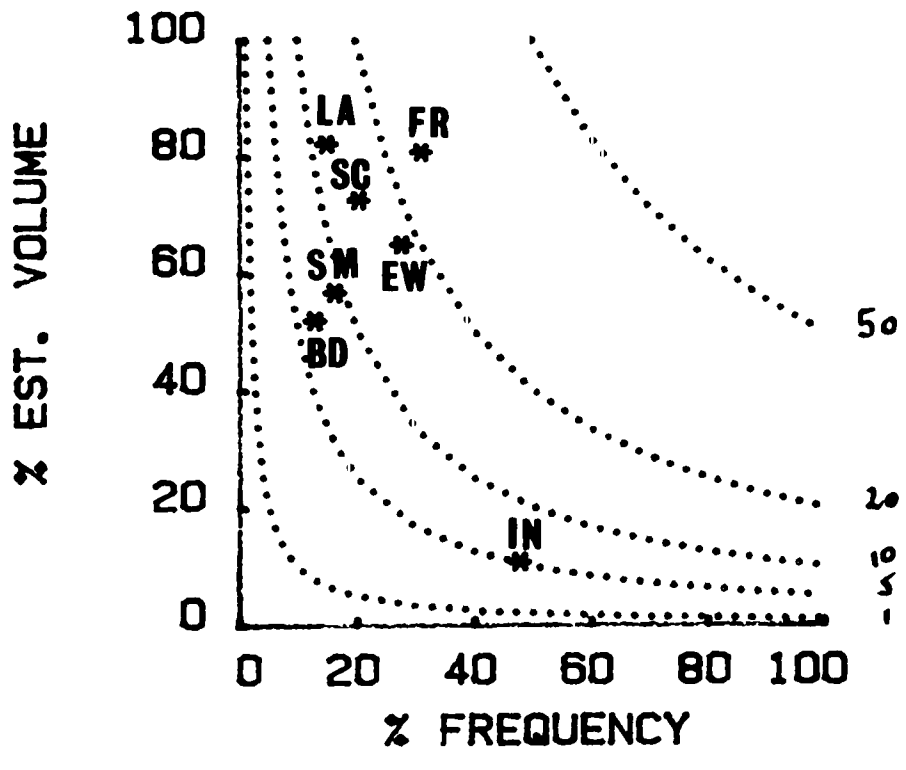
a. spring
b. summer
c. autumn
d. winter


100
90
80
70
60
50
40
30
20
10
0
% ESTIMATED VOLUME
LAG
SCA
FR
SO
SM
BD
INV
0 10 20 30 40 50 60 70 80 90 100
% FREQUENCY
SM SMALL MAMMAL
INV INVERTEBRATES
FR FRUIT
BD BIRDS
LAG LAGOMORPH
SCA SCAVENGE
SO EARTHWORMS
50 % VOL IN TOTAL DIET
20 % VOL IN TOTAL DIET
10 % VOL IN TOTAL DIET
5 % VOL IN TOTAL DIET
1 % VOL IN TOTAL DIET

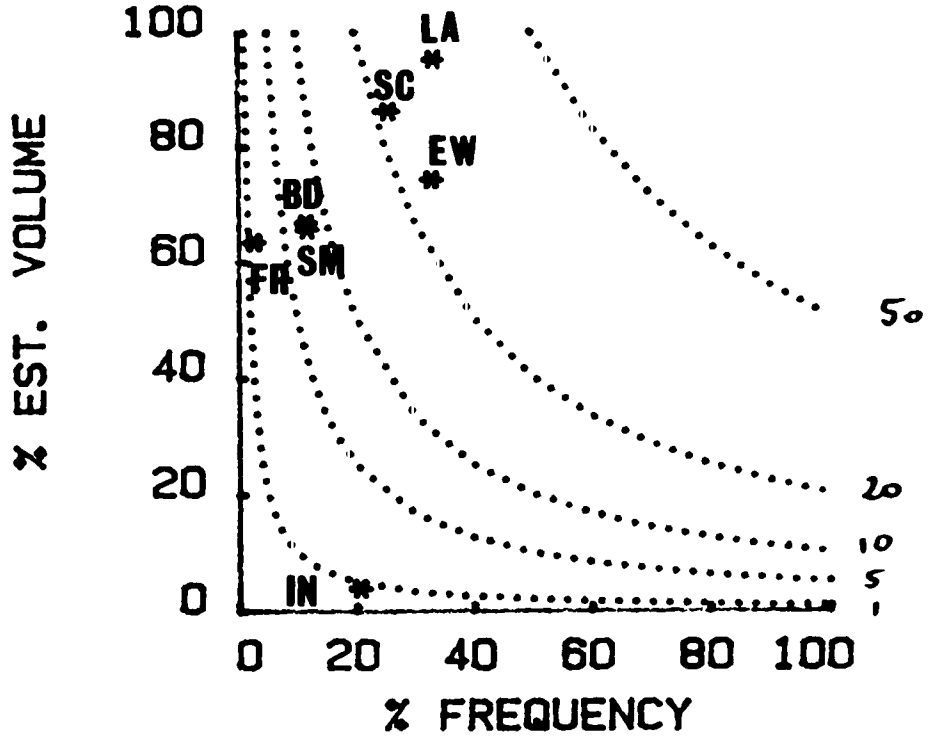
b.


% EST. VOLUME
100
80
60
40
20
0
LA
SC
EW
SM
BD
FR
IN
50
20
10
5
1
0 20 40 60 80 100
% FREQUENCY

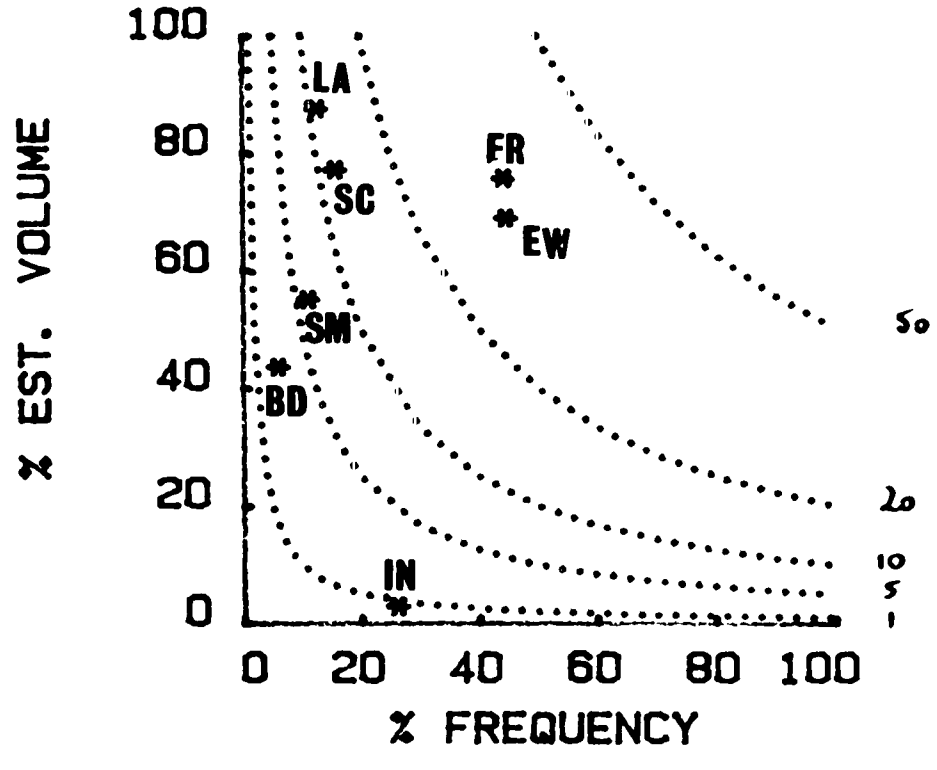
c.


% EST. VOLUME
100
80
60
40
20
0
LA
FR
SC
SM
EW
BD
IN
50
20
10
5
1
0 20 40 60 80 100
% FREQUENCY

6.


% EST. VOLUME
100
80
60
40
20
0
LA
SC
EW
BD
FR
SM
IN
50
20
10
5
1
0 20 40 60 80 100
% FREQUENCY

d.


% EST. VOLUME
100
80
60
40
20
0
LA
FR
SC
EW
SM
BD
IN
50
20
10
5
1
0 20 40 60 80 100
% FREQUENCY

4.3 the mean percent estimated volume of those scats where a given food type occurred is plotted against its frequency of occurrence. The dotted lines again indicate how much each prey type contributes to the total diet. Some of the food types contribute a fairly constant proportion to the overall diet (small mammals in all seasons; birds in three out of four, only declining in season 4, autumn), while others show a marked seasonal variation. For instance, invertebrates (largely beetles) contribute less than 1% usually but increase to 5% in summer. Fruits are barely consumed in winter and spring, but become the most important part of the diet in summer and (together with earthworms) in autumn. On the contrary, lagomorphs are the most important element in summer and autumn. Scavenge is most important in spring while less important during other seasons. Earthworms show a peak contribution in winter, spring, and autumn but decline in summer.

Fig. 4.5. shows a more detailed analysis of the relative contribution of each food type to the overall diet split by months. The dotted lines represent the annual means while the bars show the proportion for each month and thus indicate the extent of deviation from each annual mean. Note that the December sample is inadequate for analysis.

Small mammals peak in August and decline in autumn but vary little during the rest of the year. Invertebrates increase during the summer months (June to September) with beetles usually being the most dominant item.

Marked monthly changes are shown by fruits. They increase rapidly from 5% to over 40% of the total diet from July to September. This is mainly due to the ripening of blackberries (Rubus fruticosus) in August and September. However, foxes consume other types of fruits and berries (see Table 4.3) which explains fruit consumption until February. Most birds are eaten in May and June while few are consumed during the winter months. Lagomorphs reach a peak in March and April, decline during late spring and summer and

Table 4.3 Identity of prey found in the droppings of fox and badger faeces in Wytham summarized undeer certain prey types

a) small mammals (latin names according to Corbet and Southern (1977))

rat	Rattus norvegicus
hedgehog	Erinaceus europaeus
mole	Talpa europaea
wood mouse	Apodemus sylvaticus
field vole	Clethrionomys glareolus
grey squirrel	Sciurus carolinensis
shrew	Sorex spec
water shrew	Neomys fodiens
hazel dormouse	Muscardinus avellanarius
house mouse	Mus musculus

b) invertebrates

beetles
snails
yellow underwing
earwig
orthoptera
caterpillar

c) birds

passerines
galliformes
columbiformes
ralliformes

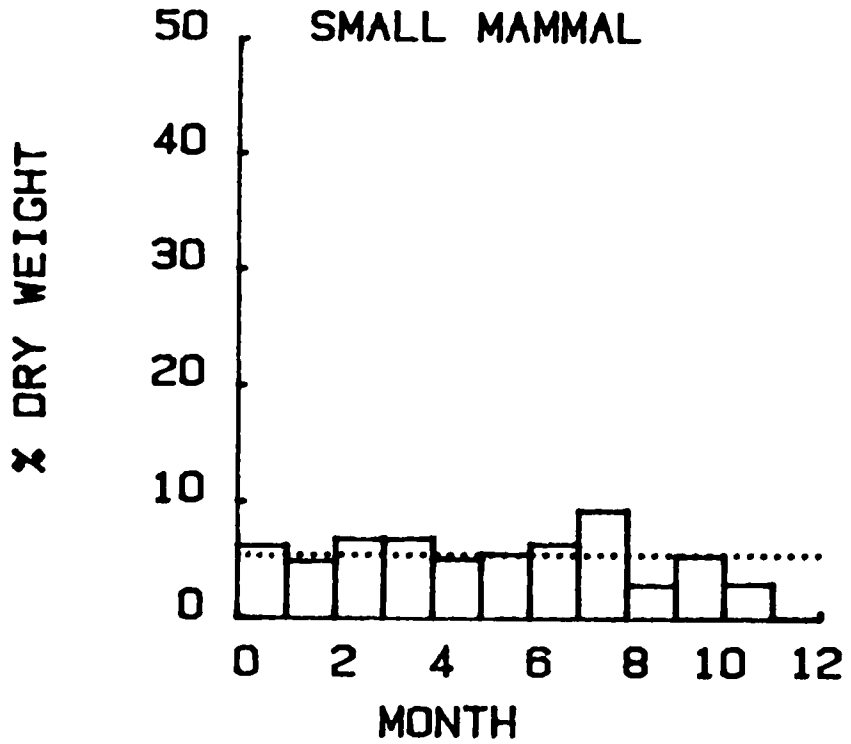
d) fruits and berries (latin names according to Clapham et. al. (1978))

plum	Prunus domestica
cherry	Prunus avium
apple	Malus malus
bramble	Rubus fruticosus
strawberry	Fragaria spec
rosehip	Rosa spec
hawthorn	Crataegus monogyna
spindleberry	Euonymus europaeus
sloe	Prunus spinosa
elderberry	Sambucus nigra
gooseberry	Ribes uva-crispa
blackcurrant	Ribes nigrum

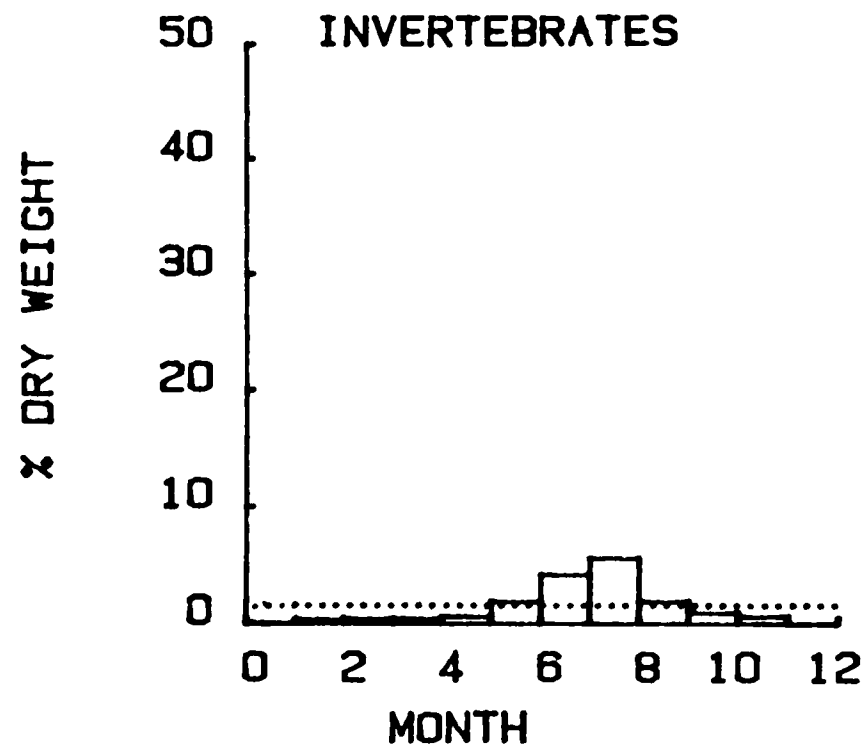
Fig. 4.5. Monthly changes in the diet of Wytham's foxes as determined by estimated dry weight.

4-5

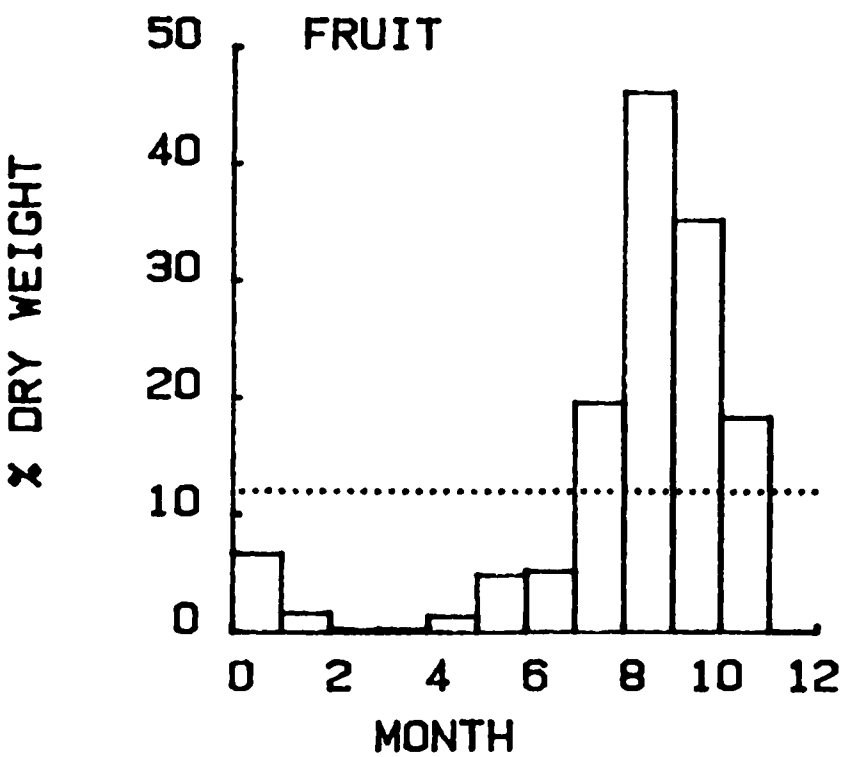
a.


SMALL MAMMAL
% DRY WEIGHT
50
40
30
20
10
0
0 2 4 6 8 10 12
MONTH

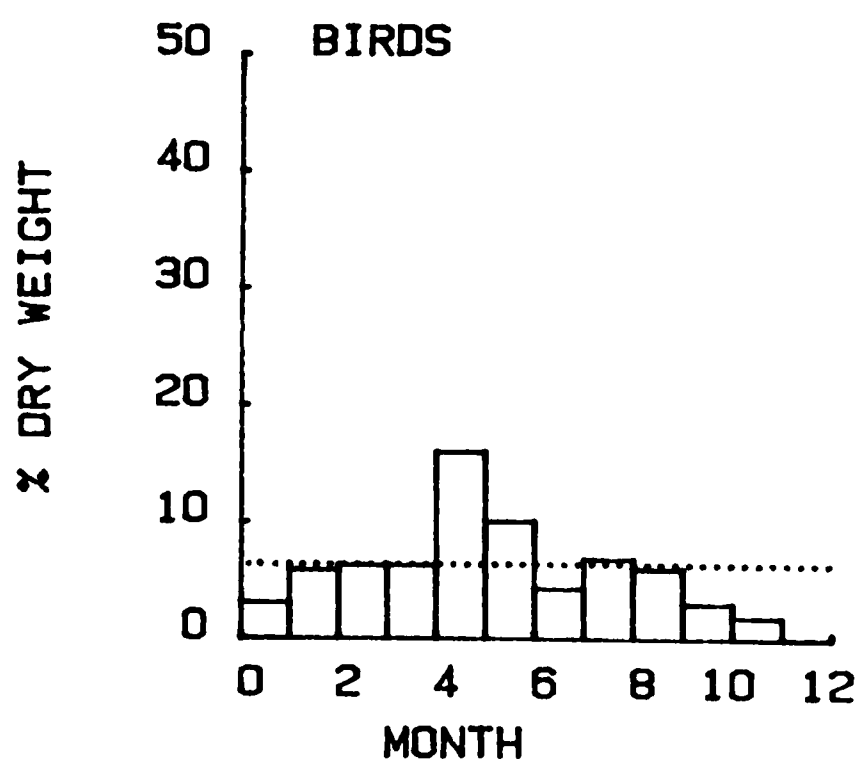
b.


INVERTEBRATES
% DRY WEIGHT
50
40
30
20
10
0
0 2 4 6 8 10 12
MONTH

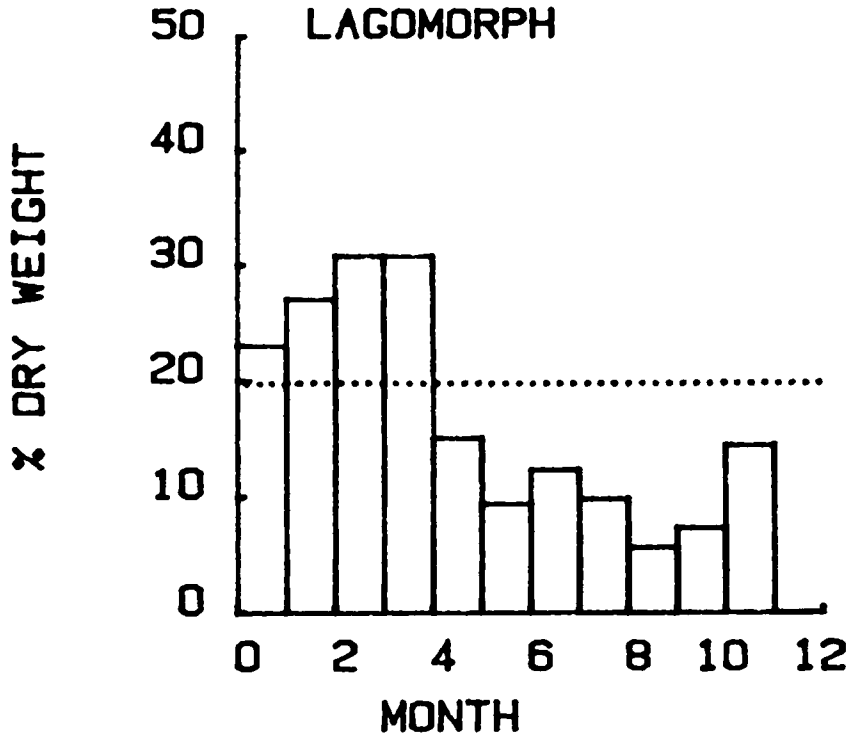
c.


FRUIT
% DRY WEIGHT
50
40
30
20
10
0
0 2 4 6 8 10 12
MONTH

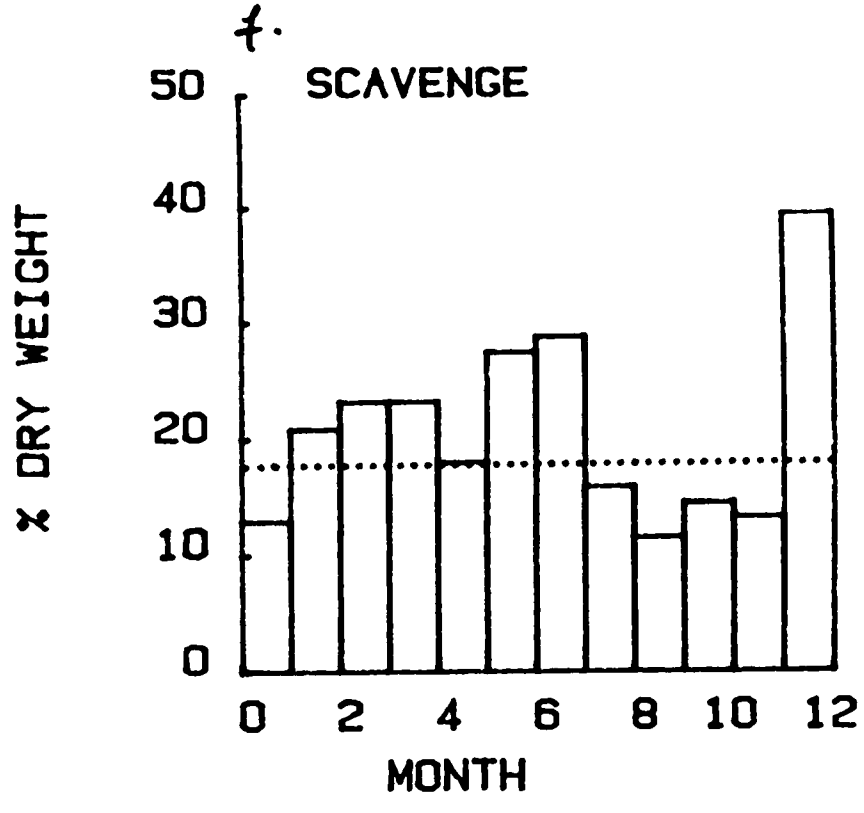
d.


BIRDS
% DRY WEIGHT
50
40
30
20
10
0
0 2 4 6 8 10 12
MONTH

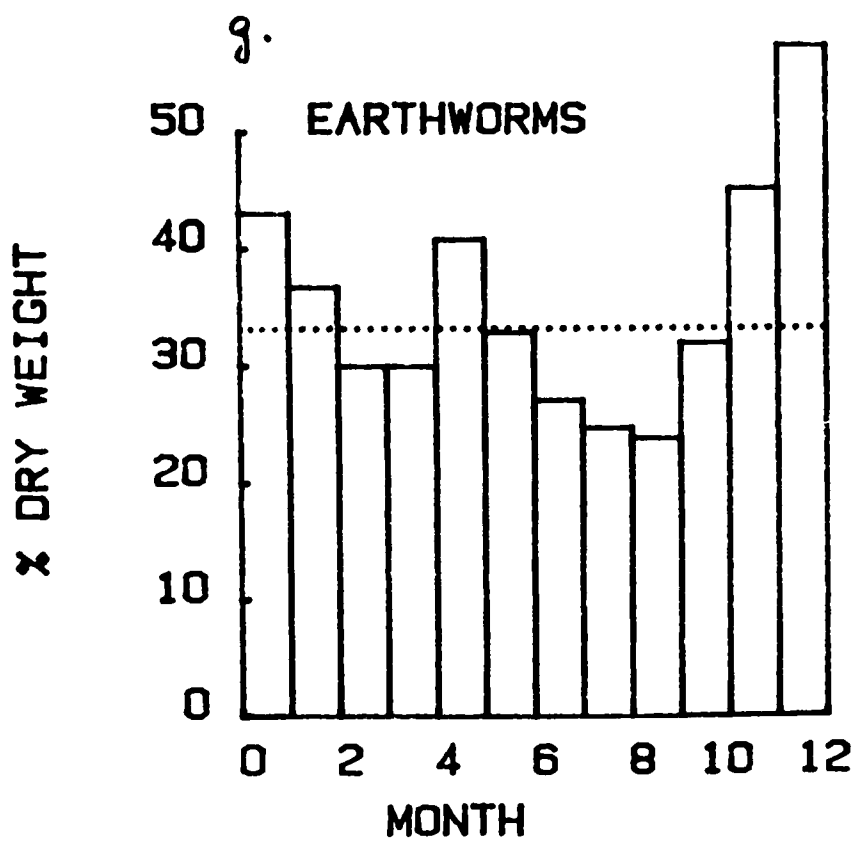
e.


LAGOMORPH
% DRY WEIGHT
50
40
30
20
10
0
0 2 4 6 8 10 12
MONTH

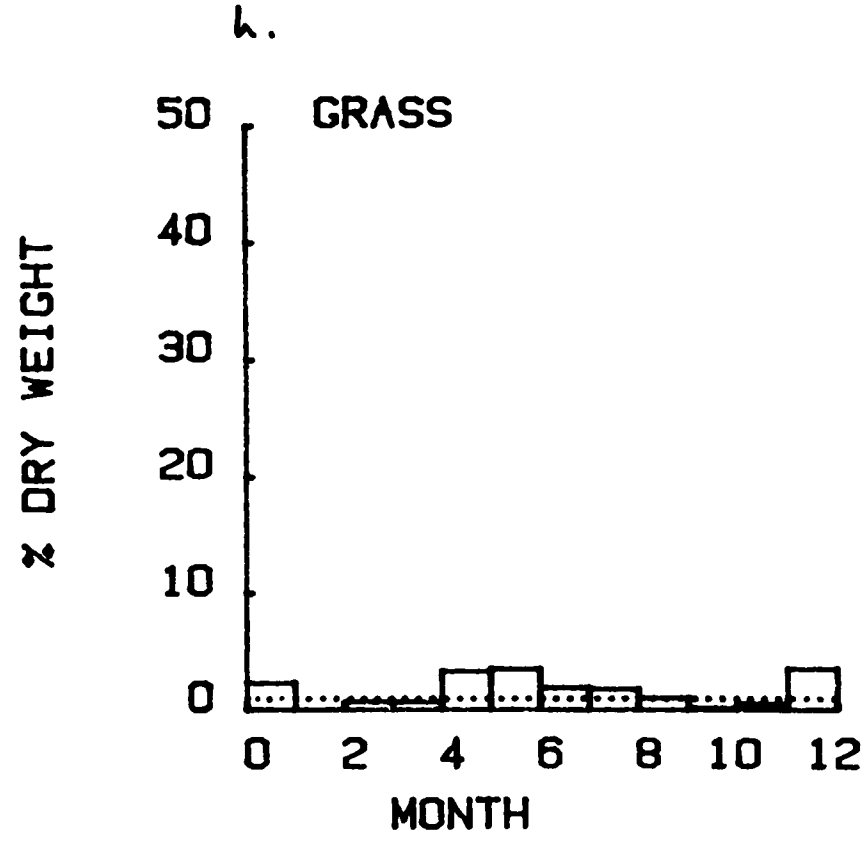
f.


SCAVENGE
% DRY WEIGHT
50
40
30
20
10
0
0 2 4 6 8 10 12
MONTH

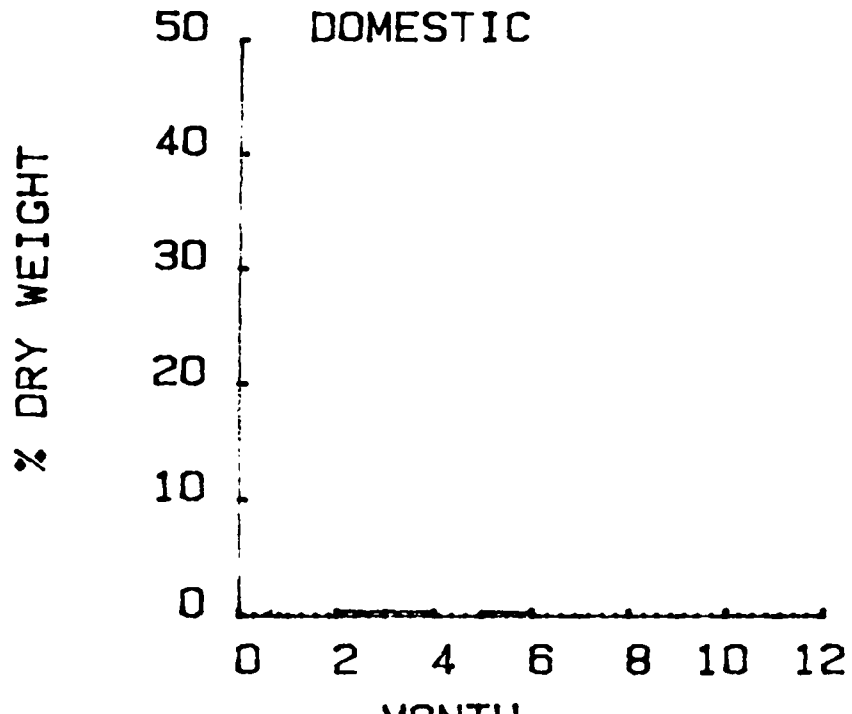
g.


EARTHWORMS
% DRY WEIGHT
50
40
30
20
10
0
0 2 4 6 8 10 12
MONTH

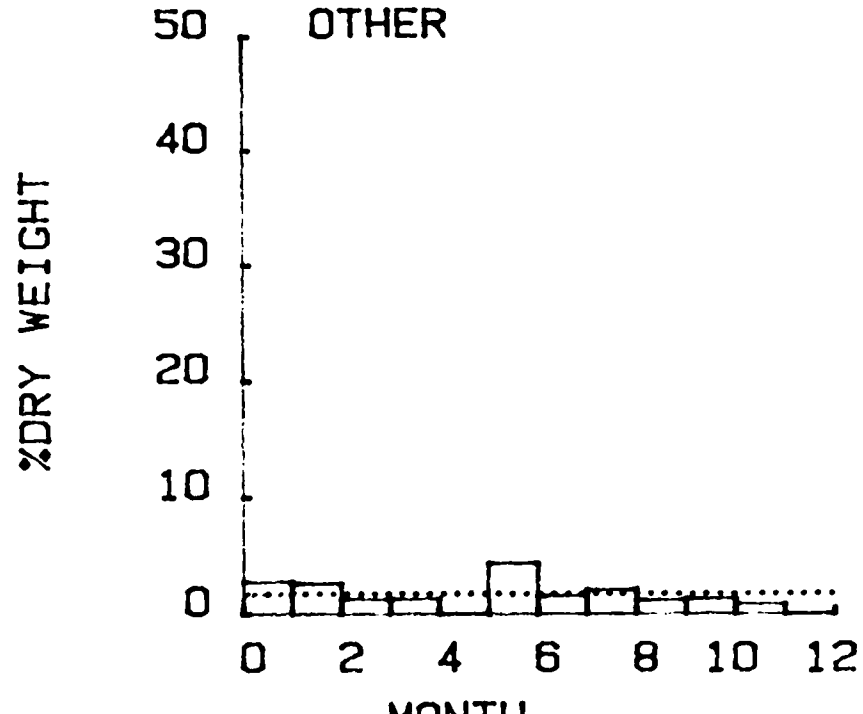
h.


GRASS
% DRY WEIGHT
50
40
30
20
10
0
0 2 4 6 8 10 12
MONTH

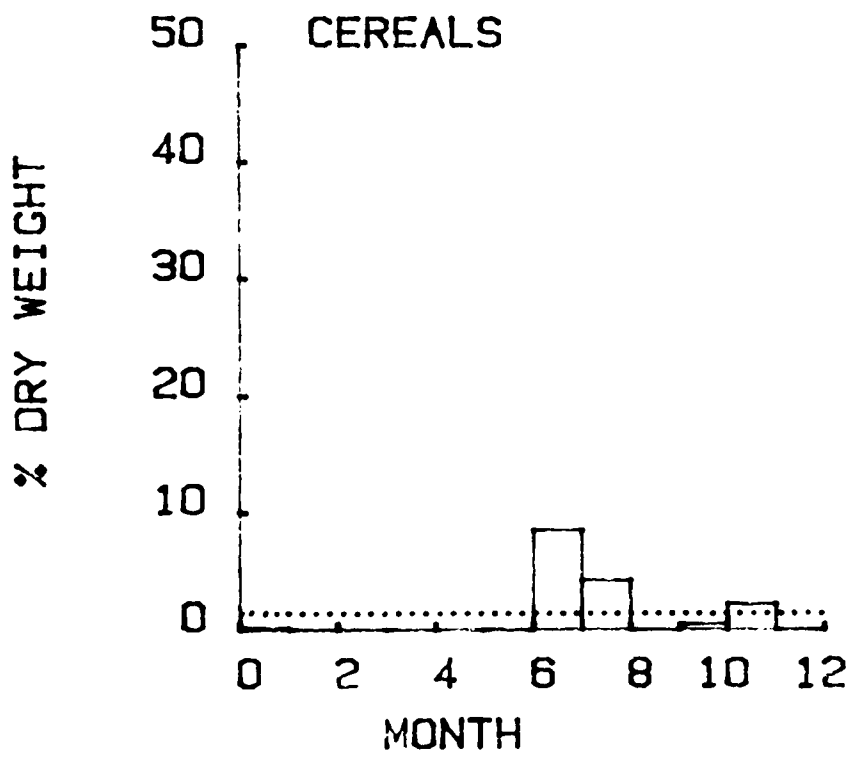
i.


DOMESTIC
% DRY WEIGHT
50
40
30
20
10
0
0 2 4 6 8 10 12
MONTH

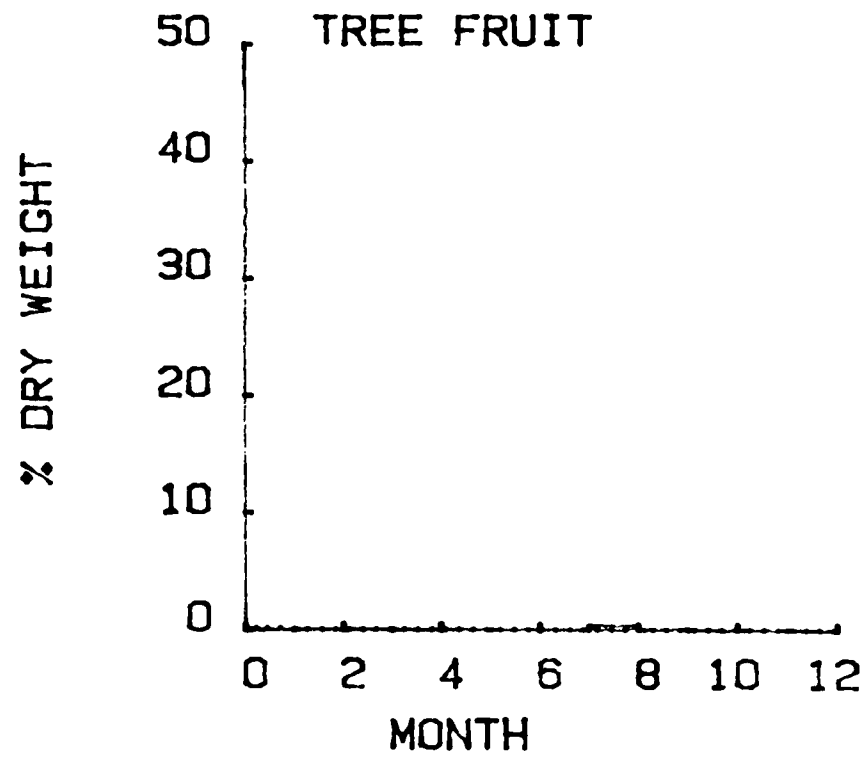
j.


OTHER
%DRY WEIGHT
50
40
30
20
10
0
0 2 4 6 8 10 12
MONTH

k.


CEREALS
% DRY WEIGHT
50
40
30
20
10
0
0 2 4 6 8 10 12
MONTH

l.


TREE FRUIT
% DRY WEIGHT
50
40
30
20
10
0
0 2 4 6 8 10 12
MONTH

increase once more in autumn and winter. Scavenge increases steadily from late winter to summer but features less prominently in late summer and autumn. Earthworms show one peak in May and a second one in late autumn and winter but decrease during summer. The contribution by the other five categories is negligible. Cereals show a peak in July and August and also occur in November, perhaps stemming from the gut contents of birds caught by the foxes.

As Table 4.4 shows, the differences between seasons as well as months are highly significant.

4.2.3.3. Variation in the diet of different ranges

4.2.3.3.1. General diet composition of ranges

As it was not possible to predict the spatial distribution of ranges in advance, so in retrospect the sampling effort appears to be distributed quite unevenly between the ranges (Table 4.1). After the filtering procedure where all droppings from zones of overlap were excluded, 1195 droppings could be used to analyse possible differences in diet composition between ranges. However, of the 10 group ranges recognized (see Chapter 5), only five ranges had reasonable sample sizes (Table 4.1).

Fig. 4.6 shows the overall composition of the diet of foxes occupying the five ranges for which seasonal analysis could be performed. From the group of seven important prey categories the only significant differences were found for small mammals, scavenge and lagomorphs with lagomorphs varying between 14 and 45% in their contribution to the total diet. The variation in fruits and earthworms appears to be considerable but nevertheless is not statistically significant (Table 4.5). In the food categories 8 to 12 there is little variation.

Table 4.4 Kruskal-Wallis one-way analysis of variance on temporal variation in the composition of the diet of Wytham's foxes

a) differences between seasons

Seasons were defined as in Table 4.1 (n = 2026, df = 3)

Prey category	H (adjusted for ties)	significance (α)
small mammals	13.82	< 0.005
invertebrates	390.6	< 0.001
fruits	468.9	< 0.001
birds	19.29	< 0.001
scavenge	26.48	< 0.001
earthworms	17.83	< 0.001

b) differences between months

All months except December (n = 2021, df = 10)

Prey category	H (adjusted for ties)	significance (α)
small mammals	27.04	< 0.005
invertebrates	413.0	< 0.001
fruits	554.9	< 0.001
birds	36.50	< 0.001
lagomorphs	154.1	< 0.001
scavenge	49.94	< 0.001
earthworms	33.44	< 0.001

Table 4.5 Kruskal-Wallis one-way analysis of variance on variation between ranges in the composition of the diet of Wytham's foxes. Only ranges with reasonable sample sizes (see text) were admitted (Ranges 1,5,6,7,11)

a) differences between ranges

Prey type	H (adj. for ties)	significance (p)
small mammals	10.12	< 0.05
invertebrates	8.51	ns
fruits	8.22	ns
birds	8.43	ns
lagomorphs	63.72	< 0.001
scavenge	12.96	< 0.025
earthworms	8.59	ns

b) differences between ranges for each season; only significant results are listed

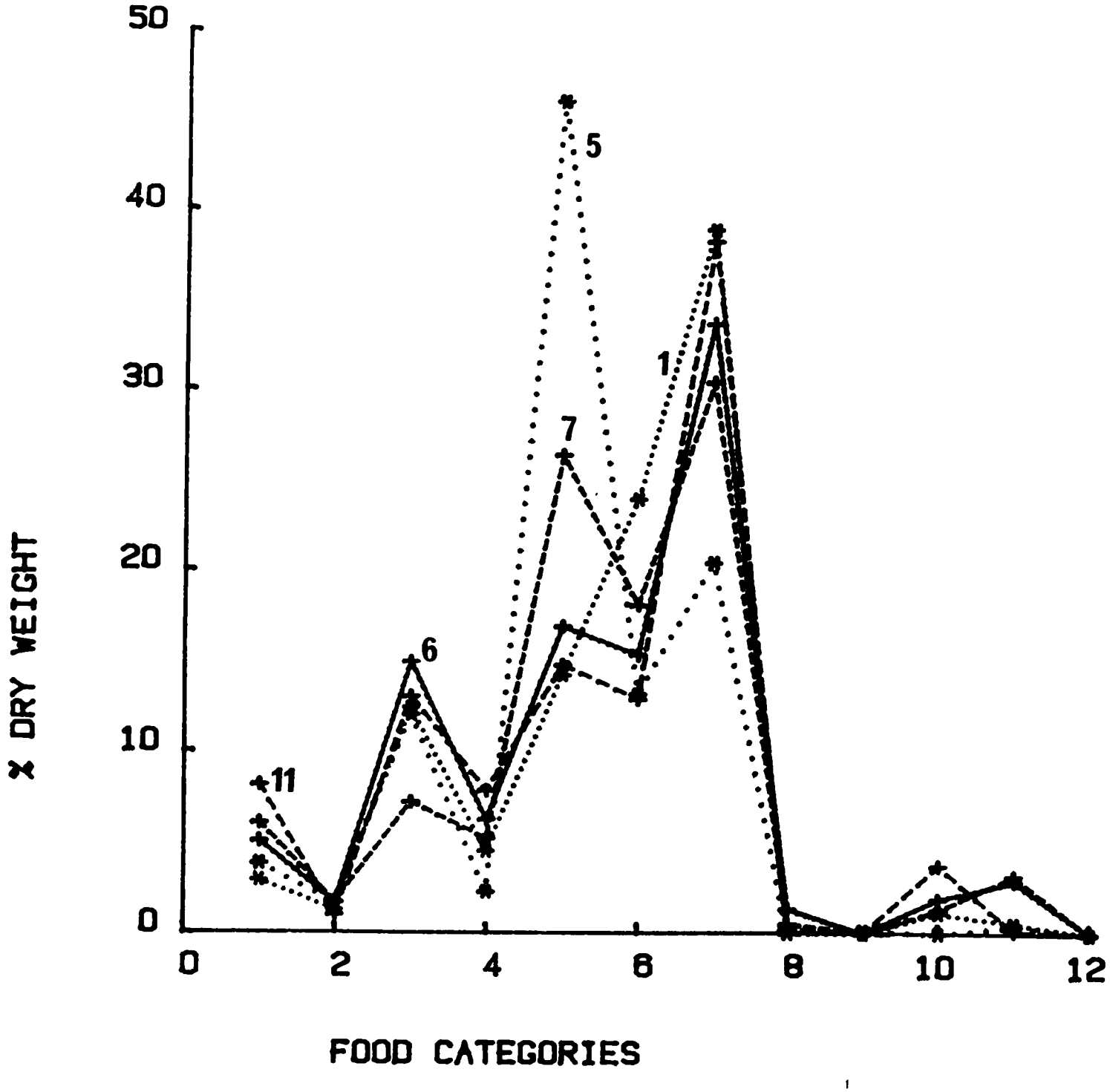
Season	Prey type	H (adj.)	significance
Winter	lagomorphs	9.94	< 0.05
Spring	small mammals	9.51	< 0.05
	invertebrates	10.61	< 0.05
	lagomorphs	29.51	< 0.001
	scavenge	10.33	< 0.05
Summer	fruits	10.76	< 0.05
	scavenge	14.84	< 0.01
Autumn	invertebrates	9.84	< 0.05
	fruits	11.90	< 0.025
	lagomorphs	21.23	< 0.001

c) differences between seasons for each range; only significant results are listed

Range	Prey type	H (adj.)	significance (α)
1	invertebrates	30.44	< 0.001
	fruits	24.42	< 0.001
5	invertebrates	24.19	< 0.001
	fruits	34.13	< 0.001
6	small mammals	9.80	< 0.025
	invertebrates	148.2	< 0.001
	fruits	156.8	< 0.001
	lagomorphs	53.87	< 0.001
7	invertebrates	25.89	< 0.001
	fruits	156.8	< 0.001
	birds	9.91	< 0.025
	lagomorphs	10.98	< 0.025
11	invertebrates	15.96	< 0.005
	fruits	28.74	< 0.001

Fig. 4.6. Differences in the diet of five fox groups as determined by estimated dry weight. Food categories plotted in identical sequence to Fig. 4.5. and Table 4.2

4-6



1 - HOME FARM
5 - WOODEND
6 - SINGING WAY
7 - HILL END CAMP
11- MARLEY

A posteriori multiple comparison tests were carried out for the three food types with significant variation to investigate which ranges differed from which others. The results are summarized in Table 4.6.

From small mammals, only three pairs of ranges showed significant differences: Range 11 (Marley Wood) consumed more small mammals than Ranges 1 (Home Farm) and 5 (Woodend Farm) and Range 6 (Singing Way) consumed more than 5 (Woodend Farm). Looking at the results for scavenge, Range 1 (Home Farm) had by far the highest intake of scavenge, significantly higher than any of the other ranges while none of the other ranges were different from each other.

Lagomorphs showed the most consistent variation between ranges. Range 5 (Woodend Farm) had a higher proportion of lagomorphs in its diet than all other ranges except the neighbouring Range 7 (Hill End Camp) which was different from the other three ranges as well. These three ranges (No.1 (Home Farm), No. 6 (Singing Way), and No. 11 (Marley Wood)) were similar in lagomorph consumption.

The results of the multiple comparison tests indicate some interesting differences for prey categories: for two food categories (scavenge and lagomorphs), one and two ranges respectively had a much higher proportion of the prey type in question and thus dominated the others. For the third prey category (small mammals) variation was generally little and only sufficient for three pairs to yield significant differences. Two ranges emerge that are dominated by one prey item: Range 5 (Woodend Farm) and Range 1 (Home Farm) while the other three ranges seem to have a more even share of the various prey types.

Differences in the diet of the five ranges are graphically illustrated in Fig. 4.7 for four prey types which also shows their spatial relationship to each other (Fig. 4.7a). For both lagomorphs and earthworms there exist spatial gradients running in opposite directions to each other. The peak of

Table 4.6 A posteriori multiple comparison tests for differences between pairs of ranges. Only food types considered that showed significant differences in a Kruskal-Wallis analysis of variance. Only pairs with significant differences listed. In this and the following tables with the results of a posterior multiple comparison tests the critical value displayed is for $\alpha = 0.05$

Part I: general differences

a) small mammals

Range with high prey value	Range with low prey value	actual value	Critical	significance (α)
11 Marley	1 Homefarm	49.3	47.66	< 0.05
6 Singing Way	5 Woodend	38.2	31.53	< 0.05
11 Marley	5 Woodend	61.2	40.33	< 0.01

b) scavenge

1 Homefarm	5 Woodend	99.6	57.23	< 0.001
1 Homefarm	6 Singing Way	80.8	49.05	< 0.1
1 Homefarm	7 HEC	79.6	56.7	< 0.01
1 Homefarm	11 Marley	82.3	57.75	< 0.01

c) lagomorphs

5 Woodend	1 Homefarm	190.3	68.31	< 0.001
7 HEC	1 Homefarm	75.4	66.68	< 0.05
5 Woodend	6 Singing Way	173.5	44.93	< 0.001
5 Woodend	7 HEC	114.8	56.01	< 0.001
5 Woodend	11 Marley	191.9	57.48	< 0.001
7 HEC	6 Singing Way	58.7	43.98	< 0.01
7 HEC	11 Marley	77.1	56.74	< 0.01

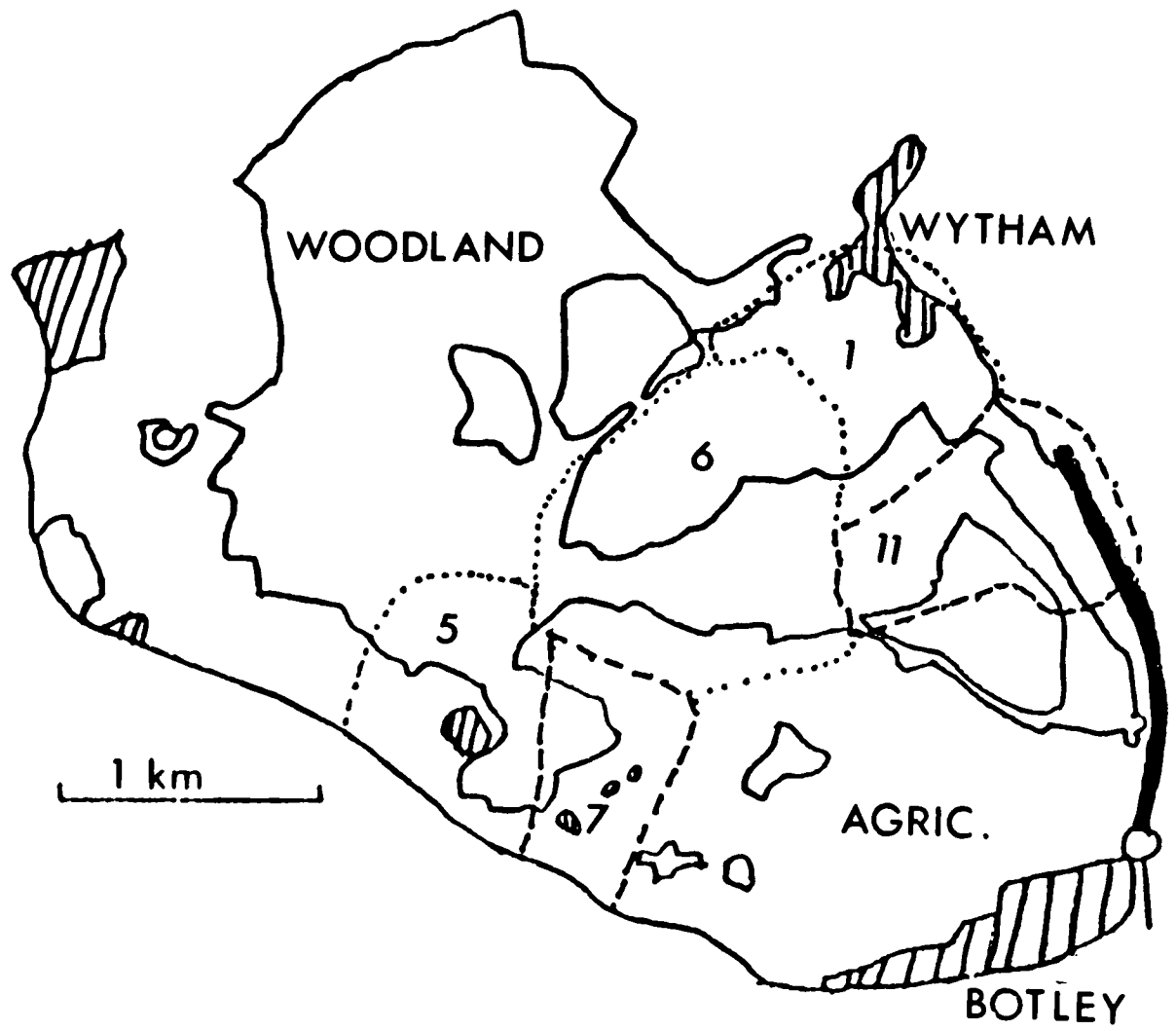
Fig. 4.7. Differences in the diet of five fox groups, as determined by estimated dry weight.

a. Map with main woodland and field boundaries and approximate range boundaries of fox groups.

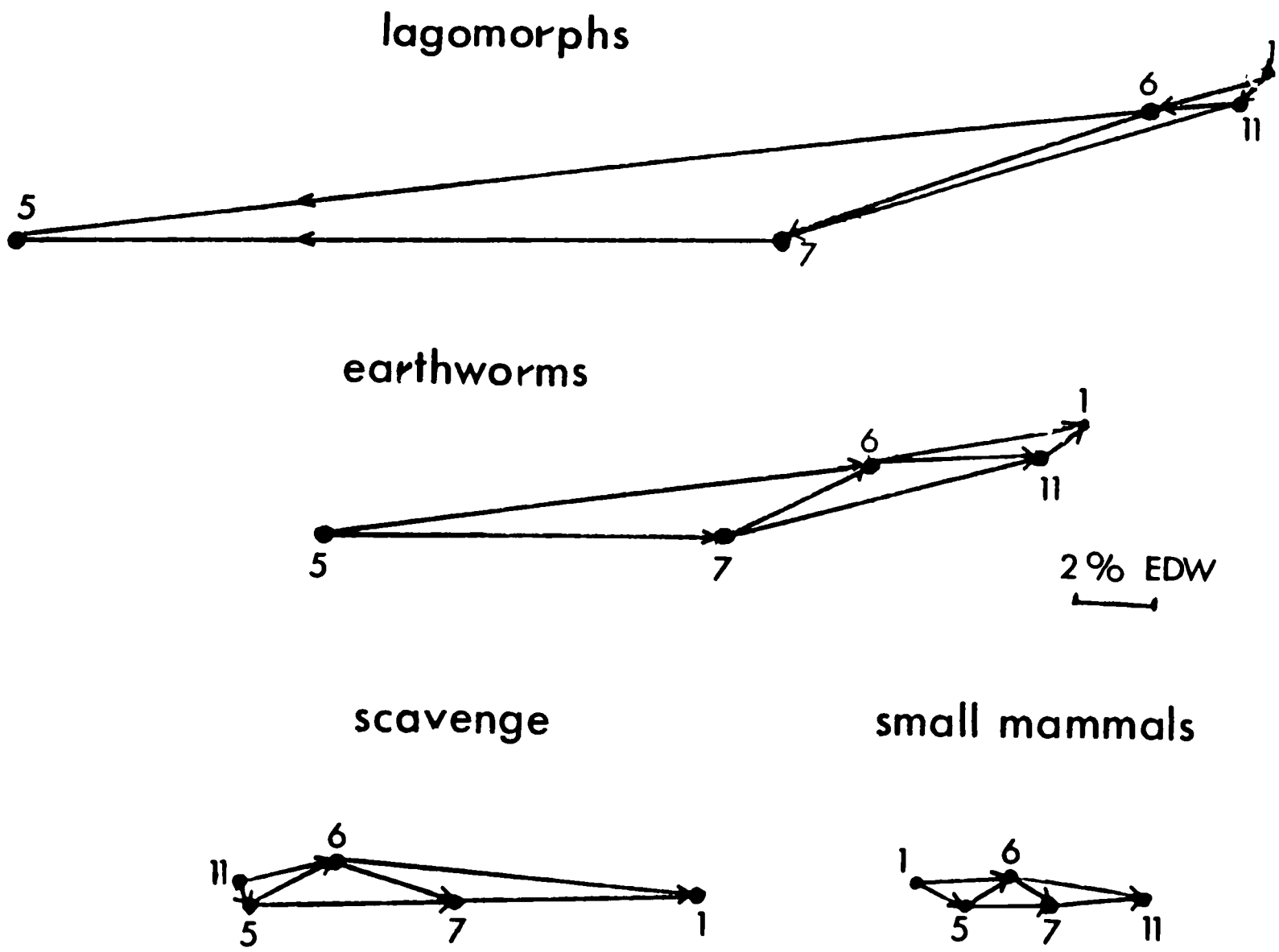
b. Differences in consumption of main prey items. Numbers are group numbers, arrows indicate an increase in the consumption of a particular item. Arrows drawn to scale.

Fig. 4.7

a


WOODLAND
WYTHAM
1
6
11
5
7
Q
1 km
AGRIC.
BOTLEY

b


lagomorphs
6
11
5
7
earthworms
1
6
11
5
7
2% EDW
scavenge
11
6
5
7
1
small mammals
1
6
5
7
11

earthworm consumption is in Range 1 (north east) corresponding to the lowest consumption of lagomorphs which reaches its peak in the southwest. Both scavenge and small mammal consumption show a non-uniform spatial trend: the three Ranges 5,6, and 7 have an intermediate consumption while Ranges 1 and 11 show an extreme high or low consumption. A high proportion of scavenging in Range 1 corresponds to the lowest proportion in small mammals; the opposite is true for Range 11.

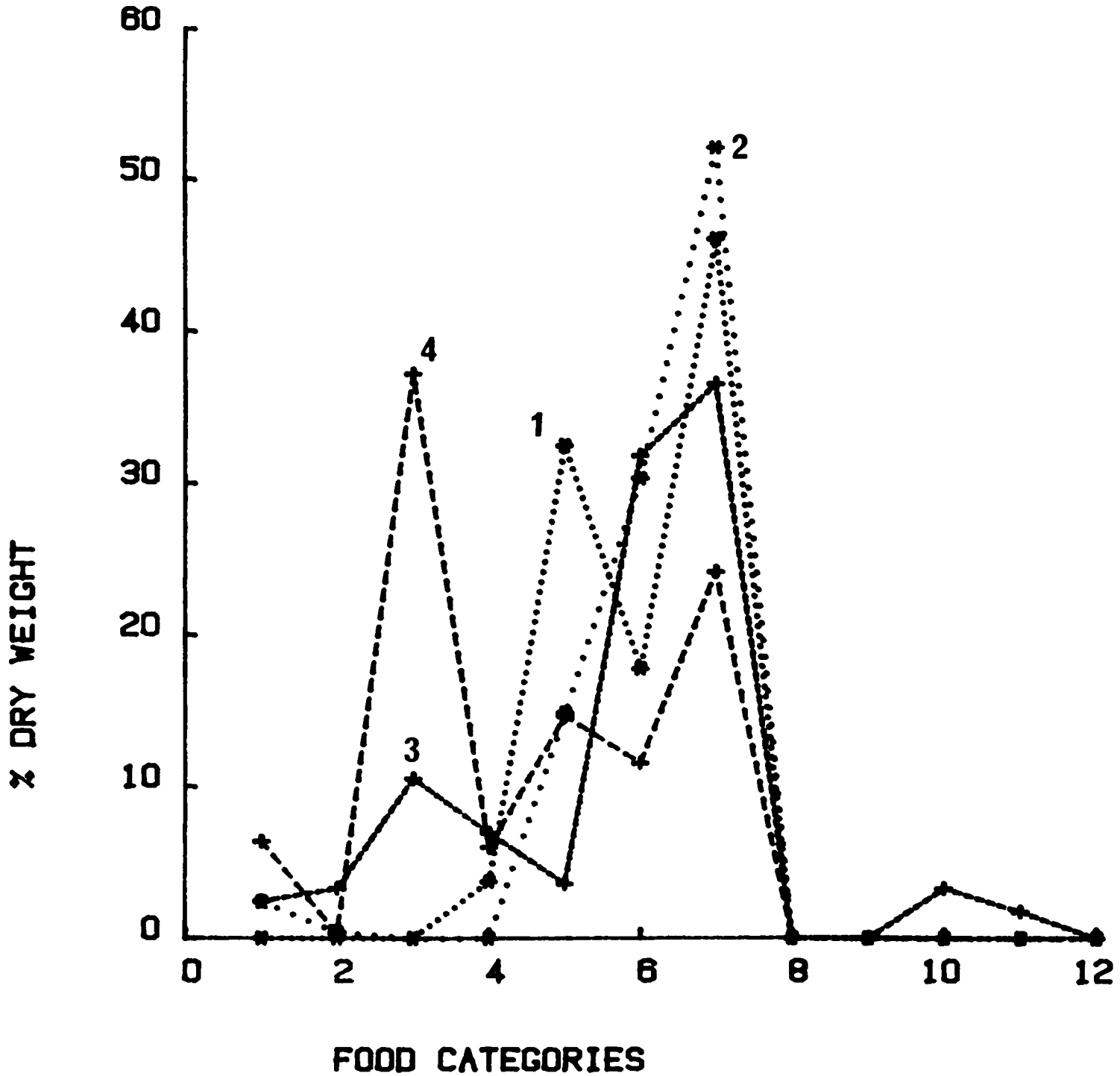
4.2.3.3.2. Seasonal variation in the diet of ranges

There are at least three different ways of looking at seasonal effects on the composition of the diet of foxes in different ranges. One way is to follow each individual range through the various seasons and investigate changes in the diet composition. This is depicted for Ranges 1,5,6,7, and 11 in Fig. 4.8 to 4.12 and the corresponding statistical analysis can be found in Table 4.5c. The second way is to look at each season in turn and to compare the diet of all ranges within that season. This approach indicates how much variation there is between single ranges for one season and gives an impression of how well the seasonal trends found for the entire study area (section 4.2.4.2) correspond to those in individual ranges. For this second presentation, the relevant statistics are listed in Table 4.5b and 4.7. The third way is to look at the degree of synchrony in the composition of the diet of ranges in their temporal fluctuations. The results of this analysis can be found in Table 4.12a.

Changes within individual territories Fig 4.8 to 4.12 show the seasonal distribution of prey categories for each of the five ranges. The results are presented first for each range and then summarized for each food type in turn. Significant differences indicate that the means of estimated dry weight of a given food category vary more than can be explained by chance

Fig. 4.8–4.12. Seasonal changes in the diet of five fox groups. Diet items plotted in sequence identical to Fig. 4.5 and Table 4.2.

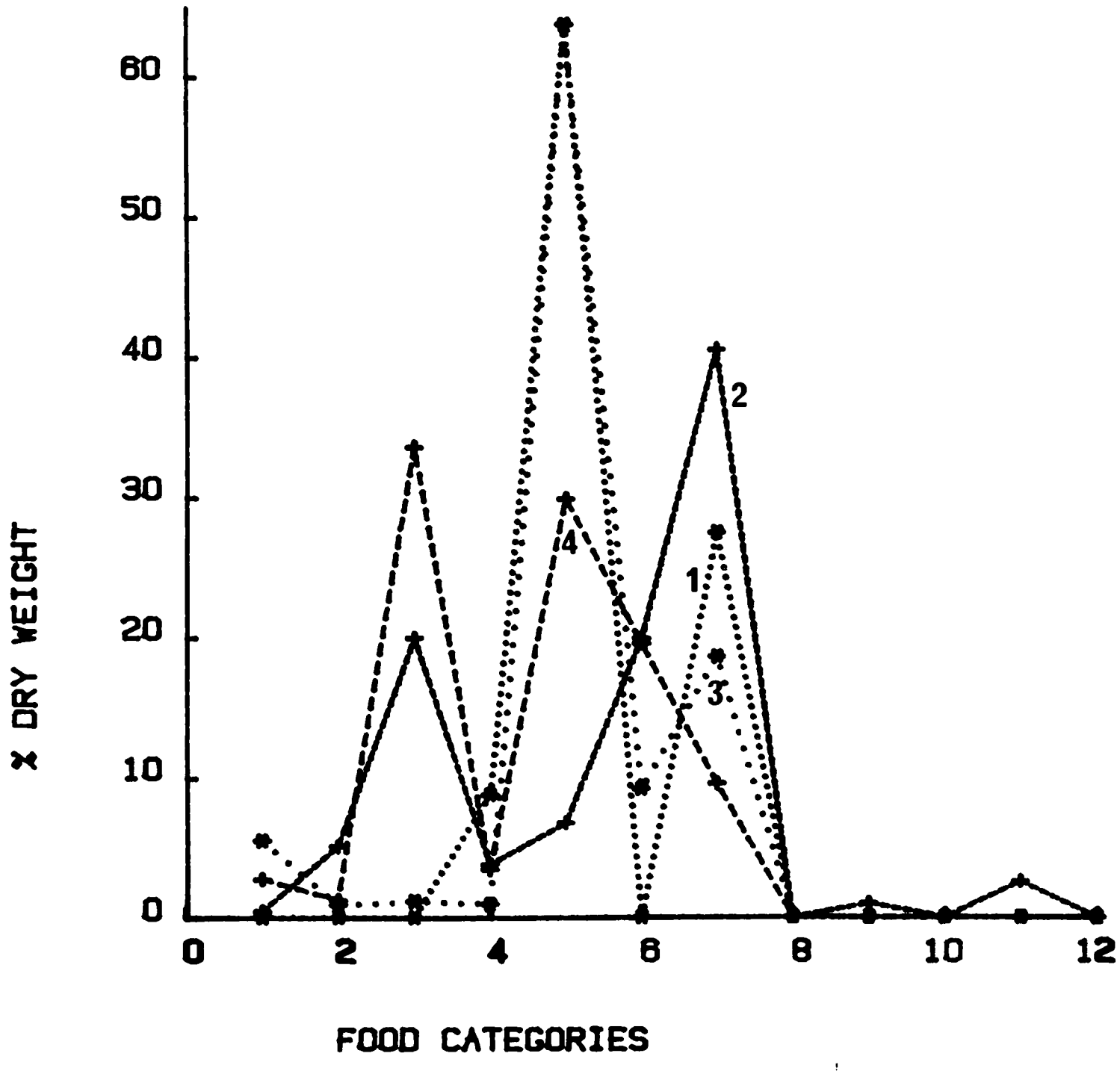
Fig. 4.8: group 1 HOMEFARM
4.9: group 5 WOODEND
4.10: group 6 SINGING WAY
4.11: group 7 HILL END CAMP
4.12: group 11 MARLEY



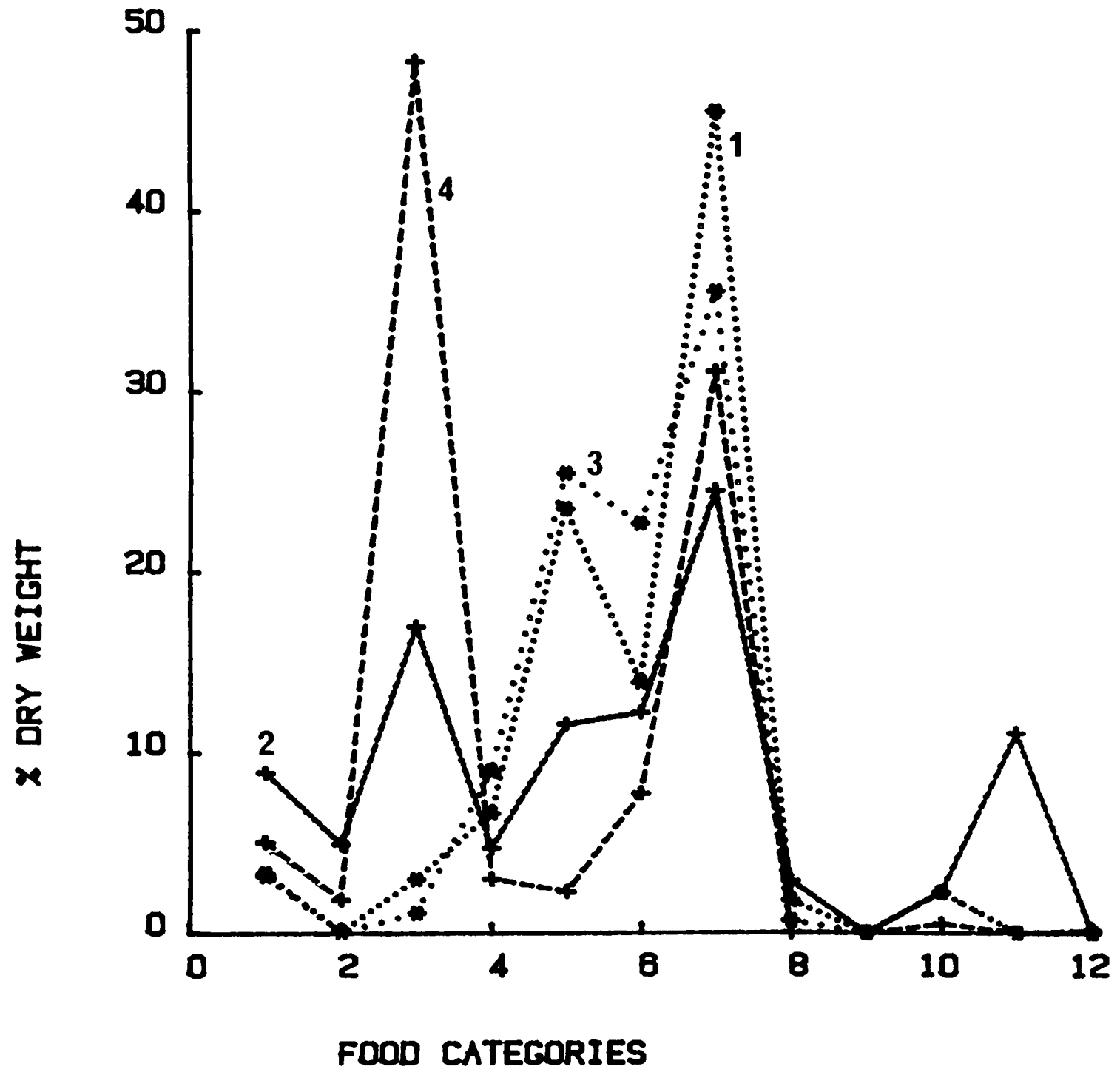
1 : DECEMBER - FEBRUARY
2 : MARCH - MAY
3 : JUNE - AUGUST
4 : SEPTEMBER - NOVEMBER

F 1

4-9

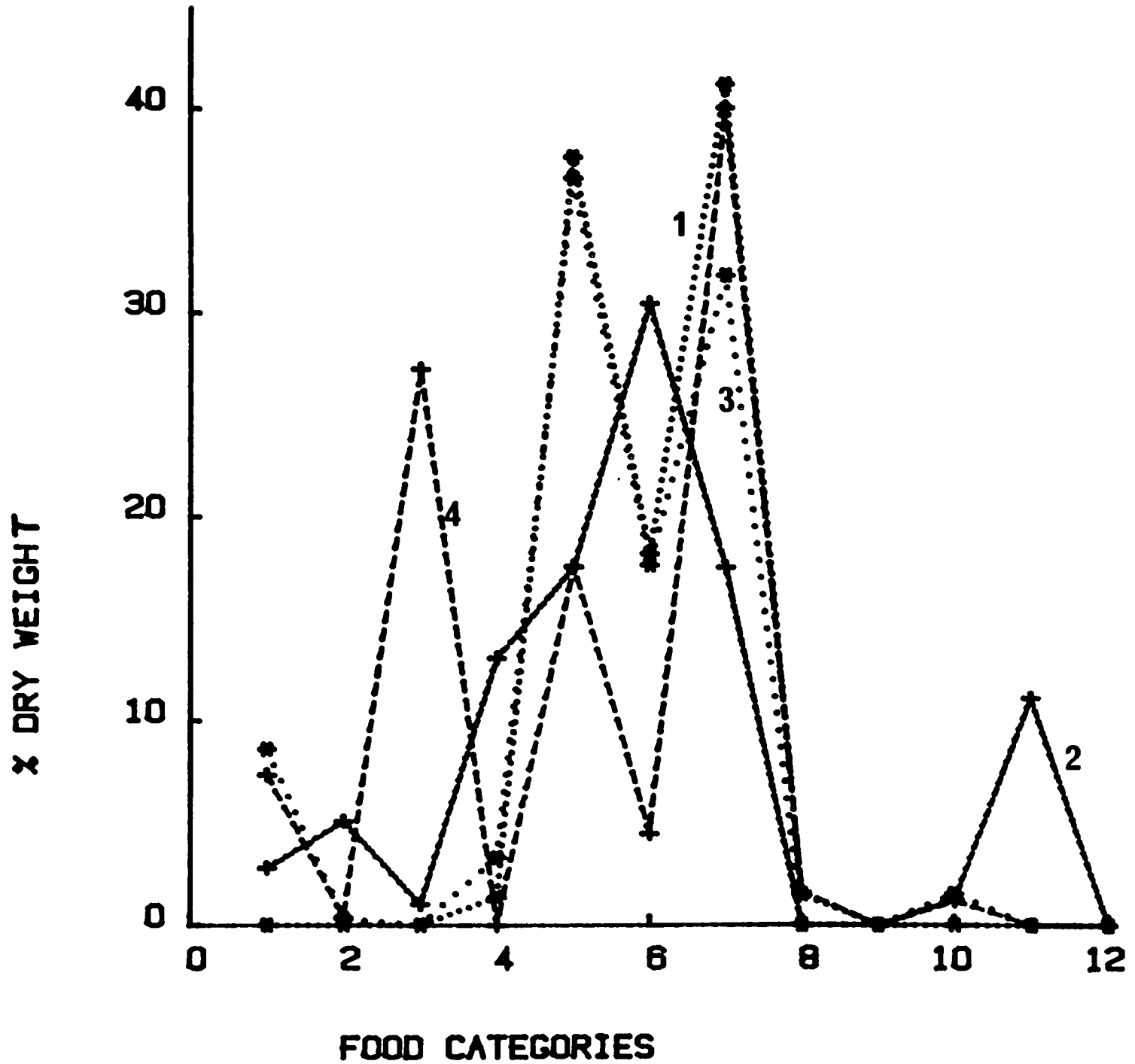

1 : DECEMBER - FEBRUARY
2 : MARCH - MAY
3 : JUNE - AUGUST
4 : SEPTEMBER - NOVEMBER
% DRY WEIGHT
0
10
20
30
40
50
60
0
2
4
6
8
10
12
FOOD CATEGORIES

F 5



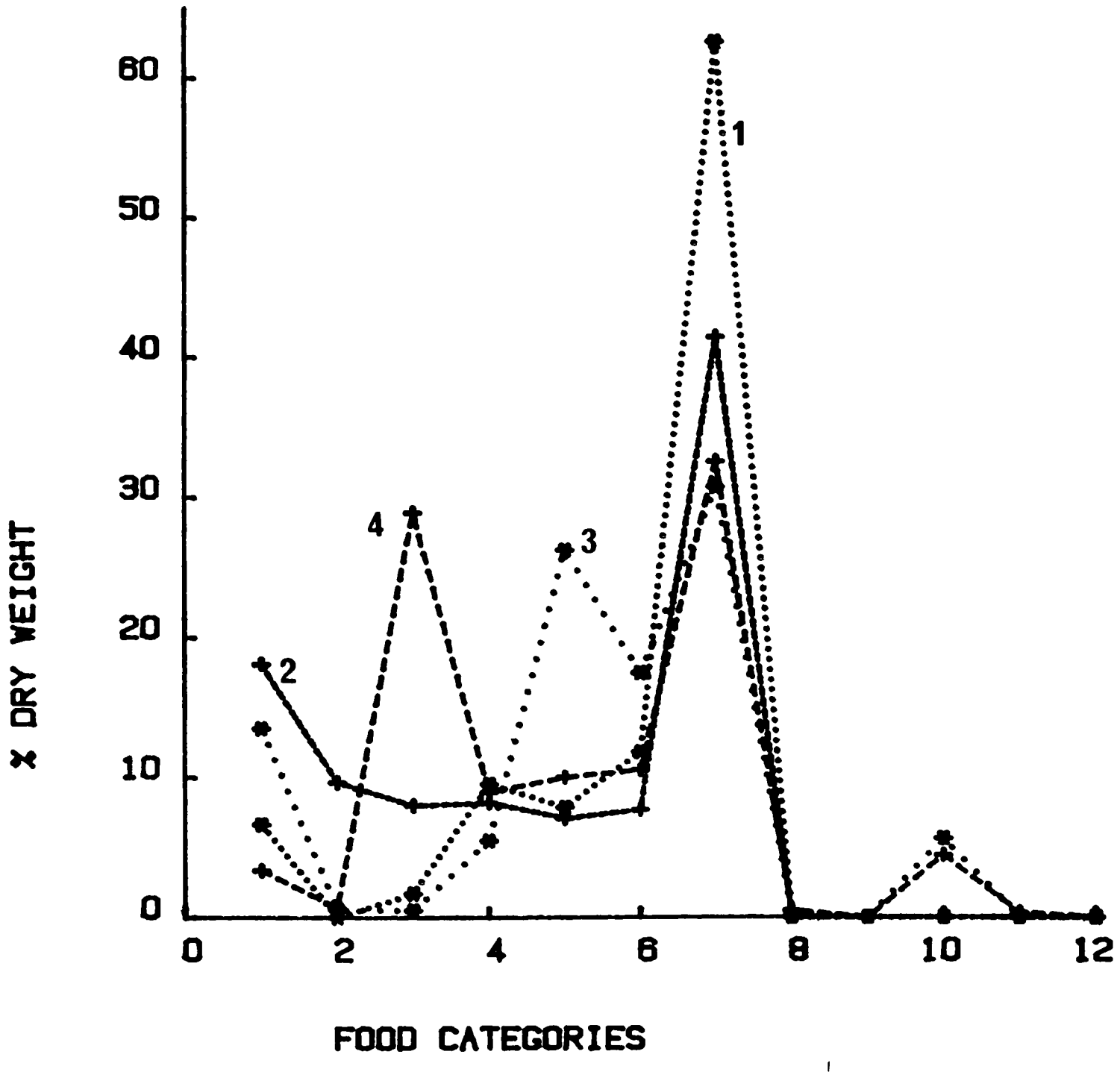
1 : DECEMBER - FEBRUARY
2 : MARCH - MAY
3 : JUNE - AUGUST
4 : SEPTEMBER - NOVEMBER

F 6



1 : DECEMBER - FEBRUARY
2 : MARCH - MAY
3 : JUNE - AUGUST
4 : SEPTEMBER - NOVEMBER

4-12



1 : DECEMBER - FEBRUARY
2 : MARCH - MAY
3 : JUNE - AUGUST
4 : SEPTEMBER - NOVEMBER

F 11

alone. Usually the food categories with significant seasonal changes are discussed first while categories without such significant changes may not be mentioned specifically.

Range 1 (Home Farm) Only invertebrates and fruits show significant seasonal variation, both being more often consumed during summer and autumn. Although the variation in other prey categories is not statistically significant, it appears that lagomorphs are mostly consumed in winter and least in summer and earthworms mostly in winter and spring.

Range 5 (Woodend) Here, invertebrates, fruits and lagomorphs show significant seasonal changes. Again, invertebrates and fruits are mostly consumed during summer and autumn. Lagomorphs dominate the diet in winter and spring, are little consumed during summer but increase during autumn. Of the food types with no statistically significant changes, scavenge is worth mentioning: practically none is consumed during winter while summer and autumn are equal. Most earthworms are taken in autumn, fewest in summer.

Range 6 (Singing Way) Significant seasonal differences were found for small mammals, invertebrates, fruits, and lagomorphs. This range was the only one with significant seasonal variations in small mammals although it is not the range with the highest proportion of small mammal consumption. They were mainly taken in summer but much less in autumn and very little in winter and spring. The changes in fruits and invertebrates follow the pattern already described for the two previous ranges; so do the changes in lagomorphs with the exception that more lagomorphs were taken in summer than in autumn. Of those prey categories with no significant differences, earthworms were the main prey in three out of four seasons; only fruits had a higher share during autumn. In contrast to other ranges, a high proportion of cereals was eaten in summer.

Range 7 (Hill End Camp) Significant seasonal changes occur in

Table 4.7 A posteriori multiple comparison tests for differences between pairs of ranges. Only food types considered that yielded significant differences in Kruskal-Wallis one-way analysis of variance.

Part II: comparisons for each season separately. Only pairs of ranges with significant differences are listed

Range with high prey value	R. with low prey value	actual value	critical value	significance
a) small mammals	SEASON: spring			
11 Marley	1 Homefarm	33.4	30.49	< 0.05
11 Marley	5 Woodend	28.6	21.11	< 0.01
11 Marley	6 Singing Way	23.9	19.01	< 0.02
b) invertebrates	SEASON: spring			
1 Homefarm	6 Singing Way	26.9	23.15	< 0.05
5 Woodend	6 Singing Way	15.4	13.48	< 0.05
11 Marley	6 Singing Way	19.4	16.29	< 0.02
	SEASON: autumn			
6 Singing Way	1 Homefarm	26.8	24.96	< 0.05
6 Singing Way	7 HillEnd Camp	24.8	20.63	< 0.02
6 Singing Way	11 Marley	21.0	18.32	< 0.05
c) fruits	SEASON: summer			
5 Woodend	7 Hill End Camp	41.5	27.95	< 0.01
6 Singing Way	7 Hill End Camp	27.3	17.53	< 0.01
6 Singing Way	7 Hill End Camp	35.9	24.21	< 0.01
6 Singing Way	11 Marley	28.5	21.50	< 0.01
d) lagomorphs	SEASON: winter			
5 Woodend	6 Singing Way	33.8	33.69	< 0.05
5 Woodend	11 Marley	54.5	27.14	< 0.01
6 Singing Way	11 Marley	20.7	19.43	< 0.05
	SEASON: Spring			
5 Woodend	1 Homefarm	83.5	45.67	< 0.001
5 Woodend	6 Singing Way	65.3	25.17	< 0.001
5 Woodend	7 Hill End Camp	39.7	33.38	< 0.02
5 Woodend	11 Marley	68.3	33.78	< 0.001

Table 4.7 (Cont.)

		SEASON: autumn			
5	Woodend	6 Singing Way	38.4	16.22	< 0.001
5	Woodend	11 Marley	28.1	17.65	< 0.01
7	Hill End Camp	6 Singing Way	19.9	15.06	< 0.01
e) scavenge		SEASON: spring			
1	Homefarm	5 Woodend	47.8	36.15	< 0.01
1	Homefarm	7 Hill End Camp	40.8	38.37	< 0.05
6	Singing Way	5 Woodend	23.9	19.93	< 0.02
		SEASON: summer			
1	Homefarm	5 Woodend	37.9	33.37	< 0.05
1	Homefarm	6 Singing Way	45.3	23.98	< 0.001

invertebrates, fruits, birds and lagomorphs. This is the only range that showed significant differences for birds. This was due to intensive consumption during summer. Again lagomorphs were mainly taken during winter and spring and less so in summer and autumn. Earthworms constituted the major food type in winter and autumn and were consumed less in summer. There were big changes in the amount of scavenge taken (although not significant): most of it was taken during summer and least taken in autumn.

Range 11 (Marley wood) Only invertebrates and fruits showed significant seasonal changes. This is the range with the fewest significant changes, together with the neighbouring Homefarm range (no.1). Invertebrates and fruits were eaten more in summer and autumn. There seemed to be some seasonal differences in the amount of small mammals consumed. Earthworms dominated the diet in all four seasons.

The following paragraphs summarize the preceding results for each food category:

Small mammals Only one range showed a significant seasonal variation (Range 6). In all five ranges, small mammals usually constituted less than 10% of the seasonal diet with the exception of Range 11 (Marley) where the proportion increased significantly from 6.6% in winter to 13.5% in spring and 18% in summer.

Invertebrates and fruits In all ranges they were mostly consumed during summer and autumn and far less during the remaining seasons. Invertebrates comprised up to 10% of the seasonal diet while fruits reached close to 50% (Range 6).

Birds Only Range 7 (Hill End Camp) showed significant seasonal variation for birds. In all five ranges, birds never exceeded 10% of the seasonal diet except for summer in Range 7.

Lagomorphs Significant seasonal changes were found in Ranges 5, 6 and 7.

In four ranges the greatest seasonal incidence of lagomorphs was during winter and spring. In four ranges they were taken least in summer, only Range 6 during autumn.

Scavenge Despite apparently considerable variation, no significant seasonal variation was found; no consistent seasonal pattern of consumption appears either. In two ranges most scavenge was taken in spring, in three in summer.

Earthworms None of the ranges showed seasonal changes in the consumption of earthworms, which constituted a very important prey category (at least if measured by dry weight). Generally, fewer worms were eaten in summer than in any other season. There was at least one range where in each of winter, spring or autumn earthworms had the highest share of all food categories in the seasonal diet.

Differences between ranges within single seasons Table 4.5b and 4.7 summarize the results of the statistical analyses performed to discern the spatial variation within a season. Within each season, there is at least one prey item for which significant differences exist between ranges. However, the number of prey categories that show significant differences varies from season to season:

Winter	1 prey category
Spring	4 prey categories
Summer	2 prey categories
Autumn	3 prey categories

Thus, seasons with high spatial diversity of diet are followed by seasons with a spatially more uniform consumption of prey types.

Winter Lagomorphs are the only prey type with significant spatial variation. This is a time of peak consumption of lagomorphs.

Spring Four prey categories (small mammals, invertebrates, lagomorphs, and

scavenge) vary in their consumption by different ranges. This is the season with the highest spatial diversification; it is also the season when the cubs are brought up.

Summer Fruits and scavenge show significant spatial variation.

Autumn Invertebrates, fruits, and lagomorphs vary significantly between ranges.

Of the seven prey categories considered, five show significant spatial variation in at least one season, only birds and earthworms are consumed at more or less constant proportions in all ranges throughout the year.

Small mammals The only significant spatial variation was found for spring, not a time of peak consumption of small mammals.

Invertebrates They vary significantly between ranges in spring and autumn, but not during the time of peak consumption (summer).

Fruits They vary between ranges in summer and autumn which are peak seasons of consumption.

Lagomorphs They show the most consistent spatial variation (three seasons out of four), excluding only summer which is a time of low consumption of lagomorphs.

Scavenge Significant spatial variation was found for spring and summer which are times of peak consumption. Here we have the interesting situation that in none of the ranges does the level of scavenging change seasonally (see preceding sections), yet the differences between various ranges change seasonally such that the spatial variation is significant in peak consumption times (spring and summer) but not for the remaining seasons.

Comparing the two most important elements (if measured by dry weight) of the fox diet in Wytham, earthworms and lagomorphs, there are obvious and interesting differences. Considering earthworms, no significant spatial or

temporal variation in the amount consumed could be detected, whether on a general level or for either different temporal or spatial units; in short, earthworms form a consistently important part of the diet. On the other hand, there is a lot of variation in lagomorphs: in general between seasons and ranges, within seasons between ranges and within ranges between seasons.

A posteriori multiple comparison tests were performed to investigate differences between ranges within single seasons (Table 4.7). In five out of ten cases one range with a particularly high score on one prey type dominates all other ranges and is responsible for the significant spatial variation within the particular season and food type. This is on two occasions Range 6 (invertebrates and fruits in autumn) and once each Range 1 (scavenge in summer), Range 5 (lagomorphs in spring) and Range 11 (small mammals in spring). Thus, the results of Table 4.6 where differences between ranges were noted over the entire year are corroborated.

Synchrony of the direction of temporal fluctuations between ranges In addition to asking whether there is spatial variation for a given time unit, one may ask whether the direction of temporal fluctuations is synchronized between ranges. This was tested using Kendall's coefficient of concordance. Results are presented in Table 4.12a. Fox ranges show a significant synchronization for invertebrates, fruits, and lagomorphs. This means that even though significant differences may have been found between ranges at a given time the change in consumption from one season to the next follows the same direction for all ranges.

4.2.4. Fox diet: summary

1. 2030 fox droppings were collected between April 1981 and October 1983 including samples from every month of the year.

2. Lagomorphs and earthworms were the most important consituents of the diet (as measured by dry weight). Lagomorphs occurred less often than earthworms and contributed one half as much estimated dry weight to the total diet as earthworms, but far more if corrected for digestibility and calorific intake. Scavenge and fruits ranked next in importance (scavenge: 20% frequency of occurrence (FO), 18% estimated dry weight (EDW); fruits: 18% FO and 13% EDW), followed by birds (11% FO and 6% EDW), small mammals (13% FO and 5% EDW) and invertebrates (25% FO and 2% EDW).

3. Of the twelve major prey types, five occurred in less than 10% of the samples and constituted only small proportions of the diet.

4. There is marked temporal variation in the proportion of most food types as measured by EDW. Invertebrates, fruits and small mammals show peaks in July, August and July respectively. Birds are consumed preferentially in May and June, lagomorphs in late winter and spring (January until April) and far less during the remaining months. Earthworms show peaks in the diet twice in the year: first, during late spring (May) and second during autumn and winter (November until January) with lower consumption at the end of winter/beginning of spring and in summer. Scavenge is more or less equally consumed between February and April and June and July but far less during autumn. All these changes are highly significant.

5. There is some variation in the composition of the diet of different fox ranges with significant spatial variation in small mammals, lagomorphs, and scavenge. For scavenge and lagomorphs one and two ranges respectively had a much higher share of these prey types than the other ranges. Usually, the number of significantly different pairs of ranges were small in comparison

with the total number of pairs. Only for lagomorphs were more pairs significantly different than not. Variation in the diet is spread widely but quite unequally amongst ranges.

6. Within each range, some prey types usually varied greatly between seasons while others did not. Fruits and invertebrates were the only prey categories that showed significant temporal variation in all ranges while scavenge and earthworms did not show any at all. The variation in the three other main prey categories was for most of the ranges significant (lagomorphs) or insignificant (small mammals, birds). Fruits, invertebrates and lagomorphs invariably showed the same pattern of peak consumption in different ranges (summer and late winter/spring, respectively), ie. the ranges were synchronized. No pattern emerged for scavenge. Although changes were not significant for earthworms, there was some variation with winter, sping and autumn having at least one range with its peak in that particular season. Summer was the season when fewer worms were eaten than at any other time of the year. Thus variation was similar in direction in some prey categories but highly different in magnitude for different ranges.

7. There is considerable variation between seasons in the amount of variation between ranges. No seasonal differences were found between ranges for the consumption of birds and earthworms. A season with high spatial diversification in diet is followed by a season with a low one (spring/summer, autumn/winter). Lagomorphs show the most consistent spatial variation in three out of four seasons. Scavenge varies in spring and summer, fruits in summer and autumn and invertebrates in spring and autumn, small mammals in spring only. Looking at pairs of ranges for each prey type with significant spatial variation it turns out that in five out of ten cases one range with a disproportionate prey value dominates all other

ranges and is responsible for the significant spatial variation. In all cases the number of pairs that differ significantly is less than the number of pairs that does not.

4.2.5. Comparison with other studies

The results of the preceding section will initially be contrasted with three other studies from Oxford areas before a comparison is made with studies from areas outside Oxford.

Newdick (1983) investigated the diet of foxes in the City of Oxford. Scavenge was the most important diet component with 47% frequency of occurrence and 37% estimated dry weight, followed by earthworms (38% and 25%). Other important food categories were small mammals (16% and 7%), birds (17% and 7%) amd lagomorphs (9% and 6%). Thus the most notable difference is the importance of scavenge in town and the reduced presence of lagomorphs. Two neighbouring areas, the "Shoot", an agricultural area with shooting interests and the Boars Hill area were investigated by D.W. Macdonald (1977[a] and unpubl.). The shoot area is a rural area where much the same food was taken as in Wytham. Lagomorphs were the principal diet, at a proportion higher than in Wytham if measured by estimated dry weight (30%), followed by earthworms and scavenge (22% and 20%). In the adjacent Boars Hill area, a suburban area of detached housing with lawns and orchards among farmland, earthworms accounted for 50% estimated dry weight, followed by scavenge (28%) while all other items were much below 10%. Preliminary results from another study area, the Cumnor area adjacent to Wytham, indicate that earthworms are the principal diet as well, followed by fruits and then by lagomorphs and scavenge (Macdonald, unpubl.).

Results from other studies emphasise one overriding aspect: the fox's versatility in adapting to the spectrum of locally available prey. Mulder

(1982) in a study of red foxes in a Dutch coastal dune reserve with a high rabbit population found that 91% of the bulk diet consisted of rabbits. The next significant items were birds, fruits and small mammals. In a study of foxes in southern Sweden, von Schantz (1980) found that foxes ate mostly rabbits (86%) while other prey categories contributed only minute amounts. In another study of suburban fox habits, Harris (1981) found earthworms and scavenge to be important parts of the diet, but emphasised the high diversity of prey types consumed at any time of the year. In the Camargue, Reynolds (1979) found rabbit to be predominant in the diet amongst a highly diverse assemblage of other prey categories. Matejka et al. (1977) found field voles and other rodents dominating the diet of foxes in a German rural area. Many other studies could be cited (for a review see Sequiera (1980)) which indicate how the main components of the diet change according to the local conditions of the study site. Most of these studies have the limitation, however, of presenting data only on the frequency of occurrence of prey categories, indicating only qualitatively which items constitute the bulk of the diet. In most studies seasonal changes are marked for most important prey items. Aside from Macdonald (1977a), who found similar patterns of spatial and temporal variation, this is the only study that compares the diet between ranges and its possible seasonal variation within ranges.

4.3. Badger diet

4.3.1. Methods of sampling

A total of 1053 badger droppings were collected over the 'core' area (see section 4.2.1.) between May 1982 and October 1983. In contrast to foxes which deposit their faeces everywhere in their ranges, badgers

generally defaecate at certain specially prepared sites called latrines (Neal (1977)). These are sites where the badgers dig little holes or pits of 5 to 30 cm diameter, with a depth of between a couple of cm up to 50 cm. These deeper pits are often blind entries to badger setts. A latrine may consist of 1 to 80 pits and cover an area between 10 by 10 cm up to 15 m maximum length and 10 m maximum width.

Latrines are often found at transitions of microhabitats and at conspicuous landmarks such as fence posts, tracks, ditches and setts. In Wytham, badgers usually defaecate into latrines. It is also known that they defaecate underground (Kruuk & Parish (1982)).

After emerging from their winter break at the beginning of March, badgers usually dig a whole set of new latrines and enlarge some old ones. Therefore I searched from the end of March onwards for latrines. Detailed searching involved walking transects through the entire study area, but concentrating on the 'core area' as defined in section 4.2.1. These transects were walked at a slow pace and spaced at variable distances so that the field of view overlapped slightly with that of neighbouring transects. In dense vegetation this usually meant a width of five to ten meters or less, while in vegetation with less undergrowth (e.g. beechwood plantations) transect widths were larger. To cover the entire area in a relatively short time I usually spent nine hours every day on transect walking from the end of March until the end of April. In spring 1982 I was greatly helped by Nick Styles and in spring 1983 by Christa Helmer. Their assistance enabled me to cover almost every square meter of the core area so that I could be sure to find most of the latrines. This was a very important requirement to ensure that my samples of faeces and the data on the activity of latrines were representative for the entire population of latrines. During the remainder of the year no further systematic search was undertaken but whenever a new latrine was encountered, the details were

taken down and this latrine included in future check rounds. As I checked each latrine at least once a month I still covered quite a large area and probably discovered the majority of new latrines created as the year progressed. In addition I was aided by members of the Edward Grey Institute of Field Ornithology who told me if they found any new latrines. As a result I found altogether 70 latrines in spring 1982 and 119 new latrines in spring 1983 (while some of the 1982 latrines were still going), and altogether 274 latrines in the core area between March 1982 and October 1983. By comparison, Kruuk (1978, pers. comm.) found in 1974 a total of 89 latrines in Wytham, but searched a larger area which included the Great Wood and the areas around the reservoir in the west.

The deposition of faeces at particular sites by the badgers facilitated the collection of samples enormously. This made the design of a sampling scheme necessary. Amongst the various sampling designs conceivable I shall evaluate the adequacy of two.

Sampling Design 1: Collection of a fixed number of samples from each latrine. Sampling more or less unrelated to the activity of the badgers.

Sampling Design 2: Collection of samples proportionate to the activity of badgers. Possibility of unequal sample sizes for different latrines within one monthly check round and for the same latrine between different check rounds.

Sampling design 1 (SD 1) has the advantage of being simple, resulting in fixed sample sizes for different latrine check rounds which may be advantageous for statistical analysis. However, as the badgers distribute their attention unequally among latrines (in each check round there are at least some latrines without any fresh droppings) some samples would either have to contain old droppings or some latrines would have to be omitted.

Reduction of the number of samples taken from each latrine (fixed under SD 1) would minimize the necessity to collect old droppings, but also reduce overall sample sizes and would result in a strong underrepresentation of very active latrines. Selection of only a few samples from a very active latrine is likely to introduce some bias.

Under SD 2 the number of samples collected from a latrine is proportionate to the activity of badgers at that latrine. If there are no fresh droppings, no samples are taken. If there are fresh droppings in several pits, a sample from each pit is taken, but no more than 10 samples from any latrine. Thus, the droppings (and therefore the diet) are adequately sampled, although there is an element of subjectivity in the decision of how many samples to take from each latrine. As I considered proportionate sampling and thus a representative sample as the most important criterion, I decided to apply sampling design 2, the proportionate sampling scheme.

While mapping latrines during March and April, no samples of droppings were collected. Although I realized the potential use of such data, collection was impossible for several reasons. During March, each badger sett was baited for at least two weeks with a mixture of peanuts, syrup and plastic pellets of different colurs. In consequence the diet samples would have been distorted by my baiting activities. During the period from end of March to the end of April all my effort was devoted to locating badger latrines, trapping and radiotracking foxes. As several setts were baited during this time for trapping purposes, diet samples would again have been affected.

From May until November latrines were visited at least once a month but in June only a few samples were taken. Usually each latrine was visited and its state of activity checked. If fresh droppings were present, a sample was collected. If the number of fresh droppings was very small, then it was

sometimes necessary to collect all droppings. However, if the number of fresh droppings exceeded ten, a selection of droppings was taken. Droppings were selected so that all pits with fresh droppings were represented at least once in the sample for that latrine. The dropping was gently separated from its substrate (either another dropping or bare ground) and placed in a plastic bag on which the number of the sample, the number of the latrine and the date were noted. The plastic bag was closed with rubber band and first stored in the deep freeze before being dried in an oven at 50° C.

4.3.2. Methods of analysis

The analysis of the scats basically followed the scheme adopted for the analysis of fox droppings. This has the advantage of analysing the diet of the two species with comparable methods. A "wet" analysis as was performed by Kruuk (e.g. 1978b) would have taken far too long and had little advantage except to disclose more of the infrequent, small, softbodied prey. The categorization of prey types was the same as described for fox faeces (see section 4.2.2.). Data were typed into a paper-tape machine and then transferred to the university's ICL-2988 computer where the paper-tape was read in and the files edited. Statistical analysis was performed on the university's VAX-11/780 computer with procedures which I wrote for the statistical package MINITAB, analogous to the procedures used for the analysis of the fox diet.

The analysis of the baiting actions in 1982 and 1983 plus the results of radiotracking permitted the determination of badger home range borders (Chapter 5). Each latrine was assigned the status of being either a "border" or a "non-border" latrine. If a latrine was assigned the status of a border latrine, at least two, sometimes three neighbouring ranges shared

the latrine and could be responsible for faeces there. Program BORLAT inserted the status of the latrine number together with its range number(s) into the file containing the results of the scat analysis. All analyses performed on ranges only considered non-border latrines, ie. those that lay inside one range and away from any borders (section 4.3.3.3.). A comparison of the contents of border and non-border latrines can be found in section 4.3.3.4.

4.3.3. Results

4.3.3.1. General composition of the diet

In 1982 and 1983, 1053 badger droppings were collected between May and November. The distribution of sample sizes for various subsets of the data are shown in Table 4.8.

Although no samples were collected during March and April, there is nevertheless information available to suggest what badgers ate during these two months. First, most fresh droppings had the darkish brown colour and liquid texture typical for faeces dominated by earthworms. In addition, detailed observations at the Jews Harp sett (Range B4) in April showed that badgers caught and ate mostly earthworms at the surface and ate hardly anything else around the sett. Of course these observations are of limited value as the badgers could not be observed away from the sett but the incidental observations available (from the work of Nickie Wadham, see Chapter 3; and observations during radiotracking) it became clear that earthworms were a big part of the diet.

Table 4.9 lists the diet of Wytham's badgers as calculated by the three available measures (frequency of occurrence, estimated volume and estimated dry weight). Earthworms constitute by far the most important component of

Table 4.8 Numbers of badger droppings collected. Data from both years (1982 and 1983) combined

a) sample sizes for different months (all latrines)

May	128	
June	11	
July	230	
August	181	
September	169	
October	178	
November	156	TOTAL: 1053

b) sample sizes for different types of latrines

non-border latrines	639	
border latrines	414	TOTAL: 1053

border latrines of borders between two neighbours	377
border latrines of borders between three neighbours	37
	414

c) sample sizes for different ranges

Range number	Name	No. of (non-border) droppings	
0	Binsey	19	
1	Botley Lodge	24	
2	Upper Follies	49	
3	Marley Wood	71	
4	Jews Harp	181	
5	Sundays hill	83	
6	Nealings Copse	45	
7	The Mount	16	
8	Lower Seeds	6	
9	Common Piece	2	
10	Radbrook Common	128	
11	The Chalet	0	
12	The Big Oak	15	TOTAL: 639

d) sample sizes for selected ranges for each month (June was excluded as no samples were collected from any of these ranges)

Range number	Name	5	7	8	9	10	11	Total
1	Botley	0	12	5	2	0	5	24
2	Upper Follies	0	10	20	4	15	0	49
3	Marley Wood	17	9	9	16	11	9	71
4	Jews Harp	21	29	32	31	42	26	181
5	Sundays	15	36	9	8	1	14	83
6	Nealings	0	5	8	6	25	0	45
10	Radbrook	5	31	14	34	16	28	128

the diet on all three measures. Cereals are second in importance followed by fruits and invertebrates. These are also the prey categories which were considered for an investigation of temporal and spatial variation in the diet composition of Wytham's badgers (see the following sections). All other prey types occur fairly seldom and are not very important parts of the diet. Comparing the three measures (Table 4.9 and Fig. 4.13) it appears that most prey categories occur more frequently than corresponds to their actual proportion in the diet, ie. the points lie below the straight line in Fig. 4.13. In Fig. 4.14 the mean percent estimated volume when present is plotted for each prey category against its frequency of occurrence. Despite the big differences in the size of prey species, earthworms not only constitute the major part of the diet (the only prey type beyond the 50% volume line) but are also the prey type with the highest frequency of occurrence and the highest mean percent estimated volume when present. This indicates that worms are consumed regularly and massively and confirms the impression derived from Table 4.9. Eight of the twelve prey types occur in less than 10% of the droppings which means that seven of them contribute less than or equal 1% of the total diet. Thus, this study confirms the results of earlier studies from Wytham (Kruuk (1978b), Hancock (1973), Hubertz (1978), and other areas (Skoog, (1970), Kruuk and Parish (1981)) which describe the earthworm as the major item of the badger's diet.

4.3.3.2. Temporal variation in the diet

Figs. 4.15a to 4.15c illustrate the monthly changes in the proportion each food type contributes to the total diet. Small mammals are consumed in spring and early summer more often than later in the year. A marked increase can be seen for invertebrates from June to August which equally quickly declines towards the late autumn. Fruits are mainly consumed during

Table 4.9 The diet of Wytham's badgers, estimated by three measures. The percentage values are the percentage contribution of each prey category to the overall result. For a definition of the measures see Table 4.2

	% freq.	% est. volume	% est. dry weight
SM	2.184	1.264	1.22
INV	21.083	7.198	5.425
FR	7.882	5.869	3.498
BD	0.475	0.271	0.286
LAG	1.614	0.803	0.681
SCA	3.324	1.550	1.465
EW	69.326	53.946	63.523
GR	3.894	0.878	0.952
DOM	0	0	0
OTH	2.944	0.985	1.094
CER	36.562	23.508	17.742
TR	3.989	3.726	4.212

SM small mammals
INV invertebrates
FR fruits
BD birds
LAG lagomorphs
SCA scavenge
EW earthworms
GR grass
DOM domestic
OTH other
CER cereals
TR tree fruits

Fig. 4.13. Plot of estimated dry weight of prey items in the diet of Wytham's badgers against frequency of occurrence. Interpretation of plot identical to Fig. 4.2. Abbreviations as before and in Table 4.9.
Some poorly represented diet items have not been specifically labelled; precise data for these as well as the labelled prey types are listed in Table 4.9.

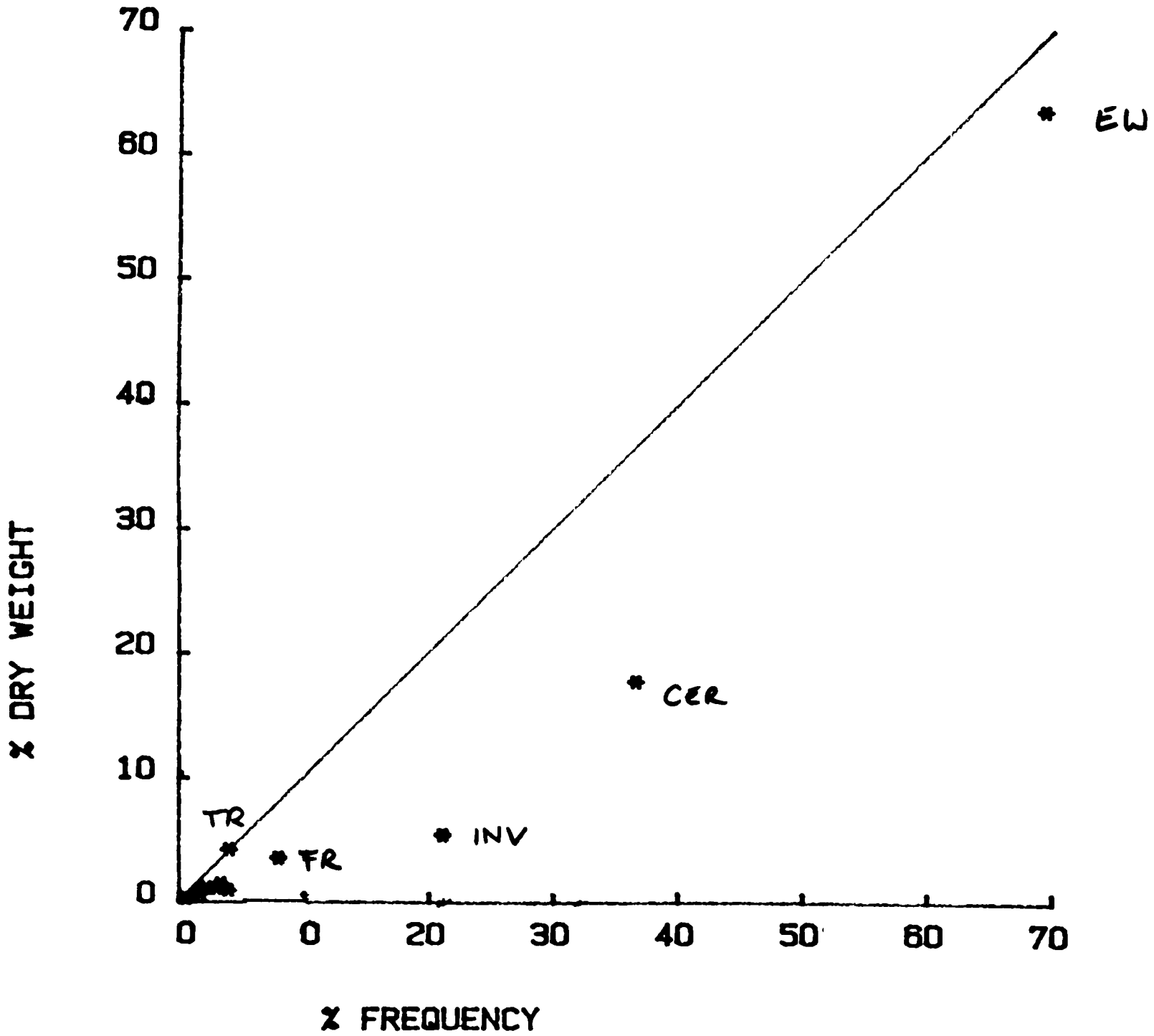
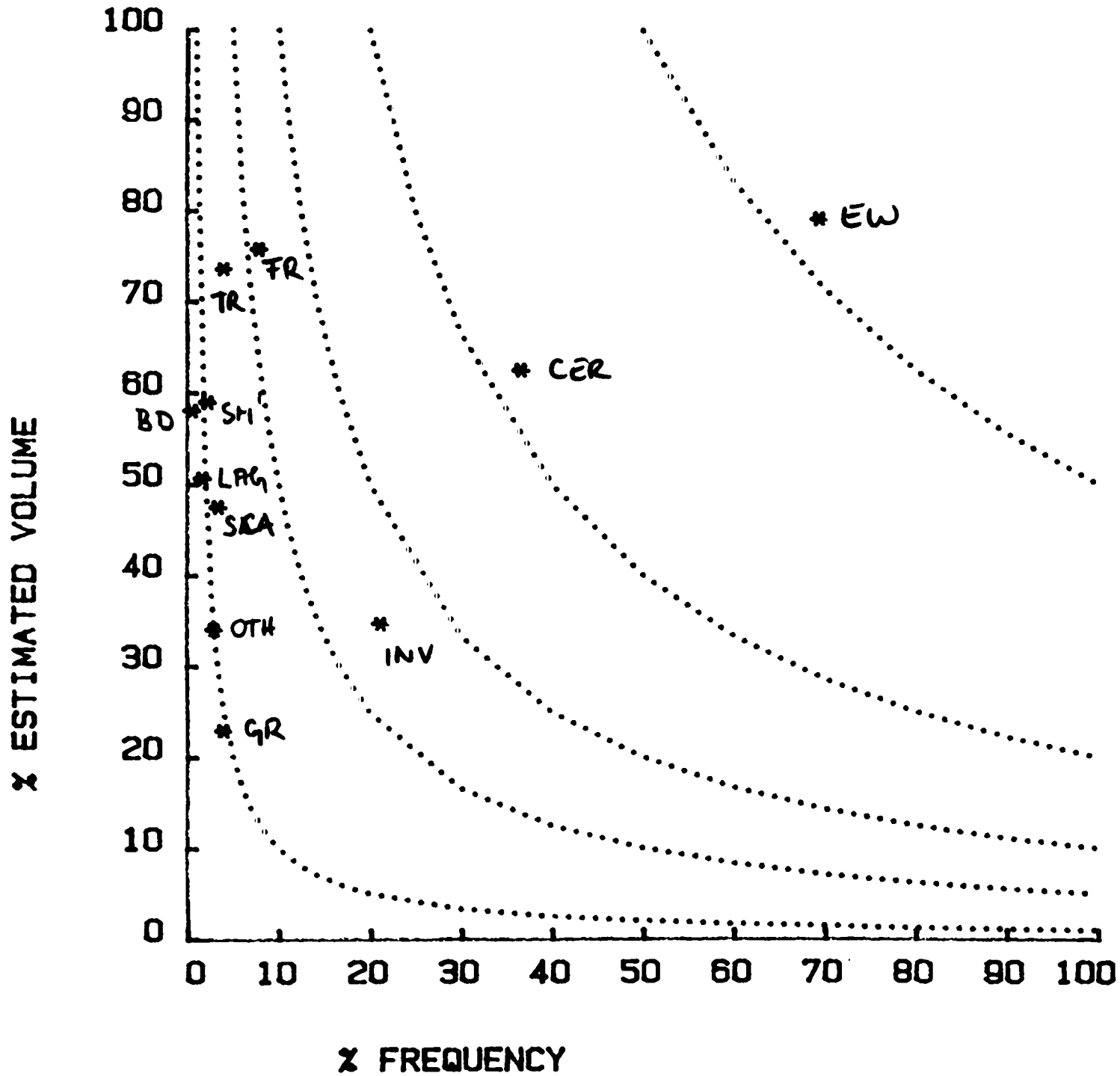

70
60
50
40
30
20
10
0
0
0
20
30
40
50
60
70
% DRY WEIGHT
% FREQUENCY
EW
CER
INV
FR
TR

Fig. 4.14. 'Kruuk-plot' (see Fig. 4.3.) of the badger diet, as determined by percent volume per faeces.



SM SMALL MAMMAL
INV INVERTEBRATES
FR FRUIT
BD BIRDS
LAG LAGOMORPHS
SCA SCAVENGE
SO EARTHWORMS
GR GRASS
OTH OTHERS
CER CEREALS
TR TREE FRUIT

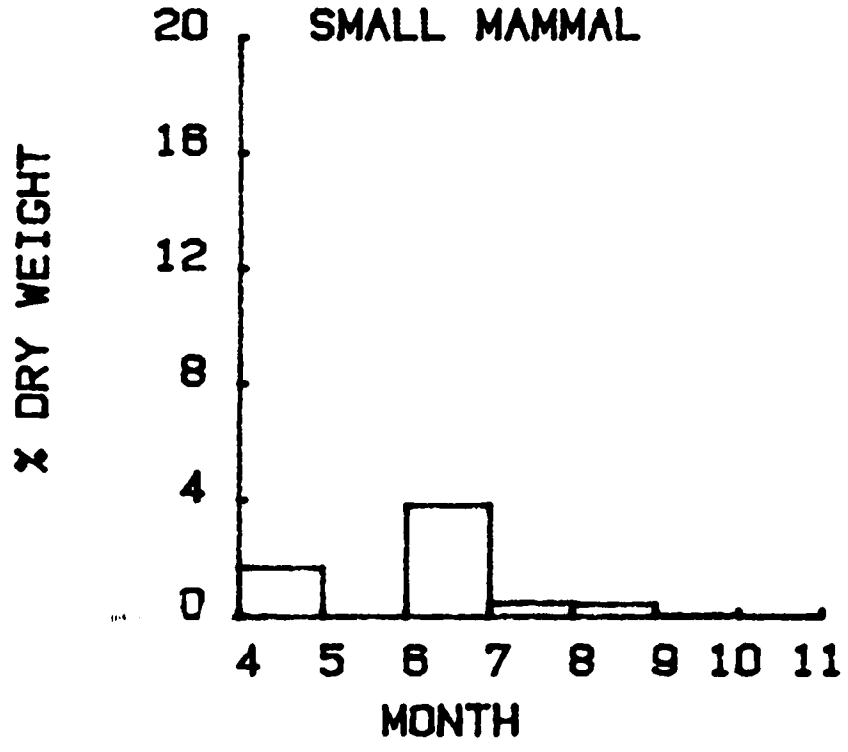
50 % VOL IN TOTAL DIET

20 % VOL IN TOTAL DIET

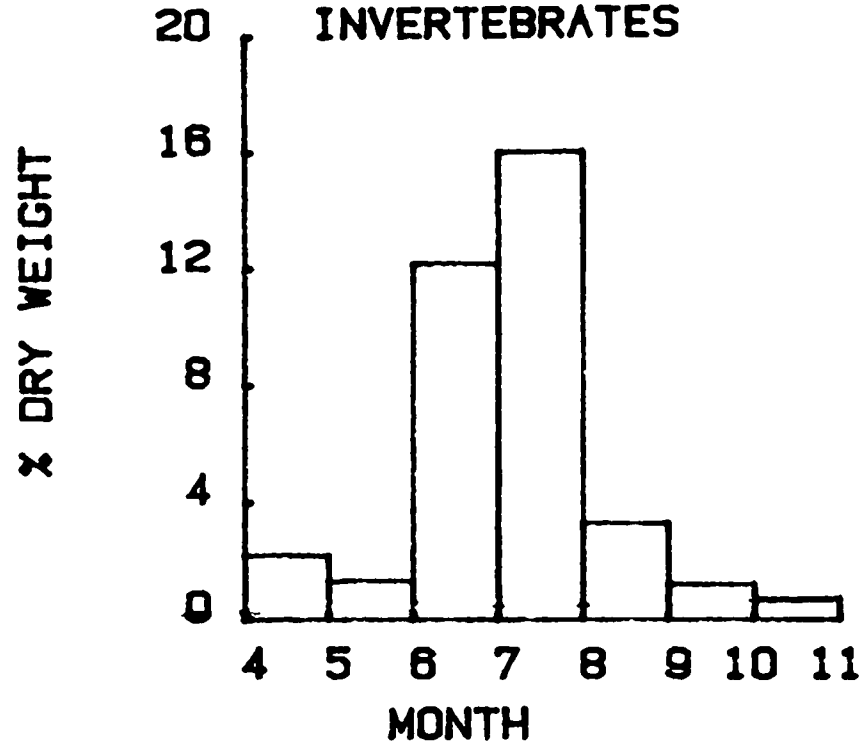
10 % VOL IN TOTAL DIET
5 % VOL IN TOTAL DIET
1 % VOL IN TOTAL DIET

Fig. 4.15. Monthly changes in the diet of Wytham's badgers, as determined by estimated dry weight. Sequence of prey types identical as in Fig. 4.5 for foxes.

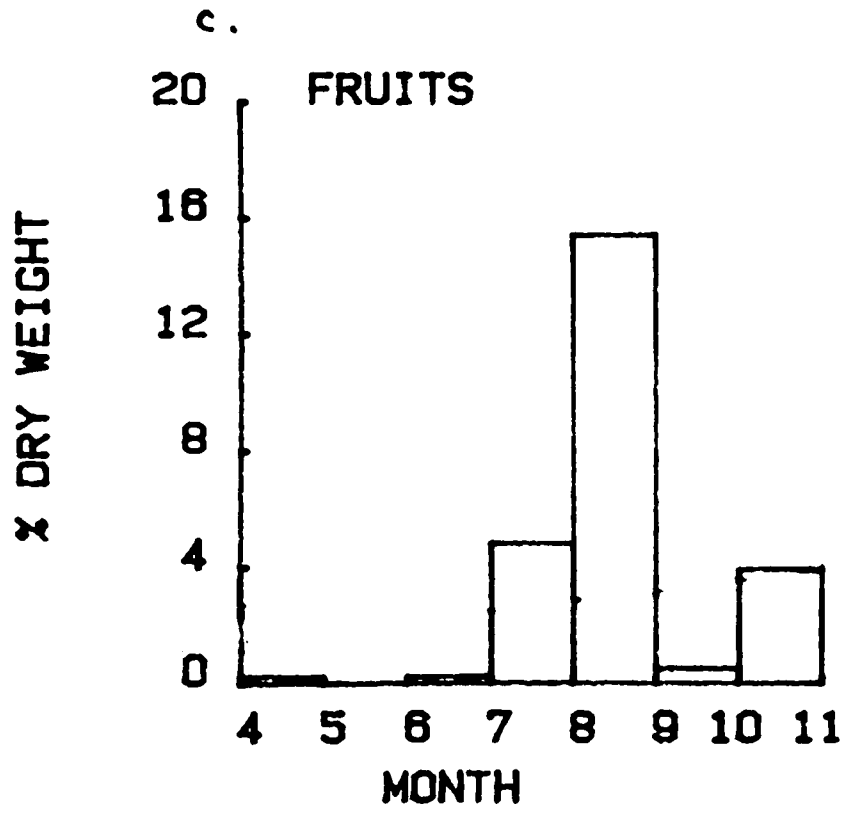
a.


SMALL MAMMAL
% DRY WEIGHT
20
16
12
8
4
0
4 5 6 7 8 9 10 11
MONTH

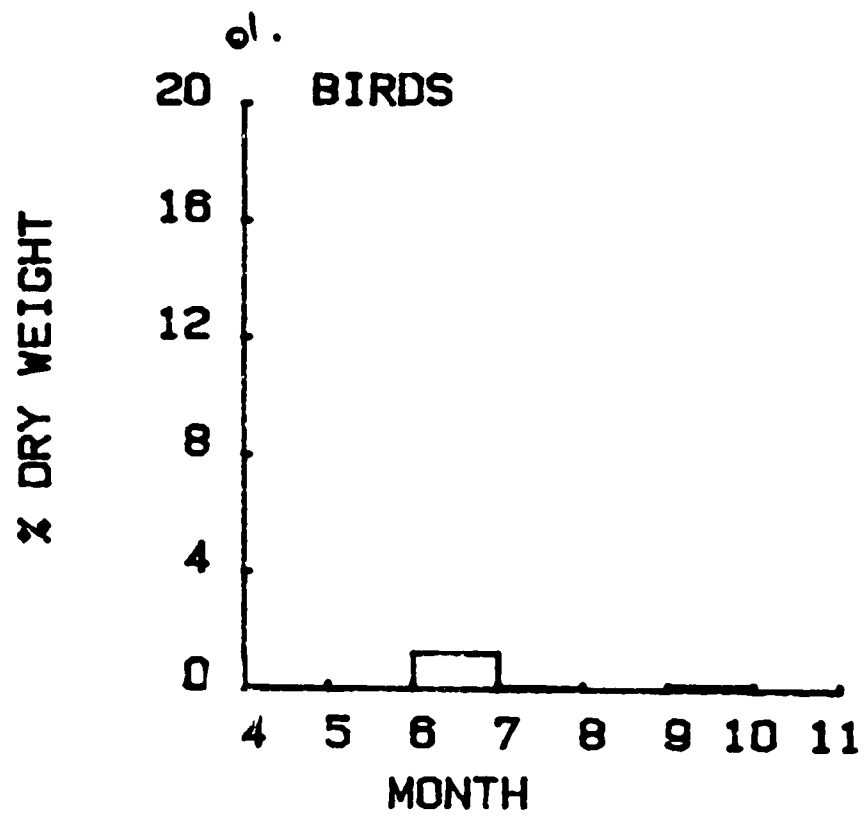
b.


INVERTEBRATES
% DRY WEIGHT
20
16
12
8
4
0
4 5 6 7 8 9 10 11
MONTH

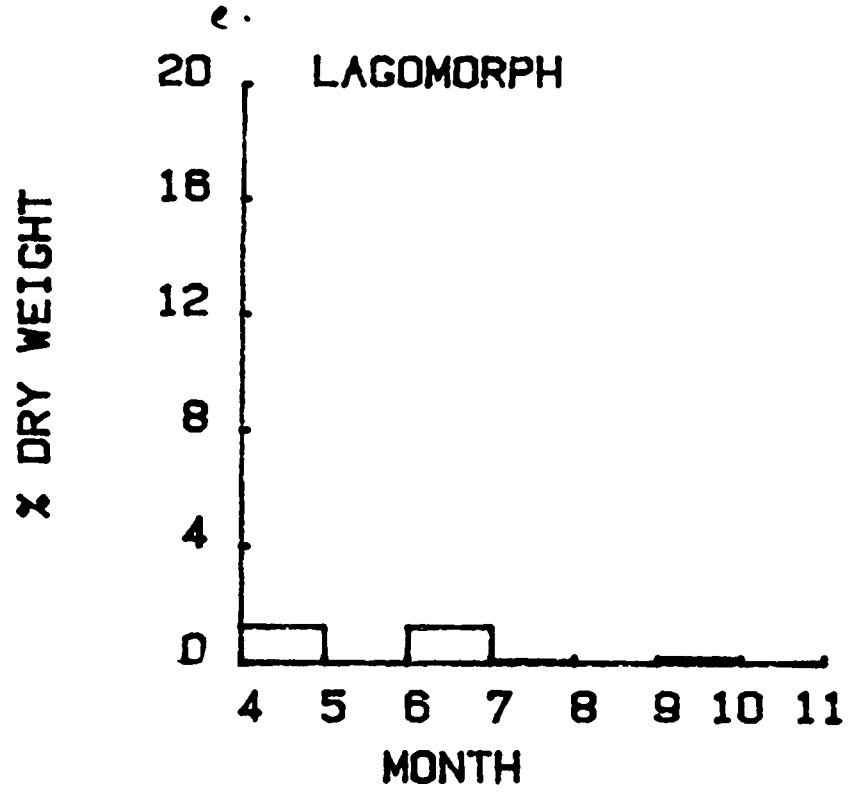
c.


FRUITS
% DRY WEIGHT
20
16
12
8
4
0
4 5 6 7 8 9 10 11
MONTH

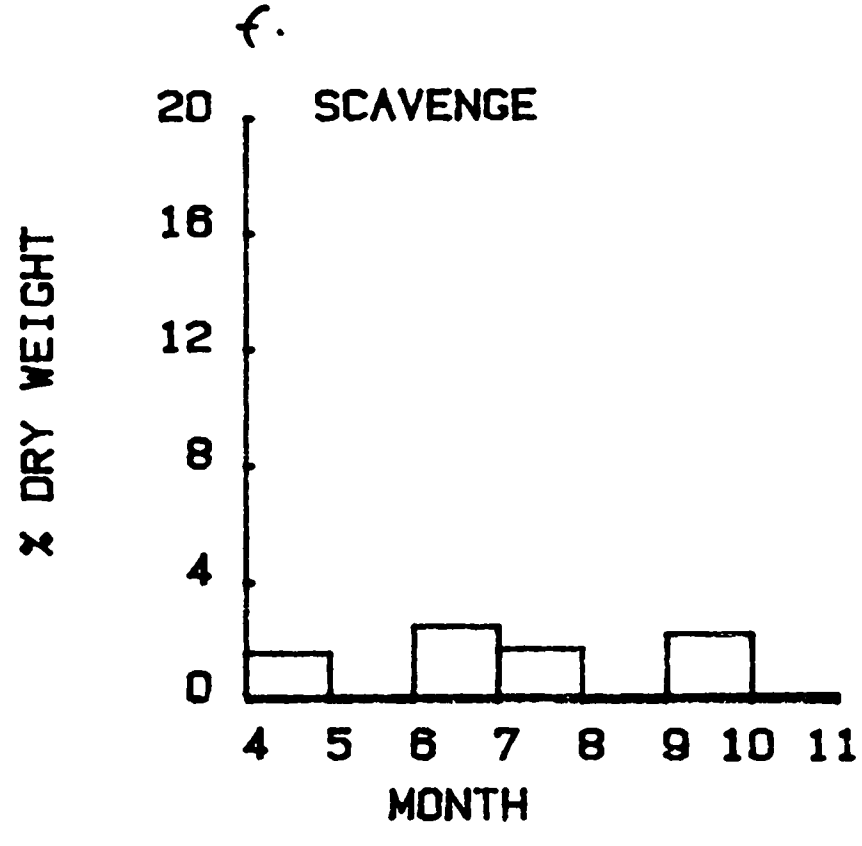
d.


BIRDS
% DRY WEIGHT
20
16
12
8
4
0
4 5 6 7 8 9 10 11
MONTH

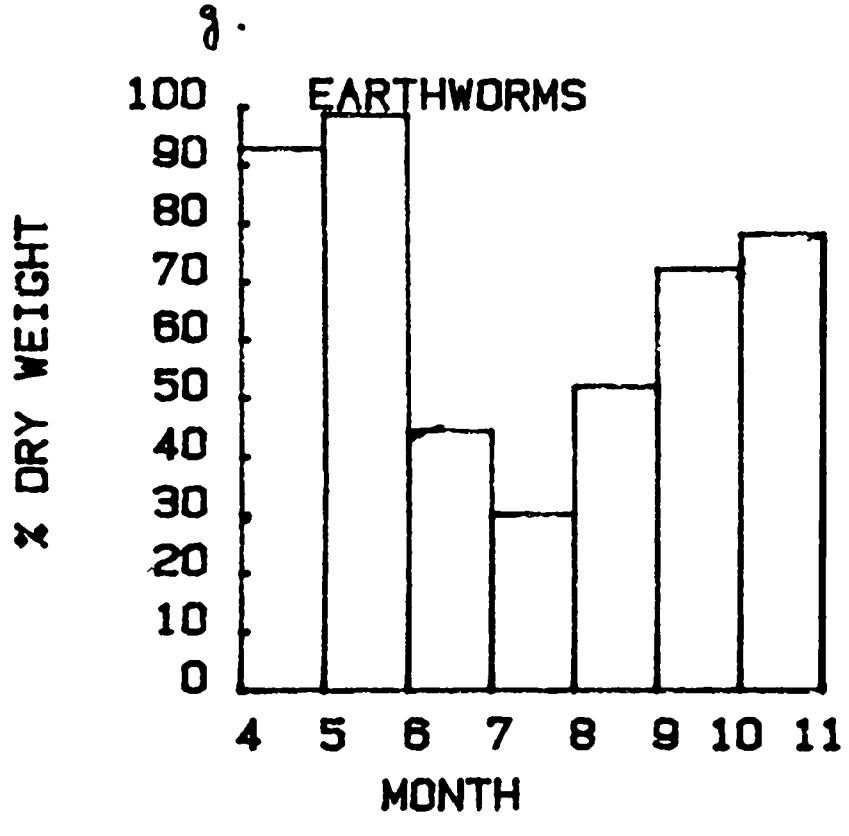
e.


LAGOMORPH
% DRY WEIGHT
20
16
12
8
4
0
4 5 6 7 8 9 10 11
MONTH

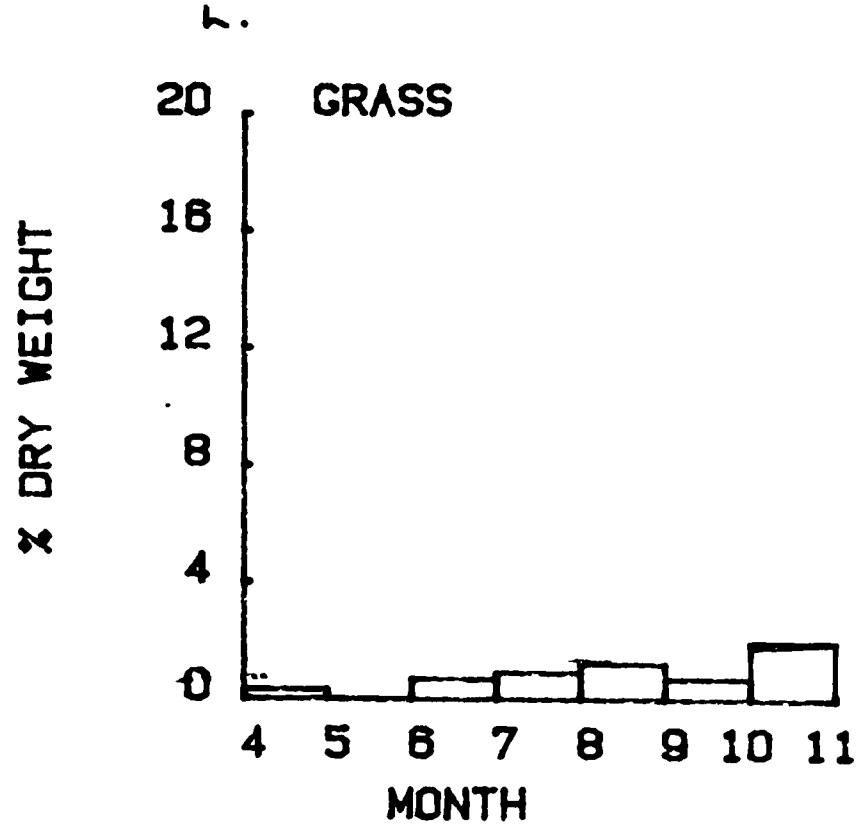
f.


SCAVENGE
% DRY WEIGHT
20
16
12
8
4
0
4 5 6 7 8 9 10 11
MONTH

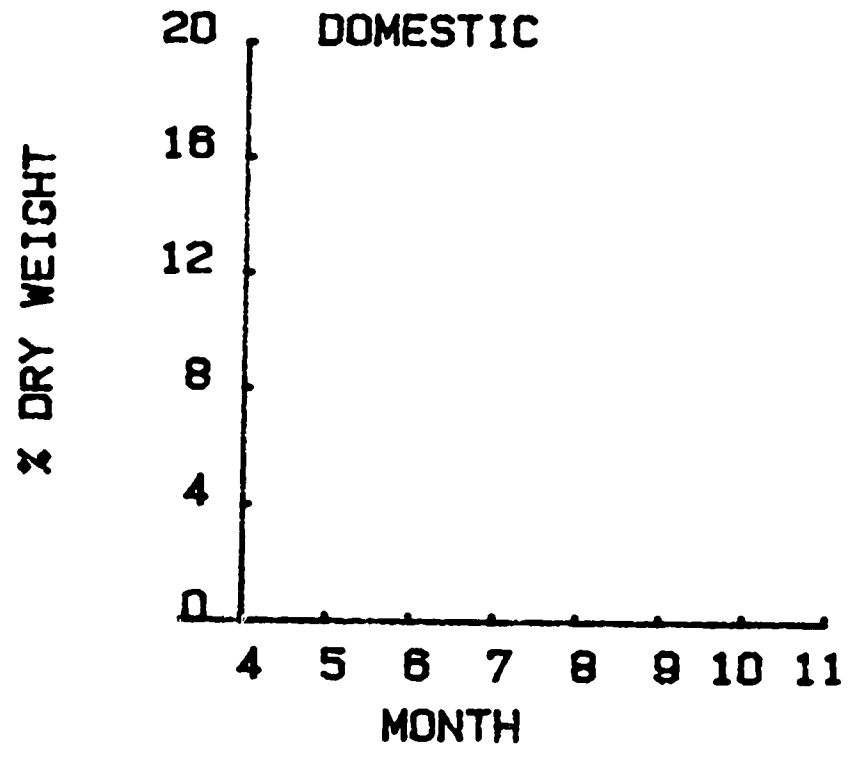
g.


EARTHWORMS
% DRY WEIGHT
100
90
80
70
60
50
40
30
20
10
0
4 5 6 7 8 9 10 11
MONTH

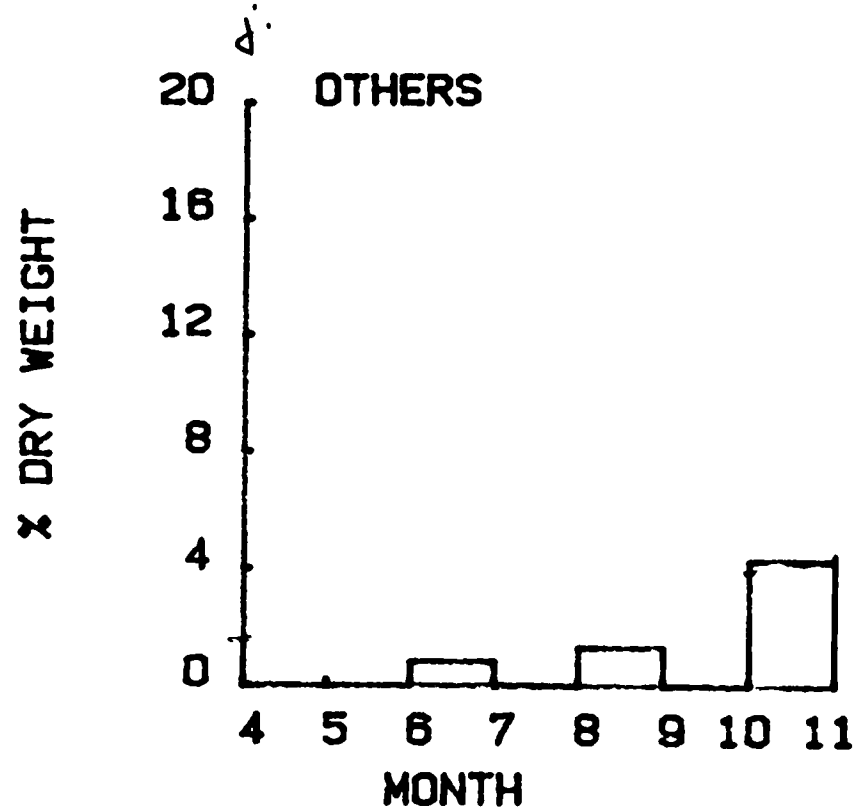
h.


GRASS
% DRY WEIGHT
20
16
12
8
4
0
4 5 6 7 8 9 10 11
MONTH

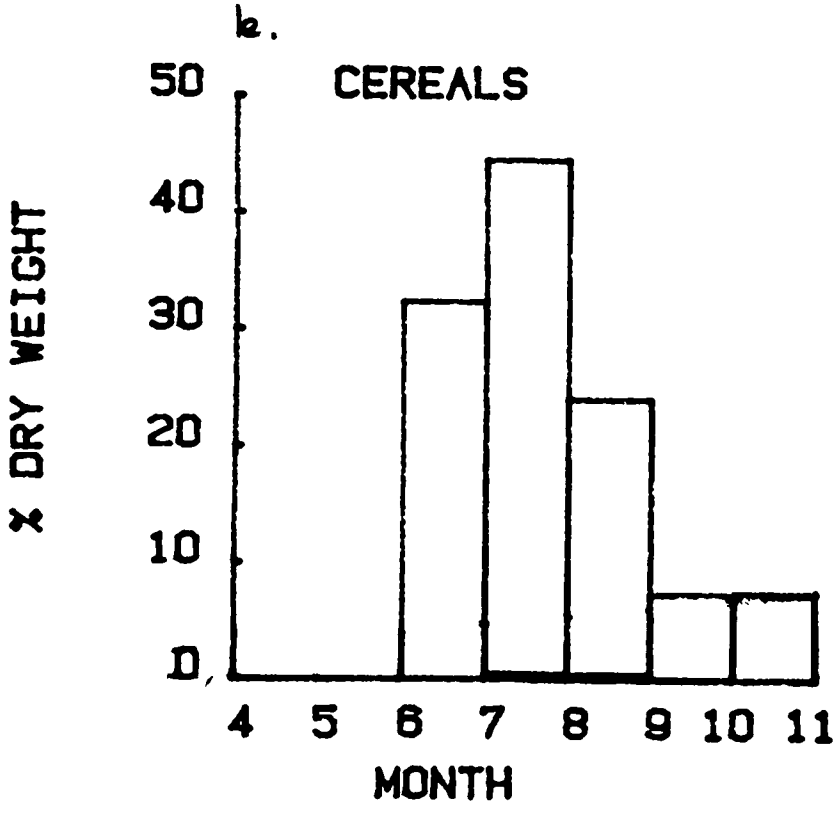
i.


DOMESTIC
% DRY WEIGHT
20
16
12
8
4
0
4 5 6 7 8 9 10 11
MONTH

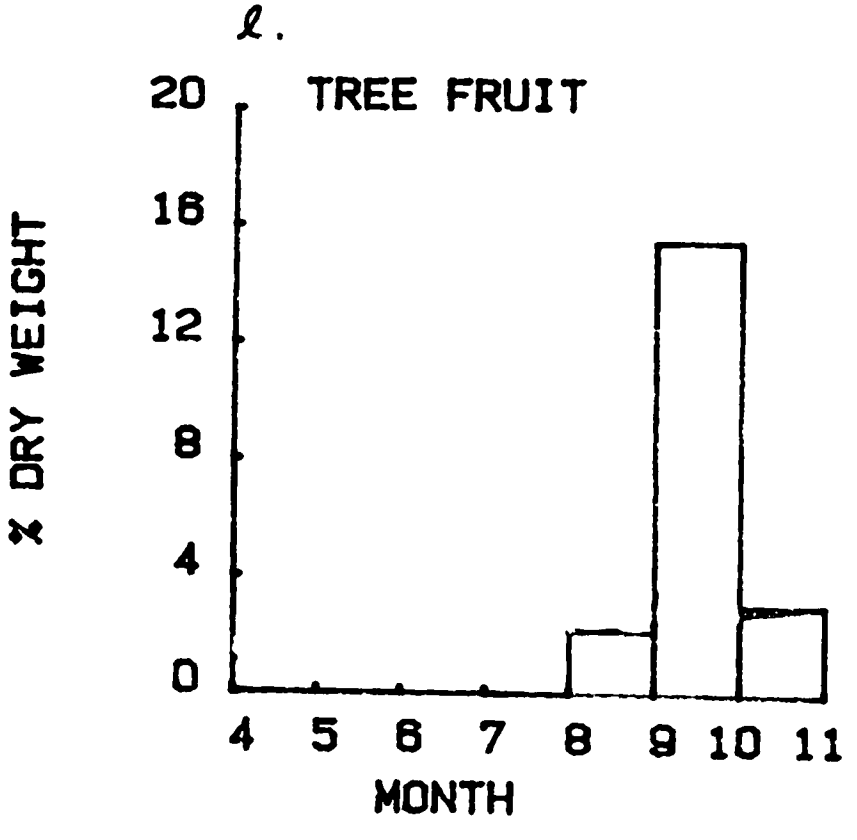
j.


OTHERS
% DRY WEIGHT
20
16
12
8
4
0
4 5 6 7 8 9 10 11
MONTH

k.


CEREALS
% DRY WEIGHT
50
40
30
20
10
0
4 5 6 7 8 9 10 11
MONTH

l.


TREE FRUIT
% DRY WEIGHT
20
16
12
8
4
0
4 5 6 7 8 9 10 11
MONTH

September and to nearly the same extent in August and November. In August and September the ripening of blackberries (Rubus fruticosus) is responsible for the big contribution of fruits while the November peak is due to some cultivated fruits (apple, etc.). Birds are only eaten in July, lagomorphs in May and July (this is in common with small mammals). Scavenge is taken to some extent in each of the three seasons represented, as is grass. Earthworms, however, show a marked decline from spring to a minimum in July and August and an increase during autumn. Tree fruits are mainly consumed in October (due to the sweet chestnut mast). Cereals peak in August but are still heavily consumed during September and to some extent in October and November. This is most likely due to the fact that cereals remain available at the edges of fields even after they have been harvested (September) while the consumption in middle and late autumn is probably due to the collection of newly sown grain.

Table 4.10a shows the results of a Kruskal-Wallis one-way analysis of variance on differences between months. Here, only the six most important food types were investigated. All prey types show significant differences between months.

4.3.3.3. Variation in the diet of different ranges

The following analysis is based on latrines of non-border status only.

4.3.3.3.1. General composition of the diet

Of the thirteen ranges that could be recognized (Chapter 5) some had to be excluded because of insufficient sample sizes (Ranges B8, B9 and B11, Table 4.8) while for others there was not enough information available to determine the range borders reliably (Ranges B0, B7 and B12, Chapter 5).

Fig. 4.16a and 4.16b depict the diet composition for the seven remaining ranges. It emphasises the importance of earthworms for all seven ranges but indicates that there was some variation between ranges, particularly in earthworms but also in cereals, invertebrates and tree fruits. The Kruskal-Wallis test confirms that these variations were significant (Table 4.10b). Spatial variation in fruits and small mammals, however, were not significant.

A posteriori multiple comparison tests (Table 4.11) were used to examine differences between range pairs. In three out of four prey categories two ranges with high prey values dominate all other ranges. With the exception of Ranges B1 and B5 that do not occur in any of the significant pairs when examining earthworms, each range appears at least once in each of the prey categories considered. The high proportion of pairs with significant differences indicate that variation is wide and well spread amongst ranges for each prey type.

4.3.3.3.2. Temporal variation in the diet

Following the approach used in the analysis of the fox diet I shall first discuss seasonal changes within each range before I look at the spatial variation within a temporal unit and the degree of synchrony between ranges in the direction of temporal fluctuations.

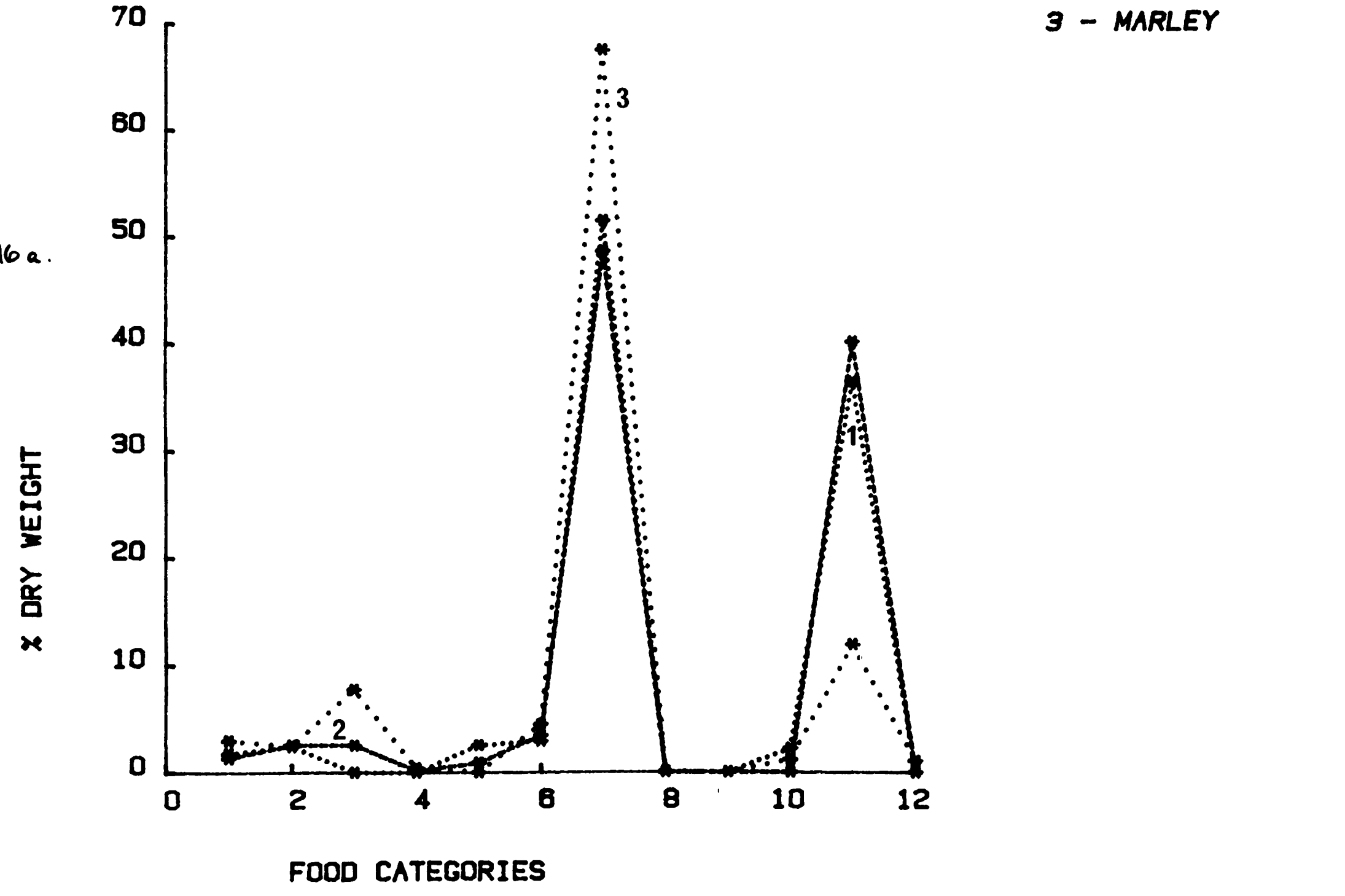
Changes within individual ranges Fig. 4.17 depicts the temporal variation in the composition of the diet of two ranges, Jews Harp (Range B4) and Radbrook (Range B10) for the four major prey categories. The graphs exemplify how different the proportions can be between ranges and how radically the proportions of any particular food type might change from month to month. Consider for instance the rapid decline of invertebrates in Range B10 from a peak in August to almost nothing in September and the

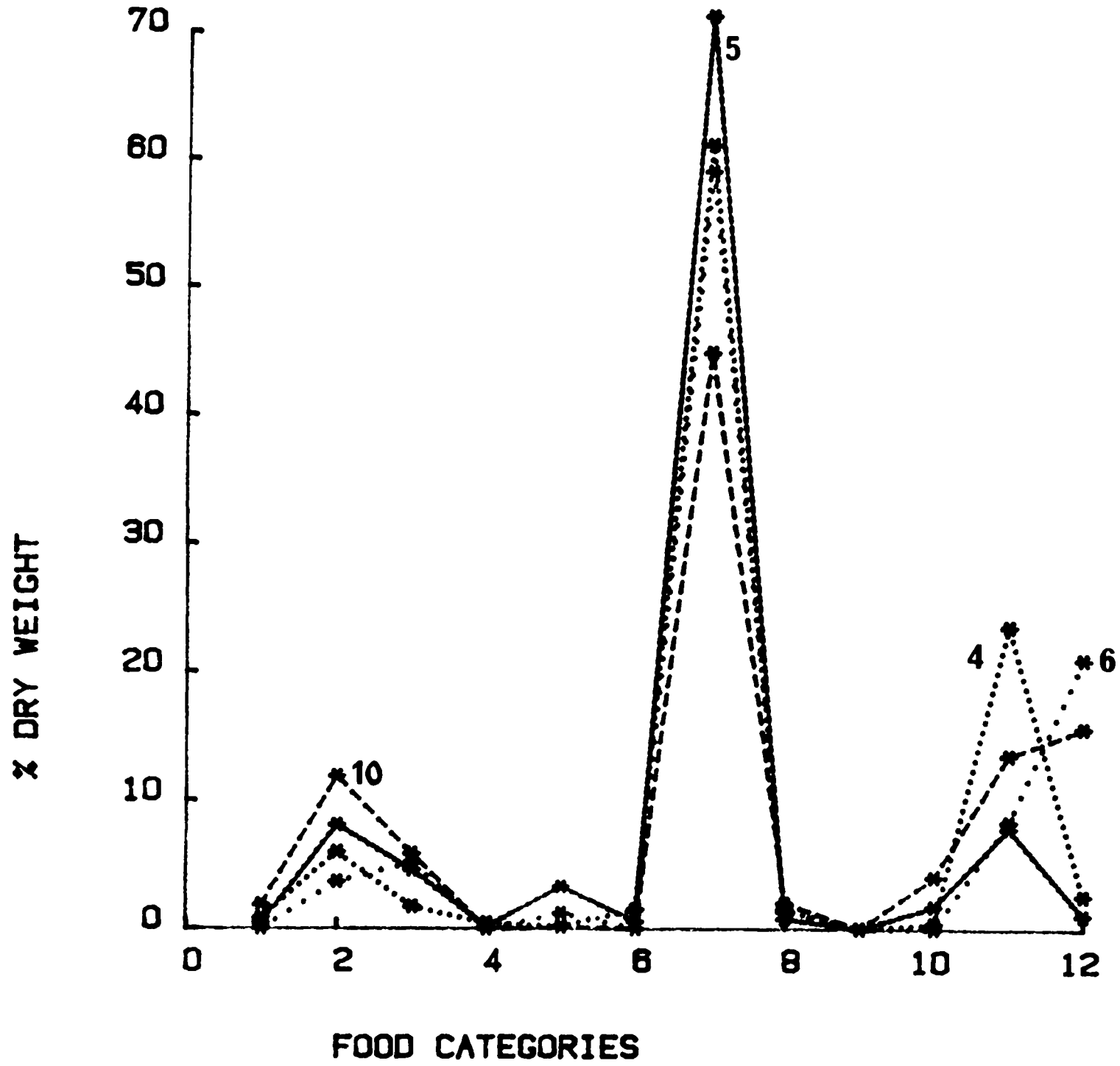
Fig. 4.16. Differences in the diet of seven badger groups, as determined by estimated dry weight.

a. Ranges B1, B2, B3.

b. Ranges B4, B5, B6, B10.

4-16a.

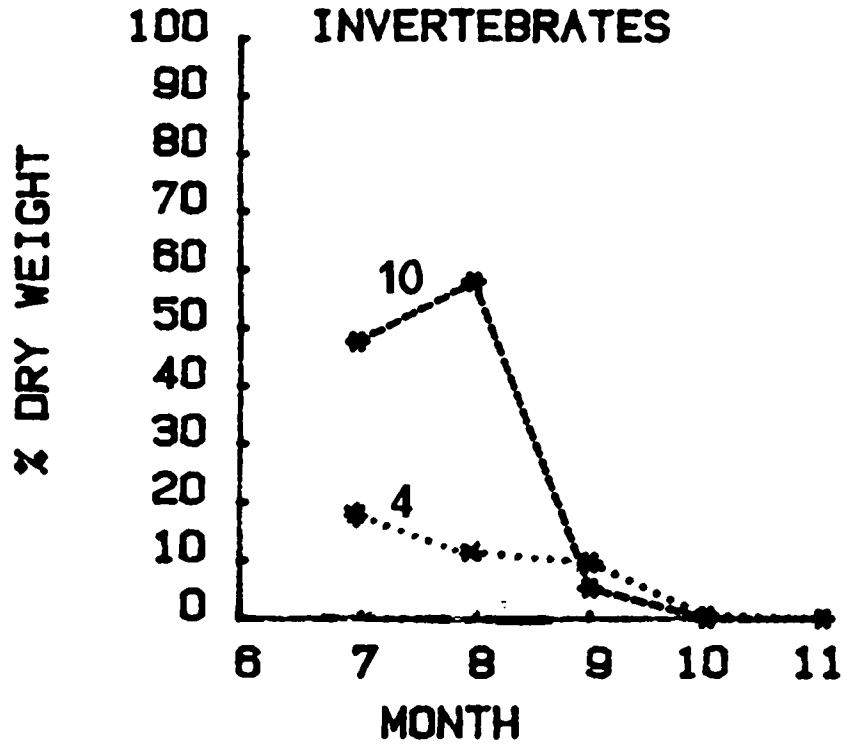

1 - BOTLEY
2 - UPPER FOLLIES
3 - MARLEY
70
60
50
40
30
20
10
0
0
2
4
6
8
10
12
3
2
1
% DRY WEIGHT
FOOD CATEGORIES



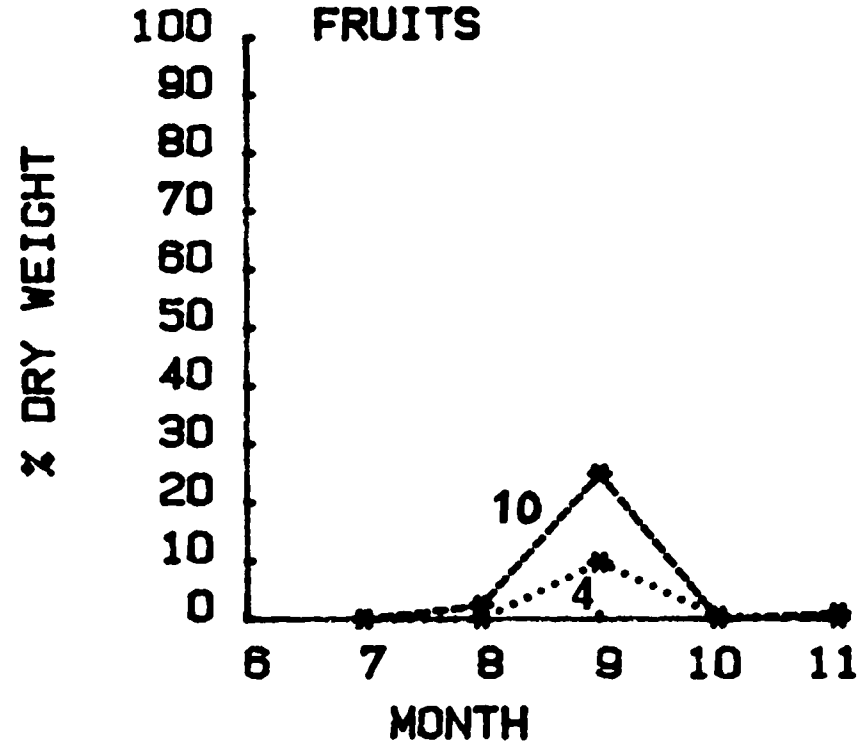
4 - JEWS HARP
5 - SUNDAY'S HILL
6 - NEALING'S COPSE
10- RADBROOK COMMON

Fig. 4.17. Monthly changes in the consumption of the four major prey types by badger groups B4 (JEWS HARP) and B10 (RADBROOK COMMON).

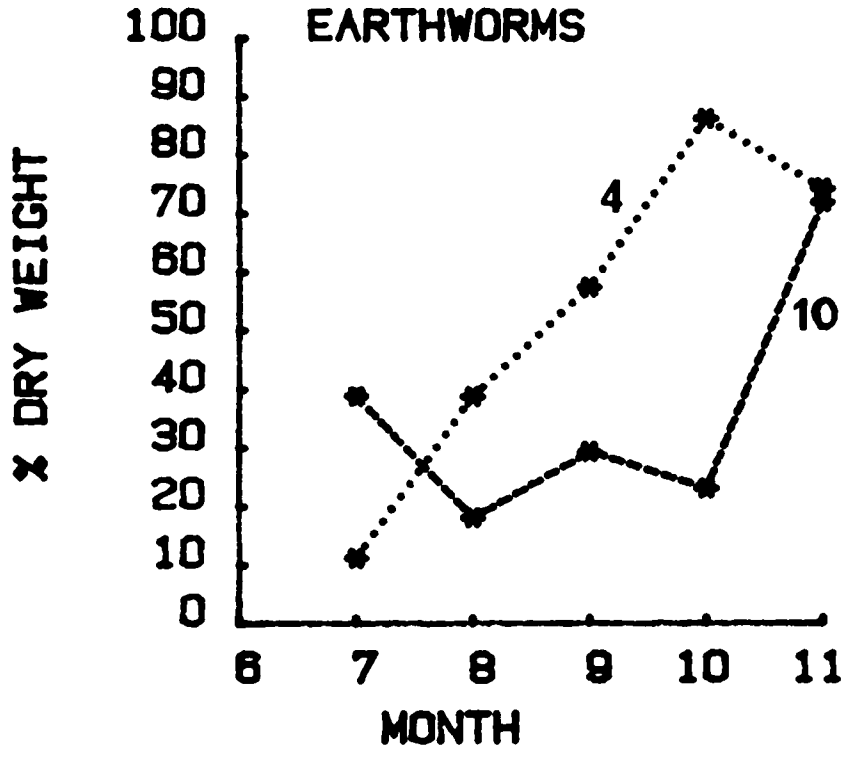
a.


INVERTEBRATES
% DRY WEIGHT
100
90
80
70
60
50
40
30
20
10
0
10
4
6
7
8
9
10
11
MONTH

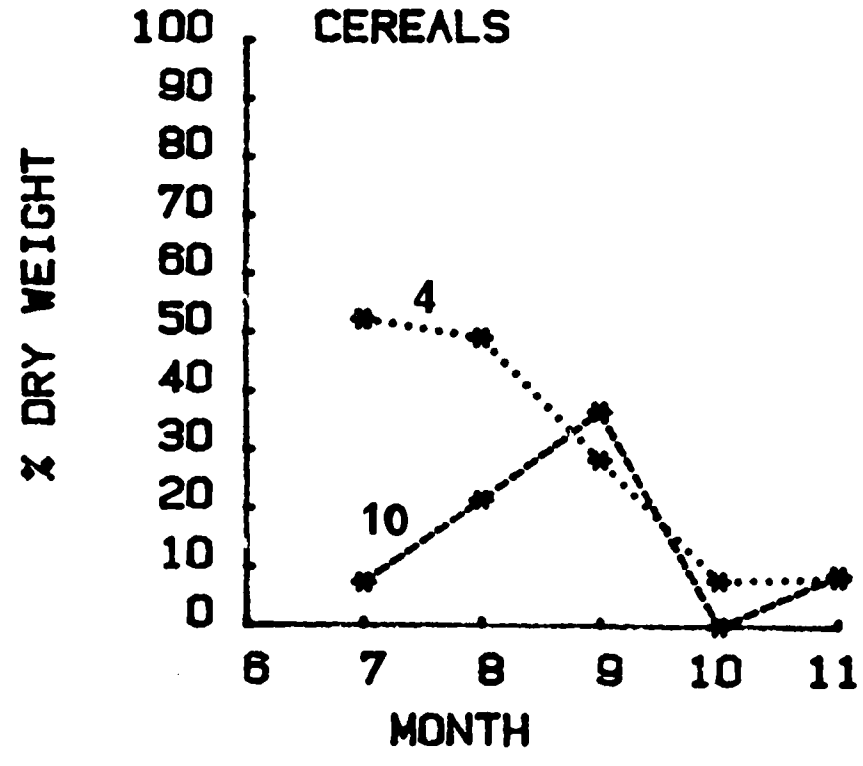
b.


FRUITS
% DRY WEIGHT
100
90
80
70
60
50
40
30
20
10
0
10
4
6
7
8
9
10
11
MONTH

c.


EARTHWORMS
% DRY WEIGHT
100
90
80
70
60
50
40
30
20
10
0
4
10
6
7
8
9
10
11
MONTH

d.


CEREALS
% DRY WEIGHT
100
90
80
70
60
50
40
30
20
10
0
4
10
6
7
8
9
10
11
MONTH

equally steep rise in earthworms from October to November in the same range. This temporal trend corresponds well with the overall trend noted in section 4.3.3.2. The two ranges chosen for Fig. 4.17 illustrate the general trend found for all ranges, but also the extremes of the variation between ranges: note the differences in absolute amount of invertebrates and the differences in the increase of the proportion of earthworms taken in autumn.

Table 4.10 summarizes the result of a Kruskal-Wallis one-way analysis of variance to reveal significant changes between months for the four major food types (invertebrates, fruits, earthworms and cereals) for each range.

Range 2 (Upper Follies) Significant temporal variation only for earthworms and cereals but no significant changes for invertebrates and fruits (both are equally little consumed during the months considered).

Range 3 (Marley) No significant changes for invertebrates and earthworms due to consistently high consumption of earthworms and low consumption of invertebrates.

Range 4 (Jews Harp) One of two ranges with significant changes in all items. This is due to high consumption of invertebrates in July and a steady decrease towards late autumn, an even more rapid decline in cereals from summer to autumn and a noticable peak for fruits in September (Fig. 4.17).

Range 5 (Sundays Hill) All prey types with significant monthly changes except for invertebrates which show a consistently high consumption.

Range 6 (Nealings Close) The only range with no significant temporal changes at all. This is due to consistently low consumption in earthworms and invertebrates and a higher consumption of cereals and fruits, particularly those of cultivated origin (boosting the autumn proportions of fruit).

Range 10 (Radbrook Common) The second range with significant changes in all four prey types. Fig. 4.17 indicates the rapid changes in all four prey

Table 4.10 Kruskal-Wallis one-way analysis of variance on spatial and temporal variation in the composition of the diet of Wytham's badgers

Prey type			H (adjusted for ties)	significance
a) differences between months (months 5 to 11)				
small mammals			19.84	<0.005
invertebrates			161.5	<0.001
fruits			105.0	<0.001
earthworms			292.6	<0.001
cereals			202.3	<0.001
tree fruits			147.1	<0.001
b) differences between ranges: (Ranges B1,B2,B3,B4,B5,B6,B10)				
small mammals			7.47	ns
invertebrates			32.90	<0.001
fruits			10.52	ns
earthworms			24.87	<0.001
cereals			34.80	<0.001
tree fruits			44.88	<0.001
c) differences between months within single ranges. Only four food categories considered: invertebrates, fruits, earthworms, cereals. * critical value = 11.07				
INVERTEBRATES				
B2	Upper F	7,8,10	3.40	ns
B3	Marley	5,7,8,9,10,11	11.04	(ns)*
B4	Jews H	5,7,8,9,10,11	25.81	<0.001
B5	Sundays H	5,7,8,9,11	5.75	ns
B6	Nealings	7,8,9,10	4.982	ns
B10	Radbrook	7,8,9,10,11	72.43	<0.001
FRUITS				
B2	Upper F	7,8,10	1.25	ns
B3	Marley	5,7,8,9,10,11	16.09	<0.01
B4	Jews H	5,6,8,9,10,11	21.52	<0.001
B5	Sundays	5,7,8,9,11	34.99	<0.001
B6	Sundays	7,8,9,10	7.45	ns
B10	Radbrook	7,8,9,10,11	27.29	<0.001
EARTHWORMS				
B2	Upper F	7,8,10	30.62	<0.001
B3	Marley	5,7,8,9,10,11	10.62	ns
B4	Jews H	5,7,8,9,10,11	60.48	<0.001
B5	Sundays H	5,7,8,9,11	31.28	<0.001
B6	Nealings	7,8,9,10	3.04	ns
B10	Radbrook	7,8,9,10,11	49.40	<0.001
CEREALS				
B2	Upper F	7,8,10	28.05	<0.01
B3	Marley	5,7,8,9,10,11	27.14	<0.001
B4	Jews H	5,7,8,9,10,11	41.85	<0.001
B5	Sundays	5,7,8,9,11	11.00	<0.05
B6	Nealings	7,8,9,10	3.779	ns
B10	Radbrook	7,8,9,10,11	19.10	<0.001

Table 4.11 A posteriori multiple comparison tests for differences between pairs of ranges. Only food types considered that yielded significant differences in a one-way Kruskal-Wallis analysis of variance. Only significantly different pairs are listed

a) Invertebrates

Range with high prey value	R. with low prey value	actual value	critical value	significance (α)
B10 Radbrook	B 1 Botley	65.6	52.66	<0.02
B 5 Sundays H	B 2 Upper F	60.7	42.65	<0.01
B10 Radbrook	B 2 Upper F	84.8	39.77	<0.001
B 5 Sundays H	B 3 Marley	58.6	38.27	<0.01
B10 Radbrook	B 3 Marley	82.7	35.03	<0.001
B10 Radbrook	B 4 Jews H	55.0	27.34	<0.001
B10 Radbrook	B 6 Nealings	56.4	41.03	<0.01

b) Earthworms

B 3 Marley	B 2 Upper F	97.7	58.89	<0.01
B 4 Jews H	B 2 Upper F	80.2	51.06	<0.01
B 3 Marley	B 6 Nealings	61.1	60.42	<0.05
B 3 Marley	B10 Radbrook	88.0	46.92	<0.001
B 4 Jews H	B10 Radbrook	70.5	36.62	<0.001

c) Cereals

B 1 Botley	B 3 Marley	88.5	65.72	<0.01
B 1 Botley	B 5 Sundays H	102.5	64.51	<0.01
B 1 Botley	B 6 Nealings	119.7	70.38	<0.001
B 1 Botley	B10 Radbrook	86.7	61.92	<0.01
B 2 Upper F	B 3 Marley	98.4	51.70	<0.001
B 2 Upper F	B 4 Jews H	62.6	44.83	<0.01
B 2 Botley	B 5 Sundays H	112.4	50.15	<0.001
B 2 Botley	B 6 Nealings	129.6	57.47	<0.001
B 2 Botley	B10 Radbrook	96.6	46.76	<0.001
B 4 Jews H	B 5 Sundays H	59.8	36.9	<0.01
B 4 Jews H	B 6 Nealings	67.0	46.37	<0.01
B 4 Jews H	B10 Radbrook	34.0	32.17	<0.05

d) Fruits

B 6 Nealings	B 1 Botley	57.8	30.97	<0.001
B10 Radbrook	B 1 Botley	34.5	27.25	<0.02
B 6 Nealings	B 2 Upper F	57.8	25.29	<0.001
B10 Radbrook	B 2 Upper F	34.5	20.58	<0.01
B 6 Nealings	B 3 Marley	46.0	23.34	<0.001
B10 Radbrook	B 3 Marley	22.7	18.13	<0.02
B 6 Nealings	B 4 Jews H	56.1	20.41	<0.001
B10 Radbrook	B 4 Jews H	32.8	14.15	<0.001
B 6 Nealings	B 5 Sundays	51.1	22.68	<0.001
B10 Radbrook	B 5 Sundays	27.8	17.27	<0.01
B 6 Nealings	B10 Radbrook	23.3	21.23	<0.05

types. Particularly noteworthy is the peak of cereal consumption in September.

Invertebrates Only two of the six ranges showed significant differences for invertebrates, namely the two ranges with the highest temporal diversification of diet, Range B4 and B10.

Fruits Two ranges with generally low temporal diversification were the only ones with no significant changes for fruits, one with a consistently low and one with a consistently high consumption.

Earthworms A similar result as for fruits: four of the six ranges with significant changes and the two not significant ranges with one with a consistently low and one with a consistently high consumption.

Cereals The prey category with the highest number of ranges with significant changes. Only Range B6 had a consistently high consumption of cereals throughout the months considered.

Summarizing we can say that temporal variation of the proportion of different prey categories in the diet is an important and regular phenomenon in most ranges.

Changes between ranges within single months Table 4.12 lists the results of the analysis to look at the spatial variation in the diet composition for each point in time considered. There can be no doubt that there is some variation between months in the amount of variation between ranges! No significant differences were found for May between Ranges B3, B4 and B5 fo each of the four major prey categories. There is an increase through early summer in the degree of spatial variation (measured by the number of prey types with significant spatial variation) to a peak in August with a subsequent decline towards November (Fig. 4.19c):

May	0	prey categories
July	3	" "
August	4	" "

Table 4.12 Kruskal-Wallis one-way analysis of variance on differences between badger ranges within a single month. Only significant results are presented

a) Results of the Kruskal-Wallis test for each month

Month	Ranges considered	Prey category	H (adj.)	signifi-cance (α)
July	1,2,3,4,5,6 10	invertebrates	32.53	<0.001
		earthworms	31.50	<0.001
		cereals	19.09	0.01
August	2,3,4,5,6,10	invertebrates	17.01	<0.005
		fruits	21.66	<0.001
		cereals	14.87	0.025
September	3,4,5,6,10	invertebrates	12.94	<0.025
		earthworms	24.84	<0.001
October	2,3,4,6,10	earthworms	24,21	<0.001
November	3,4,5,10	fruits	32.34	<0.001

b) Multiple comparison tests

Month	Prey	Range prey value high	low	Actual value	Critical value	Sig.
July	invertebrates	B 5	B 2	32.4	23.93	<0.01
		B10	B 2	62.5	24.35	<0.001
		B10	B 3	38.4	25.35	<0.005
		B10	B 4	38.8	17.3	<0.001
		B10	B 6	41.1	29.86	<0.01
	earthworms	B 3	B 2	39.5	31.67	<0.02
		B 2	B 2	42.2	24.64	<0.001
		B 3	B 4	38.7	26.3	<0.005
		B 5	B 4	41.4	17.2	<0.001
		B10	B 4	22.5	17.80	<0.001
		B 5	B10	18.9	16.89	<0.05
	cereals	B 2	B 3	45.5	43.69	0.05
		B 2	B 5	43.5	43.09	0.05
		B 2	B10	44.0	43.75	0.05
		B 4	B 3	27.5	23.96	0.01
		B 4	B 5	25.5	24.2	0.05
		B 4	B 6	25.2	27.6	0.05
		B 4	B10	26	24.14	0.05
August	invertebrates	B 4	B 2	11.7	11.60	<0.05
		B10	B 2	23.8	14.18	<0.002
		B 4	B 3	16.1	15.36	<0.05
		B10	B 3	28.2	17.39	<0.005
		B 4	B 6	20.2	16.09	<0.02
		B10	B 6	32.3	18.04	<0.001

August	fruits	B 5	B 2	23.0	11.09	<0.001
		B 3	B 4	10.6	10.42	<0.05
		B 5	B 3	14.6	13.02	<0.05
		B 5	B 4	25.2	10.42	<0.001
		B 6	B 4	12.6	10.92	<0.05
		B 5	B 10	19.1	11.80	<0.005
	earthworms	B 4	B 2	19.0	12.57	<0.005
		B 6	B 2	22.1	18.45	<0.05
		B 3	B 5	21.2	20.79	<0.05
		B 4	B 5	27.1	16.64	<0.005
		B 4	B10	20.3	14.13	<0.01
		B 6	B 5	30.2	21.43	<0.01
		B 6	B10	23.4	19.54	<0.05
	cereals	B 2	B 5	28.0	22.30	<0.01
		B 4	B 5	44.0	13.66	<0.001
		B 4	B10	35.0	20.79	<0.01
September	invertebrates	B10	B 3	14.1	9.63	<0.005
		B10	B 4	11.0	7.89	<0.01
		B10	B 5	14.1	12.48	<0.05
	earthworms	B 3	B 4	15.1	14.38	<0.05
		B 3	B 5	49.6	20.22	<0.001
		B 3	B 6	31.8	22.36	<0.01
		B 3	B10	30.4	14.16	<0.001
		B 4	B 5	34.5	18.52	<0.001
		B 4	B10	15.3	11.60	<0.02
		B10	B 5	19.2	18.35	<0.05
October	earthworms	B 2	B 3	24.8	22.32	<0.05
		B 2	B 6	28.9	18.36	<0.005
		B 2	B10	46.3	20.21	<0.001
		B 4	B 6	19.4	14.2	<0.01
		B 4	B10	36.8	16.52	<0.001
November	fruits	B 3	B 4	21.4	6.24	<0.001
		B 3	B 4	21.4	6.9	<0.001
		B 3	B10	20.0	6.19	<0.001

September	2	"	"
October	1	"	"
November	1	"	"

Invertebrates There is significant spatial variation during peak consumption times (July and August) and during a general decline in consumption (September).

Fruits Significant spatial variation occurs before peak consumption time in August and after peak consumption time in late autumn (November).

Earthworms Earthworms is the prey category with the highest spatial diversification: there is significant variation for all months except May and November, which are times of peak consumption while the other months form the mid-year "trough".

Cereals Significant spatial changes occur in times of peak consumption (July and August).

Thus there is considerable variation for all food types, but the spatial variation may occur either at times of peak or low consumption.

Synchronization in the changes of the diet between ranges As Fig. 4.17 indicated, ranges might show similarities in the way a diet component changes in its proportion from month to month (e.g. fruits) but also differences (marked differences in cereals, also some variation in earthworms). In Table 4.13b the results of the statistical analysis using Kendall's coefficient of concordance are presented. As could have been guessed from Fig. 4.17, the similarities between ranges in the direction of changes in the proportions of prey types are significant only for fruits and invertebrates, but not for cereals or earthworms.

4.3.3.4 Comparison of border and non-border latrines

So far the analysis of the badger diet in Wytham largely involved

Table 4.13 Degree of synchrony of fluctuations of the components of diet between different ranges, as expressed by W. Kendall's coefficient of concordance. As test statistic was used the statistic T_2 derived from Friedman's test, (Conover (1980), p.299-305). A significant result indicates synchronization.

a) Badgers: ranges 3,4,6, and 10 compared for the months July to October: (T_2 tested against F_{crit} with df = 3 and 9)

Prey type	T_2	T_3	W	Significnce
Invertebrates	3.985	6.846	0.571	<0.05
Fruits	5.604	7.816	0.651	<0.025
Earthworms	2.714	5.700	0.475	ns
Cereals	3.000	6.000	0.500	ns

b) Foxes: ranges 1,5,6,7, and 11 compared for the four seasons as defined in Table 4.1: (T_2 tested against F_{crit} with df = 3 and 12)

Prey type	T_2	T_3	W	Significance
Small mammals	1.464	4.020	0.268	ns
Invertebrates	17.667	12.231	0.815	<0.001
Fruits	28.25	13.14	0.876	<0.001
Birds	0.75	2.368	0.158	ns
Lagomorphs	7.417	9.745	0.65	<0.005
Scavenge	1.076	3.18	0.212	ns
Earthworms	1.688	4.451	0.297	ns
Cereals	1.573	4.234	0.282	ns

latrines that could be associated with one range only. I now want to investigate whether faeces collected from latrines on the border between ranges differ in their composition from those collected from latrines that lay inside the neighbouring ranges. If for instance two neighbours had a radically different diet and utilized the border latrines to equal amounts, differences should occur between border latrines (which comprise a sort of compromise of the diets of the two ranges) and the latrines lying inside the range of each neighbour.

There is no published evidence so far that badgers can detect the components of faeces. However, it is reasonable to assume that they can do so both by appearance and odour. It is known that badgers smell their prey, particularly earthworms (Kruuk, 1978b, pers. obs.) and that they are also able to distinguish individual badgers from their own group from badgers from another group by smell (Kruuk et al., 1984, Gorman et al., 1984). Beauchamp (1976) showed that guinea pigs (Cavia)can distinguish different metabolites in the urine of conspecifics. Badgers may therefore have some information about the diet of their neighbours. This may not be particularly useful during favourable times (e.g. in spring when all badgers eat a plentiful supply of earthworms). But at times when conditions are generally unfavourable (e.g. summer with its short, dry nights reducing the available earthworm populations) it would be of great value for badgers to assess what food resources the neighbouring ranges were exploiting. If badgers in one range have a disproportionate amount of a desirable resource it would seem to be beneficial to conceal this fact.

I investigated possible differences between border and non-border latrines in three steps:

1. For each range, border and non-border latrines were compared for possible differences in diet composition (always only the four major prey

types considered).

2. All border latrines were split according to the neighbouring range and for each possible differences between border latrines shared with different neighbours were investigated. For instance, Range B4 (Jews Harp) shared border latrines with neighbouring Ranges B 3 (Marley), B5 (Sunday Hills) and B6.

Results can be summarized briefly. No differences were found for any comparisons with two interesting exceptions: there were significant differences between border and non-border latrines in the amount of invertebrates consumed in July (Kruskal-Wallis test, H (adjusted) = 8.102, df = 2, n = 230, $p<0.025$) and there were differences in the amount of earthworms consumed in August (t-test, t = 1.99, df = 174, p = 0.049). In both cases the non-border latrines had a higher proportion of the food type in question than the border latrines. As these are results when the border latrines and non-border latrines are lumped over all ranges it is not possible to say whether these effects are restricted to particular borders accounting for the significant variation or whether this is actually the case for all borders. As Table 4.12 shows, there is significant spatial variation both for invertebrates in July and earthworms in August. If the composition of samples from the borders are a compromise of the diet of the neighbours, then there should be no significant differences between border and non-border latrines unless there is an active selection process by the badgers. Whether this is the case or not has to be determined by experimental procedures but the decision to distinguish between border and non-border latrines is certainly justified in the light of these results. An alternative explanation would be that males and females had different diets (at least for this period) and also different tendencies to use border latrines and non-border latrines. Although nothing is known about possible

sex differences, the results of the radiotracking seem to indicate that female badgers at least visit border latrines regularly. This of course does not exclude the possibility that males visit the border latrines even more frequently, but the proportion of 'active' latrines is lower during summer than in spring or autumn. Previous studies (e.g. by Kruuk and others) never indicated whether they distinguished between border and non-border latrines for their sampling scheme or during analysis. However, Kruuk (pers. comm.) states that he usually excluded border latrines from his sampling scheme.

4.3.4. Badger diet: summary

1. 1053 badger droppings were collected between May 1982 and October 1983 with samples in each month from May until November each year.

2. Earthworms were the most important component of the diet with 69% of samples containing earthworms and 61% of the estimated dry weight (EDW). Cereals are the second most important component with 36.5% frequency of occurrence (FO) and 17.7% EDW, followed by invertebrates (21.1% FO and 5.4% EDW), fruits (7.9% FO and 3.5% EDW) and tree fruits (4% FO and 4.2% EDW).

3. Of the twelve prey categories considered, eight occurred in less than 10% of the samples and seven of them contributed less than 1.5% EDW each.

4. There is marked temporal variation in some food types but not in others. The main components of the diet (earthworms, cereals, fruits, invertebrates) show a marked variation. Invertebrates, fruits, and cereals are mostly consumed during July and August, while earthworms are mostly consumed in spring and autumn with a trough in consumption in July and August. These

changes are highly significant.

5. There is a highly significant variation in the diet composition of different badger ranges for four prey types (invertebrates, earthworms, cereals, tree fruits). Only small mammals and fruits are equally consumed in different ranges. Each range appears in at least one pair of significantly different ranges for each food type that showed an overall significant spatial variation. The only exceptions are Ranges B1 and B5 for earthworms. Variation in the diet composition is highly and equally well spread amongst ranges.

6. Within each range, there is marked temporal variation in the amount of each of the four major prey types consumed (invertebrates, fruits, earthworms, cereals), with the exception of invertebrates where only two out of six ranges varied significantly. Variation is similar in direction but partly different in magnitude between different ranges.

7. There is some variation between months in the amount of variation between ranges. Significant spatial variation in invertebrates occurs from July to September and in fruits in August (time of peak consumption) and November (time of low consumption). Earthworms showed significant spatial variation from July to October at a time when all ranges generally increased their consumption of earthworms but at different rates of change, converging in November. Ranges show also significant differences in the amount of cereal consumption in July and August (peak consumption time). Ranges were synchronized in the direction of temporal fluctuations of prey consumption only for invertebrates and fruits but not in their changes of cereal or earthworm consumption.

8. Comparisons of border and non-border latrines for each range did not yield significant differences, nor did a comparison of border latrines shared with different neighbours, if all months are lumped. However, if data are lumped over all ranges, there was a significantly higher proportion of invertebrates represented in non-border latrines than in border latrines in July and the same was valid for earthworms in August.

4.3.5. Comparison with other studies

Fortunately, the diet of Wytham's badgers has been studied several times before (Hancox (1973), Hubertz (1978) and Kruuk (1978b)). Despite apparent differences between the studies in sampling design, purpose and duration, a broad consensus emerges. Hancox (1973) found that earthworms occurred in 91% of over 2000 badger faeces he collected from Wytham Woods, making up a total volume of 61%, a figure that comes very close to my result of 63.5% (estimated dry weight (EDW)) and 54% (estimated percent volume, ie. not corrected for the weight of the dropping). Kruuk (1978b) found in a sample of 39 droppings from September/October 1974 earthworms the most important element, followed by cereals, insects, bird remains and acorns. Hubertz (1978) found from a sample of two periods during summer (beginning and end of July) similar results as my study for July. Together with my study there is unequivocal evidence for the consistently important role earthworms play for the badger population at Wytham. Other studies from Britain (Kruuk et al., (1979), Kruuk and Parish (1981), Neal (1977)) support this impression and serve to confirm the notion of the badger as an 'earthworm specialist' (Kruuk and Parish (1981)). An interesting exception was found by Harris (1982, 1984). He investigated the social structure and the diet of a suburban population of badgers around Bristol and found scavenged items to be the generally most important element of the diet, only

surpassed by fruits in late summer and early autumn. Earthworms generally constituted between 20% and 30% of the diet (estimated by percent volume) with less marked seasonal variation as in this study. From other European countries there are the notable studies of Andersen (1954) from Denmark, Skoog (1970) from Sweden, Wiertz (1976) from Holland and a brief study by Kruuk and De Kock (1981) on the diet of badgers in northern Italy. Earthworms were again the most or one of the most important elements of the diet with the interesting exception of the Italian badgers which almost exclusively ate olives. However, there are also local variations. Wiertz (1976) emphasised the regularity by which small mammals and birds are consumed all year around by Dutch badgers (measured by FO). Skoog (1970) distinguished between a group of primary foods (most importantly earthworms; also insects, plant foods and mammals) and secondary foods (birds, molluscs, amphibians, reptiles and garbage plus carrion) in the diet of the Swedish badger. He also found a seasonal decline in earthworm consumption during summer and related this to the suboptimal soil temperatures with their detrimental effects on the activity and size of earthworm populations. Andersen's (1954) results on the diet of the Danish badgers showed similarities to Skoog's (1970) results both for the general composition and the seasonal variations. The large number of insectivores, especially shrews, that were eaten by Danish badgers was notable.

Excluding the two atypical studies of Harris (1982, 1984) and Kruuk and De Kock (1981), the seasonal trends found at different study sites emerge as remarkably similar for the prey types considered. However, there is only one study available with a full investigation of spatial trends: Kruuk and Parish's study (1981) on the diet of the Scottish badger (differences between several sites were also partly evaluated by Skoog (1970) and Wiertz (1976)). They compared the results of six study areas, ie. six different populations of badgers. So far, my study is the only one to have

investigated spatial variation within one study population. Comparing the results of the different study populations in Scotland with the results of the different ranges within the Wytham populations, some similar spatial and temporal trends appear. Invertebrates and fruits peak at the same times for both studies (if measured by percent volume); also the spatial units in both studies are synchronized for both prey items. Cereals peak at the same times in both studies; in Scotland the study areas were synchronized in their temporal fluctuations of cereal consumption while in my study the badger ranges were not. No synchronization between spatial units were found in either of the studies for earthworms. Interestingly, the Scottish badgers did not consume more earthworms in autumn than in summer (measured by percent volume) but decreased in their consumption slightly, while the FO of earthworms in samples was much higher in Scotland than in Wytham.

So far, no study except this one has distinguished between border and non-border latrines explicitly; in actual fact, hardly any study reports on the sampling scheme applied (most authors simply referred to the 'collection of droppings from latrines at setts and in the vegetation'). Therefore it is not possible to estimate the errors associated with the results of each study except in very general terms (e.g. sample size). From the results of my study some conclusions can be drawn on an appropriate sampling scheme. For instance, the sharp changes that can occur from month to month as detailed in previous sections (and also found to some extent by Skoog (1970) and others) are not adequately brought out by sampling latrines every two months (examples are Kruuk's and co-worker's studies). Most studies used only frequency of occurrence as a measure of diet and thus ignored most of the information that can be extracted from an analyis of the food remains. Whether the amount of underground defaecation follows temporal fluctuations of some kind is not known. Presumably the droppings placed underground are a similar, representative sample of the total diet as the droppings above

ground, so that ignoring them does not introduce a systematic bias but merely reduces the number of droppings available for sampling.

4.4. Comparison of fox and badger diet

The following comparison of the results of the analyses of the diet of Wytham's foxes and badgers emphasises patterns that emerged in sections 4.2 and 4.3. It was not possible to sample the faeces of both species in a directly comparable manner, since the patterns of deposition are different. This does not impede comparison of the diets of the two species since the collection resulted in a representative sample of faeces for both. Due to the reduced activity of the badgers in winter and the priorities of the study in spring, it was not possible to sample all seasons for the analysis of the badger diet. As a result concise information on the badger diet exists only for part of the year, although there is some indication as to what they consume during winter and spring. This of course reduces a quantitative comparison of the diet of the two species to the time from May until November.

From the results of the overall diet a measure of proportional overlap in resource utilization was computed (Colwell & Futuyma (1971), Southwood (1978):

$$\text{resource overlap} = 1 - 0.5 \sum_{i=1}^{11} \left| p_{i\,fox} - p_{i\,badger} \right|$$

with p_i: the proportion of estimated dry weight for a given prey category for a given species

The proportion of each prey category was recalculated after "others"

had been extracted. "Others" were excluded because it was not a taxonomic unit but an assemblage of various 'curiosities', and each type of curiosity occurred only once or twice. Resource overlap for the general diet as calculated by equation (1) was 0.46 for Wytham's foxes and badgers; this value is half-way between perfect separation (overlap = 0) and perfect overlap (overlap = 1).

Of the twelve major prey types considered, four items turned out to be important for badgers (earthworms, cereals, invertebrates, fruits) while there was a group of seven items important to foxes (earthworms, lagomorphs, scavange, fruits, birds, small mammals, invertebrates). Even though the badger diet was sampled only for late spring, summer, and autumn, this conclusion would presumably still hold for the entire year, as the cereals and fruits proved to be such an important part of the diet during summer.

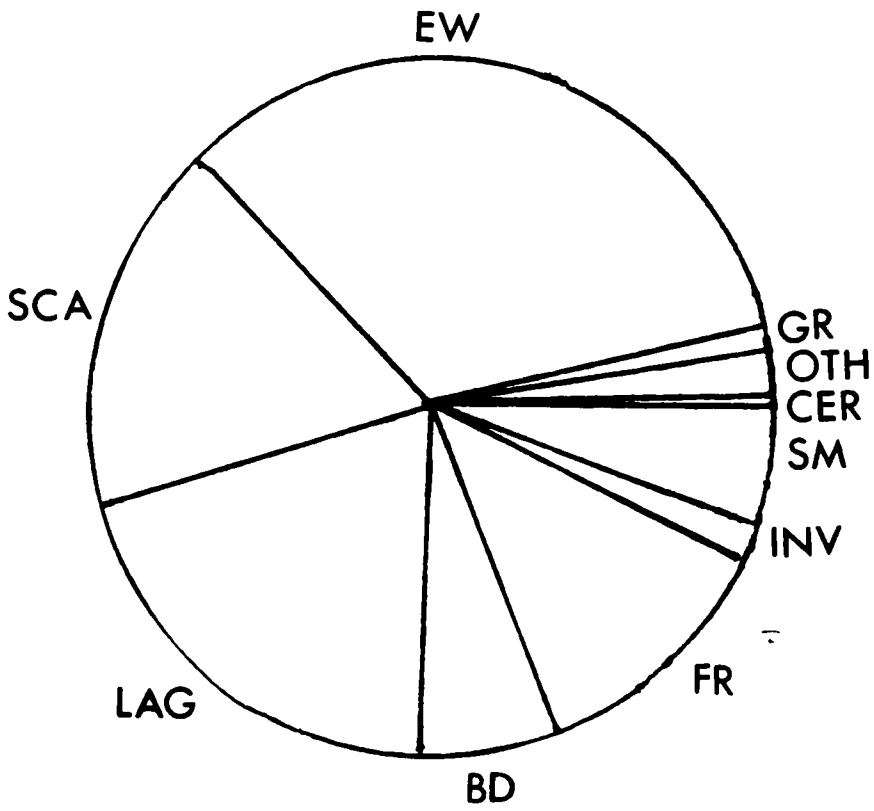
In general, food types show the same marked, temporal variation in magnitude and direction for both species: invertebrates and fruits peak during summer (so do small mammals for foxes and cereals for badgers and foxes). There are peaks of earthworm consumption in late spring and autumn for badgers (presumably also in early spring) and in late spring, autumn and winter for foxes. In addition, foxes ate lagomorphs mainly in late winter and spring and birds in May and June (badgers in July).

There is some variation in the diet composition of animals in different ranges for both foxes and badgers. The picture here is a little bit more complicated: fruits and small mammals are consumed equally in all badger ranges considered, but all other prey types (invertebrates, cereals, earthworms, tree fruits) vary significantly between ranges. In contrast, the three types of prey that showed significant spatial variation in foxes were small mammals, scavenge and lagomorphs. Variation between badger ranges is generally large and well spread as indicated by the high number of pairs of ranges with significant differences between the ranges of that pair

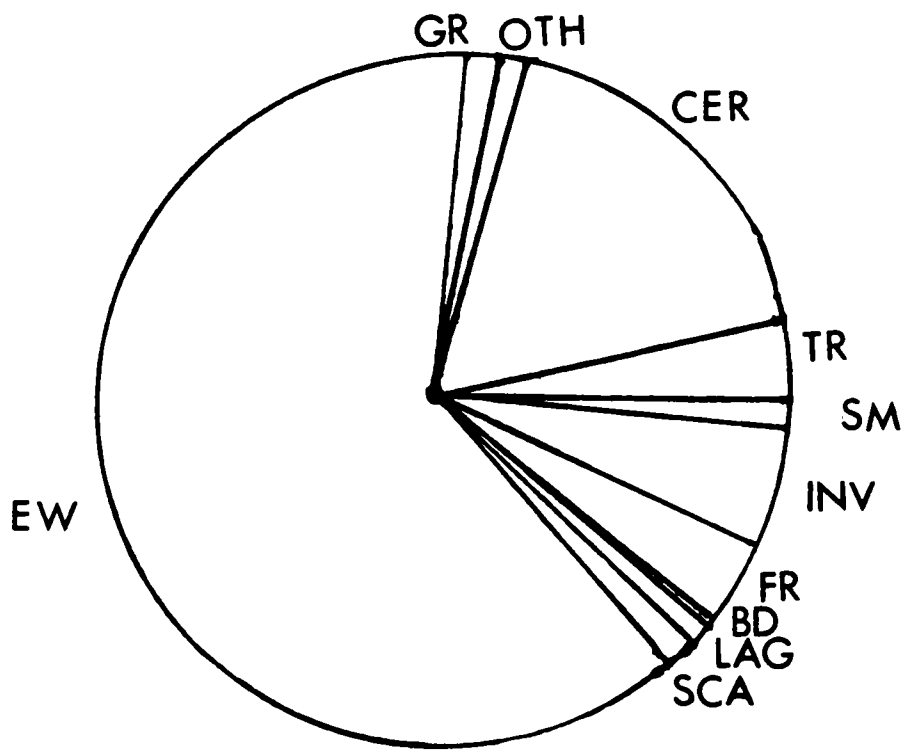
Fig. 4.18. Pie charts of the diet of Wytham's foxes and badgers as determined by estimated dry weight. Abbreviations for prey items as before.

Fig. 4. 18

FOXES



BADGERS



and the fact that with two exceptions all ranges appear in at least one pair of significantly different ranges for each food type. In contrast, the number of significantly different pairs was small for foxes except for lagomorphs and usually one or two ranges had a much larger proportion of a certain prey category in their diet than all others.

There are some differences in the degree of temporal variation in the diet of animals from different ranges. In badgers, all ranges show a significant temporal variation for all food types except invertebrates (only some ranges). The direction of the temporal variation is generally the same but the magnitudes might vary considerably between ranges. Foxes consumed fruits, invertebrates and lagomorphs in all ranges to the same of earthworms and no pattern discernible in the time of peak consumption of scavenge. Scavenge did not show any temporal variation in any of the ranges.

However, for both foxes and badgers there is some variation between months and seasons in the amount of spatial variation. Interesting contrasts are the significant spatial differences for earthworms in badgers for late summer and early autumn while there are no such differences in foxes. Both foxes and badgers show a significant spatial variation in fruit consumption in summer and autumn. Invertebrates show significant spatial differences in spring and autumn for foxes and in summer and autumn for badgers. Small mammals vary significantly for foxes in spring, lagomorphs in three out of four seasons and birds not at all. In Fig. 4.19c the number of prey categories with significant spatial variation is plotted against time (different time scales for foxes (seasonal) and badgers (monthly) as sample sizes were insufficient for monthly evaluations of the fox diet). Because of the different time scales, the results are not directly comparable for foxes and badgers but a more fine grained analysis for foxes would presumably have confirmed the results depicted in Fig. 4.19c and 4.18d. Looking at the results for summer, a general increase in

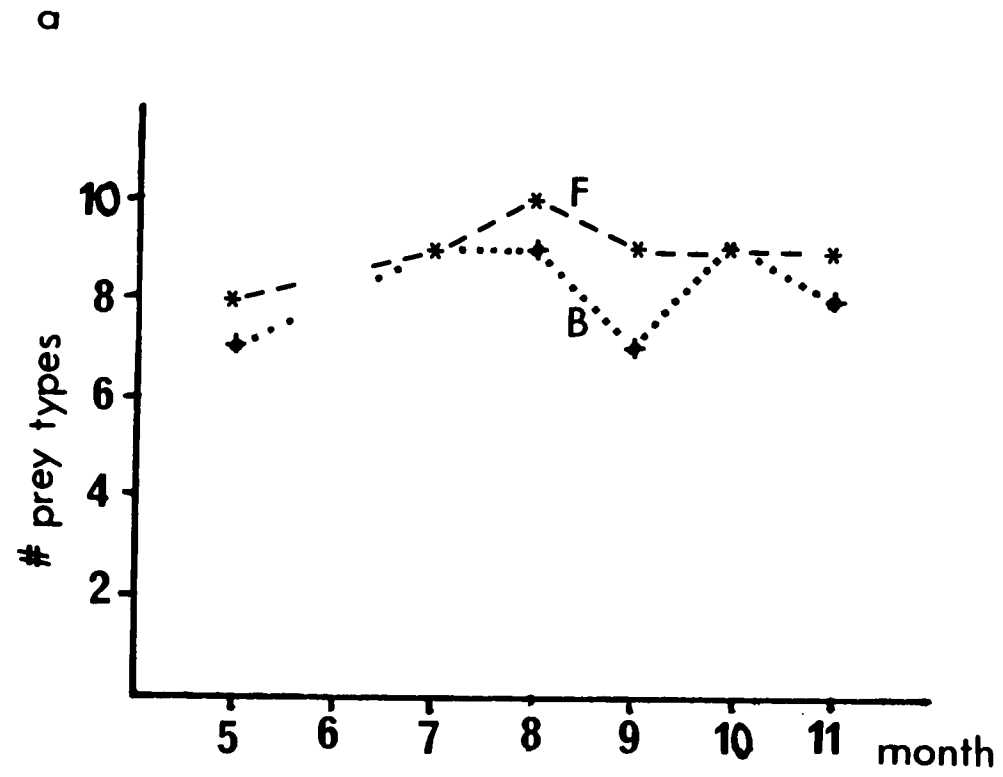
Fig. 4.19. Comparison of seasonal changes in the diet of Wytham's foxes and badgers in

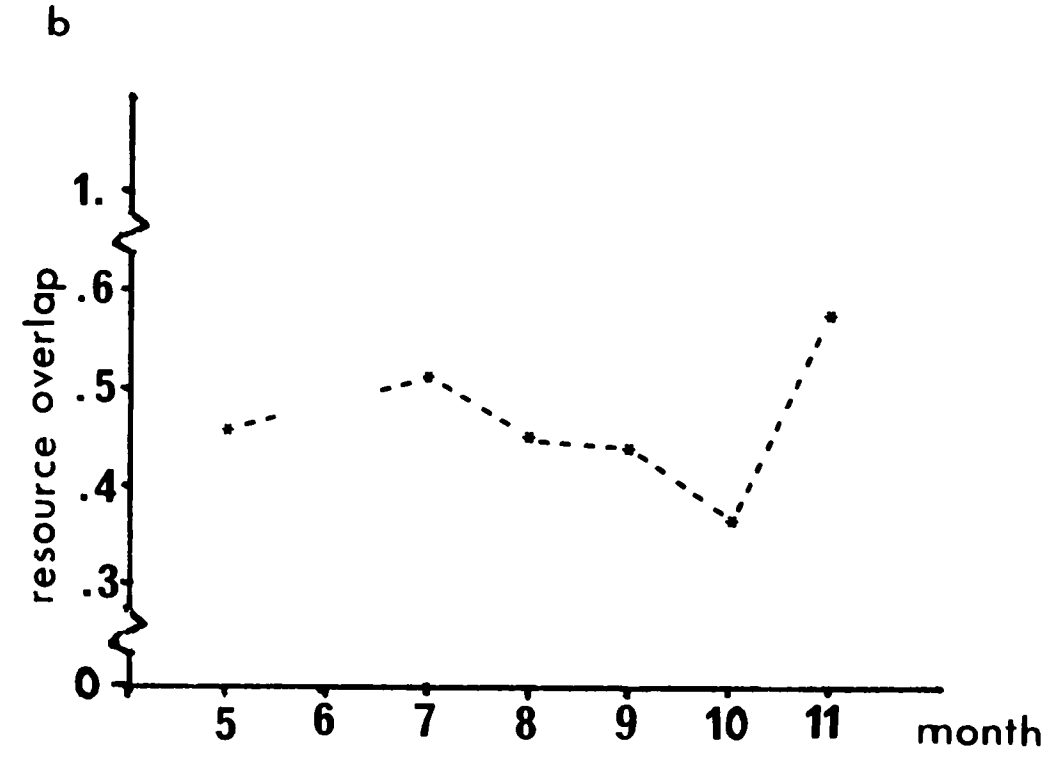
a. number of prey types present in the diet per month, for entire populations.

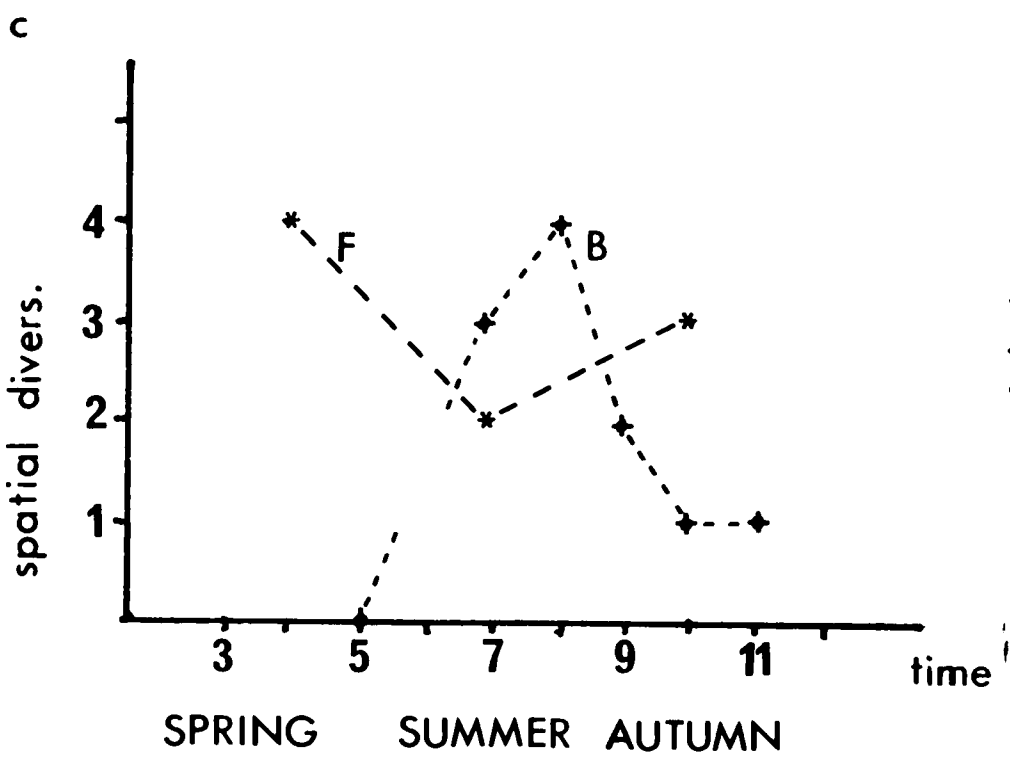
b. resource overlap between foxes and badgers as computed by Colwell & Futuyma's (1971) formula (see text); data from entire populations.

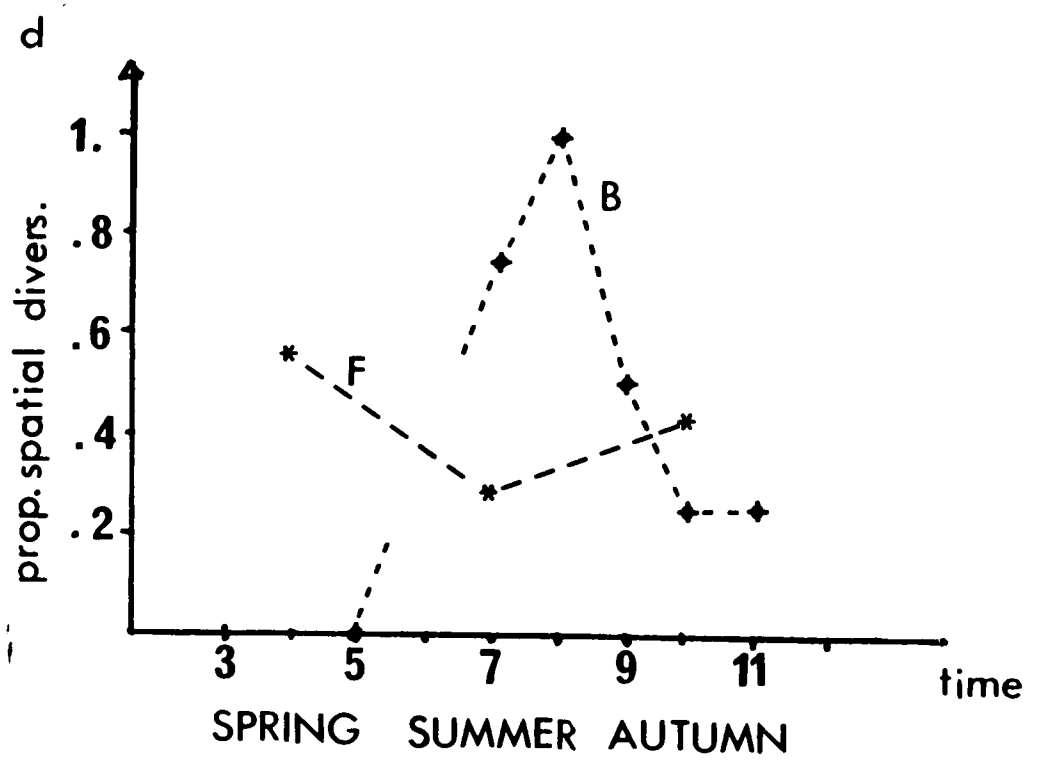
c. spatial diversity of diet, ie. the number of prey items with significant differences in consumption between groups; for badgers evaluated per month, excluding June; for foxes evaluated per season and plotted for the central month of each season.

d. proportional spatial diversity of diet, ie. spatial diversity in relation to total number of different prey types consumed per time unit.


a
prey types
10
8
6
4
2
F
B
5
6
7
8
9
10
11
month


b
resource overlap
1.
.6
.5
.4
.3
0
5
6
7
8
9
10
11
month


c
spatial divers.
4
3
2
1
F
B
3
5
7
9
11
time
SPRING
SUMMER
AUTUMN


d
prop. spatial divers.
1.
.8
.6
.4
.2
F
B
3
5
7
9
11
time
SPRING
SUMMER
AUTUMN

diversification of the fox diet (Fig. 4.19a) is paralleled by a process of increasing spatial uniformity (Fig. 4.19c and 4.19d). Corresponding to this is the increase of the resource utilization overlap with badgers (evaluated monthly and shown in Fig. 4.19c and 4.19d) but also in spatial diversification (Fig. 4.19c and 4.19d). The parallel development of general diversification of badger and fox diet and the utilization overlap between the two indicates that both consume first more and then fewer prey types to a similar extent. This is the result of a comparatively uniform consumption pattern of different fox ranges while the badger ranges show an extreme spatial variation. As the important prey types are mostly the same for both species (invertebrates, fruits, earthworms, cereals; in addition scavenge and lagomorphs for foxes) they face probably parallel trends in prey availability. Local variations in prey availability are compensated far more by foxes than by badgers. Whether this is an indication of competitive inferiority of badgers is doubtful and shall be discussed below in detail.

It is obvious that some badger groups become specialists on one prey e.g. cereals for periods of time (e.g. Ranges B2 and B4 for July) when they seem to abandon their usual foraging tactics (as glimpsed from the results of the majority of other temporal units). Range B4 for instance has a significantly smaller consumption of earthworms in July than Range B10 (Table 4.12b and Fig. 4.16c), an 'invertebrate specialist'. This has already changed in the next month (August) and remains so until the consumption of earthworms in the two ranges reaches a similar level in late autumn. Of the important food categories for both species at the time of the peak in resource utilization overlap in July only earthworms are in a 'bottle-neck' situation while cereals and invertebrates (beetles) appear to be superabundant (see Chapter 3). From the point of view of possible competition between the two species a comparison of the fluctuations in consumption of earthworms seems most promising. As Table 4.5b and 4.5c

show, there are no significant differences in temporal fluctuations for each fox range nor in spatial fluctuations for each season in earthworm consumption. In contrast, earthworm consumption varies between badger ranges significantly, each range shows significant temporal changes and each month considered shows a significant spatial variation. The only exceptions are two ranges (Range B3 with a particularly high and Range B6 with a particularly low earthworm consumption) and one month (November when all ranges consumed equally high amounts of earthworms).

The most sensible explanation for this pattern seems to arise from a consideration of the actual amounts of earthworms consumed in relation to population density and range size. During summer, when earthworm consumption by badgers is low and at a maximum spatial diversification, it is actually as high as the consumption by foxes (25% EDW for foxes in July and 30% for badgers; Fig. 4.5 and 4.14), although badgers' ranges are roughly half the size of foxes' ranges (Chapter 5) and the group size of badgers is usually larger than that of foxes (ie. there is a potentially higher earthworm hunting pressure per area unit by badgers than by foxes). Despite the potentially higher hunting pressure by badgers they manage to consume still more earthworms than the foxes do although the earthworm population availability is in a bottle-beck period during summer! This, if anything, indicates that badgers are at least as successful in earthworm predation as foxes are and there is some evidence that they are actually superior (Chapter 3).

Additional support for this explanation can be seen from a consideration of the situation in November. From October to November there is a steep rise in the resource utilization overlap reaching its highest value (Fig. 4.19b). Now the trends in spatial diversification are just the opposite of the situation in summer: badgers show a low spatial diversification, ie. the food consumption is fairly uniform over all ranges while there is a higher

spatial diversification in foxes. However, foxes have a very high consumption of earthworms (45% EDW, badgers 79% EDW). This is a large difference but it is smaller than those of previous months. At the same time, earthworms are plentifully abundant and thus there is the opposite of the bottle-neck situation in summer. Considering the super-availability of earthworms in November, it is not surprising that both foxes and badgers consume lots of them and there is little indication of competition between the predators.

Summarizing we can say that there are two peaks in the resource utilization overlap between the diet of foxes and badgers, one coinciding with a trough of earthworm availability in summer when badgers reduce their earthworm consumption to the level of consumption by foxes (as measured by percent contribution to the diet of the range) and the other peak coinciding with a peak of earthworm availability. In the first case, competition is possible between foxes and badgers, while for the peak in November competition seems unlikely when a high utilization overlap coincides with high prey availability. This indicates how resource utilization overlap may vary independently of the degree of competition and that one cannot necessarily be deduced from the other. The analysis shows furthermore how a detailed understanding of the temporal and spatial variation in resource utilization is absolutely necessary to gain an adequate understanding of the relationship of two species (this is perhaps even more important if k-selected species are involved in the comparison). In the light of these results, much of the current discussion on competition and resource utilization based on relatively coarse-grained data, such as one value for resource overlap for the whole year, may look like scratching only the tip of the iceberg.

5. Fox and badger home ranges

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5.2.3. Observations

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5.4.1. Description of badger group ranges

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.1. Distribution of latrines

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5.5. Fox group ranges

5.5.1. Description of fox group ranges

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5.6. Habitat composition of and resource use in group ranges

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5. Fox and badger home ranges

In this chapter I consider how foxes and badgers partition the resource space into home ranges for individual use. After a description of group ranges and scent-marking patterns which may be relevant to the maintenance of the ranges, I will deal with the resource distribution and abundance within home ranges, as evidenced by their habitat composition. In particular, I will explore how home range features relate to habitat and resource use, as indicated by the diet of the groups. Finally, models are discussed that describe how individual and group ranges should be dispersed in space given a certain set of conditions of resource dispersion and availability.

5.1. Review of home range concepts

Burt (1943) defined home range as the area over which an animal normally travels during activities associated with feeding, resting, reproduction, and shelter-seeking. This excluded 'occasional sallies' outside this area as well as dispersal by adolescent animals. This concept has been recognized as extremely useful, even if some authors differ in their opinion as to how excursions should be defined (Wilson 1975, Southwood 1978, Harestad & Bunnell 1979 and others). Home ranges discussed in this chapter exclude outside sallies.

Despite general agreement in principle, as to what constitutes a home range, there is a wealth of methods for determining range configuration and size. Several of them constitute models in that they assume a certain utilization distribution and construct range borders from an assumed utilization distribution rather than taking into account the distribution of the original data points. A survey of these and other methods is presented

in Table 5.1, together with examples for applications from the literature.

As I shall show in Chapter 6, utilization distributions of fox and badger ranges are extremely variable and do not fit any of the proposed distributions (e.g. bivariate normal). Furthermore, many of the non-parametric probabilistic models assume independent data points, which are extremely difficult to obtain (see Appendix 4), and therefore are of limited usefulness. This leaves methods that do not make assumptions about utilization distributions and other qualities of ranges, ie. the hand-drawn method, the minimum convex polygon and the grid method. Since hand-drawn home ranges suffer from observer bias and absence of rigorous rules, I prefer the grid method and under some circumstances, the minimum convex polygon (MCP).

5.2. Methods of data collection

Information on home ranges of foxes was derived from radio-tracking of animals that had previously been captured and fitted with a transmitter. Capturing and tagging followed the standard techniques employed by members of the Oxford Foxlot for many years and have been described in detail elsewhere (Macdonald 1978, Newdick 1983, Doncaster 1985).

Information on home ranges of badgers was combined from radio-tracking of animals and the results of the non-invasive bait marking technique developed by Kruuk (1978a) and described in more detail in Section 5.2.2. Badgers were caught in large steel cage traps that were placed close to setts and prebaited with peanuts for at least a week. Trap doors were either released by the badger's weight on a tredle or operated from a hide by a long cord (see Cheeseman & Mallinson 1980). Traps were checked once daily early in the morning. The trapping was in accordance with an NCC licence issued to Dr. D.W. Macdonald. Captured invididuals were

Table 5.1. A comparison of methods for the determination of home range size and configuration.

Method	Principle	Advantages	Disadvantages	Example & Ref.
Hand drawn method	Draw range border by hand	incorporates other useful informations from behavioural observation allows detailed construction of perimeter	subject to observer bias constant level of field knowledge in each range assumed no rigorous rules to define construction of range border	Vulpes vulpes Macdonald 1977a
Minimum area(convex polygon)	connect peripheral locations such that all internal angles are < 180 degrees	easy to do by hand many studies for comparison available non-parametric	considerable sample size bias assumes range border to be convex	Vulpes vulpes Hough 1980
Grid	count locations in grid cells	construction of detailed perimeter poss. non-parametric independent data points not required	size of grid cells defined post hoc or arbitrarily exact definition of range dependent on observer decision	Vulpes vulpes Newdick 1983
Regression	data from well-sampled individuals used to predict ranges of less well-sampled individuals	empirically based unbiased for small sample sizes considers size,symmetry and skewness of utilization	assumes similar utilization distribution of several ranges complicated in application many individuals required	lizards Schoener 1981
Probabilistic methods				
Bivariate normal	Draw x % confidence ellipses around arithmetic mean of locations	calculation simple	biological importance attributed to arithmetic home range centre normality of data assumed sensitive to temporal contingency	Vulpes vulpes Macdonald, Bolitani Barrasso 1980
Ornstein-Uhlenbeck method	as bivariate normal, correcting for lack of temporal independence	allows for correlation between successive locations (data need not be independent)	biological importance attributed to arithmetic home range centre assumption of normality of data	Vulpes vulpes Macdonald, Rall, Hough 1980
Population utilization distribution method (PUD)	simulate space-use pattern using frequency distribution of distances between all pairs of points estimate minimum area containing a specified proportion of animal's space use	non-parametric gives fairly good estimates with few data	sensitive to temporal contingency present program implementation offers only a 7x7 grid on which space use is based	Calidris melanotos (pectoral sandpiper) Ford & Myers 1981
Harmonic mean	compute isopleths (lines of similar use) around a harmonic mean centre	mimics skewed placement of centres of activity	assumes a centre of activity in home range sensitive to temporal contingency	Dixon & Chapman 1980
Fourier ransform	models utilization by generating a smoothed function through Fourier transformation	non-parametric estimates close to true values in all cases	assumes independent observations	Cervus elaphus nelsoni (wapiti) Anderson 1982

anaesthetized with ketamine hydrochloride, a safe and widely used immobilization drug (see Beck 1976, Ramsden et al. 1976), before they were taken out of the trap. Each individual was measured, weighed and fitted with eartags made by Dalton Supplies Ltd, Nettlebed, Oxon. Eartags were numbered and an attempt was made to mark members of the same group with different colours. Adult badgers were then fitted with radio-transmitters around their neck. The transmitter collar was made of first-class saddle leather which proved to be ideal for balancing the need of firm attachment to the body while at the same time not impeding its movements. A beta-light, manufactured by Saunders & Roe Ltd and embedded in translucient acrylic was fixed to the upper side of the collar to facilitate observations in the dark. Animals were then placed close to the sett entrance from which they had emerged, to facilitate their orientation after rewakening. I stayed with the animals for at least half an hour to check that they were well and safe after regaining consciousness.

5.2.1. Radio-tracking

Radio-tracking was principally carried out from a car, since home ranges were generally too large to be covered effectively on foot. Some attempts were made to follow foxes through woodland on foot; invariably, the foxes were lost within two hours. Following badgers on foot was more successful and I could follow individuals even through dense plantations for several hours, largely due to the betalight which could be seen for up to two hundred metres. Intensive radio-tracking on foot was done in Autumn 1982 for fourteen days in the Jews Harp Range (see below), not only to register the movements of individuals but also observe their activities and monitor their emergence patterns from setts.

On the roof of the car a three element yagi antenna was mounted and

connected to an AVM LA12 receiver (AVM Instrument Co. Ltd., 2368 Research Drive, Livermore, CA 94550). The antenna could be rotated by a handle from the inside of the car. A direction indicator and a protractor fitted to the rotating handle completed the tracking device and enabled me to monitor signal strength and direction while driving. Benefits of such a design include rapid recording of locations, minimizing errors by always stopping at sites with optimal signal strength and reduced waste of time, since driving in the wrong direction was quickly noticed. With an experienced operator, this design made it possible to record locations every minute.

Recording of locations followed one of two schemes: either several animals were tracked, or one individual was followed continuously. With the first approach, data on several individuals were collected quickly. This is especially important if several animals have been equipped with radios within a few days, since it was our experience that transmitters either stop functioning after four or five days, or go on for a long time. With growing experience, and following preliminary data analysis, it became clear that the greatest benefit was derived from intensive monitoring lasting for several days, so in the last radio-tracking season an attempt was made to follow particular indidivuals for consecutive nights. Since foxes were infrequently, but regularly seen active during the daylight, I also followed the movements of indidivual foxes continuously for 60 hours on three occasions (here I am indebted to Chris Bowden, Helen Dolk, Marion East, Gillian Kerby, David Macdonald and Colin Pringle who followed the animals during the hours I was asleep).

If an animal was followed continuously, a location was recorded if it moved its position from the previous location. This could mean that a location was taken every minute, if the animal moved quickly through an area, but often an animal would stay within the same area of ca 20 by 30 metres for up to an hour. In this case, the same location was recorded

every 15 minutes, to indicate that the animal was still there and I still awake. As a result, time intervals between recording times of successive locations were very variable, but the record of movements was complete.

Locations were determined by triangulation (see Macdonald & Amlaner 1980, Deat et al. 1980). This was straightfoward with animals that were either inactive, or moving slowly. With rapidly moving animals, triangulation demanded successive bearings that were only a few seconds apart and this sometimes necessitated taking fixes from otherwise suboptimal sites. The vast majority of locations were obtained from rather slow moving animals, so larger errors possibly associated with fast moving animals will have little influence.

Accuracy of radio fixes was estimated to average about 30 metres. This estimate is based on experiments with hidden transmitters, chance observations, and years of experience in the Oxford Foxlot. The accuracy of much of the data is better than the 30 metre error margin since my tracking often resembled what Macdonald (1978) has called 'predictive tracking'. For example, while tracking members of the Botley Lodge badger clan in Marley Plantation, I would see the individual at least a dozen times during the night and stay as close as 50 metres sometimes for several hours in a row. The positions of my favourite triangulation places were determined during the day by reference to the Wytham Forestry grid system and the Wytham Atlas (see Chapter 2) and marked on the tracking maps. These were sites where radio signal reception was especially strong. By confining myself mostly to such sites, I sought to reduce errors by building up a mental picture of the transmitting qualities which differed greatly between individual radio-collars.

In summary, there are many possible sources of error in radio-tracking (see Amlaner & Macdonald 1980 for reviews). In this study I was fortunate to overcome most of them and to generate data to a much greater level of

accuracy than is customary in radio-tracking studies.

5.2.2. Bait marking and badger latrine checks

Bait marking is a non-invasive technique that was developed by Hans Kruuk (1978a) and first successfully applied in his earlier study on Wytham badgers in 1974. Each badger sett is supplied with a mixture of peanuts and small plastic pellets (length ca 2-3 mm) coated in golden syrup. Each sett was supplied with a different colour of plastic pellets. Small mounds of the bait were placed in several holes and covered with soil or sand so that birds, particularly crows, did not take them. As some fox faeces indicated, this was not entirely successful with respect to other animal groups. Badgers ate the mixture and passed the pellets to their faeces in latrines, where the origins of the individuals using a latrine could then be traced due to the different colour codings. Baiting continued every day for two or three weeks in March, July, October 1982 and March 1983. Setts were baited in July 1982 since the decision was taken to enlarge the area of interest, thus including the setts of the Radbrook Common area and the first line of setts west of the Chalet (Fig. 5.4). However, due to reduced utilization of latrines in summer, delineation of range borders remained doubtful and a third baiting period was chosen for the same year. I am indebted to Adrian Barnett and Rory Howlett for supplying the badger setts with peanuts and beads in July and October respectively. Setts were selected for baiting (i) if badgers had been active there in previous weeks, (ii) because setts were included in the Annual Badger Census (ABC) of the Animal Ecology Research Group in May, or (iii) because they had been used by badgers in Kruuk's (1978a) study. A detailed list of setts baited is presented in Table 5.4, sett locations are indicated in Fig. 5.1 - 5.6

Latrines were classified as 'border' or 'non-border' latrine. A latrine

was assigned border status of it was shared by neighbouring ranges, usually indicated by the recovery of plastic beads originating from different setts. In ranges at the fringe of the core study area, existence of neighbours was occasionally uncertain. In these cases, some of the latrines that were used to delineate the range border (e.g. SW-corner of Range B1, BOTLEY LODGE, Fig. 5.5) were excluded from analysis of range diet (Chapter 4) and latrine activity (section 5.4.2).

Latrine utilization was gauged by three kinds of parameters:

(a) number of new latrines founded and total number of latrines available (ie. total of recently and previously found latrines);

(b) proportion of latrines with at least one recent dropping ("active" latrines) of all latrines available and checked in a given month;

(c) measures of intensity of use per latrine:

(i) AREA: the area of a rectangle (in m^2) with side lengths equivalent to the maximum length and maximum width of a latrine measured at right angles;

(ii) TOTAL: the total number of pits per latrine, ie. shallow excavations either empty or filled with anal sac secretion and/or dung;

(iii) FILLED: number of pits per latrine that contained at least one badger dropping or anal sac secretion;

(iv) FRESH: number of pits per latrine with at least one recent dropping (deposited within the last 48 hours) or anal sac secretion.

5.2.3. Observations

Observations of the behaviour of foxes and badgers were of three kinds (Section 4.2.1.): observing radio-tracked foxes and badgers, watching from hides as badgers emerged from their setts (and returned to them), and chance observations of animals. Observations during the night were made either using an image-intensifier or infrared binoculars, and notes were spoken into a dictaphone. Monthly checks of badger setts, fox earths and rabbit warrens were used to locate fox litters. Earths with fox litters are characterised by a large area of cleanly swept bare soil in front of the entrances, flies, fox tracks, scats and prey remains (Lloyd 1980). If a litter was located in a den, observations were occasionally undertaken at dusk to confirm the presence of fox cubs and determine litter size.

5.3. Methods of analysis

5.3.1. Processing procedures for telemetric data

Tracking locations were recorded as pairs of x,y coordinates to the nearest 10 metres on the National Grid System. These coordinates, together with date, time, an estimate of the confidence (error) for the location, activity of the animal, observation, weather conditions (air temperature, wind direction and wind speed according to the Beaufort scale, degree of precipitation, relative humidity, cloud cover) were typed into computer files, one each for each individual. Program SRCH2H (written by Ken Royall and Malcolm Newdick) tagged each location with its appropriate patch and habitat number with reference to the computerized habitat map (see Chapter 2). Program ICELLH, a modified version of program ICELL (written by Malcolm Newdick) was used to plot all radio-tracking fixes on a grid based map, so

typing errors could be checked (e.g. indicated by anomalous position). All data files were checked line by line and compared with the original data sheets. Later, program VELOCITY fitted polynomials to calculate movement speeds. All very fast speeds were checked again and the last typing errors eradicated. These procedures took a very long time, but as a result I feel that at least 99% of all locations typed in have their correct coordinates attached to them.

Home range sizes of individual animals and of fox group ranges were analysed by evaluating tracking data on a grid of 50 by 50 metre cells. This size was considered a satisfactory compromise between the estimated tracking error, sample size considerations, the desired spatial resolution of space use patterns and the average habitat heterogeneity per cell. A cell size of 25 metres is not particularly useful, since the suggested maximum error of radio tracking, 30 metres, exceeds the cell size. Larger cells, e.g. 100 metre cells, decrease sample size considerably and represent quite a heterogeneous assemblage of different habitats, thereby increasing the difficulties of interpreting movements with reference to habitat types. Also, larger sizes do not permit a fine spatial resolution of the exact delineation of the range border and range utilization patterns (see Chapter 6).

Selection of tracking data poses a problem for most applications, including the determination of range sizes and the habitat composition of ranges, since a common assumption is independence of data points. However, this condition is rarely fulfilled by tracking data. The problem is discussed in Appendix 4 in detail, and procedures are suggested to overcome it. It was concluded that selecting data at an interval of 15 minutes ("independence interval") results in approximate and, for our purposes, sufficient independence of data points. Therefore, tracking data were selected by this criterion, unless data from intensive tracking periods with

'time-tabling' of movements could be used.

Individual home range sizes were usually based on the grid method (Voigt & Tinline 1980), where the number of cells with radio locations multiplied by the cell size yields the range size. The effect of data selection procedures on estimates of range size was explored by adopting the following measures:

(1) "15 MIN RADIO": fixes selected according to the 15 min independence interval; only cells with radio locations.

(2) "15 MIN OCCUPIED": as (1), plus cells immediately surrounding a radio cell ("influence cells"), unless they are at the border of the range. Every individual must have passed through at least one of the eight influence cells surrounding a radio cell to reach the point of radio location. With discontinuous tracking schemes, the record of the movement path of an individual is incomplete and the correct neighbouring cell may have been missed by the researcher. Hence, Newdick (1983) suggested to correct this deficiency by including influence cells in range calculations. Delineation of range border remains unchanged, but the inner area of the range is 'filled up'.

(3) "15 MIN TOTAL": as (2), plus cells that are completely enclosed by radio and/or influence cells but do not belong to either of the categories (empty spaces, so-called "lakes"). While inside the border of the range, these cells do not belong to the actively used sections of the range.

(4) "0 MIN OCCUPIED": as (2), but no independence interval, all fixes admitted.

(5) "0 MIN TOTAL": as (3), but no independence interval, all fixes admitted.

(6) "MCP"(Minimum Convex Polygon): all fixes admitted, range border delineated according to the minimum convex polygon method (Table 5.1).

Measures (1) to (3) and (4) to (5) are distinguished by the time

interval of data selection while within both groups measures are distinguished according to procedures intended to correct for deficiencies in recording procedures. Estimates of range sizes according to measures (1) to (5) were produced by program ICELLH (modified from Newdick 1983), estimates according to measure (6) were produced by program CV written by Malcolm Newdick. Results for individual lifetime ranges are presented in Table 5.2. Size estimates show differences up to 900 %. Obviously, the choice of data selection and method of computation is not a trivial one, if absolute range size is important, e.g. if range size is considered in relation to body size, metabolic needs etc (Harestad & Bunnell 1979, Gittleman & Harvey 1982).

Do the six measures produce a similar trend for estimates of range size for foxes and badgers ? The results of calculations of Kendall's coefficient of concordance (see Appendix 3) listed in Table 5.3 show that this is the case. According to multiple comparisons between different measures (Conover 1980), measures are ranked as follows (listed from producing small to large estimates):

Foxes: 15 MIN RADIO < 15 MIN OCCUPIED < 0 MIN OCCUPIED =
15 MIN TOTAL < 0 MIN TOTAL = MCP

Badgers: 15 MIN RADIO < 15 MIN OCCUPIED < 15 MIN TOTAL =
0 MIN OCCUPIED < 0 MIN TOTAL = MCP

For both species, 15 MIN RADIO yields on average the smallest range size estimate and MCP the largest. Differences between species in ranking of the measures concerns the positions of 0 MIN OCCUPIED and 15 MIN TOTAL. This is probably an effect of different recording schemes (Chapter 6). In contrast to foxes, badgers were very intensively tracked (fixes often only a few

Table 5.2 A comparison of home range sizes (ha) of individual foxes and badgers calculated by different methods. Range sizes were computed by programs ICELLH and CV using the following options:

15-RAD: 15 min independence interval; radio cells
15-OCC: 15 min independence interval; radio cells plus influence cells (see text)
15-TOT: as 15-OCC, plus unused cells completely surrounded by radio or influence cells
0-OCC : as 15-OCC, but all locations admitted
0-TOT : as 15-TOT, but all locations admitted
CV : minimum convex polygon method.

Name	15-RAD	15-OCC	15-TOT	0-OCC	0-TOT	CV	Perime-ter (m)
a) Badgers							
Ali	19.00	31.00	31.25	31.00	31.25	30.64	2122
Eliane	15.25	34.75	37.00	37.25	39.00	36.85	2312
George	13.00	30.25	32.25	40.00	42.75	37.86	2478
Jo	14.00	34.25	36.25	37.50	39.50	37.85	1904
Nani	17.50	23.50	23.50	23.50	23.50	24.68	2189
Noears	17.75	52.00	53.75	58.00	58.50	54.99	2952
Peaceful	25.75	39.00	39.25	39.75	40.00	41.67	2536
Sara	17.00	25.00	25.00	28.50	28.75	28.68	2284
Wilf	28.25	53.75	57.00	53.75	57.00	54.71	2887
b) Foxes							
Bramble	32.00	73.75	98.25	75.75	101.75	121.27	4188
Elke	56.25	110.50	130.25	124.50	139.50	148.91	4922
Gasper	20.25	47.75	91.25	55.25	102.75	179.92	5767
Grizzle	17.00	47.75	49.50	52.00	53.25	49.24	2657
Kali	45.75	101.50	138.75	128.75	164.75	196.62	5280
Kboom	78.00	157.75	200.00	173.75	213.00	259.28	6122
Kobuk	24.00	61.50	103.25	65.50	103.75	169.31	5729
Lio	26.00	71.00	92.00	97.25	121.00	190.70	5796
Oldmahog	73.75	160.75	192.50	166.75	200.25	241.88	5966
Pintooth	44.25	73.50	76.00	75.00	78.75	71.43	3162
Podge	43.75	83.50	99.50	94.50	105.25	121.35	4635
Surprise	22.25	65.75	91.00	69.75	91.00	85.71	3811
Taru	7.00	22.50	23.50	26.50	28.25	34.58	2543

c) are the methods consistent in their effect on range size estimates within a species ? (estimate of synchrony of influence by Kendall's coefficient of concordance, W)

Badgers: $W = 0.73$, $df = 5, 40$, $p < 0.001$
Foxes : $W = 0.82$, $df = 5, 60$, $p < 0.001$

For both species, the different methods are highly consistent in their influence on estimates of range size.

Table 5.3 Analysis of the effects of data selection method on the estimation of individual range sizes: Multiple comparison tests.

Measure producing a high estimate	Measure producing a low estimate	actual value	critical value	significance
(1) BADGERS				
15 OCCUPIED	15 RADIO	13.0	8.6	< 0.01
15 TOTAL	15 RADIO	24.0	8.6	< 0.01
0 OCCUPIED	15 RADIO	27.5	8.6	< 0.01
0 TOTAL	15 RADIO	39.5	8.6	< 0.001
MCP	15 RADIO	31.0	8.6	< 0.001
15 TOTAL	15 OCCUPIED	11.0	8.6	< 0.05
0 OCCUPIED	15 OCCUPIED	14.5	8.6	< 0.01
0 TOTAL	15 OCCUPIED	26.5	8.6	< 0.01
MCP	15 OCCUPIED	18.0	8.6	< 0.01
0 TOTAL	15 TOTAL	15.5	8.6	< 0.01
0 TOTAL	0 OCCUPIED	12.0	8.6	< 0.01
(2) FOXES				
15 OCCUPIED	15 RADIO	13.0	8.4	< 0.05
15 TOTAL	15 RADIO	38.5	8.4	< 0.001
0 OCCUPIED	15 RADIO	32.0	8.4	< 0.001
0 TOTAL	15 RADIO	54.5	8.4	< 0.001
MCP	15 RADIO	56.0	8.4	< 0.001
15 TOTAL	15 OCCUPIED	25.5	8.4	< 0.01
0 OCCUPIED	15 OCCUPIED	19.0	8.4	< 0.01
0 TOTAL	15 OCCUPIED	41.5	8.4	< 0.001
MCP	15 OCCUPIED	43.0	8.4	< 0.001
0 TOTAL	15 TOTAL	16.0	8.4	< 0.01
MCP	15 TOTAL	17.5	8.4	< 0.01
0 TOTAL	0 OCCUPIED	22.5	8.4	< 0.01
MCP	0 OCCUPIED	24.0	8.4	< 0.01

minutes apart), hence a relatively high proportion of data is excluded by the application of a time interval and therefore the difference between 15 MIN OCCUPIED and 0 MIN OCCUPIED is larger than for foxes. The often discontinuous tracking scheme for foxes produced smaller homogeneous areas completely covered by radio cells, hence more "lakes" are produced and therefore the difference between 15 MIN OCCUPIED and 15 MIN TOTAL larger.

To exclude these effects of different recording regimes and facilitate intra- and interspecific comparisons, I decided to use estimates of range sizes as determined by the most conservative measure, 15 MIN RADIO, both for the establishment and the determination of the habitat composition of fox group ranges.

Fox group ranges were established by combining all cells visited by the members of a fox group. Table 5.23, section 5.5., lists the radio-tracked members of each group. Membership of an individual to a group was identified by a large proportion of overlap of an individual's range with those of other foxes in the same area. This posed no problems at all, since ranges were clearly separated from each other (Fig. 5.30-5.33). In three groups (Ranges 5, 6, and 7), males of the group (OLDSABRE, BOOTS, RABBITS) were only tracked for brief periods; their ranges showed complete overlap with those of their respective females (KBOOM, OLDMAHOG, PINTOOTH). In most other groups, only one group member was caught and radio-tracked, despite extensive trapping efforts. Only in the HOMEFARM group, several, probably all group members were caught and tracked. Group range size, delineation of range border, habitat composition and diet (Chapter 4) were based on a range that was cleansed from overlap zones with neighbouring ranges. Overlap zones were determined by the procedures described in Appendix 3, ie. cells visited by individuals of both neighbouring ranges in the border ones were excluded from both ranges. Not considered in this pruning procedure were occasional excursions by individuals into neighbouring ranges or even further away.

Examples of such excursions are (i) an excursion by the vixen PODGE (HOMEFARM Range) of more than 2 km outside her usual range during the mating season (26-27.1.1982), (ii) several day-time visits by the dog-foxes GASPER and KOBUK (HOMEFARM Range) to an area approximately 3 km outside their usual range, and (iii) several excursions of KBOOM (WOODEND Range) into the neighbouring range of PINTOOTH (HILL END CAMP Range). Excursions show a pattern of movement distinct from the usual ranging behaviour (e.g. Hough 1980): usually, the individual starts quite late (ca 2 to 3 a.m.) and moves rapidly into a specific direction over a long distance. Movements in border zones are not distinguished from movements well inside a group range, as far as radio-tracking can tell.

By restricting myself to the pruned sections of fox group ranges I hope to have minimized the uncertainty regarding the ownership of a particular area and included only those sections of a range that are exclusively used by a group. Any remaining errors due to misidentification of the ownership of a particular area will, however, work against any conclusions to the effect that a given characteristic differs between groups.

5.3.2. Habitat and diet description of ranges

Each grid cell that was (by previous procedures) identified as part of a home range served as the base area for extracting 9 equidistant points (program HABCOR2), that were subsequently tagged with their respective habitat and patch numbers according to the computerized habitat map (Chapter 2; program SRCH2HAB). Programs HABSEL2 and HABLUMP summarized the output of SRCH2HAB by habitat and by cell respectively. Thus, an estimate of the proportion of habitats represented in a range (in absolute as well as relative values) was derived, and the habitat composition of each cell identified.

Variability of the absolute and relative proportion of a habitat in group ranges was assessed by Levene's test (Van Valen 1978, Schultz 1983). Since the mean values of the area (in % or ha) occupied by different habitats differed widely, it seemed sensible to assess relative rather than absolute variability, as expressed by the coefficient of variation. For each habitat category, the median over all group ranges was identified and new variables calculated according to

$$y_{ij} = | x_{ij} - x_{med,i} | / x_{med,i}$$

with y_{ij} the new variables

x_{ij} the area in % or ha of the i-th habitat category in the j-th group

$x_{med,i}$ the median for the i-th habitat category

There has been much debate recently as to what kind of measure(s) of variation perform best for biological problems, especially in systematics (Van Valen 1978, Sokal & Rohlf 1981, Schultz 1983). Several authors cited by these studies agree that Levene's test is the most robust, yet simplest test presently available. On Schultz's (1983) recommendation I used the median instead of the mean as an estimate of central location. The new variables y_{ij} were then tested on differences between habitat categories with the Kruskal-Wallis one-way analysis of variance because of its usual advantages (Appendix 3).

A stepwise discriminant analysis was run using the BMDP package, in order to prove whether, despite considerable inter-group variability in habitat composition of ranges, species were consistent in their choices relative to each other. Program BMDP7M was run with option FORCE=0. Then, only habitat types are included in the classification function, if they are

above a certain limit (F-to-enter was set as 4.0). The resulting classification indicates which habitat variables are best suited to distinguish fox and badger home ranges.

The procedures used to determine the diet of groups have been explained in sections 4.2.2. and 4.3.2.

5.4. Badger group ranges.

The results of the sett baiting actions in 1982 and 1983 are presented in Table 5.5 and Fig 5.1-5.4 (only those latrines from which beads were recovered are plotted). The proportion of active latrines from which beads were recovered varied between 32.2 and 58.6 %. The small number of active latrines in spring 1982 made an unambiguous identification of some sections of range borders difficult. Since the proportion of bead recoveries in 1982 was similar for latrines later assigned border or non-border status (binomial test, summed probabilities, one-tailed, p=0.435, 0.601 and 0.705), additional information on the movements of individuals was used for the determination of range boundaries. Spring 1983, however, saw a threefold increase in the number of active latrines (Table 5.5) with more border latrines than expected containing beads (binomial test, summed probability, one-tailed, p = 0.006). Since the level of latrine activity during the remainder of 1983 fell back to and partly below 1982 levels (section 5.4.3.), spring 1983 should be interpreted as a time of intense marking activity leading to (i) well-defined range borders and (ii) high efficiency in deduction of range borders by bead recovery.

I shall now discuss each range in detail, starting in the south-east corner of the study area.

Table 5.4 Main badger setts selected for bait-marking. Numbering of setts follows the list kept for the Annual Badger Census (ABC) of the A.E.R.G.

Sett No.	Sett name	Bait marking action Mar 82	Jul 82	Oct 82	Mar 83	Kruuk's sett No.
1	The Mount	yes	yes	yes	yes	9
2	Common Piece	–	yes	yes	yes	10
3	First Turn	–	–	–	–	–
4	Holy Hill	–	–	–	–	12
5	Thornycroft	–	–	–	–	11
6	Great Ash Hill	–	–	–	–	13
7	Great Wood	–	–	–	–	(13)
8	The Chalet	–	yes	yes	yes	14
9	Hill/Lord's Copse	–	yes	yes	yes	7
10	Rough Common	–	yes	yes	yes	16
11	Lower Seeds	–	yes	yes	yes	–
12	Brogden's Belt	yes	yes	yes	yes	8
13	Radbrook Common	–	yes	yes	yes	–
14	Burkett's Plant.	–	yes	yes	yes	7
15	Sunday's Hill	yes	yes	yes	yes	–
16	Nealing's Copse	yes	yes	yes	yes	6
17	The Pasticks	yes	–	yes	yes	–
18	Jew's Harp	yes	yes	yes	yes	4
19	Bracken	yes	–	–	–	(3)
20	Marley Main	yes	yes	yes	yes	2
21	Singing Way	–	–	–	yes	–
22	Upper Follies	yes	yes	yes	yes	1
23	Botley Lodge	–	yes	yes	yes	–
24	The Park	–	yes	yes	yes	–
25	The Platform	yes	–	–	–	3
26	Hill End Camp	yes	yes	yes	yes	5

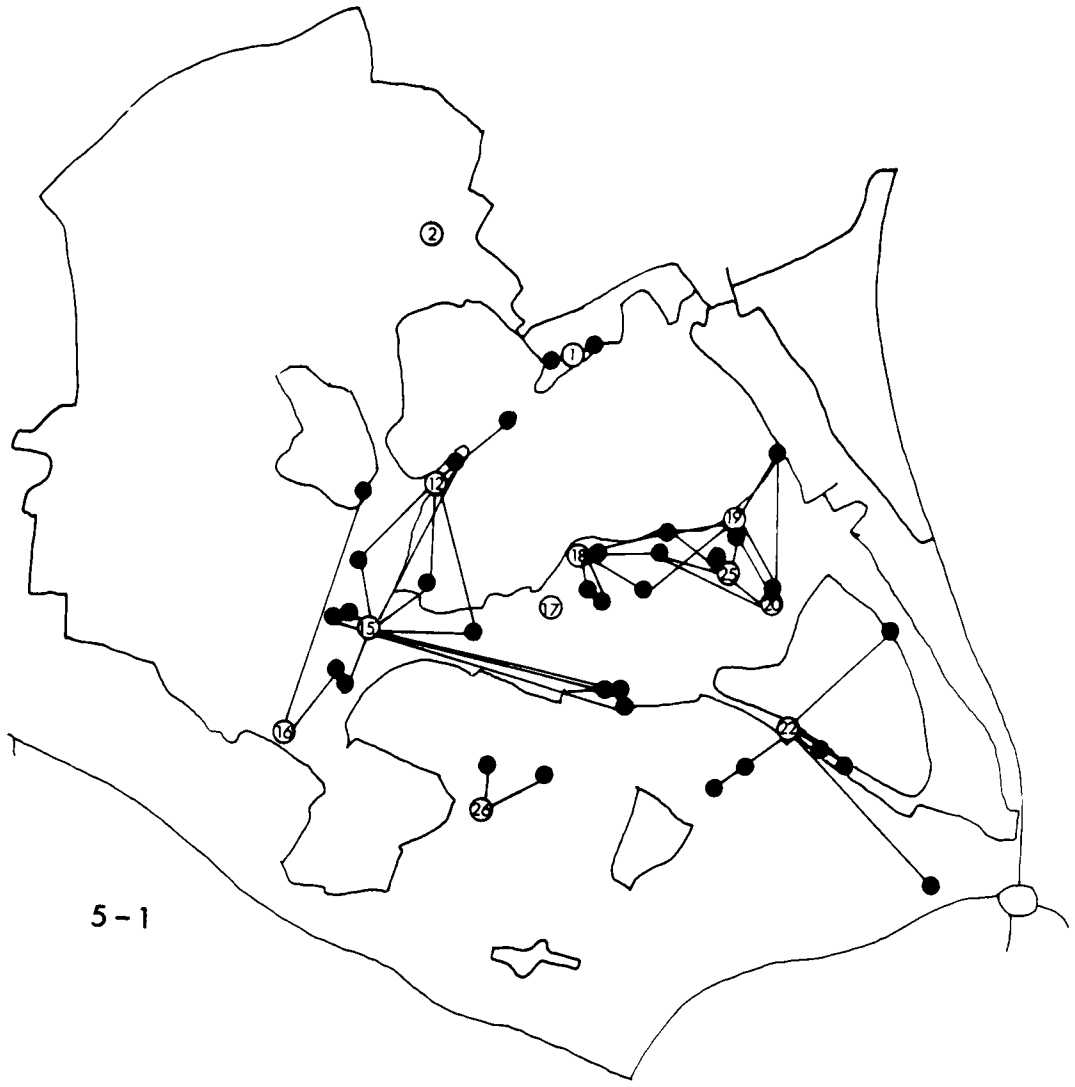
Table 5.5 Proportion of 'active' badger latrines from which plastic beads were recovered. (L = Latrines)

Variable No.	Latrine Type	Mar 82	Jul 82	Oct 82	Mar 83
1	No. of L checked	68	62	105	256
2	No. of active L (ie. containing fresh droppings	58	37	59	185
3	No. of L with beads	34	14	19	79
4	Proportion 3/2 (%)	58.6	37.8	32.2	42.7
5	No. of active border L	24	19	22	56
6	No. of border L with beads	13	8	7	35
7	Proportion 6/5 (%)	54.2	42.1	31.8	62.5
8	No. of active non-border L	34	18	37	129
9	No. of non-border L with beads	21	6	12	44
10	Proportion 9/8 (%)	61.8	33.3	32.4	34.1
-	Binomial test (prob.)	0.705	0.435	0.601	0.006

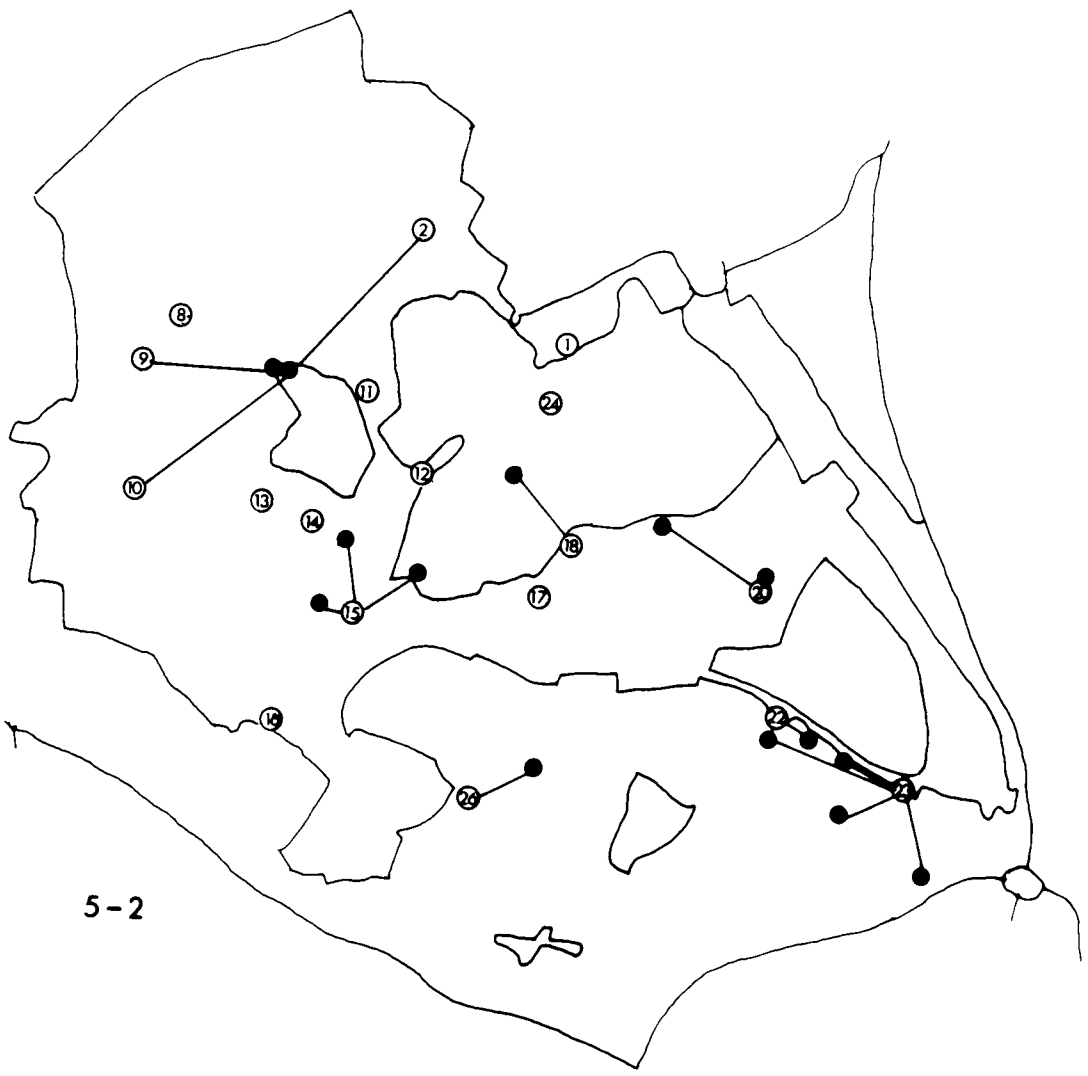
Fig. 5.1-5.4

Results of baiting actions of badger setts, for spring 1982, summer 1982, autumn 1982 and spring 1983, respectively.

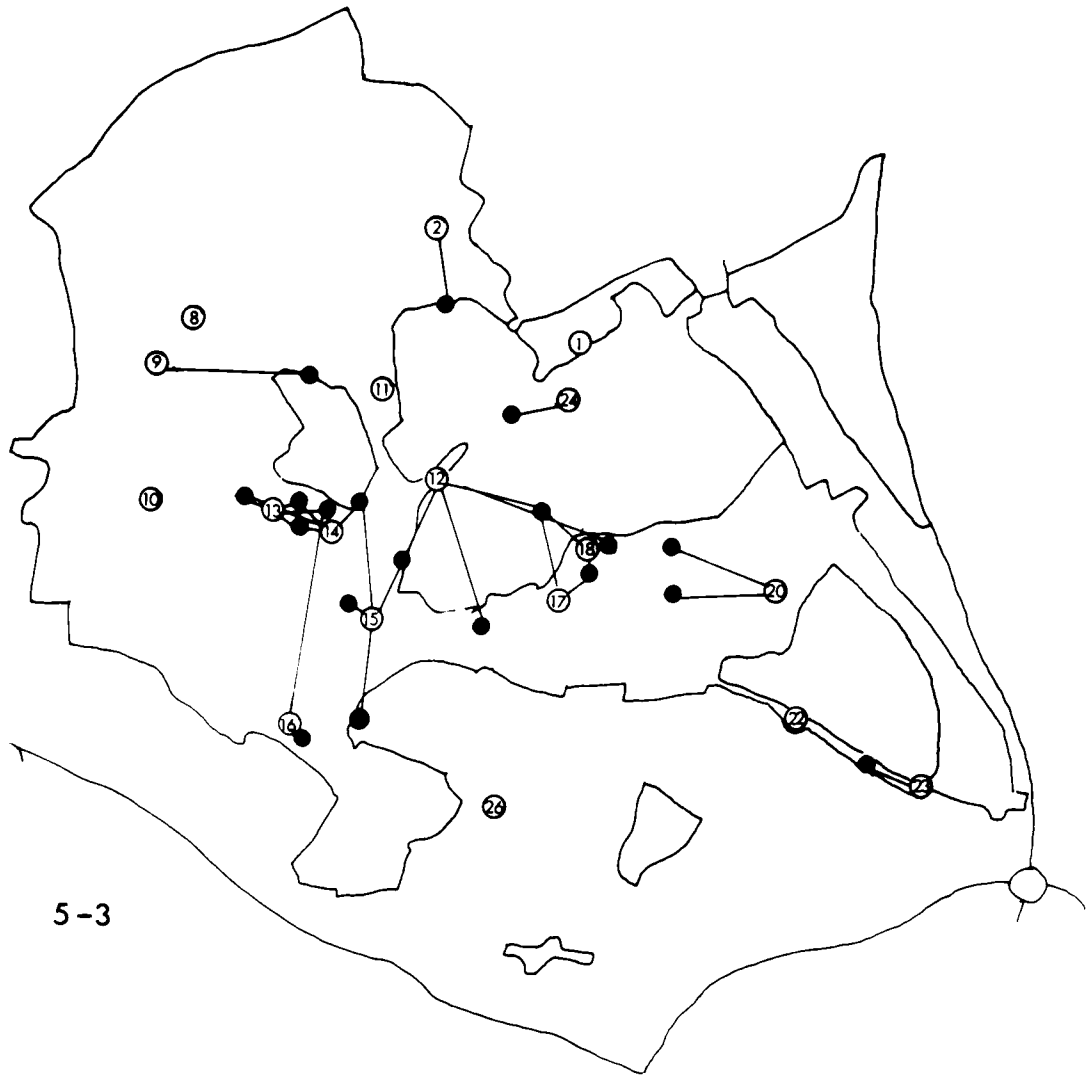
The thin lines delineate the major woodland borders, and the western bypass (eastmost line) and the Eynsham Road (southern line). Encircled numbers indicate identity of setts according to Table 5.4. Latrines from which beads were recovered are indicated as filled circles; the lines connecting latrines with setts indicate the origins of beads recovered from the latrines.


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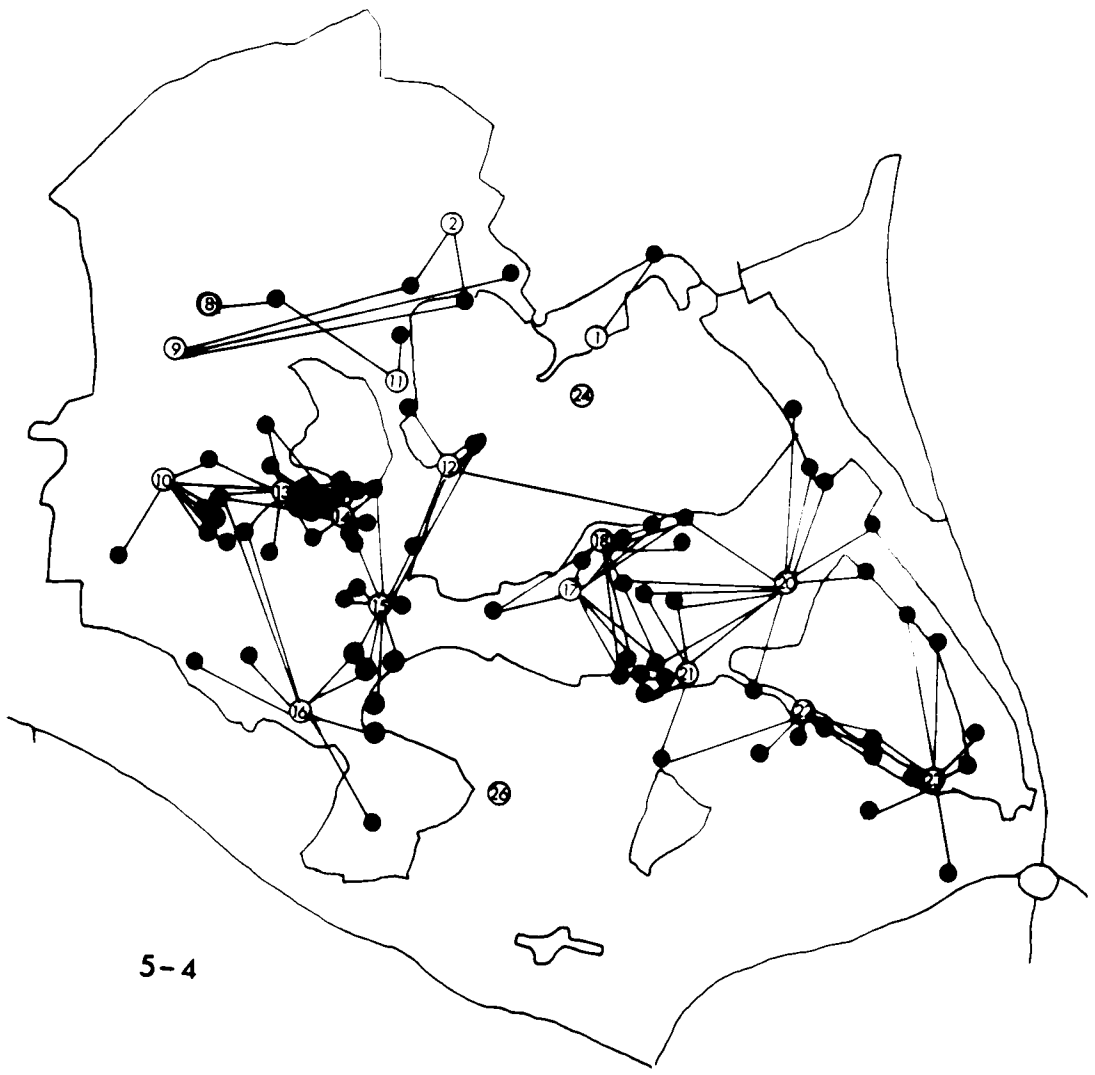
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5.4.1. Description of badger group ranges.

Range B1 (BOTLEY LODGE). Sett 23, the Botley Lodge sett (Table 5.4, Fig. 5.6) is situated on a steep slope close to a track road and hidden behind dense elderberry thickets. Digging activity was pronounced throughout the study period and more intense than at any other sett. In spring 1982, one sett and one outlier were present; in autumn 1982 and spring 1983 two more outliers were dug (Table 5.7).

Range B2 (UPPER FOLLIES). This range contains one main sett (22, Fig. 5.6) but no outliers. 11 border and 24 non-border latrines were located in this range (Table 5.6). The history of latrines is similar to the BOTLEY Range; the majority of 1983 latrines were placed along the edges of pasture fields (e.g. Fig. 5.10). Range B2 shares its eastern border with Range B1 and the north and north-west sections with Range B3. The exact delineation of the western section was difficult, since it could not be established whether there was a direct neighbour group to this side. Since the resident badgurs ranged extensively in the south-west pasture field (Fig. 5.10-5.12), I used as borter line the straight connection of the local latrine to the latrine north of Higgin's Copse from which beads were recovered (Fig. 5.4). During the ABC, two adults were observed in 1982 and none in 1983, although in August 1983 three adults were caught (Table 5.9). Similar to Range B1, the male WILF and one female NANI were quite old while the second female ALI appeared to be younger. Since the Upper Follies sett was well used throughout the study period (Table 5.7), I conclude that the captured animals were resident - albeit not seen - during the ABC. The extensive excursions of WILF (Fig. 5.12) into Range B1 are discussed in more detail in section 5.4.2 and Chapter 7.

Table 5.6 Number of new latrines per range in 1982 and 1983. 1 = Spring 1982; 2 = remainder of 1982; 3 = Spring 1983; 4 = remainder of 1983; T = Total. TOTALS (bottom line): each latrine counted once only !

Range	Border latrines					Non-border latrines					All latrines				
	1	2	3	4	T	1	2	3	4	T	1	2	3	4	T
BOTLEY	5	2	2	–	9	1	5	9	2	17	6	7	11	2	26
UPPER F.	6	2	3	–	11	5	2	13	4	24	11	4	16	4	35
MARLEY	8	2	5	–	15	6	9	15	2	32	14	11	20	2	47
JEWS HARP	10	3	7	–	20	6	12	7	4	29	16	15	14	4	49
SUNDAYS H.	10	4	6	1	21	7	1	8	1	17	17	5	14	2	38
NEALINGS C.	6	–	9	1	16	–	5	10	9	24	6	5	19	10	40
THE MOUNT	1	3	3	–	7	3	1	5	–	9	4	4	8	–	16
LOWER S.	5	1	7	–	13	–	–	6	2	8	5	1	13	2	21
COMMON P.	1	1	4	–	6	–	–	3	–	3	1	1	7	–	9
RADBROOK C.	7	2	9	–	18	4	2	15	3	24	11	4	24	3	42
CHALET	3	–	6	–	9	–	–	2	–	2	3	–	8	–	11
ROUGH C.	1	–	8	–	9	5	2	4	–	11	6	2	12	–	20

Table 5.7 Number of setts and outliers per badger range. 1 = Spring 1982; 2 = Autumn 1982; 3 = Spring 1983; S = number of active setts; SH = number of used holes, summed over all setts per range; O = number of active outliers; OH = number of used holes summed over all active outliers per range; TOTAL = numbers of setts and outliers present, but not necessarily used per range; x) does not consider setts or outliers outside the study area.

Range	Setts						Outliers						TOTAL		
	1		2		3		1		2		3				
	S	SH	S	SH	S	SH	O	OH	O	OH	O	OH	S	O	
BOTLEY	1	2	1	2	1	2	–	–	1	1	2	2	1	3	
UPPER F.	1	5	1	7	1	10	–	–	–	–	–	–	1	0	
MARLEY	3	11	2	8	5	23	1	1	1	2	2	3	5	5	
JEWS HARP	2	6	2	8	2	13	4	6	5	7	2	3	2	16	
SUNDAYS H.	2	5	2	7	2	19	–	–	–	–	2	5	2	9	
NEALINGS C.	–	–	1	3	1	2	–	–	–	–	–	–	1	0	x)
THE MOUNT	1	5	2	8	2	20	4	6	–	–	–	–	2	4	
LOWER SEEDS	2	7	1	1	1	11	4	6	–	–	–	–	2	8	
RADBROOK C.	2	15	2	9	2	14	1	1	–	–	1	1	2	9	
ROUGH C.	1	2	1	2	1	2	–	–	–	–	1	1	1	1	x)
Total	15	58	15	55	19	116	14	20	7	10	8	13	20	55	

Table 5.8 Observations of badgers useful to the determination of (1) range boundaries or (2) group structure or (3) group size (see comment).

Range	Date	Time	Coordinates	Animal	Activity	comment
UPPER F.	16.03.83	21.30	4795 0712	1 ad	crossing track towards SW	1
MARLEY	04.06.82	00.00	4777 0817	1 ad	coming from Home Farm	1
"	11.09.82	22.45	4749 0732	1 ad	crossing track towards NE	1
"	12.09.82	21.15	4737 0736	1 juv	crossing track from N to S	1,2,3
"	19.03.83	21.20	4745 0737	1 ad	on junction rushing NW	1
JEWS HARP	18.04.83	20.20	J.H. SETT	1 ad	unmarked, emerged	3
"	16.06.83	15.00	4720 0780	LORY	resting under a tree	2,3
"	27.06.83	23.15	4685 0742	1 juv	running NW into plantations	2,3
"	28.06.83	06.15	Pasticks S.	1 juv	grooming on top of sett	2,3
SUNDAYS H.	14.09.82	00.00	4662 0749	WHITE EART. juv	coming from border latrine going SW	1
THE MOUNT	16.09.82	23.27	4706 0861	1 juv	crossing road towards sett	2,3
LOWER S.	23.09.82	20.50	4618 0860	1 ad	coming from N towards 3rd ramp but turned from latrine at road back N	1
RADBROOK	19.05.83	20.00	Burkett S.	6 ad	emerged from sett	3

Table 5.9 Badgers caught and radiotracked in Wytham 1982/83. Location: number of sett according to Table 5.4. x) transmitter mounted at second capture on April 18th, 1983.

No.	Range	Date of 1st capture	Location	Sex	Age	Name	eartag colour	ear-tag no.	trans-mitter days	fate
1	BOTLEY	20.05.83	23	M	ad	GEORGE	pink	15	37	?
2	"	17.08.83	23	F	ad	SARA	green	68	71	?
3	"	19.08.83	23	F	ad	HELEN	orange	23	52	?
4	UPPER F.	17.08.83	22	F	ad	ALI	green	69	67	?
5	"	17.08.83	22	F	ad	NANI	red	50	58	?
6	"	17.08.83	22	M	ad	WILF	blue	61	67	?
7	MARLEY	21.06.82	20	F	ad	NOEARS	-	-	58	?
8	"	01.05.83	19	F	juv	-	green	58/59	-	?
9	"	02.05.83	19	F	juv	-	red	48/49	-	?
10	JEWS HARP	11.09.82	18	F	ad	PEACEFUL	pink	13/14	412	?
11	"	11.09.82	18	M	juv	VICIOUS	red	24/25	31x)	dispersed to MOUNT in 1984
12	"	12.09.82	18	F	ad	SCARLESS	-	-	34	?
13	"	15.09.82	17	F	ad	LORY	blue	21/22	110	?
14	"	18.09.82	17	F	ad	JO	orange	9/10	283	found dead at Hill End Camp on 15.05.84
15	SUNDAYS H.	05.07.82	15	M	juv	-	white	166/167	-	?
16	"	05.07.82	15	F	ad	ELIANE	white	164/165	98	?
17	"	06.06.83	15	M	juv	-	orange	21/22	-	?
18	"	06.06.83	15	F	juv	-	green	66/67	-	?
19	"	04.07.83	15	F	juv	-	blue	39/40	-	?

Fig. 5.5

Core study area with latrines and badger range borders.

Thin lines: major woodland border

Dotted lines: range borders

Stippled lines: major tracks and foot paths

Encircled numbers: setts according to Table 5.4

Filled circles: latrines

Some latrines were not shown, if they are very close to others and a main sett



Fig. 5.6

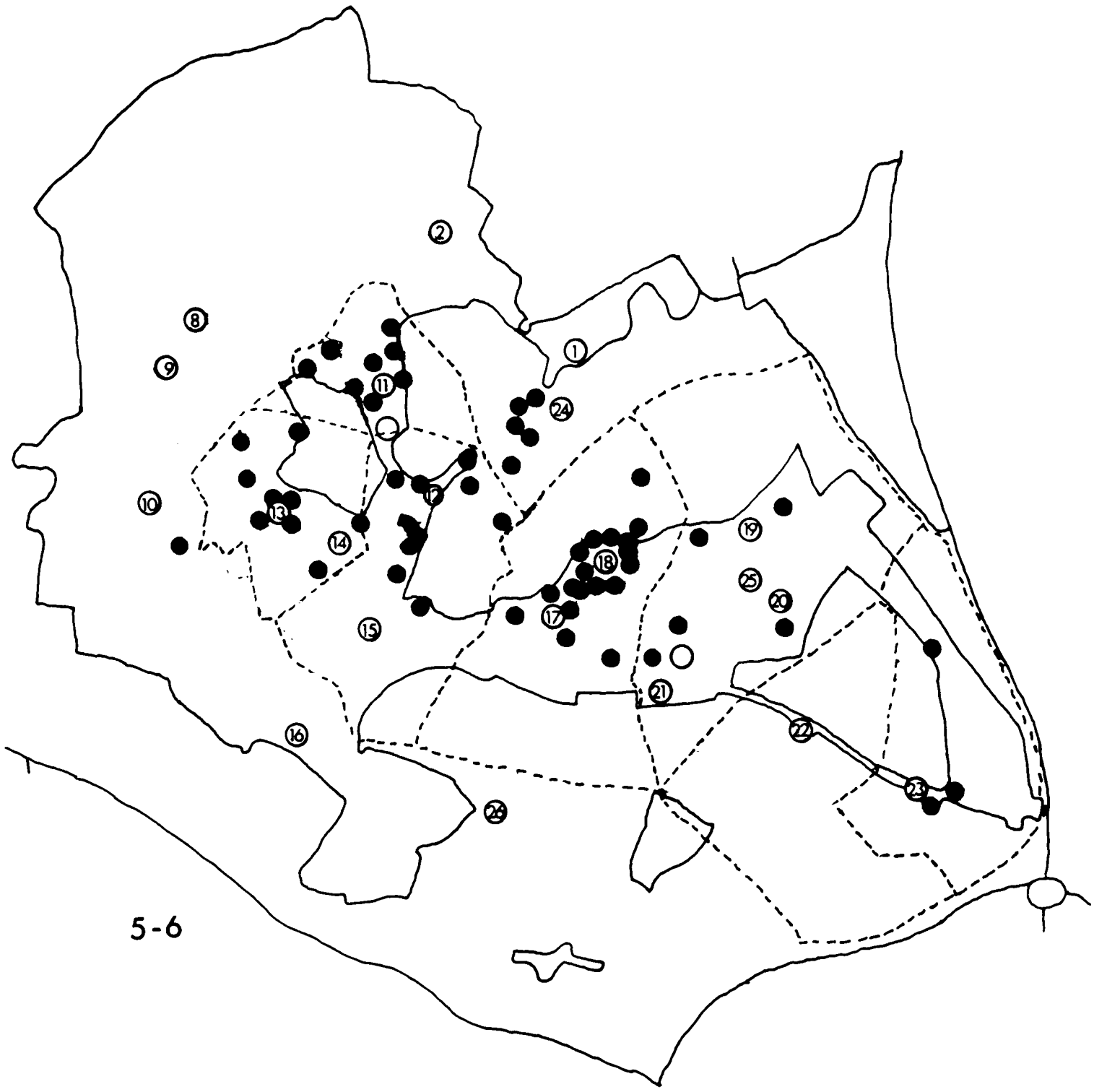
Map with known outliers and major setts.

Thin lines: major woodland boundaries

Dotted lines: range borders

Encircled numbers: setts according to Table 5.4

Filled circles: outliers


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5.7-5.19

Badger group ranges and individual ranges in relation to habitats and distribution of latrines.

Thick black lines: border of group range

Green stars: latrines

Thin lines: patch borders of the habitat map; plotted habitats include pasture and deciduous woodland

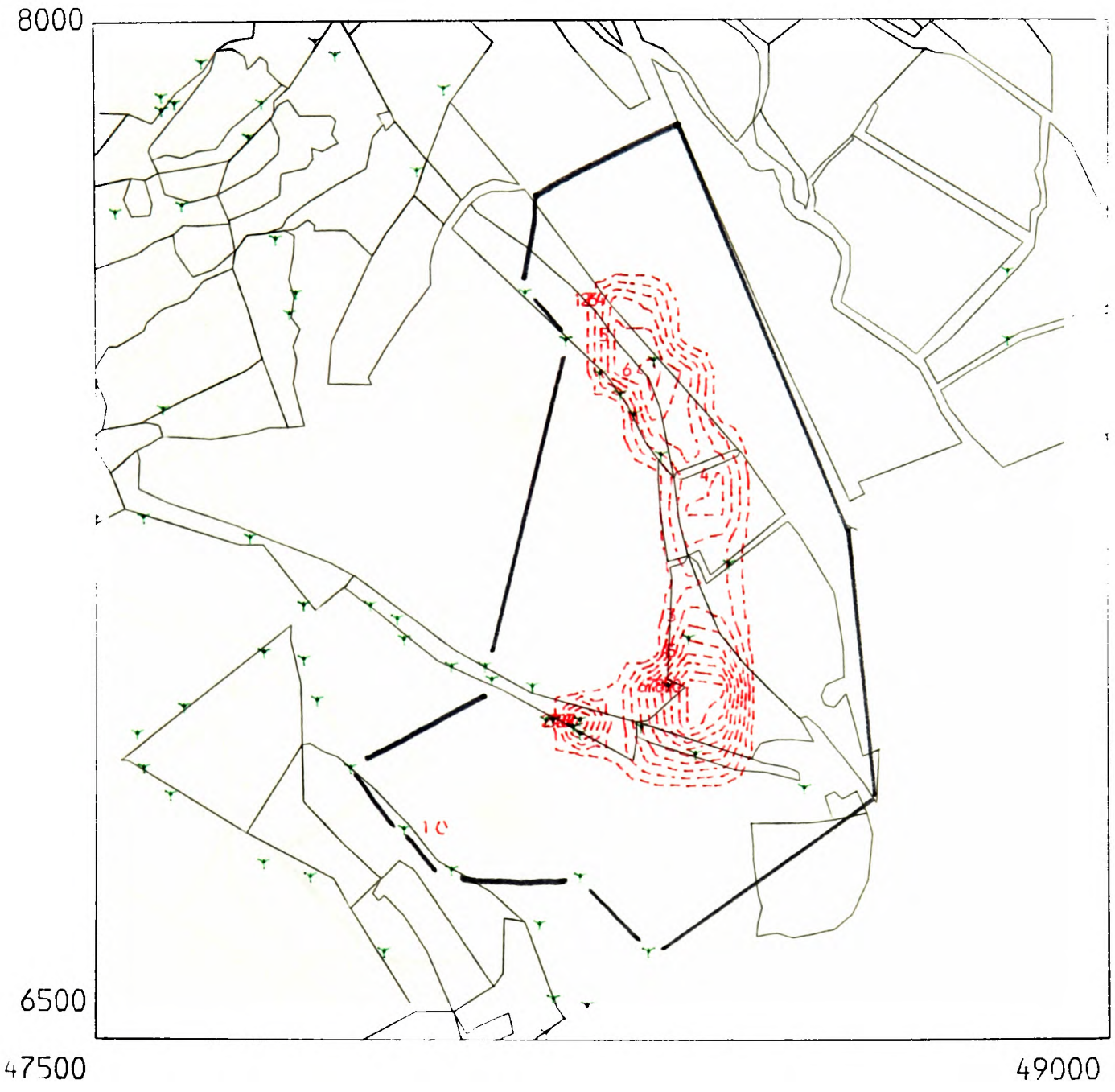
Dotted lines: contour plot of intensity of use of an individual's range, evaluated on a 50 m grid, produced by program MAPITH, using GHOST-80 graphics package. Each contour line delineates an equal level of utilization intensity of the range. Empty areas enclosed by several narrowly placed contour lines indicate plateaux where the intensity of use is higher than the top contour level chosen.

Data used for the plots were selected according to the 15 min independence interval.

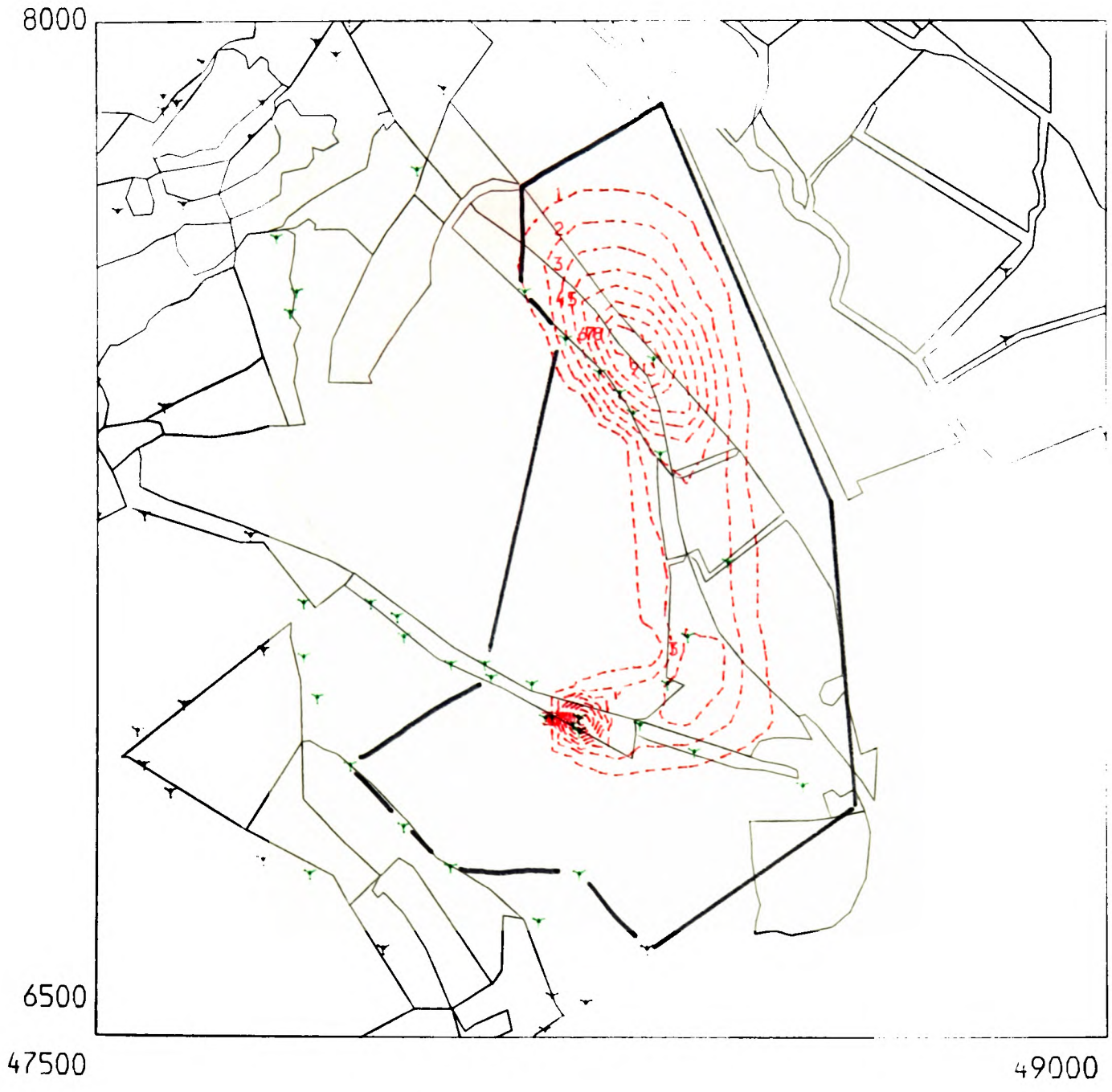
GEORGE 15 MIN INT.



HELEN 15 MIN INT.

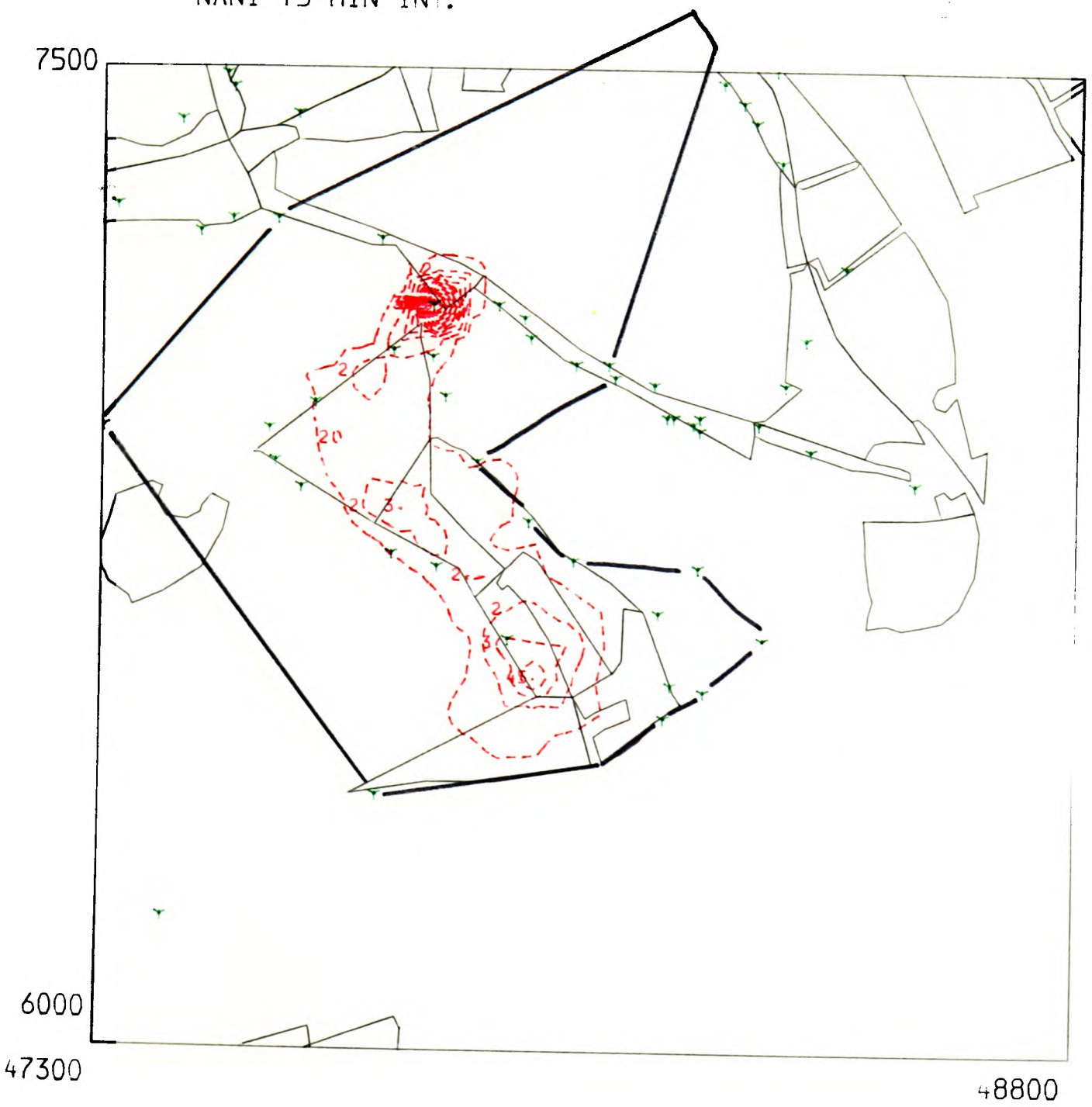


SARA 15 MIN INT.




ALI 15 MIN INTERVAL
7500
6000
47300
48800
15
16
4
34

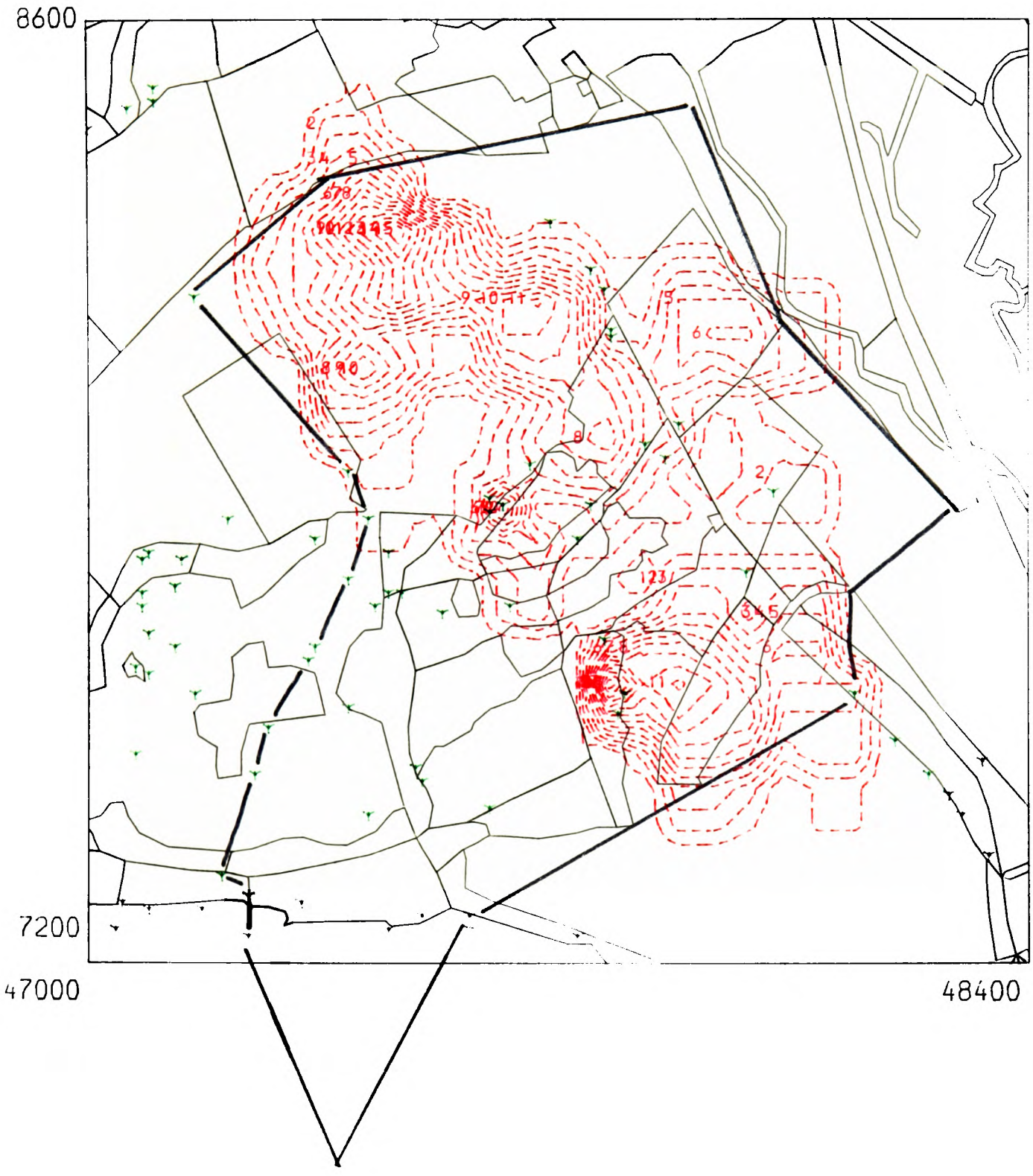
NANI 15 MIN INT.



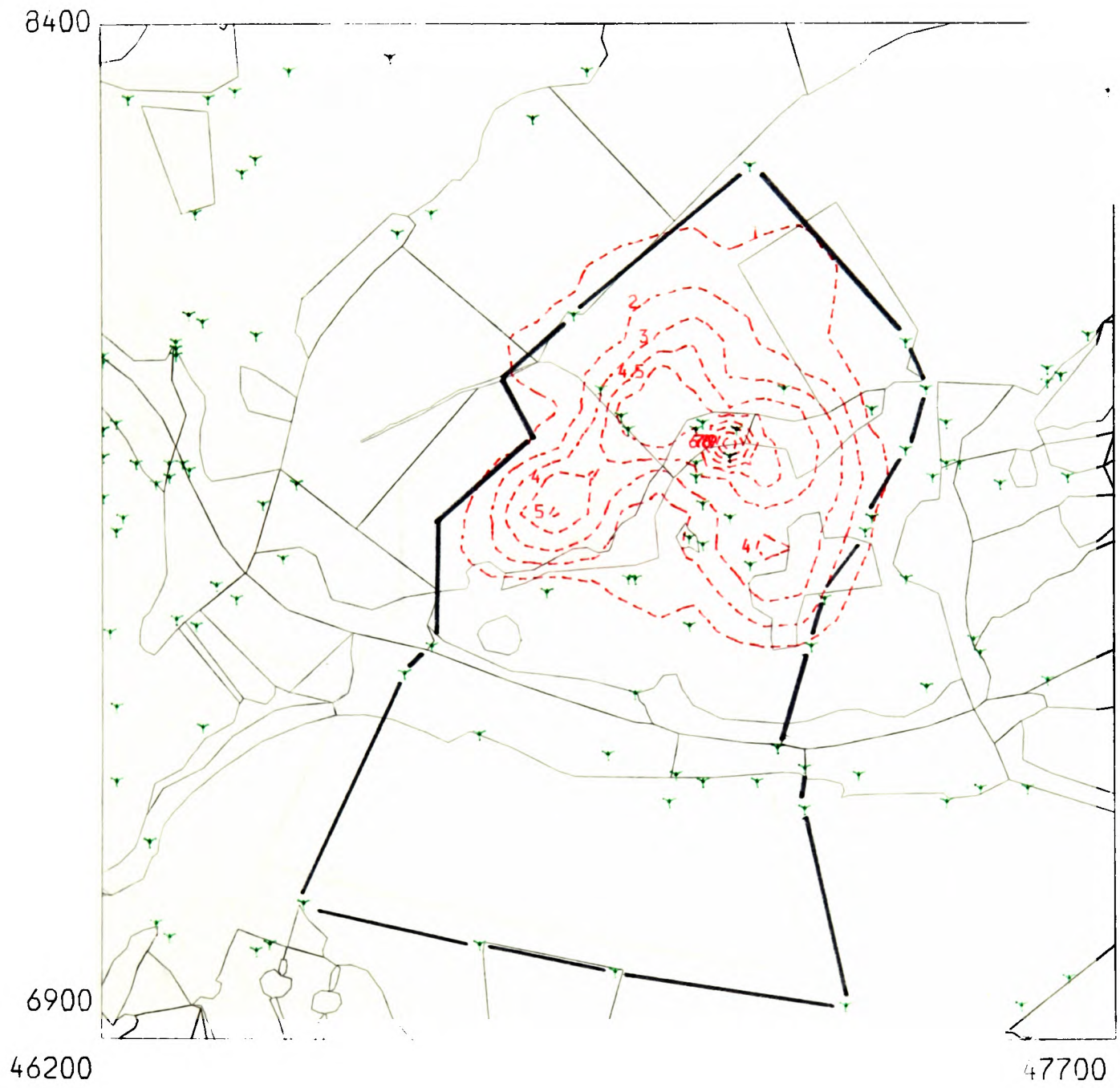
WILF 15 MIN INT.



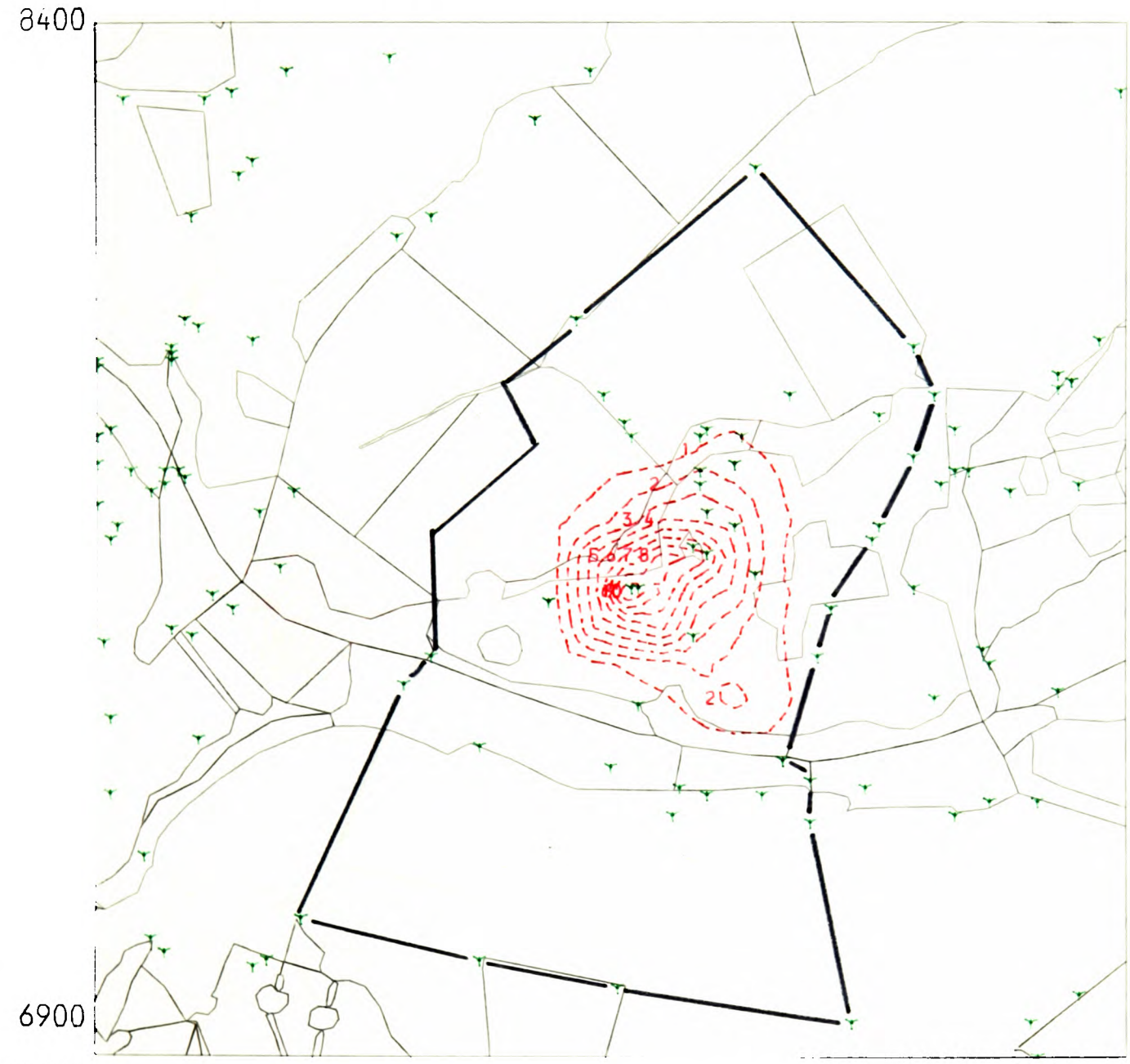
NOEARS 15 MIN INT.



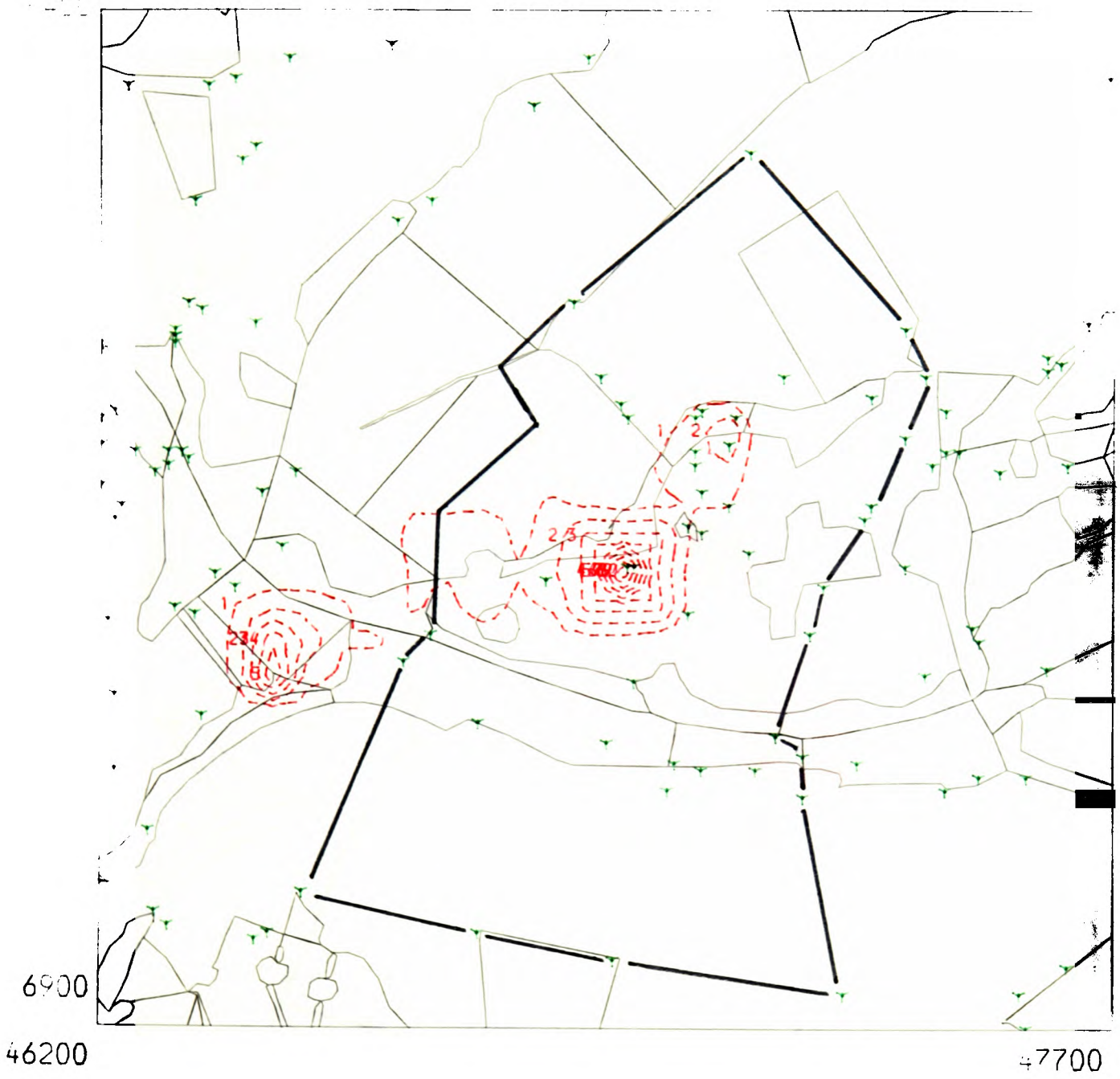
PEACEFUL 15 MIN INT.



JO 15 MIN INTERVAL

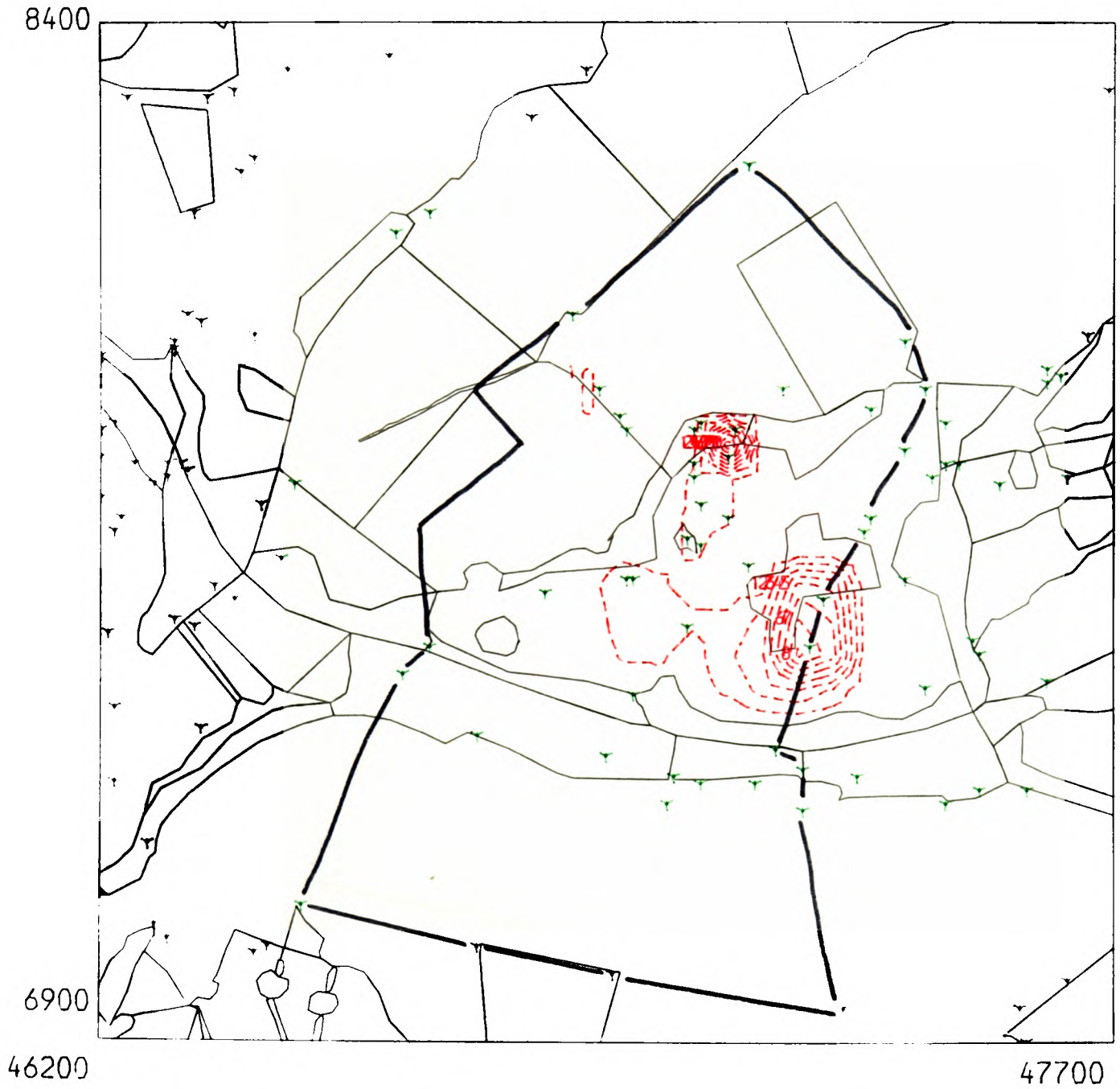


LORY 15 MIN INTERVAL

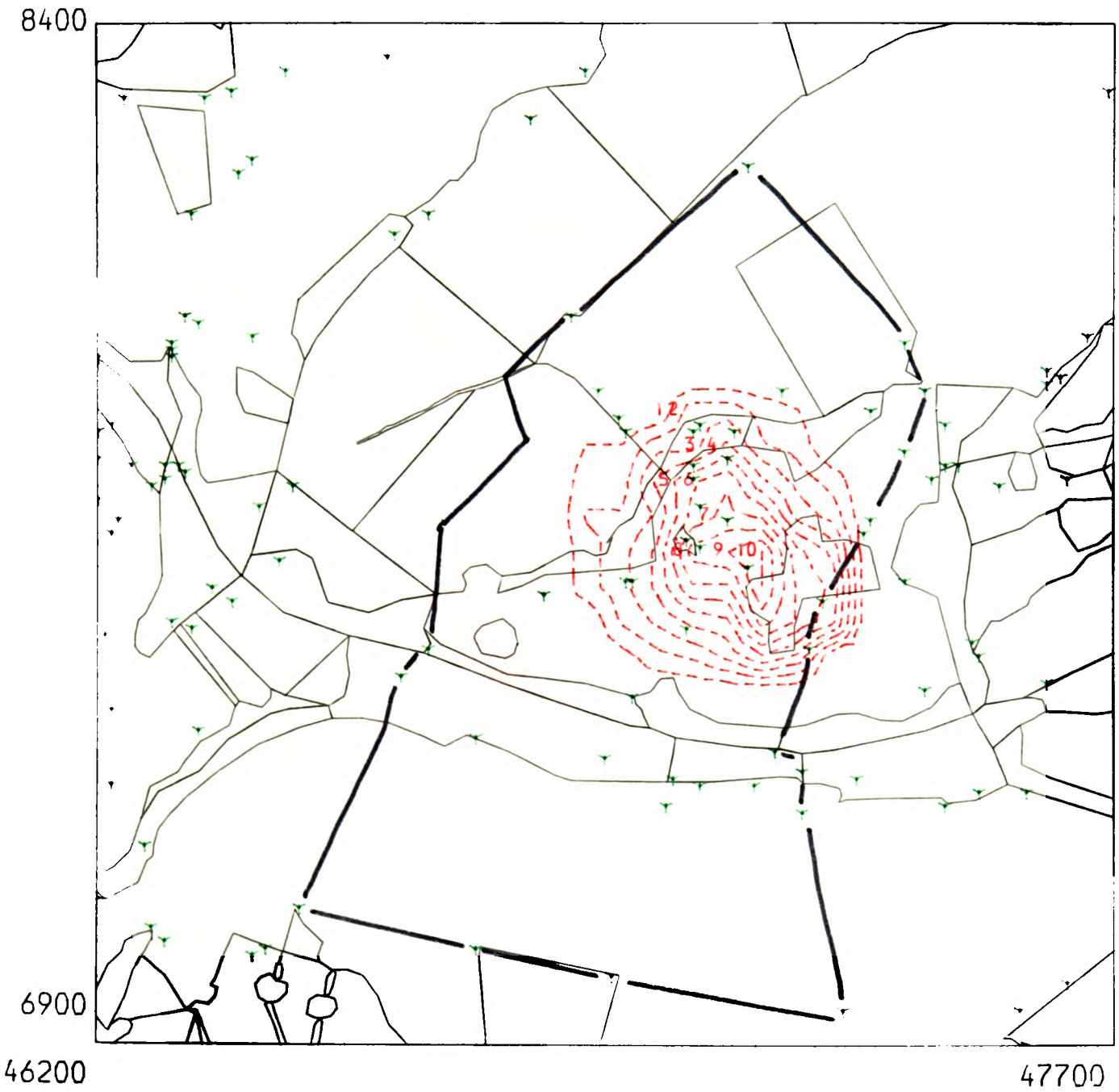


5-17

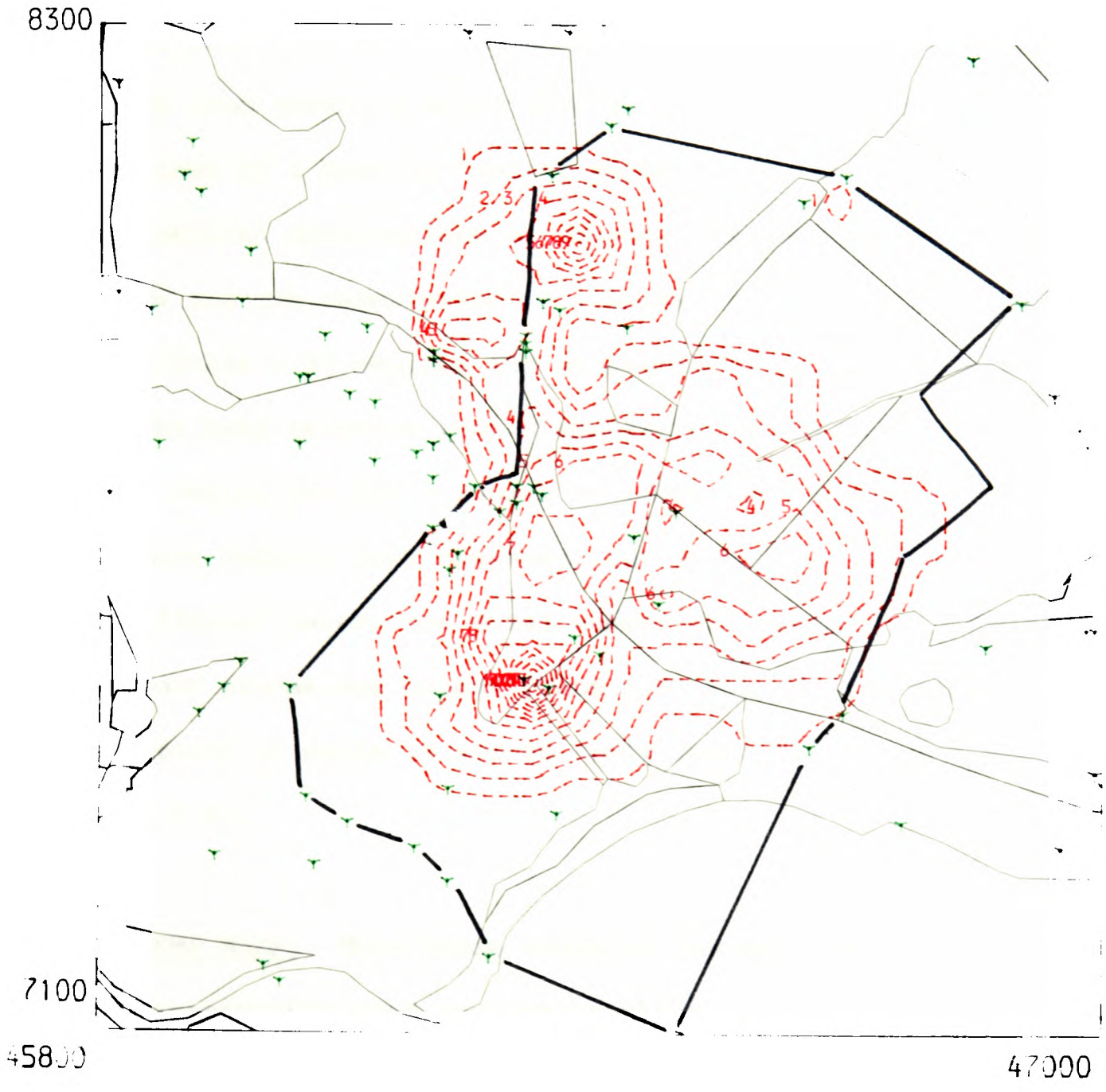
SCARLESS 15 MIN INT.



VICIOUS 15 MIN INT.



ELIANE 15 MIN INT.



Range B3 (MARLEY). This is the largest known range in Wytham (Table 5.10). At least 5 excavations qualify as setts (Fig. 5.6), three of which are checked during the ABC (19, 20, 21, Fig. 5.6). One sett (25, Fig. 5.6), formerly the centre of Hans Kruuk's (1978a) bachelor clan, is now mostly occupied by foxes and rabbits, and another hole (unnumbered, Fig. 5.6) is occasionally used by badgers. 15 border latrines and 32 non-border latrines were found. One of the best documented range boundaries is shared by the MARLEY Range with its western neighbour, the JEWS HARP Range. This border section runs from north to south through the Pastick's Plantation and is clearly defined by a heavily trotten badger track and 10 latrines (Fig. 5.5 and 5.13). Several observations of unmarked badgers in the south-west corner of the range and the observation of a badger returning from Home Farm in the north-west (Table 5.8) besides the movements of the female NOEARS (Fig. 5.13) and the bead recovery record emphasize the extension of the range of this group. During the ABC 3 adults in 1982 and 2 adults in 1983 were observed. More badgers were observed, but since they emerged from different setts at different dates, the total number is unknown. In June 1982, one old female without pinnae was caught (Tabe 5.9, Fig. 5.13). Despite intense trapping efforts at setts 19 and 20, only two cubs were caught in spring 1983 (Table 5.9).

Range B4 (JEWS HARP). This range contains two main setts (17 & 18, Fig. 5.6), both intensively used throughout the study period, and 16 outliers, some of which were used in 1982 (Table 5.7). The observed increase in use of outliers in autumn 1982 could indicate dispersal pressure since juveniles and subdominants ready to disperse tend to stay in outliers in autumn (Kruuk (1978a), Neal (1977), Long & Killingley 1983). JEWS HARP is the only range with information on dispersal. JO, an old female occasionally located outside the group range (Fig. 5.15), was found dead in Range B6 at Hill End

Camp. VICIOUS, a male cub recaught as a young adult dispersed in its second year to range B7 (ABC, 1984). Both animals dispersed to neighbouring ranges, less than 1 km apart. 20 border and 29 non-border latrines were identified (Table 5.6). Eastern, northern, and western sections of the range border were well-defined (Fig. 5.1-5.4, 5.14-5.18). Although I did not recover beads from the southern border I believe the extension of the range beyond the wood is justified, since two radio-tracked animals were located in the midst of the arable fields south of the woodland. According to the ABC and my own observations group size varied between 5 and 7 adults (Table 5.8, 5.10). Four females were caught, two old ones (PEACEFUL and JO) and two in their prime (LORY and SCARLESS) and one male cub later recaught as a young adult (VICIOUS). Contour plots of their movements are shown in Fig. 5.14-5.18.

Range B5 (SUNDAYS HILL). This includes two setts (12 and 15, Fig. 5.6) and 9 outliers. Sett no. 12 was included in this range since bead recoveries from both setts overlapped (Fig. 5.1-5.4) and during each baiting period several faeces were found that contained beads from both setts, implying that at least one individual has been eating beads at both setts. In this range 21 border latrines were found, the highest score of all ranges. Also, the highest number of border latrine foundations outside spring occurred here (Table 5.6). The border to range B10, its western neighbour, is littered with border latrines and non-border latrines nearby (Fig. 5.5, 5.19). The south-east corner of the Lower Seeds field seemed to be attractive to both ranges, as indicated by ELIANE's excursions in autumn 1982 (Fig. 5.19) and a series of latrine foundations along the track leading to the south-east corner in spring 1983, mostly claimed by Range B10 (Fig. 5.4). All other border sections were well defined except for the south-east corner. Any of the latrines 254, 255 or 59 was a likely candidate as a cornerstone of the

border to the eastern neighbour, the JEWS HARP Range. Here I decided to take the medium line between the two extremes, following in principle Kruuk's (1978a) procedure. In 1982 a male cub and a small old female called ELIANE and in 1983 three juveniles were caught. Despite one chance observation (Table 5.8) none of the marked cubs has been observed since its capture.

Range B6 (NEALINGS COPSE). This is a range with one main sett within the Wytham Wood area and no outliers and extending over Denman's Farm to Cumnor Hill, south of the study area (Fig. 5.20). A male badger caught by D.W. Macdonald at Cumnor was radio-tracked throughout the Cumnor area, Denman's Farm and the Radbrook Common area in Wytham (D.W. Macdonald pers. comm.). Badgers were also repeatedly observed to cross the Eynsham road from Hill End Camp to Denman's Farm; one female was killed by a car while crossing. Beads placed at the Nealing's Copse sett (16, Fig. 5.6) were recovered from latrines at Cumnor Hill (Fig. 5.20). Close inspection of the latrines at the Nealing's Copse sett in autumn 1982 and 1983 revealed the presence of cultivated fruits in badger faeces that are unknown from Wytham but grown in the orchards at Denman's Farm. This considerable body of evidence implies regular exchange of badgers between areas on both sides of the Eynsham road and supports the idea that both areas are part of one range. Thus, absence of badgers from Nealing's Copse during the ABC does not indicate an empty range; rather group size estimates are incomplete. Within the study area 16 border and 24 non-border latrines were located. The position of the Hill End Camp sett (26, Fig. 5.6) is uncertain; the bead recoveries do not present conclusive evidence to establish it as the centre of a separate range next to B6.

Range B7 (THE MOUNT). This range includes two setts (1,24, Fig. 5.6). 16 latrines were located in parts of the study area that could be unequivocally

assigned to this range. Its extension to the north and the east (towards the village) remains unknown (Fig. 5.20). In autumn 1981 and 1982 I repeatedly observed badgers in the village and once saw a large adult cross the parking area of the local pub at 22.00 hours while radiotracking a fox nearby. The relationship of B7 to its western neighbour B9 is unknown. In spring 1982 and 1983 excavation activity was very pronounced (Table 5.7) but thereafter sett 1 showed little signs of use. 2 adults and 1 cub were seen in 1982, 5 adults and 2 cubs in 1983 and 3 adults and 4 cubs in 1984 (Table 5.10).

Range B8 (LOWER SEEDS). The smallest of all known ranges in Wytham includes one main sett and another old and infrequently used excavation at its southern border. This range had no access to pasture fields except some fallow land slowly converting to grassland. The asphalt road from the village to the Chalet was determined as its north-western border, since few of the many badgers seen close to the road actually crossed but usually turned back in the direction from which they came, and the track was littered with latrines (Fig. 5.5). Animals were observed in 1982 and 1984, but not in 1983.

Range B9 (COMMON PIECE). This range covers the north-eastern part of the Great Wood around sett 2 (Fig. 5.20). 9 latrines could be associated with it. Animals were observed at the main sett in 1982 and 1984 (Table 5.10).

Range B10 (RADBROOK COMMON). Similar as Range B8, this is a range without access to pasture fields and includes two main setts (13, 14, Fig. 5.6) surrounded by a host of outliers (Table 5.7, Fig. 5.6). 18 border and 24 non-border latrines were identified (Table 5.6). The baiting periods in autumn 1982 and spring 1983 showed conclusively that the two setts belong together and are apparently used inter-changeably by the resident badgers

(Fig. 5.3, 5.4). Faeces with beads from both setts were recovered several times. Although the second smallest of all known ranges, group sizes can compete with or exceed those of larger ranges (e.g. B3 and B4, Table 5.10), and reproductive output was consistently high (Table 5.10). Range borders were well defined except for the northern section across the Lower Seeds field. As with the border between Ranges B4 and B5 I took the middle line and assigned the northern half of the Lower Seeds field to Range B8 and the southern half to Range B10. Despite intensive search on the Lower Seeds field no latrines were located suggesting that this was not an important border section.

Range B11 (THE CHALET). This range covers some parts of the north-west of the Great Wood and includes setts 8 and 9 (Fig. 5.6). 11 latrines could be assigned to this range within my study area (Table 5.6). Group sizes were amongst the highest encountered (Table 5.10).

Range B12 (ROUGH COMMON). This range is probably the southern neighbour of Range B11 and the western neighbour of Range B10. One sett is found in the study area (Fig. 5.6) but it is likely that a second sett at the Reservoir belongs to this range as well (Kruuk 1978a). Activity increased greatly in spring 1983 when 8 new border latrines were founded (Table 5.6), separating this range more clearly from the east (Range B10) and the southeast (Range B6). Group size appeared to be small (Table 5.10) but was probably underestimated since the second sett at the Reservoir was not included in the ABC.

Summary. Altogether 12 ranges could be identified in Wytham from bead recovery, radio-tracking and chance observations. 7 ranges could be completely delineated. Both bead recovery records and radio tracking were

useful techniques for determining the boundaries. Information from radio-tracking was essential if badgers did not mark sections of range borders in sufficient detail (e.g. eastern border sections of Ranges B1 and B3; southwestern corner of Range B2). Where their ranges enclosed arable fields at their periphery, borders were poorly defined by latrines, which may indicate that these areas were of reduced value.

The detailed study of range anatomy sheds some light on the interpretation of the results of the ABC. Since several ranges contained two or more setts, badger population size cannot necessarily be determined by adding up the group size estimates for each sett, as is common practice during the ABC (Table 5.11, "TOTAL ESTIMATE"). However, estimates of population size derived by this method are surprisingly close to population size as determined by summing up the group sizes of all badger ranges (Table 5.11, "ALL INFORMATION") which were considered to be closest to the "true" group and population sizes. Estimates derived from badger counts at any particular evening (Table 5.11, "EVENING COUNT") lead to a severe underestimation of population size and are therefore not a useful method. Overall, the Wytham population seems to have increased slightly from 1982 to 1983 (Table 5.11) corresponding to an increased activity at setts (Table 5.7) and an increase in the intensity of latrine use in spring 1983 as compared with 1982 (Table 5.6).

How isolated is the badger population of Wytham ? I have mentioned that Range B6 extends into the farmland south of the Eynsham road. In the east, badgers were observed crossing the main road in the Binsey area (Fig. 5.20) several times in spring 1982. Detailed searching and bait marking in spring 1982 revealed the presence of several setts and 17 latrines that can be assigned to one, and possibly two Binsey ranges (Fig. 5.20). To what extent these badgers have contact with Wytham is unknown; Binsey could represent a "dispersal sink" to the Wytham population (see Lidicker 1978).

Table 5.10 Range and group sizes of badger groups in Wytham. Group sizes are based on all available information. If group sizes deviate from the results of the ABC, additional reference is provided. Range sizes were determined by program BBUILD. A = adults; J = juv.

No	Range	Size (ha)	estimate of group size (May) 1982 A	J	T	1983 A	J	T	1984 A	J	T	Sett nos. (Tab.5.2)
1	BOTLEY	42.67	2	0	2	3[2]	1	4	0	0	0	23
2	UPPER F.	67.58	2	0	2	3[2]	0	3	3	1	4	22
3	MARLEY	75.31	3	1[1]	4	2	3	5	4	0	4	19,20,21
4	JEWS HARP	56.00	6	1[2]	7	5[5]	1	6	7	4	11	17,18
5	SUNDAYS H.	48.61	3	4	7	5	5	10	7	6	13	12,15
6	NEALINGS C.	-	0	0	0	2[4]	0	2	3	0	3	16
7	MOUNT	-	2	1[1]	3	5	2	7	3	4	7	1,24
8	LOWER S.	17.83	2	1	3	1	0	1	3	0	3	11
9	COMMON P.	-	5	1	6	0	0	0	2	0	2	2
10	RADBROOK C.	22.36	3	2	5	8	5[1]	13	4	2	6	13,14
11	CHALET	-	5	4	9	4	3	7	6	3	9	8
12	ROUGH C.	-	1	0	1	4	2	6	2	0	2	10

[1] see Table 5.8
[2] captured; see Table 5.9
[3] extended observations throughout April 1983 revealed the presence of at least 1 unmarked and 4 marked adults
[4] 1 male radiotracked from Cumnor area (see text); 1 female found dead at Eynsham road later in the year after having been repeatedly observed to cross into Nealings Copse area

Table 5.11 Population size of Wytham badgers as determined by three different methods. For full explanation see text. A = setts Holy Hill and Thornycroft are taken as setts of one range (as in Kruuk 1978a); B = setts Holy Hill and Thornycroft are taken as separate ranges.

No	Method	1982 ad	juv	total	1983 ad	juv	total
1	Total estimate	51	18	69	44	21	65
2	Evening count	36	11	47	31	13	44
3	A-All information	44	18	62	44	24	68
4	B-All information	44	20	64	44	24	68
	Corr. Factor 1/3	0.863	1.0	0.899	1.0	1.143	1.046
	1/4	0.863	1.111	0.928	1.0	1.143	1.046
	2/3	1.222	1.636	1.319	1.42	1.846	1.545
	2/4	1.222	1.818	1.362	1.42	1.846	1.545

Fig. 5.20

Map of the study area with all known badger ranges.

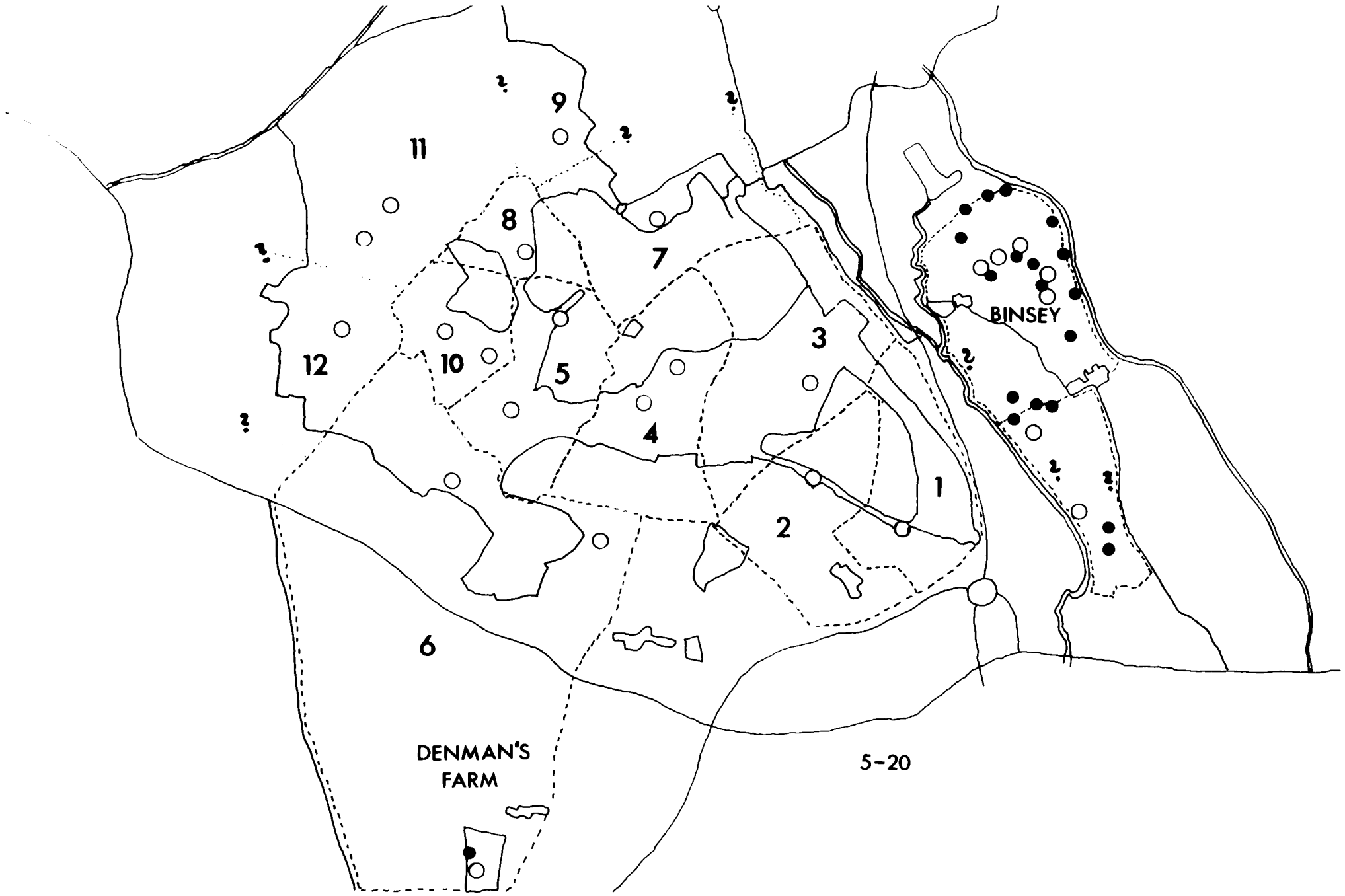
Thin lines: major woodland boundaries and roads

Thin parallel lines: rivers

Numbers: number of badger range

Empty circles: major setts of range

Filled circles: latrines in the Binsey area; lines indicate bead recovery and origin of beads


11
9
8
7
12
10
5
3
4
BINSEY
1
2
6
DENMAN'S
FARM
5-20

5.4.2. Relationships between ranges and long-term developments.

Kruuk (1978a) demonstrated that badgers in Wytham are territorial and produced evidence that ranges were actively defended. Table 5.12 lists some incidents related to intraspecific aggression. They indicate that at least some injuries are received during contests between members of neighbouring groups. Even though the evidence is necessarily indirect, I suggest that moving outside one's range can incur considerable costs. Consequently, such excursions should be fairly rare events. Whether these costs vary for different age or sex classes can at present not be decided.

Kruuk (1978a) and this study used food markers to investigate range borders. Kruuk has called the recovery of a marker well outside its range an 'incidental visit'. He had evidence of four such visits (= 5.7 % of latrine visits that resulted in the recovery of food markers). Incidental visits recorded during the present study are listed in Table 5.13. During 4 baiting periods, altogether 10 visits were recorded (= 7 %). A closer look at the most frequently visited range, the JEWS HARP Range, provides several plausible explanations of excursions.

Firstly, excursions can constitute successful or attempted dispersal movements. For instance, the female JO of the JEWS HARP Range was located outside the group range 4 times; she later dispersed to Range B6 where she was found dead (Table 5.8). The beads could then have been swallowed at the dispersing individual's home sett and deposited in the neighbouring range while looking for vacancies. In this context it is noteworthy that the majority of incidental visits occurred to range boundaries. According to Neal (1977) and Long & Killingley (1983), subordinates or adolescents with an interest in dispersing are usually allowed to stay at the fringes of ranges.

Another explanation could be that the resource holding power of members

Table 5.12 Indicators of intraspecific aggression amongst badgers in Wytham.

(a) State of animals captured in traps.

Range	Name	Date	Remarks
B1	GEORGE	20.05.83	lobe of right ear bitten off
	HELEN	19.08.83	left ear split into two halfs
B2	WILF	17.08.83	upper lip split; upper left canine missing
B4	PEACEFUL	15.09.82	big injury (10 x 4 cm) ca 5 cm above root of tail; parts of skin and flesh missing
		18.04.83	healed, but large area without fur
	JO	18.09.82	neck scar ca 1 cm deep and long
	LORY	25.09.82	large scar on throat
	VICIOUS	18.04.83	big nasty injury just over root of tail, skin and flesh partly missing, wound open

(b) other animals and observations

April 1982	blood bath at border latrine 33 between MARLEY and JEWS HARP range; badger blood, pieces of skin and flesh and chunks of badger hair scattered over 10 sq m; bloody track leading into MARLEY
October 1982	unknown badger found at Eynsham road; death due to starvation probably because animal was unable to obtain food because of a hugh injury at the back: half the anus pulled out, large chunks of the back ripped off and supra-anal gland destroyed
April 1983	dead corpse found at latrine close to sett 14 in RADBROOK COMMON range; animal had been severely wounded by several bites at throat and neck and at the back (bites at level of supra-anal gland and anus above tail-root)

Table 5.13 "Incidental visits" (see text for an explanation) as revealed by food markers.

Date	visitor from	visited range and area
Spring 82	SUNDAYS H.	border between MARLEY and JEWS HARP at the woodland/arable field transition
	NEALINGS C.	Lower Seeds field in RADBROOK C., but close to border to SUNDAYS HILL
Summer 82	BOTLEY	a field edge close to the Upper Follies sett in UPPER FOLLIES
Autumn 82	SUNDAYS H.	to a latrine close to the Jew's Harp sett in JEWS HARP
	NEALINGS C.	to a latrine close to Burkett's Plantation sett in RADBROOK COMMON
Spring 83	SUNDAYS H.	to a border latrine shared by MARLEY and JEWS HARP at a woodland/arable field transition
	MARLEY	latrine inside JEWS HARP
	CHALET	to a border latrine between COMMON PIECE and LOWER SEEDS
	LOWER SEEDS	to a latrine inside CHALET
	ROUGH COMMON	to the SE corner of the Lower Seeds field in RADBROOK COMMON close to the border to SUNDAYS HILL

of the JEWS HARP group was lower than usual and insufficient to make their neighbours readily accept a settlement based on roles. Then contests would have escalated and could have resulted in the injuries noticed on several group members (Table 5.12).

A third explanation concerns the identity of visitors. The food markers do not indicate the sex-age class of the visitor. According to intensive observations at both main setts of the JEWS HARP Range in autumn 1982 and April 1983, it is almost certain that the sex-ratio was female-biased, since apart from the four trapped females only two other animals were observed that could have been males; one of them, however, seemed to be too small for an adult male. Thus, the high proportion of visits to the JEWS HARP Range may be due to males from surrounding ranges visiting the resident females. In a similar vein, the excursion of the old male WILF from Range B2 (Fig. 5.12) into the neighbouring range B1 was probably undertaken to visit the local females. WILF was actually located once in Range B1 in an outlier <u>together</u> with SARA, one of the resident females (see also Chapter 7).

If excursions are rare and territoriality a constant feature of the local system, then long-term changes of the spatial arrangements of groups should be modest. The results of Kruuk's study provide an ideal opportunity to record the changes over a 8-year period (1974/75 to 1982/83). Fig 5.21 shows a plot of Kruuk's and my range boundaries.

The most conspicuous change is the amalgamation of the bachelor clan at The Platform sett with the MARLEY Range. The western border of the then bachelor clan still serves as boundary between the JEWS HARP Range and its eastern neighbour - a fine example of continuity ! The fusion of the bachelor clan with its eastern neighbour lead to considerable modifications in the east of the study area. A comparison of Kruuk's plots of the ranges of his females with Fig. 5.7-5.13 shows that the ranges of the local females changed less than the delineation of group range borders (Fig. 5.22). The

Fig. 5.2I. Badger territories in Wytham in I974 (dotted lines) and I982 (dashed lines). Main woodland boundary delineated

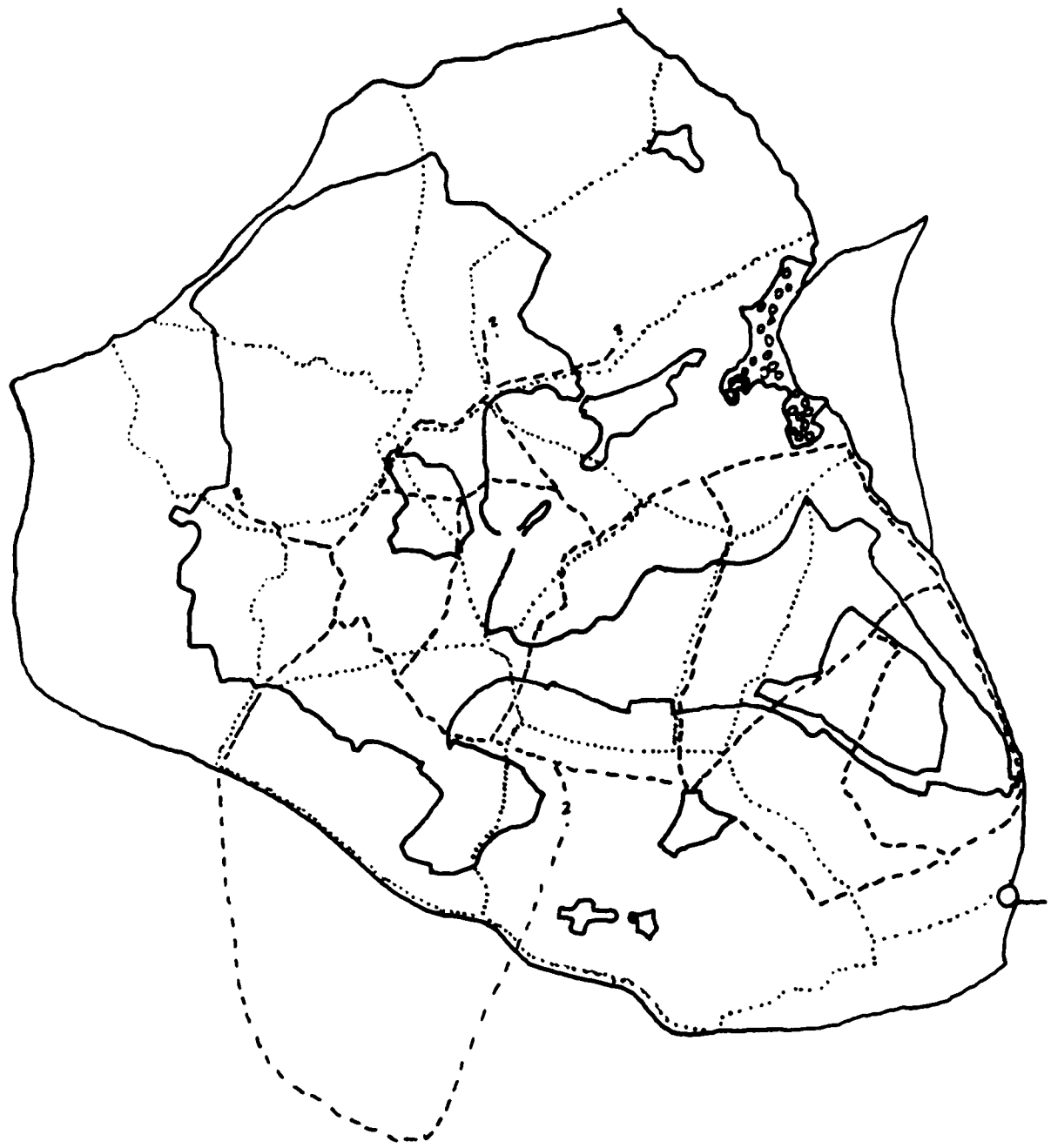


Fig. 5.22

Changes in range configuration from Kruuk's study 1974/75 to this study 1982/83, in the Marley-Botley area.

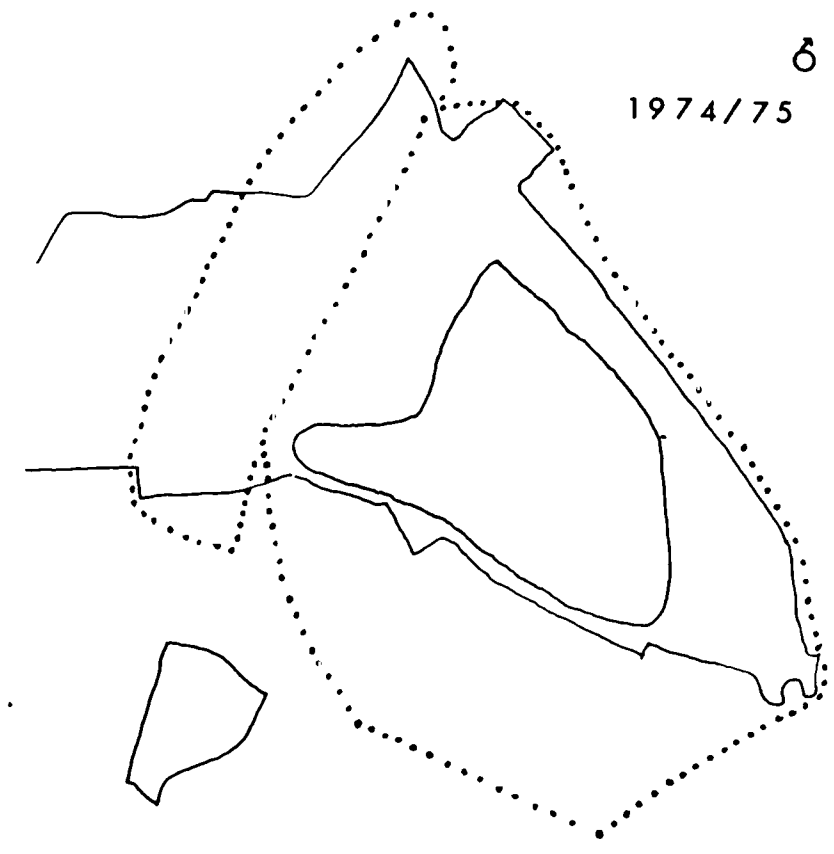
Thin lines: major woodland boundaries

Stippled lines: male ranges 1974/75

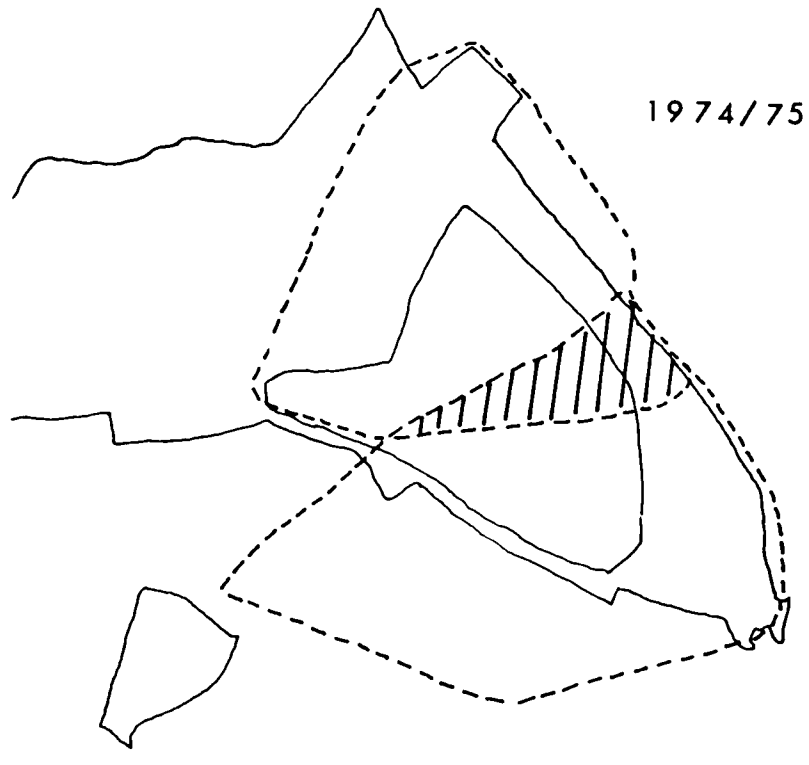
Dotted lines: female ranges 1974/75, hatched area: overlap between neighbouring females

Stippled and dotted combined: group ranges 1982/83

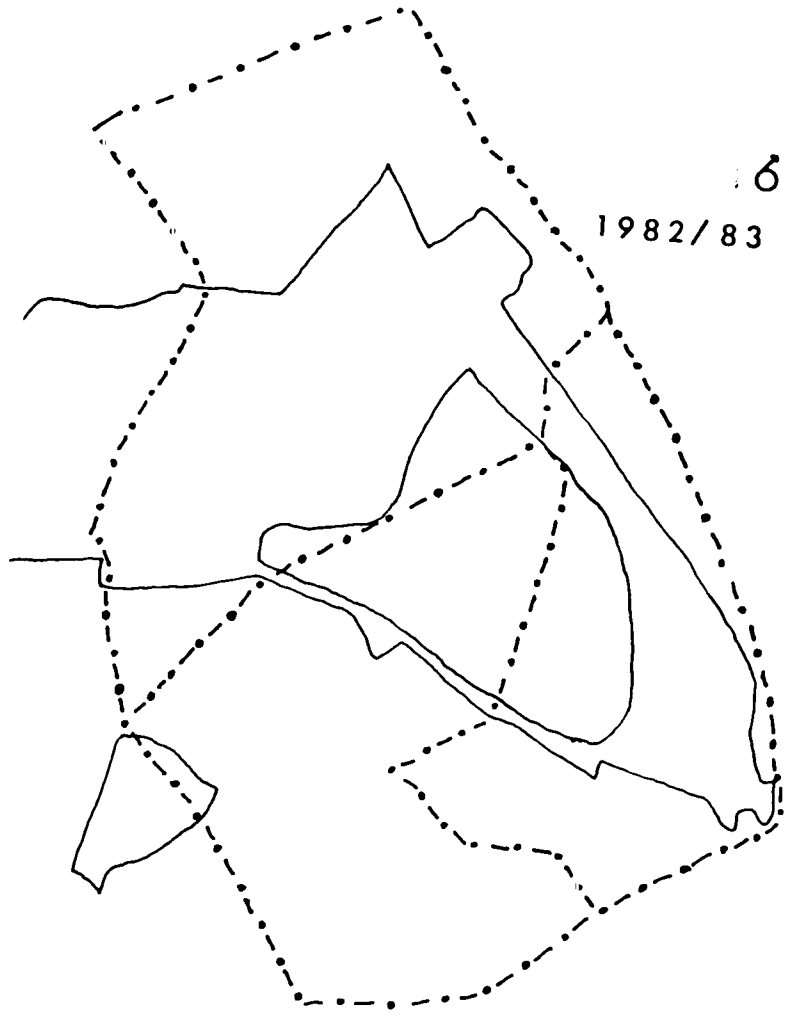
♂
1974/75



♀
1974/75



♂+♀
1982/83



border between Kruuk's "Marley" and "Botley" females is now formalized as a boundary between the MARLEY Range and its southern two neighbours. This suggests that, at least in this case, the driving force behind the rearrangement of groups was the negotiation of spheres of influence of males. (A more detailed discussion of the reasons and consequences for this is deferred to Chapter 7). The south-east area, formerly just occupied by Kruuk's "Botley" females, now supports two ranges. These two ranges (B1 & B2) extend further to the south-east and the south-west than the "Botley" females used to, and there is some evidence (e.g. the digging activity in B1) to suggest that B1 is a split from the UPPER FOLLIES Range.

The JEWS HARP Range has changed little since 1974; it lost a small area in the west and gained a similar sized area in the north-east. Further west, Kruuk's old Brogden Belt's range has moved south, leaving space for the new and small LOWER SEEDS Range still contained within large portions of the old Brogden Belt's border. By pushing south, the SUNDAYS HILL range reduced the western JEWS HARP extension and the northern NEALINGS COPSE extension. NEALINGS COPSE, however, compensated by taking chunks off the southern section of the RADBROOK COMMON Range.

5.4.3. Patterns of latrine distribution and utilization.

Following Kruuk's (1978a) results, badger latrines were identified and used as markers of group range boundaries (section 5.4.1). An analysis of latrine distribution and utilization may therefore contribute to an understanding of the procedures by which badgers establish ranges, how groups react to pressures applied by their neighbours, and how ranges are maintained. Thus, we need to know in more detail where badgers place latrines, how they use them and how the usage varies with time, space and in relation to environmental features. Since at present very little is known

about the various functions that latrines may fulfil as one possible source of information in badger societies, I also want to explore other possible functions besides territory maintenance. Therefore, my analysis is centred around the following questions:

1. Do badgers show preferences for particular sites when establishing new latrines ? For instance, efficient advertisement of range boundaries would imply a distribution of latrines that (i) conveys claims of ownership of an area and intention of defense with a minimum of effort, and (ii) is highly predictable for other badgers. Then, badgers would expect latrines to be located at such sites and this is why latrines could (in evolutionary time) have evolved into information centres.

2. Many latrines are founded inside the group range (non-border latrines). What message do they convey ?

3. Can variation of latrine distribution and utilization be explained by variation in local environmental features ? For instance, latrines could be distributed and utilized so that areas important to the range inhabitants are well marked. If high quality food patches receive increased marking attention, then variation in habitat quality (which is related to resource presence, Chapter 2 and 3) should correspond to variation in marking intensity. Such a pattern could arise directly ('intentional' placement and utilization of latrines) or indirectly (increased marking activity could be the incidental consequence of increased frequency of visits to such areas, indicating to trespassers that the risk of encountering resident badgers increases).

5.4.3.1. Distribution of latrines.

Thirteen latrines were located in large, homogeneous areas without any discernible characteristics (e.g. a ploughed field, Table 5.14). 137

Table 5.14 Frequency of occurrences of latrines at different sites.

	Border	Non-b.
(A) No particular characteristics discernible		
1. badger path recognizable	6	38
2. badger path not recognizable (e.g. freshly ploughed field)	0	13
(B) Sites with one basic feature		
3. less tham 50 meters away from sett	0	44
4. stone wall	0	1
5. hay stack	0	1
6. fence	11	18
7. ditch	0	1
8. track road	25	25
9. hedge	0	6
10. vegetation boundary (excluding hedge)	10	23
(C) Sites with two basic features		
11. fence & track road	1	0
12. fence & hedge	2	2
13. fence & vegetation boundary	5	15
14. ditch & vegetation boundary	1	3
15. track & vegetation boundary	5	7
(D) Sites with three basic features		
16. fence & ditch & vegetation boundary	1	6
17. fence & track & vegetation boundary	0	4
18. fence & ditch & hedge	1	2
(E) TOTAL	69	209

Table 5.15 Frequency of occurence of latrine sites in different habitats. Only habitats and sites with sufficient frequencies included.

GRASS = habitats 5,6,7 SHRUB = habitats 10,35,36,44
ARABLE = habitats 28,29 WOOD = deciduous wododland
PLANT = deciduous, mixed, coniferous plantations: 39,40,41
SETT = site 3 (Table 5.10) TRACK = site 8
FENCE = site 6 VB = site 10

	GRASS	ARABLE	PLANT	SHRUB	WOOD	Sum
SETT	2	2	5	5	30	44
FENCE	7	12	1	2	7	29
TRACK	6	1	11	2	30	50
VB	2	1	20	3	7	33
Sum	17	16	37	12	74	157

Test on independence: $G = 69.0$, $df = 12$, $p < 0.001$

latrines (49.3 %) were associated with human artefacts (fences, ditches, track roads etc, Table 5.14). The most important natural site characteristic was 'vegetation boundary', e.g. a woodland/grassland border. Latrines were unevenly distributed over habitats (Fig. 5.23, using the same habitat categories as in section 5.6); the difference between the observed and expected frequencies, the latter calculated from the proportion of each habitat occupied over all badger ranges (which is different from the proportion of each habitat in the study area; section 5.6), is highly significant ($G=129.5$, $df=4$, $p < 0.001$). Selection of deposition sites also varies between different habitats ($G=69.0$, $df=12$, $p < 0.001$, Table 5.15). Thus, distribution of badger latrines is highly non-random with respect to habitats and sites. Most latrines are found in woody habitats (Fig. 5.23) and fences, track roads and vegetation boundaries are preferred foundation sites.

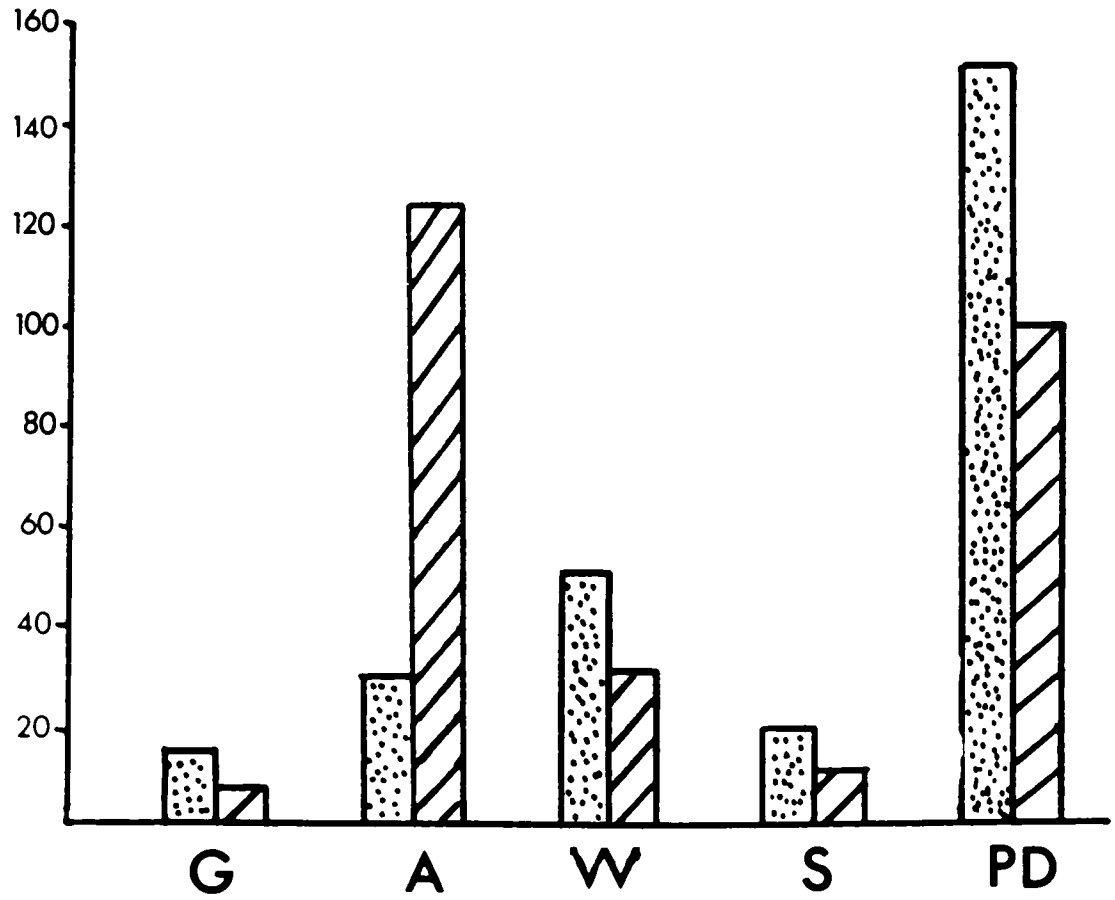
The distribution of latrines in relation to habitat quality was investigated by setting up a three-factor log-linear model considering the status of a latrine (STATUS), the habitat where the latrine is placed (HABITAT AT), and the surrounding or nearest other habitat (HABITAT CLOSE). Habitats were scored as either high quality or low quality habitat with respect to earthworm production; pasture and mature deciduous woodland (habitat types 7 and 37) qualified as high quality habitat (Chapter 3) while all other habitats were assigned to the low quality category. A log-linear model is in some ways equivalent to a multiway analysis of variance on frequencies (Sokal & Rohlf 1981) and can clarify if and how two or more parameters interact. Testing for an interaction between variables is based on the G statistic and includes two checks. Firstly, an absolute G-value is computed for each interaction. If this G-value is significant, then the predicted frequencies, based on the assumption that a particular interaction is zero, deviate so much from the observed frequencies that the model is not

Fig. 5.23 Frequency of occurrence of badger latrines in different habitats.

G	habitats 5,6.	grassland
A	habitats 28,29,3o,31,32	arable land
W	habitats 38,39,4o,41,35	woodland plantatior
S	habitats 1o,35,36,44	scrub + shrub
PD	habitats 7,37	pasture+deciduous

stippled : observed frequencies

hatched : expected frequencies calculated from the proportion each habitat occupies over all badger ranges



in accordance with the data. Thus, that interaction has to be included in the model. Even if this absolute G-value is not significant, the interaction may still be included in the model, if the <u>increase</u> in the G-value from the highest-order interaction is significant, since then the difference is too large to be ignored. The final model then specifies the simplest combination of parameters and interactions between them with the best fit to the original data.

Table 5.16 lists the data and the generation of the model, and Table 5.17 presents an interpretation of the model. Two highly significant interactions exist: for a given level of HABITAT CLOSE, quality of HABITAT AT and STATUS are interrelated, and for a given STATUS, HABITAT AT and HABITAT CLOSE are interdependent (Table 5.16). Since there was no interrelation of HABITAT CLOSE and STATUS for a given level of HABITAT AT, I excluded the three-factor interaction from the model, even though it was - if only barely - significant (Table 5.16).

How can this model be interpreted in terms of communicative function of latrine characteristics ? More border latrines than expected occurred at habitat transitions with a change in habitat quality. This could be due to a variety of reasons. For instance, badgers may be more inclined to check habitat transitions carefully for signs of other badgers, since a major proportion of heavily used badger paths run along or across transitions (section 6.2.6). Resident badgers should then place border latrines at such sites to increase the probability of information transmission. Alternatively, residents may put an increased effort in marking quality transitions as a response to increased intrusion pressure from badgers in search of high quality areas (see Chapter 7). A third possibility is that density of latrine presence is an indicator of the importance residents attach to a particular area, ie. how willing (or rather how unwilling)

Table 5.16 Log-linear model for distribution patterns of badger latrines in relation to local habitat transitions and border status of latrine.
Part I: Data and model specification.

Variables: A 1= border latrine; 2= non-border latrine
B 1= OTHERS habitat at latrine location is neither pasture nor deciduous woodland (Types 7 and 37, see Chapter 2, section on habitat map)
2= GOOD habitat at latrine location is either pasture or deciduous woodland
C 1= OTHERS habitat close to latrine location is neither pasture nor deciduous woodland
2= GOOD habitat close to latrine is either pasture or deciduous woodland

(1) Data

		border	non-border
OTHERS at	OTHERS close	16	48
	GOOD close	23	37
GOOD at	OTHERS close	11	31
	GOOD close	19	93

---

(2) Testing for interaction of variables (model generation)

1. Test for three factor interaction (test $\alpha\beta\gamma=0$)

$G_{abc} = 3.864$ df= 1; p = 0.05 Chi $sq_{crit} = 3.841$.

2. Test for two factor interaction: $\alpha\beta = 0$?

$G_{ab(c)} = 9.3615$ df = 2 , $p < 0{\cdot}01$

$G_{ab(c)} - G_{abc} = 5.4969$ df = 1 , $p < 0{\cdot}025$

3. Test for two factor interaction: $\alpha\gamma = 0$?

$G_{ac(b)} = 4.1465$ df = 2 , n.s.

$G_{ac(b)} - G_{abc} = 0.2819$ df = 1 , n.s.

4. Test for two factor interaction: $\beta\gamma = 0$?

$G_{bc(a)} = 21.4329$ df = 2 , $p < 0{\cdot}001$

$G_{bc(a)} - G_{abc} = 17.5683$ df = 1 , $p < 0{\cdot}001$

(3) Final model

$$\ln f_{ijk} = u + \alpha_i + \beta_j + \gamma_k + \alpha\beta_{ij} + \beta\gamma_{jk}$$

Table 5.17 Log-linear model for distribution patterns of badger latrines in relation to local habitat transitions and border status of latrine.
Part II: Interpretation of model

Data and variable specifications as in Part I.
FT = Freeman-Tukey deviate (an estimate of how significant an individual deviation of expected and observed frequencies is)

Interpretation			FT
(1) H_o = For a given level of C (Habitat close) no interaction of A (status) and B (Habitat at)			
rejected		FT_{crit} =	0·97
OTHERS close	as expected		
GOOD close	too many latrines at OTHERS AT to GOOD CLOSE transitions with border status		1.9744*
	too few latrines at GOOD AT to GOOD CLOSE transitions with border status		1.6759*
	too few latrines at OTHERS AT to GOOD CLOSE transitions with non-border status		1.2582*
	too many latrines at GOOD AT to GOOD CLOSE transitions with non-border status		0·91
(2) H_o = For a given level of A (status) no interaction of B (Habitat at) and C (Habitat close)			
rejected		FT_{crit} =	0·97
border	as expected		
non-border	too many latrines where Habitat at is similar to Habitat close		
		OTHERS - OTHERS	2.5477*
		GOOD - GOOD	1.7459*
	too few latrines where Habitat at is different from Habitat close		
		OTHERS - GOOD	2.3296*
		GOOD - OTHERS	2.5043*

residents are to "negotiate" ownership of this area with their neighbours. Here, border latrines may not only advertise range boundaries but also reinforce ownership claims on high quality habitat. Indirect evidence for this suggestion is the poor presence of latrines at border sections that run through arable land, a habitat of supposedly low value to badgers.

Fewer border latrines than expected were placed at high quality to high quality habitat transitions. If significance to badgers is a function of presence or absence of habitat transitions per se, then this should be distinguishable (in terms of latrine presence) from transitions in quality, since some habitat transitions occur where there is no change in habitat quality (e.g. from pasture to deciduous woodland). It is arguable (Chapter 7) that areas of high quality to high quality transitions are less subject to high intrusion pressure than areas with transitions with a quality change, perhaps because such adjacent areas are treated as a single functional patch. If density of latrines is a function of pressure from intruders, then presence of latrines at such transitions should be reduced, as is the case. If border latrines serve to reinforce ownership claims on high quality habitats, then latrine presence should be independent from the quality of neighbouring habitat; a reduced presence is inconsistent with this expectation. However, it may well be that badgers do not react to transitions between areas of similar quality as transitions at all; consequently there would be no need to maintain a marking intensity on a level comparable with that at transitions associated with a quality change.

According to the two significant two-factor interactions, non-border latrines occur more often than expected at transitions with no quality change while fewer than expected occur at transitions with a quality change. High quality habitats are frequently and intensively visited by residents (Chapter 6). Increased latrine usage may just be an incidental consequence of badgers staying in such areas for a long time, so that the need for

defaecation arises more frequently. However, if defaecation inside the range is an incidental affair, then there is no need to maintain special sites for defaecation. Alternatively, marking at non-border latrines could remind an individual whether it has already visited this particular area on a given night and how much time has elapsed since its last visit or that of a group member. (This assumes that badgers can tell from the condition of a marking how much time has elapsed since it was deposited). Foraging success (e.g. rate of energy intake) in high quality habitats is a function of the time since the area was last visited (see Chapter 7): with more time elapsed without any badger presence, more worms are likely to have returned to the surface and thus become available, provided the weather has not deteriorated. In areas of high intrinsic value, revisiting intervals are shorter than in other areas (Chapter 6), increasing the likelihood that badgers may return to an area before it has fully 'recovered', and thus depress their feeding rate, unless their movements are somehow coordinated (details see Chapter 6). Since badgers can distinguish the scent of different individuals (Kruuk et al. 1984, Gorman et al. 1984), marking as an indicator of previous usage of a patch could facilitate intra-group communication and help avoid (i) over-exploitation of patches and (ii) waste of time on fruitless searches of patches already 'harvested'. This is important, if group members want to minimize interference (Chapter 7).

The log-linear model shows that it is important to distinguish between border and non-border latrines, since the model identified patterns of latrine characteristics opposite in trend for latrines of different status.

5.4.3.2. Utilization of latrines

Data on latrine utilization are available from each month for the periods April to November 1982 and March to October 1983. 39.7 % of latrines

checked contained at least one recent dropping ("active" latrines). The majority of latrines without a recent dropping had obviously not been visited for some time and showed clear signs of decay. The following analysis only deals with "active" latrines.

The majority of latrines were founded in spring (Table 5.6, Fig. 5.24). In spring 1983, three times more new latrines were founded and active than in spring 1982. However, since the number of active latrines during the remainder of the year was similar for both years (Mann-Whitney U-test, normalized, n=7, m=7, U (border latrines)= -0.771, ns; U (non-border latrines)= -0.832, ns), data from both years were analysed together.

The size distribution of latrines as measured by numbers of TOTAL, FILLED, and FRESH pits per latrine is shown in Fig. 5.25. Four size classes were distinguished: small (1-2 pits), medium (3-9), large (10-19), and extra-large latrines (> 19 pits). 7.9 % of all checks encountered latrines with more than 19 TOTAL pits, but only 1.3 % had similarly many FRESH pits. 55.8 % of the cases concerned latrines with 1-2 FRESH pits. The size distributions differ between the three measures ($G=129.8$, $df=6$, $p < 0.001$).

The pattern of utilization varied between latrines of different status. Binomial tests (Table 5.18) were used to investigate whether observed numbers of active latrines of a given status matched expected ones. In 11 out of 16 months, observed and expected numbers corresponded. In 4 months of 1983, more border latrines were active and in June 1982, fewer border latrines were active than expected. Measures of intensity of use per latrine were significantly different for latrines of different status (Table 5.19); in all cases, border latrines were larger or contained more pits than non-border latrines.

Latrine utilization also varied greatly between different times of the year (Fig. 5.26, Table 5.19). Table 5.20 analyses differences in intensity of use of border latrines in more detail. Differences occurred both within

Table 5.18 Results of binomial tests that compared observed numbers of active latrines with expected numbers for a given status. Expected probabilities p (for border latrines) and q (non-border latrines) are derived from the number of available and checked latrines of a given status for each month. Summed probabilities are one-tailed probabilities for observed and higher numbers of active border latrines.

Month	p	q	exact prob.	summed prob.
April 1982	0.439	0.561	0.098	0.69
May	0.308	0.692	0.19	0.27
June	0.545	0.455	0.073	0.98 *
July	0.25	0.75	0.16	0.61
August	0.5	0.5	0.12	0.50
September	0.338	0.662	0.14	0.63
October	0.263	0.737	0.16	0.75
November	0.324	0.676	0.078	0.25
April 1983	0.289	0.711	0.061	0.39
May	0.219	0.781	0.033 *	0.058
June	0.171	0.829	0.11	0.16
July	0.277	0.723	0.013 *	0.026 *
August	0.28	0.72	0.029 *	0.072
September	0.282	0.718	0.0095 **	0.016
October	0.238	0.762	0.12	0.49

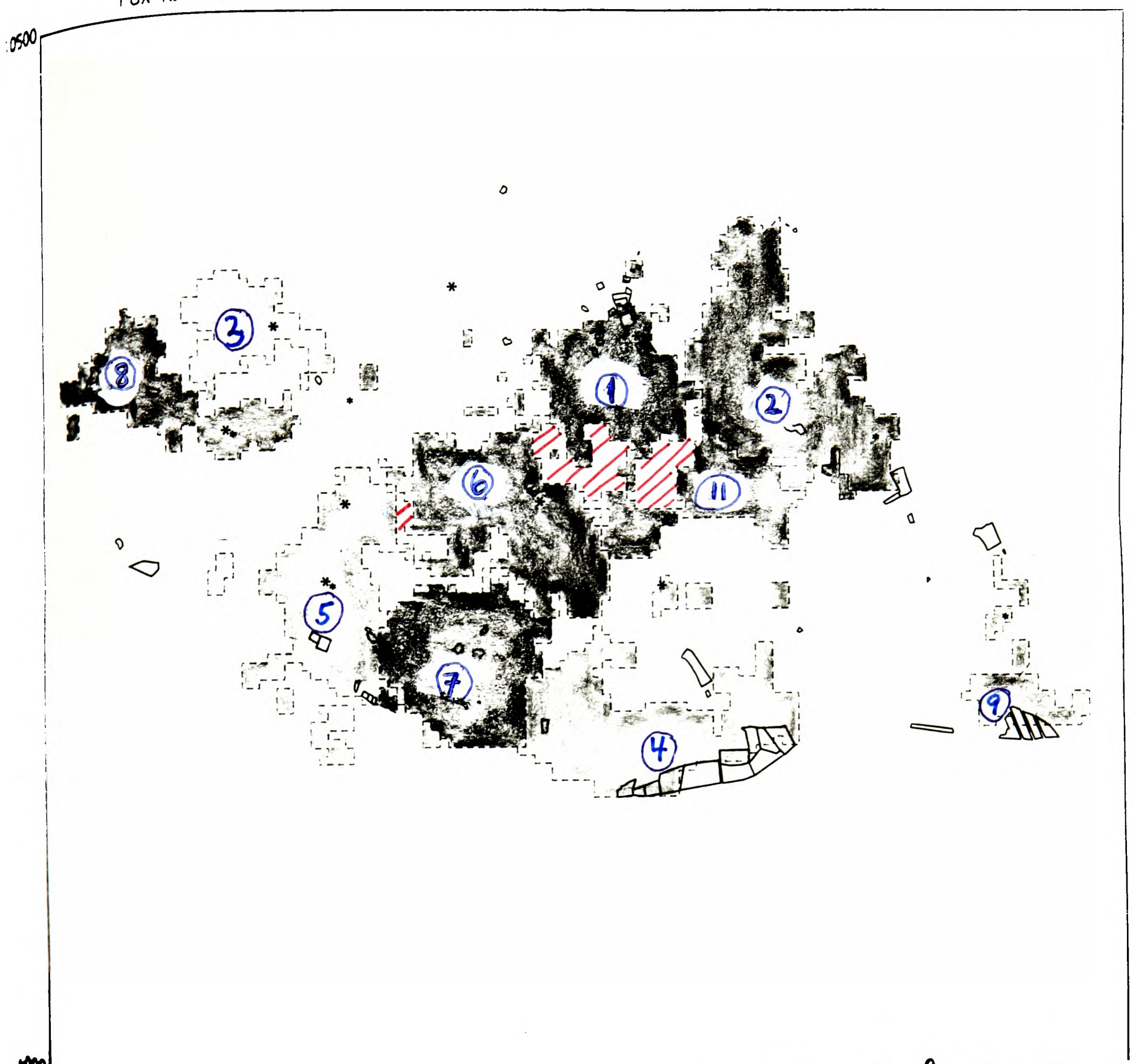
Table 5.19 Comparison of intensity of use of latrines of different status and during different seasons. H = Kruskal-Wallis analysis of variance, adjusted for ties.

(a) Comparison of latrines of different status: non-border latrines, border latrines shared by two neighbour ranges, border latrines shared by three neighbour ranges.

Variable	df	H	significance
AREA	2	54.5	< 0.001
TOTAL number of pits	2	70.7	< 0.001
FILLED " " "	2	65.6	< 0.001
FRESH " " "	2	30.3	< 0.001

TOP.

FOX R. HUMAN



Range Numbers of fox groups.

Table 5.19 Comparison of intensity of use of latrines of different status and during different seasons. H = Kruskal-Wallis analysis of variance, adjusted for ties.

(a) Comparison of latrines of different status: non-border latrines, border latrines shared by two neighbour ranges, border latrines shared by three neighbour ranges.

Variable	df	H	significance
AREA	2	54.5	< 0.001
TOTAL number of pits	2	70.7	< 0.001
FILLED " " "	2	65.6	< 0.001
FRESH " " "	2	30.3	< 0.001

(b) Comparison of intensity of use of border latrines in different months: months with sample sizes > 5, both years lumped, no distinction of number of neighbouring ranges sharing the latrine.

Variable	df	H	significance
AREA	11	26.64	< 0.001
TOTAL	11	14.83	ns
FILLED	11	10.67	ns
FRESH	11	22.22	< 0.025

(c) Comparison of intensity of use of non-border latrines in different months: both years lumped.

Variable	df	H	significance
AREA	15	43.2	< 0.001
TOTAL	15	60.5	< 0.001
FILLED	15	51.2	< 0.001
FRESH	15	43.2	< 0.001

Table 5.20 Multiple comparisons of months for differences in the intensity of use of border latrines. Only comparisons with significant differences listed. Measures of intensity of use selected were AREA and FRESH (the only ones with significant differences between months according to Table 5.19).

High	Low	AREA			FRESH		
		Actual value	crit. value	signi-ficance	actual value	crit. value	signi-ficance
Apr 82	Aug 83	39.0	35.3	<0.05	49.3	47.5	<0.01
Apr 82	Sep 83	49.7	46.7	<0.02	–	–	–
Aug 82	Aug 83	40.0	37.1	<0.05	–	–	–
Aug 82	Sep 83	50.7	48.7	<0.02	–	–	–
Sep 82	Oct 82	69.8	62.4	<0.05	–	–	–
Sep 82	Aug 83	54.7	54.0	<0.02	51.5	47.3	<0.05
Sep 82	Sep 83	65.4	64.0	<0.01	–	–	–
Nov 82	Jul 83	–	–	–	42.7	38.1	<0.05
Nov 82	Aug 83	–	–	–	57.8	52.9	<0.005
Nov 82	Sep 83	43.1	39.7	<0.05	43.1	40.8	<0.05
Apr 83	Oct 82	60.6	52.0	<0.05	–	–	–
Apr 83	Jul 83	–	–	–	38.1	37.8	<0.02
Apr 83	Aug 83	45.5	42.6	<0.005	53.2	51.1	<0.001
Apr 83	Sep 83	56.2	54.3	<0.002	38.5	35.0	<0.05
May 83	Oct 82	88.7	87.8	<0.005	–	–	–
May 83	Jul 83	60.1	55.5	<0.02	52.0	46.7	<0.05
May 83	Aug 83	73.6	69.4	<0.002	67.1	65.5	<0.005
May 83	Sep 83	84.3	79.5	<0.001	52.4	48.9	<0.05

Fig. 5.24

Changes of number of (a) new (b) total available and (c) proportion of active latrines over time (from April 1982 to October 1983)

a.

5-24

NO OF NEW L.

120
100
80
60
40
20

A M J J A S O N M A M J J A S O

b.

AVAILABLE L.

280
240
200
160
120
80
40

A M J J A S O N M A M J J A S O

c.

PROPORTION ACTIVE %

100
80
60
40
20

A M J J A S O N M A M J J A S O

Fig, 5.25 Frequency distribution of latrine size as measured by TOTAL number of pits (circles), FILLED number of pits (triangles) and fresh number of pits (squares).

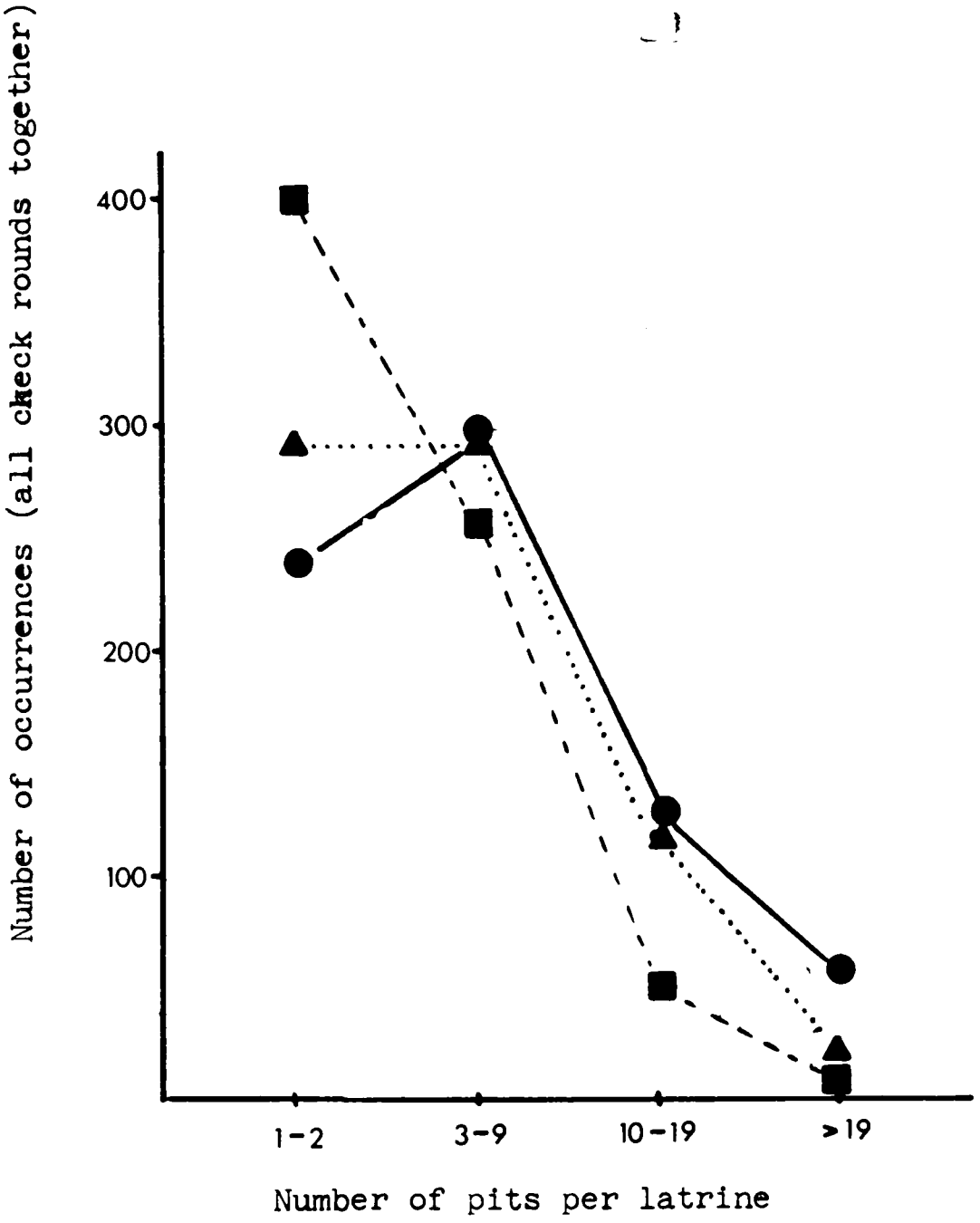


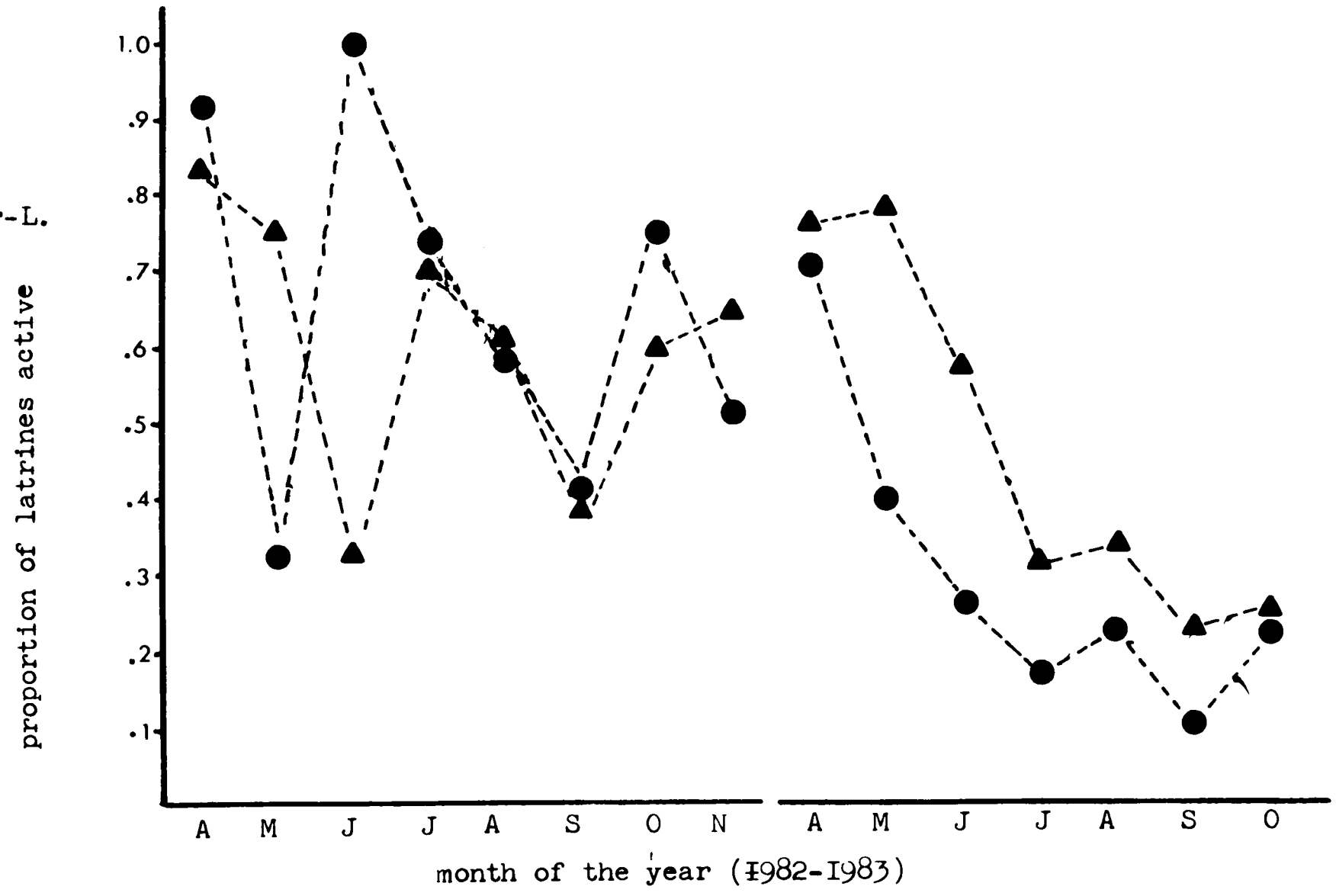
Fig. 5.26

Proportion of utilized latrines of latrines available and checked in a given month versus time (April 1982 to October 1983)

Circles: non-border latrines

Triangles: border latrines

triangles: border-L.
circles: non-border-L.



and between years. Both spring seasons were times of high activity while activity was reduced during the remainder of the year. Autumn 1982 witnessed (with the exception of October) a higher intensity of use of latrines than autumn 1983 when intensity sharply declined. During the period of low utilization in summer and autumn 1983, however, more border latrines were maintained active than expected (Table 5.18).

The relationship between the proportion of active latrines and the intensity of use per latrine deserves closer investigation. According to the results described so far, measures of intensity of use per latrine can be expected to covary with the proportion of active latrines, ie. if many latrines are used, then activity per latrine should be high, and vice versa. Fig 5.27 and 5.28 show how the measures relate to each other for border and non-border latrines. For border latrines, significant correlations were found for AREA, TOTAL and FRESH (Table 5.21). When a high proportion of border latrines is used, badgers enlarge latrines by digging new pits (AREA and TOTAL) and distributing their faeces over many pits (FRESH). Only the long-term record of latrine activity (FILLED) is an unreliable indicator of present interest in latrines. For non-border latrines, only the actual number of FRESH pits per latrine increases with the proportion of active non-border latrines.

In summary, badgers have periods with low and high levels of activity in latrines. Spring is the time when badgers are most heavily occupied with them, and when most of the existing latrines are visited, new ones are founded and new pits are dug at border latrines, often, but not always, filled with droppings, and droppings are distributed over many pits. During periods of less activity, few latrines are visited and marked, droppings are often piled in a few pits and latrines are left unchanged. However, the system is quite flexible and the timing and extent of intensive and cursory utilization variable. Here the two years showed contrasting patterns. In

Table 5.21 Comparison of different measures of latrine utilization by badgers. A priori expectation is that measures covary; thus significance values are one-tailed (positive correlation expected).

(a) Border latrines (analysis excludes March due to small sample size)

parameters compared	Spearman's rank corr.	df	significance
proportion of active border latrines of all border latrines available and checked in a given month			
and			
AREA	0.64	15	<0.01
TOTAL number of pits	0.56	15	<0.025
FILLED " " "	0.21	15	ns
FRESH " " "	0.49	15	<0.05

(b) non-border latrines

parameters compared	rank corr.	df	significance
proportion of active non-border latrines of all non-border latrines checked and available in a given month			
and			
AREA	0.41	16	ns
TOTAL	0.18	16	ns
FILLED	0.12	16	ns
FRESH	0.57	16	<0.025

Fig. 5.27-5.28

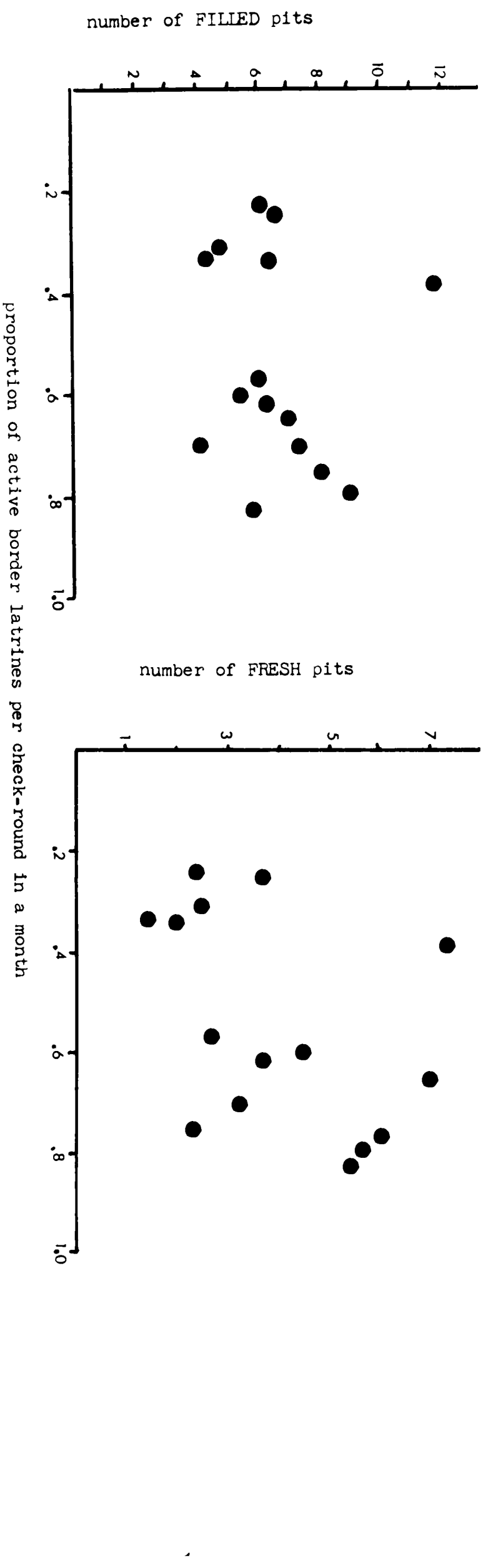
Relationship between different measures of intensity of use per latrine and the proportion of latrines active of a given category (border and non-border latrines, respectively)

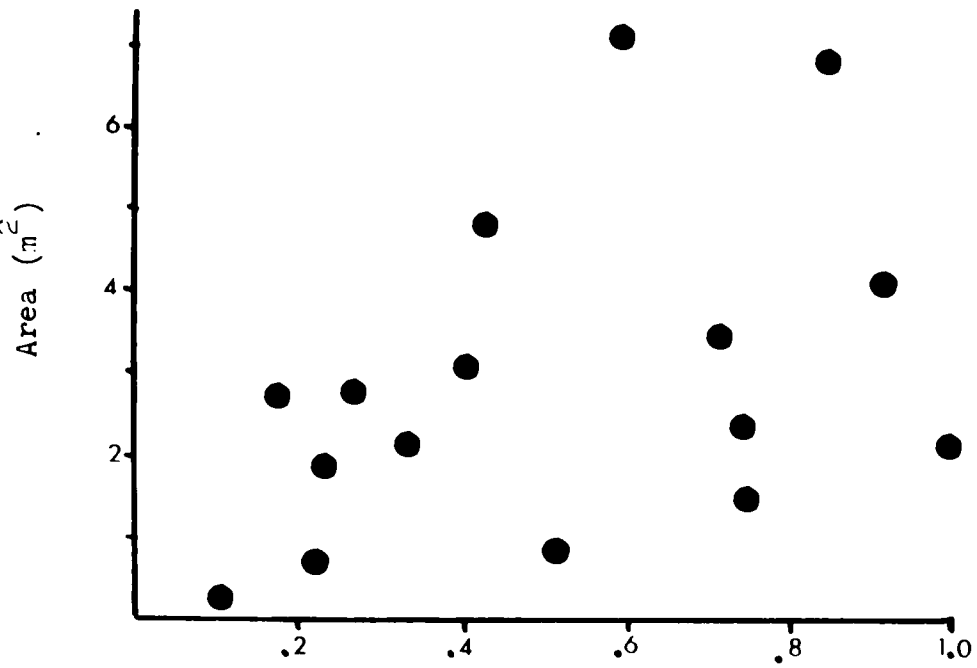
a. AREA (ha) versus proportion of active border-L

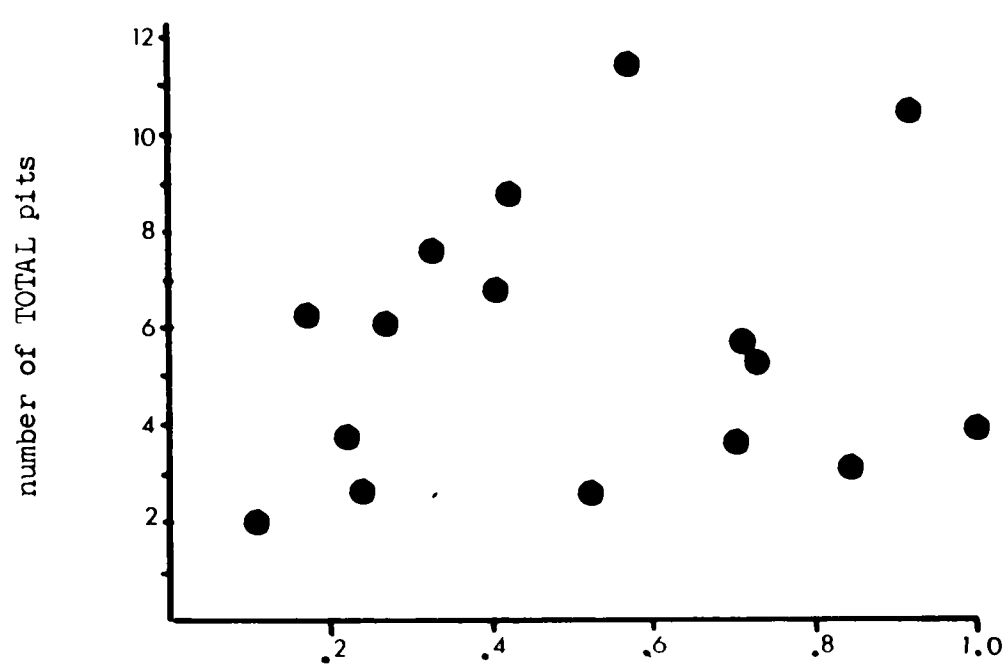
b. TOTAL " " " " "

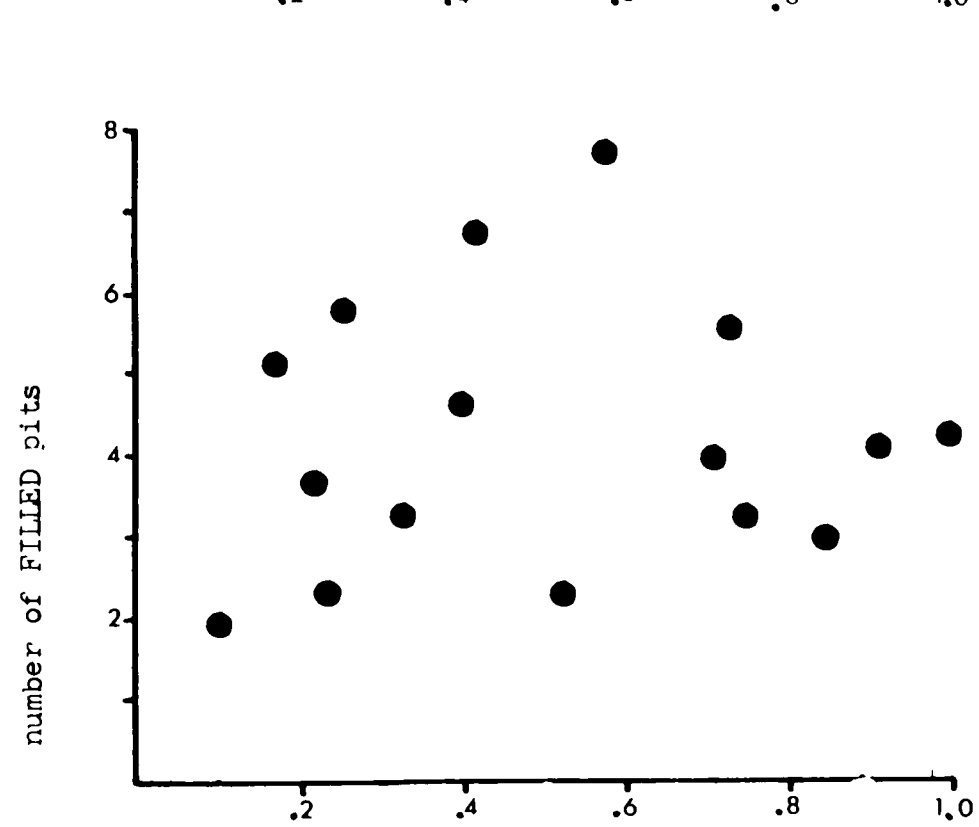
c. FILLED " " " " "

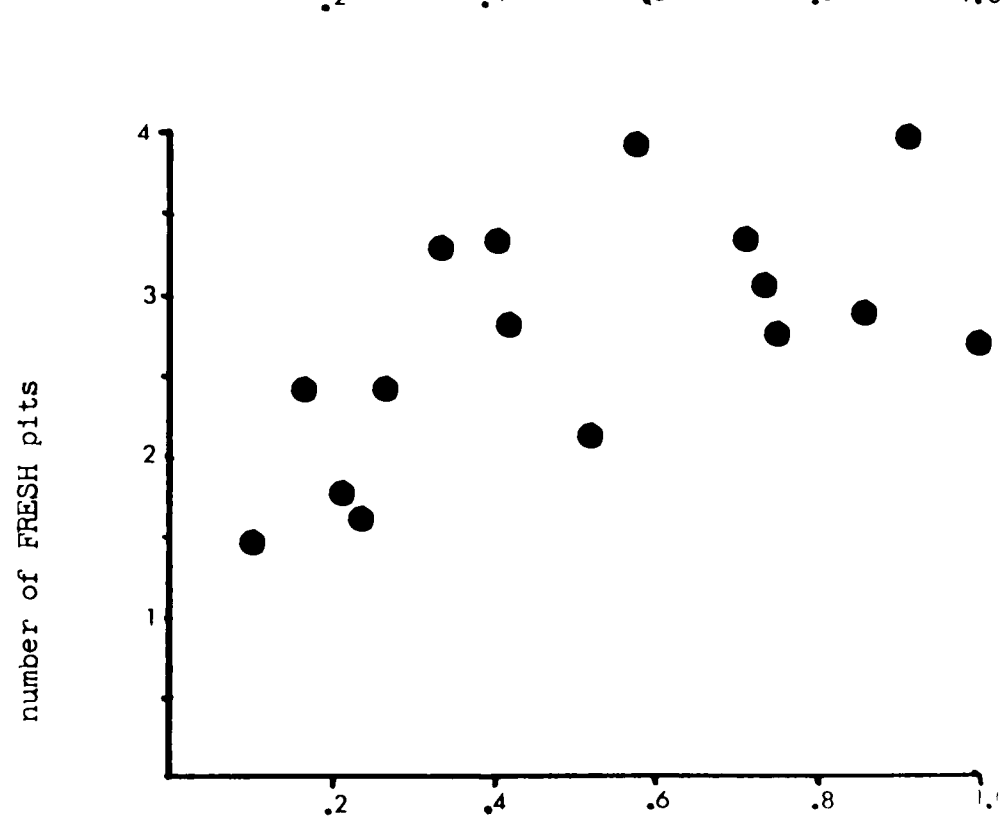
d. FRESH " " " " "


number of FILLED pits
2
4
6
8
10
12
.2
.4
.6
.8
1.0
number of FRESH pits
Area (m^2)
2
4
6
8
10
12
14
.2
.4
.6
.8
1.0
number of TOTAL pits
2
6
10
14
18
.2
.4
.6
.8
1.0
proportion of active border latrines
1
3
5
7
.2
.4
.6
.8
1.0
per check-round in a month









proportion of active non-border latrines per check-round in a month

1982, a moderate number of latrines was available, a high proportion was maintained active throughout the year and active latrines were intensively used. In 1983, foundation activity and numbers available were extremely high in spring, but intensity of use declined strongly according to all measures employed during the remainder of the year.

5.4.3.3. Function and evolution of badger latrines.

Due to their solitary movements (Chapter 6) and foraging habits (Chapter 3), badgers face the problem of transmitting information indirectly to a heterogenous group of potential receivers, some of which they know (neighbours) and some they do not (e.g. dispersing adolescents). The use of latrines, constituting a formalized marking system by which special sites are agreed upon as information centres, increases the likelihood that (i) information will be received and (ii) that it is received by the appropriate individuals. Further characteristics of the latrine marking system are (i) marking is continued throughout the year (Harris 1982, pers. obs.), ie. information flow is permanent; (ii) marking intensity never drops below a threshold; (iii) marking intensity varies and can be adjusted by the resident animals.

Fine tuning of marking intensity can best be understood as an adaptation to changing pressures, particularly intrusion pressure. Fig. 5.29 depicts a graphical model relating marking intensity, as observed in latrine utilization, to pressure. Two elements characterise the model. At low levels of pressure, marking intensity never drops below a threshold. Here, the message includes the statement "I am/we are still about and continue to occupy this range". If, as in Wytham (Kruuk 1978a, section 5.4.2.), ranges are defended territories, the message extends to "and I/we shall continue to defend it". At low levels of utilization, border latrines were more

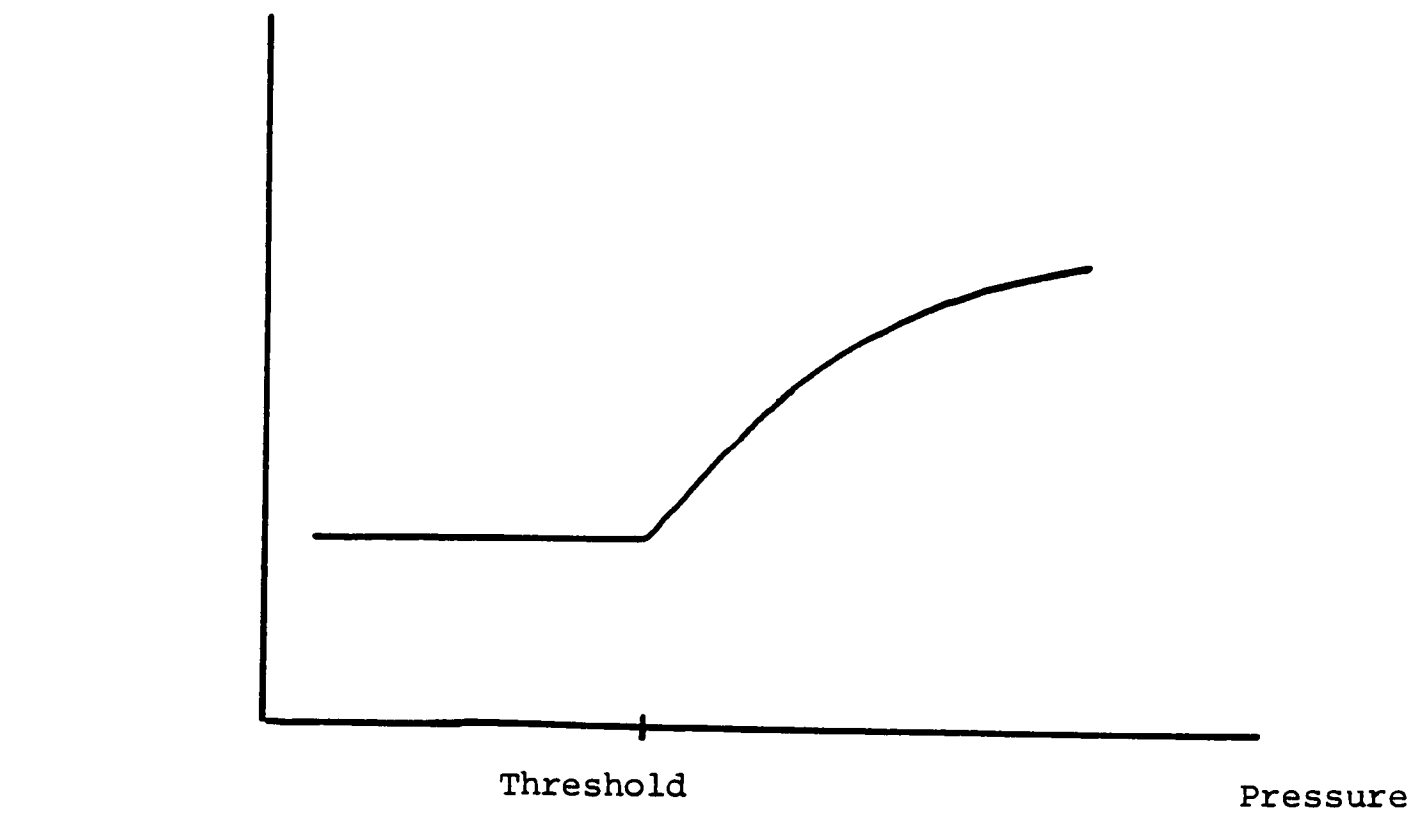
Fig. 5.29

Model of latrine marking intensity versus pressure exerted by outside badgers

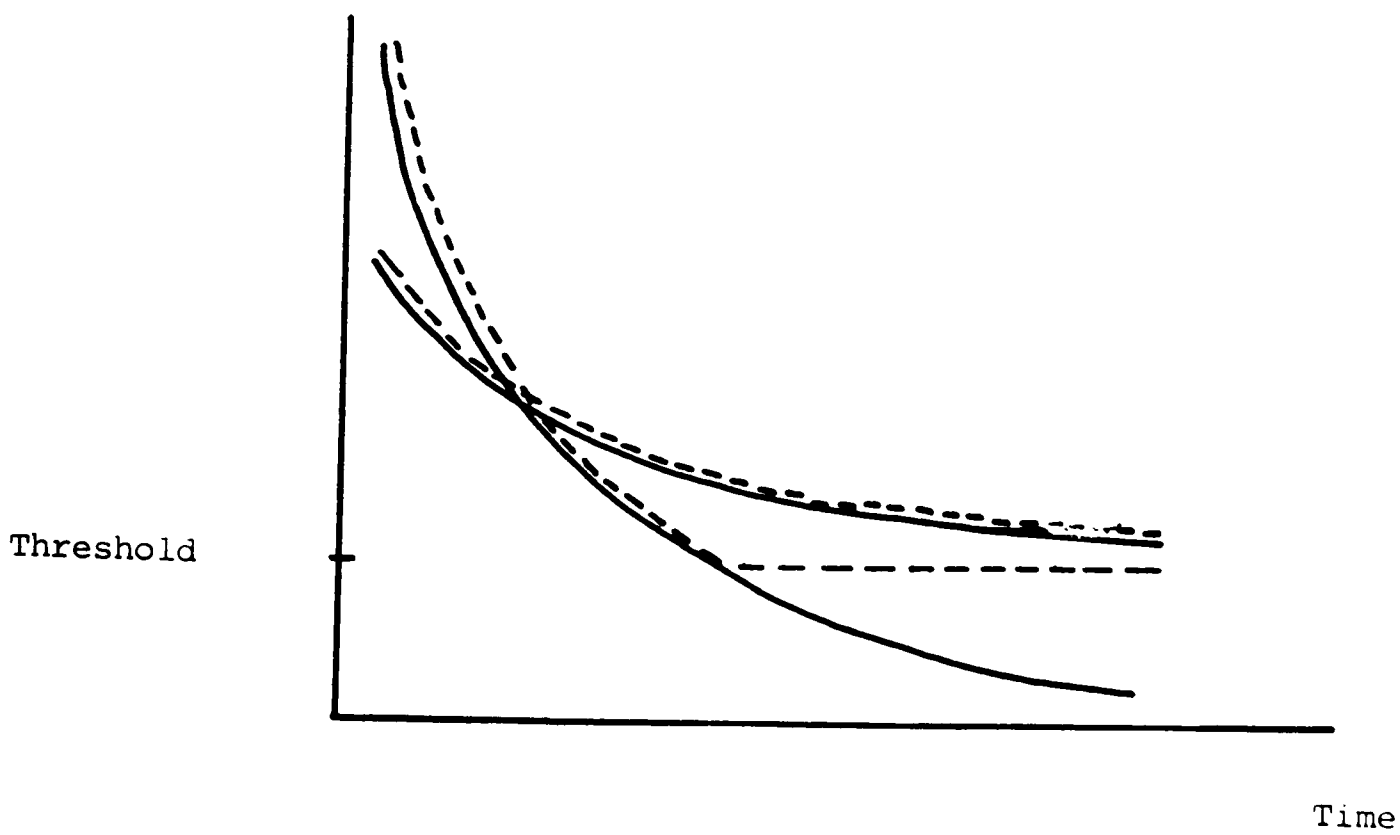
a. Model: over a wide range of minimal to moderate pressures, marking intensity increases slowly but rapidly once a certain threshold has been surpassed

b. Illustration of the relationship between pressure/marking intensity and time (ie. from spring to autumn). The two curves represent 1982 and 1983. 1982 starts at lower intensity but maintains a higher level throughout the year, while in 1983 after a flush of activity intensity reduces to very low levels

a.


M. Intensity
Threshold
Pressure

b.


Pressure
Marking Intensity
Threshold
Time

active than expected (Table 5.18). According to the model, marking intensity increases by some kind of monotonic function at intermediate to high levels of pressure. Some evidence for this is provided by the distribution of latrines (and increased density of latrines at certain habitat quality transitions) which could best be explained by interpreting them as a response to intrusion pressure. Then (i) many latrines and (ii) a high proportion of available latrines are used and (iii) each latrine is intensively used (Table 5.21). The general message is complemented by specifying the exact delineation of the boundary ("the range extends up to here") and the declaration that this area still belongs to this group ("we continue to defend"). Latrine utilization is highest, when range boundaries are negotiated and reinforced at times when specific resources attain a particular importance (high quality habitat for females during the period of lactation, females for males during the periods when the females are in oestrus, Chapter 7) to owners as well as intruders. Here, utilization of latrines can be regarded as providing vital information preceding and perhaps defusing contests.

The adaptive features of this system are numerous. The continuity of marking continually reminds neighbours, the most likely contestants, of the identity of the opponent, e.g. by matching the scent of the individual with the scent encountered previously at border latrines (Gosling 1982). Thereby, contestants can identify role asymmetries before a contest begins and reach a quick settlement following some rule, e.g. the owner wins (Maynard Smith 1982). However, this system works only if both sides accept conventions as a means to settle the conflict economically. This seems to be the case for badgers; Kruuk (1978a) has described some border fights between badgers where the dominance of an individual during the fight clearly depended on whether it was on its own range ("owner") or inside the neighbour's ("intruder").

Establishment of range boundaries is another field where the latrine marking system can help avoid escalations. Such disputes are equivalent to games with incomplete information: both partners know how much they value the resource in question, but neither knows how much the other side values it, how far the opponent is prepared to escalate the conflict. Essential features of such games are that a compromise is possible (the resource is divisible) and that a breakdown of negotiations (escalation without settlement) could occur, usually with costly consequences due to the ignorance of both sides (Maynard Smith 1982). By varying foundation activity and the intensity of use of its border latrines and checking the claims of its neighbours, a group can evaluate the intensity of pressure that it is exposed to by different neighbours and compare the 'suggested changes' with its own needs. Neighbours are probably longstanding (section 5.4.2.) and latrines ensure repeated encounters. Under these conditions, it pays both contestants to be moderate in their border disputes and to avoid clashes, since, once established, such cooperative behaviour is evolutionarily stable against nasty alternatives (Axelrod & Hamilton 1981, Axelrod 1984). However, a system like marking latrines as a surrogate for (the majority of) territorial disputes is only likely to be useful (and thus stable over evolutionary time) if changes can be moderate and if the need for changes arises infrequently (e.g. once a year). This requires some stability of the conditions that determine the spatial structure of a population, e.g. stability in resource distribution, as well as a long life expectancy for group members, so that neighbours do indeed encounter each other repeatedly and familiarise themselves with each other. This is the case in Wytham: in Chapter 3 I have shown that earthworms, the major resource for badgers in Wytham (Chapter 4), seem to occur at constant population levels in different habitats over at least 10 years. Furthermore, the long-term changes in the spatial structure of the population from 1974/75 (Kruuk 1978a) to 1982/83

are moderate; the basic structure of the spatial setup has been preserved (section 5.4.2.). Finally, if badgers survive the first year of life, their mortality rate during adulthood is low (Anderson & Trewhalla 1985).

In the light of these proposals, I suggest that spring 1982 saw a quick settlement of the territorial mosaic for that spring, but that conflicts lingered on and raised general levels of latrine utilization later in the year. Spring 1983 saw a lot of border instabilities that were resolved after an intense flush of activity leaving few disputes during the remainder of the year.

The changes in the pattern of latrine utilization from one year to the next is consistent with marking activity as expected from a situation equivalent to an 'independent-cost game' (Parker 1984), if the contestants can choose from a continuous set of behavioural strategies (e.g. vary intensity of use on a continuous scale): once a conventional rule is established by which the neighbours settle their conflicts, they should require less and less marking activity to achieve and maintain settlements, thereby reducing the cost of marking until they are so small that it pays the contestants to breach the rules, even if such a behaviour promises only small to moderate benefits. Since the level of marking intensity is then insufficient to guarantee a proper settlement, marking intensity has to increase until the opponents have again agreed to settle by their convention. (This assumes that even at high costs of marking, the benefits in terms of improved survival and avoidance of escalated conflicts still outweighs the costs of marking activity). Therefore an endless oscillation is expected between reduced and increased marking activity.

5.5. Fox group ranges.

In contrast to badger ranges, the layout of fox group ranges is less

neat and tidy, and some - although not substantial - overlap between neighbouring ranges may occur, exceptional cases notwithstanding (Macdonald 1977a). Foxes are also distinguished from badgers in that the den does not assume the same importance to the fox as the sett does to the badger. Fox dens seem to be essential only as a hide for small cubs in spring, and, in unsuitable landscapes and geological formations, may then limit the breeding density of foxes (Weber 1985). According to monthly checks of earths of all kinds and the habits of radio-tracked individuals, use of earths, badger setts or extended rabbit warrens was erratic or absent in other seasons. Foxes show great flexibility in their choice of day-time resting places. In Range 7, for instance, the two radio-tracked foxes RABBITS and PINTOOTH often slept in a large blackberry bush that stood isolated in the midst of pastures and long grassland and was surrounded by buildings, or they went to a small thicket next to the swimming pool at Hill End Camp. During summer, wheat fields were a favourite resting site. This behaviour is used by the local farmers who successfully hunt foxes from reaping machines during harvest.

Information on range characteristics was derived from radio-tracking of 20 foxes (Tables 5.22 and 5.23). Hence, the available information, particularly for group size and reproductive success per group, is not as extensive as for badger groups, where the radio-tracking supplemented the results of the baiting action and the Annual Badger Census. This information is summarized in the following section.

5.5.1. Description of fox group ranges.

Fig. 5.30-5.33 illustrate the distribution of fox group ranges in the study area in relation to four major habitat categories (HUMAN: habitat types 1, 2, 3, 23, 47; DECIDUOUS WOODLAND: habitat type 37; PASTURE: habitat

Table 5.22 Foxes caught and radiotracked in Wytham 1981/83.
Location: I – caught inside its range; O – outside (e.g. on an excursion).

No.	Date of 1st capture	Location	Sex	Name	Group	eartag colour	eartag number	transmitter days	fate
1	07.08.82	–	F	BACKFOOT	–	white	170,173	28	dispersed north
2	21.04.81	I	M	BOOTS	6	green	28,29	18	?
3	06.03.81	I	F	BRAMBLE	1	white	142,143	180	?
4	17.02.82	I	F	ELKE	2	white	153,154	66	?
5	01.03.81	I	M	GASPER	1	–	–	197	shot 31.08.81 at Home Farm
6	17.04.81	I	F	GRIZZLE	3	–	–	94	?
7	31.05.83	O	F	KALI	4	pink	33,34	155	found dead 29.12.83
8	21.04.81	O	F	KBOOM	5	green	26,27	402	found dead 15.09.85
9	02.03.81	I	M	KOBUK	1	–	–	132	shot 31.07.81 at Home Farm
10	20.09.82	I	F	LIN	1	white	199,200	45	killed by car at Wolvercote 04.04.84
11	27.01.83	I	M	LIO	11	yellow	24,25	20	?
12	13.05.81	I	F	OLDMAHOGANY	6	–	–	214	?
13	17.04.82	O	M	OLDSABRE	5	–	–	13	?
14	21.05.81	I	F	PINTOOTH	7	–	–	201	?
15	15.11.81	I	F	PODGE	1	white	151,152	325	?
16	15.05.81	I	M	RABBITS	7	–	–	16	found dead at Hill End Camp 01.12.81
17	16.09.82	I	M	RIC	1	green	45,44	7	dispersed to Farmoor in May 82
18	16.04.81	I	F	SURPRISE	8	–	–	134	?
19	March 81	I	F	TARU	9	–	–	9	?
20	14.02.83	–	M	VALENTINO	–	green	49,50	3	dispersed towards Oxford City

Table 5.23 Association of individual foxes with group ranges.
* = tracking results of this individual were used to evaluate group range characteristics.

Group	Name	Individual(s)
1	HOME FARM	Bramble*, Gasper*, Kobuk*, Podge* Lin, Ric*
2	CHURCHGROVE	Elke*
3	GREAT WOOD	Grizzle*
4	TILBURY FARM	Kali*
5	WOODEND	Kboom*, Oldsabre
6	SINGING WAY	Oldmahogany*, Boots
7	HILL END CAMP	Pintooth*, Rabbits
8	SWINFORD LODGE	Surprise*
9	BINSEY	Taru*
11	MARLEY	Lio*

animals not associated with a Wytham group: Backfoot, Valentino; both moved in from the outside and left the study area again

type 7; ARABLE: habitat type 28, 29, 30).

Range F1 (HOMEFARM). This is the best known fox range in this study. It covers the southern half of Wytham village, extends to the Wytham road in the east, covers the northern half of Marley Wood in the south and includes the eastern fields of the Wytham Park in the West. Four adults, the dog-foxes GASPER and KOBUK and the vixens BRAMBLE and PODGE, were tracked in 1981 and 1982 (Table 5.22). There is some evidence that PODGE, the vixen caught in November 1981, was a resident throughout 1981. In summer 1981, unmarked fox(es) could be frequently observed at the back of Mrs. Gardiner's garden, and at the date of capture, PODGE was quite old and hence unlikely to be a recent immigrant (Lloyd 1980). In spring 1981, BRAMBLE had a litter in a den under a tree in the backyard of Mrs. Gardiner's garden (see Fig. 5.30-5.33), but moved the cubs to the wood later in the year. In spring 1982, PODGE had cubs in the same den as BRAMBLE in 1981 in the woodland at the southern fringe of the range, but moved them probably temporarily to the backyard of Mrs. Gardiner's garden at some stage (for a detailed description of her movements during the breeding season see Chapter 6). Both males were shot by the owner of Home Farm in late summer 1981; the fate of both females remains unknown. Observed litter size in both years was two cubs. Two young individuals, the vixen LIN and the dog-fox RIC, were caught in autumn 1982, but due to premature transmitter failure a satisfactory record of their dispersal movements could not be obtained. In May 1984, LIN was run over by a car at a distance of 2 km from her natal range in Wolvercote at the age of nearly 3 years. RIC moved in autumn 1982 from the village area to Marley Wood into the transition zone between Ranges F1 and F11 and dispersed to Farmoor at the southern edge of the study area in spring 1983, where he was sighted several times (straight dispersal distance from the natal range of 4.3 km). The HOMEFARM Range is dominated by pasture and deciduous woodland;

Fig. 5.30–5.33

Group ranges of foxes illustrated on major habitat categories. Numbering of fox ranges in accordance with Table 5.23. The habitats plotted are:

5.30 pasture

5.31 deciduous woodland

5.32 human areas

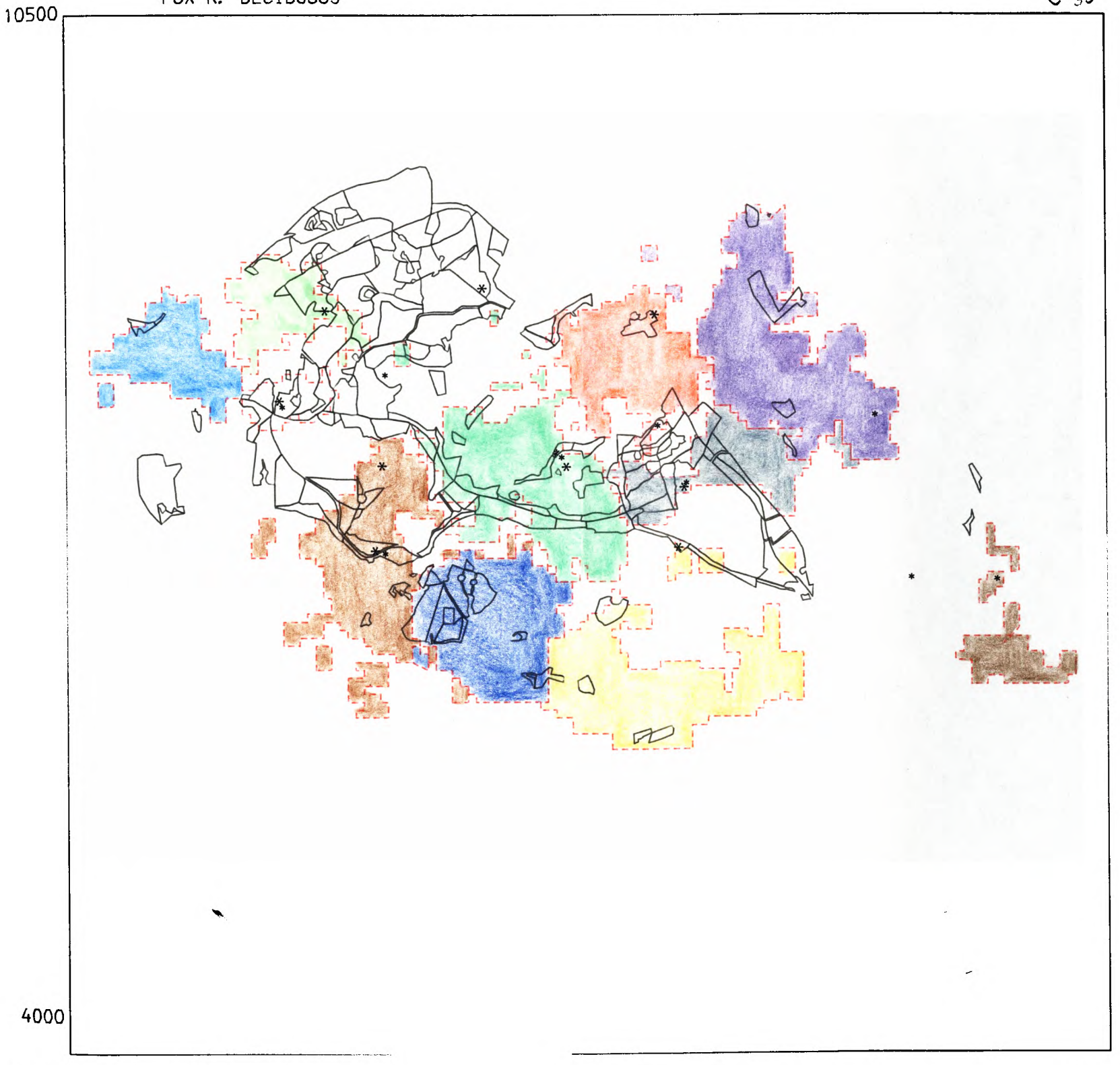
5.33 cereals

Large stars: fox breeding dens 1983

Small stars: fox breeding dens 1982

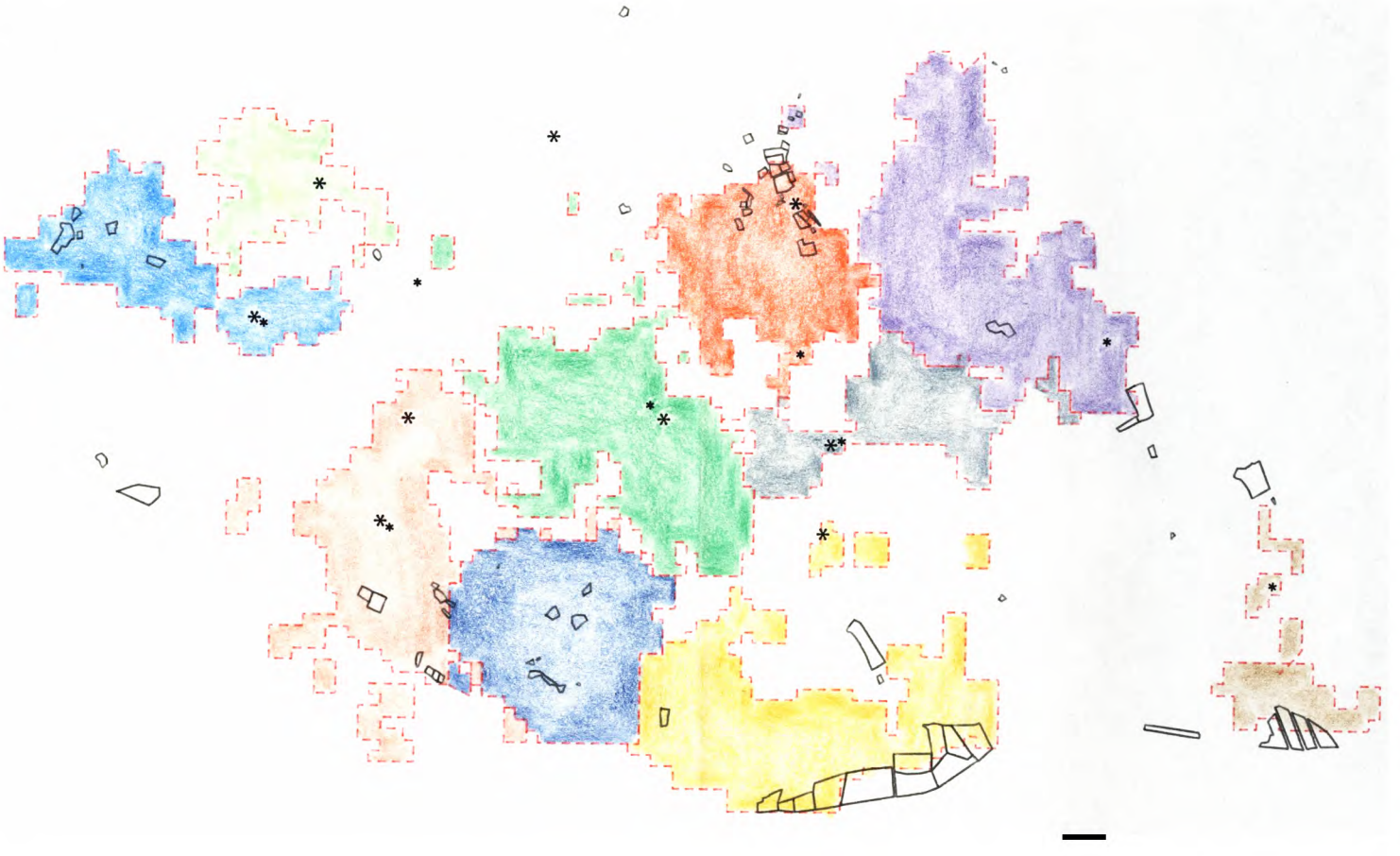
FOX R. DECIDUOUS

5-30



FOX R. HUMAN

5-31



10500

4000

44000

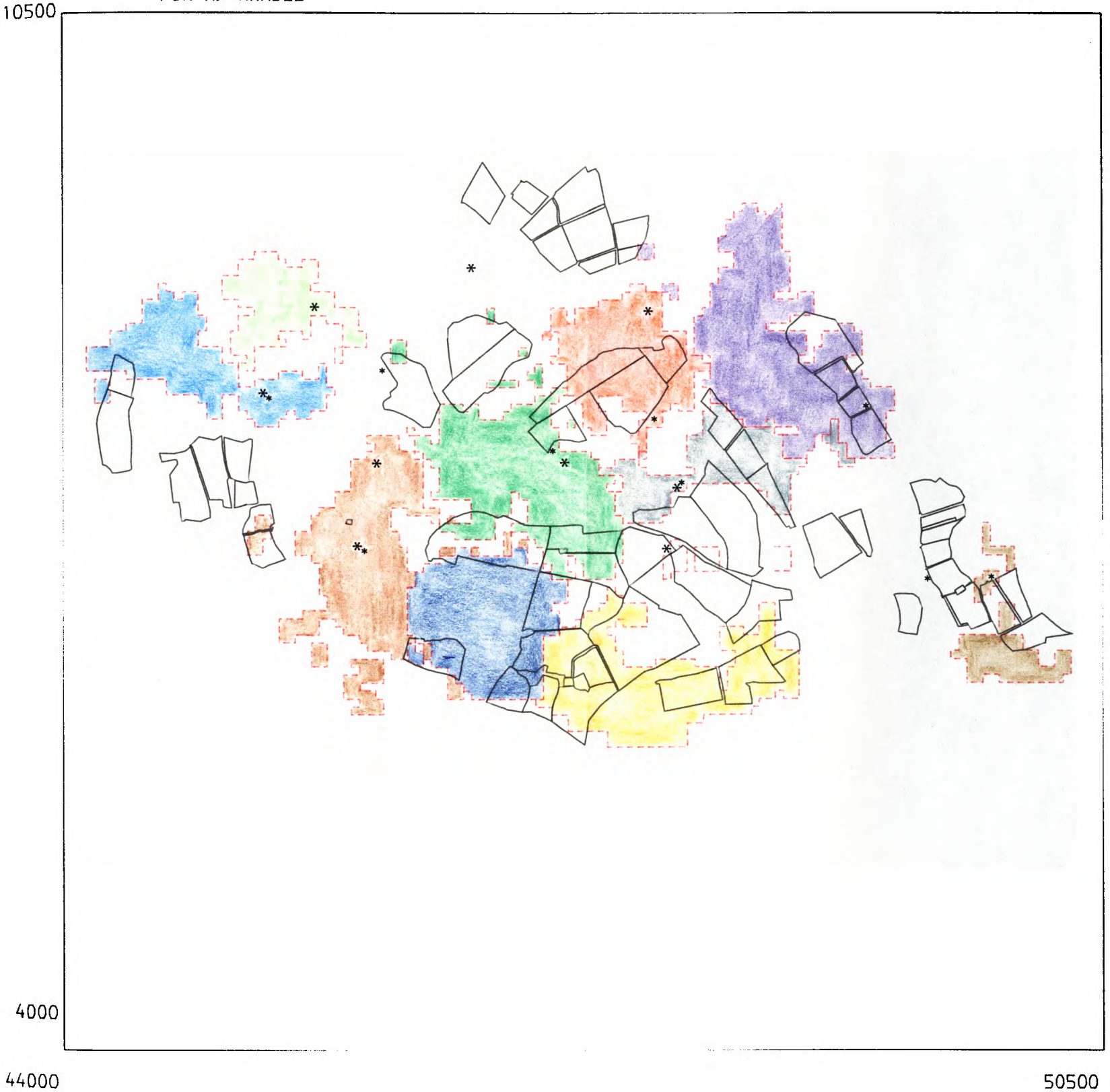
50500

FOX R. PASTURE

5-32



FOX R. ARABLE



third in area are wheat fields and root crops. Access to human-originated resources is manifold and varied (compost heaps, farms etc).

Range F2 (CHURCHGROVE). This range covers the northern half of the Binsey area. One fox, the vixen ELKE, was tracked here in 1982. Her range approximately coincides with the range of a vixen tracked several years earlier by Newdick (1983), indicating that the spatial setup of the fox ranges includes some stability. This vixen was barren when caught (17.2.1982), suggesting a group size of 3 if a breeding vixen was also present. In 1982, a breeding den was located in a hedge north of the Binsey Farm. According to the local farmer, that breeding den was regularly used. Accordingly, minimum estimate of group size is 3. Litter size could not be determined.

Range F3 (GREAT WOOD). This is a little known range where the vixen GRIZZLE was tracked in 1981. In 1983, 4 fox cubs were sighted in the Chalet badger sett in this area. The range is broadly partitioned into two sections: a short-grass pasture area in the west, and dense, heterogeneous woodland in the east.

Range F4 (TILBURY FARM). This range extends from southeastern sections of the woodland to the suburbs of Botley, including large fields, grass ley and pastures, but especially human-dominated areas (farms, allotments, detached, and semi-detached housing). Here, another barren vixen, KALI, was caught and radio-tracked in 1983. Simultaneous observation of 3 foxes during radio-tracking on 2.6./3.6.1983 lends additional support to the suggested minimum group size of 3. A fox litter was regularly observed at the Upper Follies badger sett, but since it is outside the range used by KALI, it is probably not associated with the TILBURY range. It is possible that cubs were reared

in the southern part of the range which was not included in any of the usual checks in spring time.

Range F5 (WOODEND). This range extends from the Eynsham road and Farnmoor in the south to the Singing Way and Radbrook Common in the north. The male OLDSABRE and the vixen KBOOM were tracked in this area in 1981 and 1982. Minimum estimate of group size is 2; information on possible additional group members is lacking. Close to the Nealing's Copse badger sett, a fox litter was observed with two cubs in all three years 1981-1983. Besides large areas of pasture and various kinds of woodlands, the range contains the Woodend Farm, the Buddhist Centre and other private housing.

Range F6 (SINGING WAY). The central range in Wytham covers The Pasticks Plantations in the east, most of Wytham Park in the north, part of the Radbrook Common area in the west and part of the wheat fields between the Singing Way and Hill End Camp in the south. The dog-fox BOOTS and the vixen OLDMAHOG were tracked in 1981; up to 4 foxes were observed simultaneously (DW Macdonald, pers. comm.). Breeding dens were located at varying sites every year. Litter size was 2 in both 1982 and 1983. Habitat heterogeneity is considerable, ranging from fields over pasture fields to mixed plantations, but no human habitation is present.

Range F7 (HILL END CAMP). This range covers some of Bean Wood in the west, but mostly the pastures and grasslands around the Hill End Camp Farm and the local natural history school. The dog-fox RABBITS and the vixen PINTOOTH were radio-tracked here in 1981. At dusk, other, unmarked fox(es) could occasionally be observed in the area. Presence of fox cubs could not be directly confirmed, although an earth was found at the edge of the wheat fields with signs typical for the presence of cubs in 1982 and 1983.

Range F8 (SWINFORD LODGE). This range extends from Swinford Lodge at the toll bridge to Eynsham in the west to the woodlands south of The Chalet and around the Reservoir in the east. It is again known from only one fox, the vixen SURPRISE tracked in 1981. A breeding den was found in 1982 and 1983 in a fox den in the neighbourhood of The Great Oak badger sett (Rough Common badger range).

Range F9 (BINSEY). This range covers agricultural and human-dominated area, mainly grass ley, wheat fields, allotments and terraced housing. Here, the vixen TARU was tracked in autumn 1981. Her range is nearly identical with that of previous members of Newdick's (1983) Binsey group radio-tracked several years earlier, again suggesting that long-term stability may be important.

Range F11 (MARLEY). This range is the southern neighbour of Range F1. It covers areas on both sides of the western by-pass and consists mostly of arable fields, pasture and deciduous woodland. In the east, it borders onto Range F2. Here, the dog-fox LIO was radio-tracked in 1983. A fox litter was located in the bracken area at the southwestern corner of Marley Wood both in 1982 and 1983. Litter size, could not be determined.

5.5.2. Characteristics of fox group ranges.

Several features of the range system as described in the previous section deserve special consideration.

(1) Long-term stability of range boundaries beyond the life-time of an individual seems to be common in Wytham. Evidence for this comes from at least four ranges. ELKE (Range F2) and TARU (Range F9) occupied ranges very similar to those occupied by foxes tracked several years earlier by Newdick

(1983). Furthermore, range boundaries of the HOMEFARM range as determined from the radio-tracking of PODGE in 1982 are consistent with the boundaries determined from the radio-tracking of BRAMBLE, GASPER, and KOBUK in 1981. Finally, the western edge of KALI's range (Range F4) in 1983 coincides with the eastern boundary of PINTOOTH's range (Range F7) in 1981, and the eastern edge of LIO's range (Range F11) in 1983 corresponds to the southwestern border of ELKE's range (Range F2) in 1982. Therefore I believe it is justified to consider all ranges from all three years together as one system in my subsequent analyses.

(2) Are Wytham foxes territorial ? Although there are many different views as to what constitutes territoriality (for a review see Kaufmann 1983), two commonly agreed criteria are (i) exclusive use of an area and (ii) active maintenance and defence of the area. I shall first deal with exclusive use and then turn to the maintenance and defense of ranges.

Several group ranges overlap slightly or moderately (Fig. 5.30-5.33). However, most part of the ranges are exclusively used by group members (Fig. 5.30-5.33). Overlap may be due to three causes:

(i) overlap is an artefact: assume, for instance that a river constitutes a perfect border between two neighbouring ranges but runs at an oblique angle through a cell. Foxes from different groups walking along both sides of the river would never touch the same ground, yet due to the analysis based on 50 m grid cells they would seem to share one or several cells. This artefact accounts for narrow bands of overlap (Fig. 5.30-5.33).

(ii) overlap is the result of slight seasonal or long-term changes in range use: this is again an artefact of the chosen method of analysis. Real separation of ranges may be perfect at each point in time, yet slight shifts of range boundaries from year to year may cause records of range use of neighbouring ranges from different years to produce some overlap. This effect may account for some of the overlap between Ranges F1 and F11 in

Marley Wood, since all individuals of Range F1 were tracked either in 1981 or 1982, while LIO from Range F11 was tracked in 1983. Slight seasonal shifts may have contributed to range overlap between OLDMAHOG (Range F6) and KBOOM (Range F7) who were tracked at the same time.

(iii) overlap is the result of common use by different individuals of the same area at the same time: this constitutes 'true' overlap. Commonly used areas, ie. areas of which members of both groups treat the common areas as their own, are expected to occur in high quality habitat. Overlap between ranges of OLDMAHOG and KBOOM do occur in high quality habitats, while areas of little use may result in empty spaces between ranges (PINTOOTH and OLDMAHOG).

Several lines of evidence suggest that foxes actively defend their ranges. Foxes token-urinate to mark the border of their ranges (Macdonald 1979b); they also defend ranges in the suburbs and the city of Oxford (Newdick 1983, Doncaster 1985). I was fortunate to witness a fight between KBOOM (Range F5) and an unmarked fox close to her range border. In Chapter 6, the fine-grained analysis of movements will reveal the extent to which foxes spend time and energy on marking and patrolling of the range border. Finally, the next section will investigate how the patterns of feaces deposition contribute to the advertisement of range ownership and hence the defense and maintenance of the ranges.

(3) Brief observations of fox litters at breeding dens are notoriously unreliable for the determination of litter size (Lloyd 1980). It is rarely the case that all cubs are present and observable at the den at the same time. Hence, observations of cubs were used to confirm the presence of a litter, but not as an indicator of reproductive success. Surprisingly, there may have been no breeding activities in Ranges 4 and Range 7, but fox cubs were also discovered in areas where foxes were not caught (Fig. 5.30-5.33).

(4) Most ranges have access to resources of human origin. These are usually located at the fringe of the range (Ranges 1, 2, 4, 5, 9). Food from human origins is an important part of the diet. It seems therefore plausible that the dispersion of these human 'patches' determine to some extent the delineation of the range boundary, as suggested by the Resource Dispersion Hypothesis of Bradbury & Vehrencamp (1976) and elaborated by Carr & Macdonald (in press). However, since proximity to easily accessible, human-derived food may increase the danger to cubs, breeding dens are usually placed far away from housing. In the context of range utilization and movement patterns (Chapter 6), evidence for the need to balance the desire for easy access to food with the need to protect the young will be discussed in detail.

5.5.3. Distribution of fox faeces

Red foxes are known to use a variety of odours for scent-marking, and these are both of glandular, e.g. anal and supracaudal gland, and non-glandular origin, e.g. urine (Macdonald 1985). However, little is known about patterns of faeces deposition and its possible role in scent-marking. In this section I analyse the position of fox faeces in relation to the local topography of deposition sites to investigate whether their distribution suggests a possible role in scent-marking.

The task of testing patterns of faeces distribution for a communicative function raises some difficulties in the absence of olfactory information.

Faeces may differ in their communicative significance (e.g. with or without anal sac secretion), and some may have no communicative function at all. The social significance may be affected by the circumstances at the time of defaecation and by the locality (e.g. core versus periphery of the territory), and also by the individual's status (e.g. dominant versus

subordinate). Furthermore, foxes may place faeces randomly with respect to their tracks, but their tracks may be highly nonrandom, and anyway difficult for the observer to identify. These are only some of the many difficulties hindering analysis of patterns of scent marking, as researched extensively in Brown and Macdonald (1985). In the light of these difficulties, I will restrict myself to one fundamental question: does the pattern of faeces deposition comply with conditions likely to maximize the transmission of a message? This question can be paraphrased by asking whether the deposition of fox faeces matches the criteria proposed by Kleiman (1966) and elaborated by Macdonald (1985) for diagnosing a scent mark. Clearly, the development of scent marks will be affected by the functional context, movement patterns, spatial and social organization etc., but nonetheless they should invariably include two elements:

(1) Maximize probability of faeces being encountered.

(2) Maximize probability of faeces being detected.

5.5.3.1. Patterns of distribution

Fox faeces were collected methodically throughout the study area during each month from April 1981 to October 1983, and the location and circumstances of each were recorded. Details of sampling procedures and data recording have been presented in sections 4.2.1. and 2.3.3. In addition two or more faeces were scored as "closely together", if each of them was at least within one metre of any of the other faeces present. In practice if several faeces were present, they were usually almost touching. Also, faeces found on fox dens and badger setts were habitually scored as on a path, since dens are regularly associated with trails leading to and away from them. Two samples of faeces were distinguished:

(1) those collected while habitat recording (Chapter 2) - a highly

systematic sampling regime. These data include 186 faeces found at 117 sites. 48(41.03%) of the faeces were not placed on discernally conspicuous objects; most frequent conspicuous objects were earths or setts with 83 (44%) faeces, followed by tussocks (23 faeces, 12.4%) and mole hills (13 faeces, 7%).

(ii) the remainder, collected mostly while searching for and monitoring badger latrines, but also those gathered opportunistically. This sample may be somewhat biased to faeces on fox trails, but this is unlikely to be a significant bias since my movements were determined by factors quite independent of either the availablity of trails or accessibility of the habitat. These data include 1691 faeces, found at 1117 sites. 755 faeces (44.6%) were not placed on conspicuous objects. Dens and setts were the most frequent conspicuous object (306 faeces, 18.1%), followed by tussocks and tufts (together 177 faeces, 10.5%), badger latrines (68 faeces = 4%) and soil mounds (52 cases, 3.1%). Table 5.24 summarises the different conspicuous objects on which faeces were found, while Table 5.25 shows the frequency with which these faeces were on and off paths, at the junctions of paths, and found within one metre of each other.

Using the data from the systematic sampling regime I calculated densities of fox faeces for various habitats, and within each habitat for various deposition characteristics, using the area of a particular habitat within the study site as my area measure. Densities of fox faeces varied from 0 to 1.36 faeces per ha. An analysis of those faeces associated with conspicuous objects revealed that in woodland the highest densities were found on paths, in grassland densities were similar regardless of whether the conspicuous site was on or away from a path, while in scrub the density of faeces on conspicuous objects was higher away from paths than on paths (Fig. 5.34). The increase of faeces density in woodland is related to the fact that most dens and setts were located in woodlands and 44% of all

Table 5.24 Frequencies of occurrence of different sites as conspicuous objects for deposition of red fox faeces.

	Habitat recording period	Remainding period
not conspicuous	48	755

Table 5.24 Frequencies of occurrence of different sites as conspicuous objects for deposition of red fox faeces.

not conspicuous		48	755
den/sett		83	306
mouse etc hole		1	21
mole hill		13	26
badger latrine		1	68
tree stump		3	20
tussock		23	87
animal skull		1	3
tuft		2	90
soil mound			52
bare patch of soil			11
stones			31
cow pad			4
large herbaceous plant			39
mound of grass			12
bale of straw			8
twig			10
large patch of leaves			1
clod			3
fox traps used in this study			6
dead shrew			1
on a wire of a fence			2
mound of cereals			1
fence post			7
sprig			1
tree base			13
tree root			1
bunch of feathers			1
piece of moss			5
rabbit pellets			1
old bucket			1
metal box			1
hollow tree			3
on top of a piece of bark			2
no description	11		98
TOTAL	186		1691

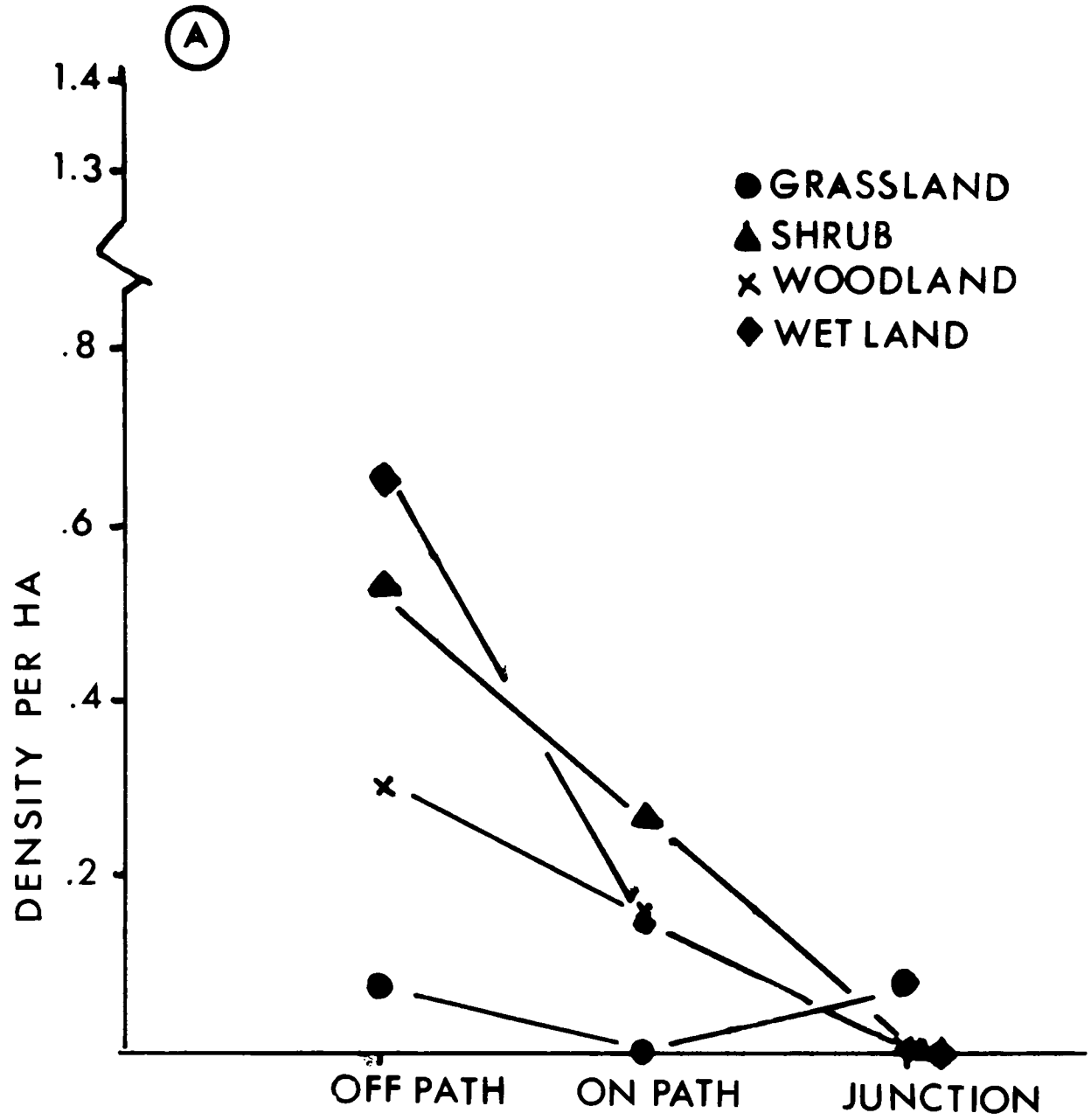
Fig. 5.34

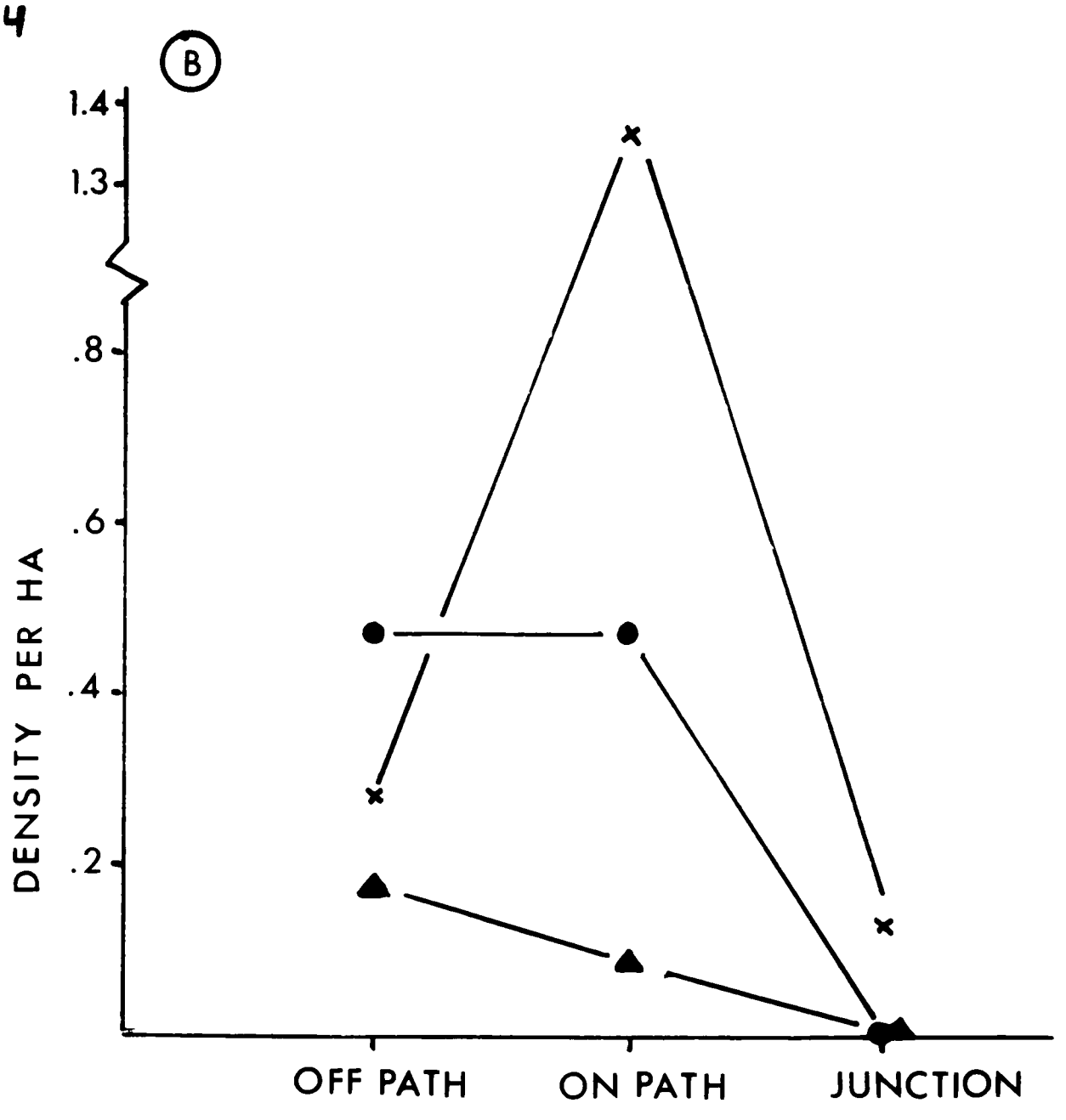
Deposition of fox faeces in relation to conspicuousness and habitat

a. faeces not on conspicuous objects

b. faeces on conspicuous objects

5-34


A
1.4
1.3
.8
.6
.4
.2
DENSITY PER HA
GRASSLAND
SHRUB
WOODLAND
WET LAND
OFF PATH
ON PATH
JUNCTION


B
1.4
1.3
.8
.6
.4
.2
DENSITY PER HA
OFF PATH
ON PATH
JUNCTION

faeces found in woodland were in association with dens. In wet lands (marsh, riverrine environment etc.) faeces were not found associated with conspicuous objects.

To summarise, fox faeces were found throughout all habitats, and off fox trails, and the majority of them are found on conspicuous objects on trails.

To explore the relationships of the characteristics of a deposition site, I generated log-linear models (see section 5.4.3) that took into account presence or absence of conspicuous objects (CONSP OBJECT) and paths (PATH) and how many faeces were found at a site (NOS PRESENT).

A priori, one might expect faeces at earths to differ from those elsewhere a) because of the social significance of dens and b) because an accumulation of faeces at a den may simply be a consequence of the fox's tendency to defecate soon after awakening. Therefore I analysed two data sets, one including faeces found on dens (data from systematic sampling during habitat recording), and the second excluding them. Data for the latter analysis were extracted from the data including all faeces found during the remainder of the study period. In Table 5.25 data and the model generation are presented for both data sets. Note that each datum is a deposition site, not a single faeces.

The final models for both data sets include two of three possible two-way interactions, one of them common to both: there is a significant mutual influence of Numbers Present and Path for a given level of Conspicuous Object. As Table 5.26 reveals (section (3)), this significant interaction is based on contrasting events. For data set I (including dens etc.), too many faeces on conspicuous objects found off-path were single faeces, while on-path too many faeces occurred as two or even larger accumulations - obviously an effect of accumula;tions at dens. If dens are excluded (data set II), too many groups of faeces are found offpath, while too few two or

Table 5.25 Log-linear model for marking patterns by the distribution of fox faeces.
Part I: Data and model specification.

Data set I: Faeces collected during the period of habitat recording in late winter 1982 (see chapter 2). Includes faeces on dens.
Data set II: Faeces collected throughout the year over the entire study area and period, excluding faeces from Data Set I, faeces on dens, and those, for which insufficient information on marking circumstances were available.

Variable A 1 = CONS on conspicuous object; 2 = NOTC not on conspicuous object
B 1 = one faeces present; 2 = two faeces present; 3 = more than two faeces present
C 1 = off a path 2 = on a path 3 = on a junction of paths

(1) Data

		Data set I (with dens)				Data set II (without dens)	
		CONS	NOTC			CONS	NOTC
	off path	20	26		off path	120	118
one	on path	21	9	one	on path	291	407
	junction	2	1		junction	58	71
	off path	2	2		off path	10	5
two	on path	5	3	two	on path	13	9
	junction	1	0		junction	2	2
	off path	1	0		off path	2	4
> two	on path	17	0	> two	on path	0	3
	junction	1	0		junction	1	1

(2) Testing for interaction of variables (model generation)

1. Test for three-factor interaction (test $\alpha\beta\gamma = 0$)

G_{abc} = 0.9035 df = 4 , n.s. G_{abc} = 2.3682 df = 4 , n.s.

2. Test for two factor interaction : $\alpha\beta = 0$?

$G_{ab(c)}$ = 13.3342 df = 6 , $p < 0.05$ $G_{ab(c)}$ = 8.2455 df = 6 , n.s.
$G_{ab(c)} - G_{abc}$ = 12.5682 df = 2 , $p < 0.005$ $G_{ab(c)} - G_{abc}$ = 5.8773 df = 2 , n.s.

3. Test for two factor interaction : $\alpha\gamma = 0$?

$G_{ac(b)}$ = 6.6337 df = 6 , n.s. $G_{ac(b)}$ 8.4347 df = 6 , n.s.
$G_{ac(b)} - G_{abc}$ 5.7302 df = 2 , n.s. $G_{ac(b)} - G_{abc}$ = 6.0665 df = 2 , $p < 0.05$

4. Test for two-factor interaction : $\beta\gamma = 0$?

$G_{bc(a)}$ = 15.5477 df = 8 , $p < 0.05$ $G_{bc(a)}$ = 13.531 df = 8 , n.s.
$G_{bc(a)} - G_{abc}$ = 14.6442 df = 4 , $p < 0.01$ $G_{bc(a)}$ = 10.7849 df = 4 , $p < 0.05$

(3) Final model

$$\ln f_{ijk} = /u + \alpha_i + \beta_j + \gamma_k + \alpha\beta_{ij} + \beta\gamma_{jk} \quad ; \quad \ln f_{ijk} = /u + \alpha_i + \beta_j + \gamma_k + \alpha\gamma_{ik} + \beta\gamma_{jk}$$

(4) Parameter estimates

$/u$ = 1.1406
α_1 = 0.1201 β_1 = 0.9385 γ_1 = 0.125
α_2 = -0.4107 β_2 = -0.7059 γ_2 = 0.6859
β_3 = -0.6684 γ_3 = -1.2469

	α_1	α_2		β_1	β_2	β_3
β_1	-0.0313	0.3218	γ_1	0.9275	0.1061	-0.5972
β_2	0.1149	0.1757	γ_2	-0.0609	0.2383	0.2585
β_3	0.3521	-0.0615	γ_3	-0.4307	0.094	0.7747

$/u$ = 2.3731
α_1 = -0.0792 β_1 = 2.5546 γ_1 = 0.2576
α_2 = 0.0792 β_2 = -0.677 γ_2 = 0.5002
β_3 = -1.8776 γ_3 = -0.7578

	α_1	α_2		β_1	β_2	β_3
γ_1	0.0985	-0.0985	γ_1	-0.4064	0.061	0.3453
γ_2	-0.0812	0.0813	γ_2	0.4144	0.1888	-0.603
γ_3	-0.0174	0.0174	γ_3	-0.0079	-0.2498	0.2576

Table 5.26 Log-Linear Model for marking patterns by the distribution of fox faeces.
Part II : Interpretation of the model.

Data set and variable specifications as in Part I.
FT Freeman-Tukey deviate (an estimate of how significant an individual deviation expec ted/observed value is)

Data Set I				Data Set II			
interpretation			FT	interpretation			FT
(1) H_o = For a given level of PATH (Var. C) no interaction of A (consp. obj.) and P (numb. pres)							
rejected			(FT_{crit} = 1.1315)	accepted			(FT_{crit}=1.1315)
off path	as expected						
on path	too many single faeces	NOTC	0.9486				
	(too few single faeces	CONS	0.4648)				
	too many duos	NOTC	0.9068	too few duos		NOTC	1.0487
	(too few duos	CONS	0.4152)	too many duos		CONS	1.1827*
	too few accumulations	NOTC	1.2416*				
	too many accumulations	CONS	1.0062				
junction	as expected						
(2) H_o = For a given level of Numb.Pres.(P) no interaction of A(consp.obj.) and C(PATH).							
accepted			(FT_{crit} = 1.1315)	rejected			(FT_{crit}=1.1315)
				one	too few off-path f.	NOTC	1.3318*
					too many off-path f.	CONS	1.4548*
too few on-path f.		NOTC	1.2999*		too many on-path f.	NOTC	0.8325
too many on-path f.		CONS	1.1295		too few on-path f.	CONS	0.9322
				two	as expected		
				> two	(too many on-path f.	NOTC	0.6132)
					too few on-path f.	CONS	1.0671
(3) H_o = For a given level of Consp.Obj.(A) no interaction of Numb.Pres.(P) and Path (C).							
	rejected		(FT_{crit} = 1.3066)	rejected			(FT_{crit}=1.3066)
NOTC	(too few duos	offp.	0.6824)		too many duos	offp.	0.9293
	too many duos	onp.	1.1141		(too few duos	onp.	0.4899)
					too many accumulat.	offp.	1.4875*
					too few accumulat.	onp.	1.0246
CONS	too many single f.	offp.	1.4709*				
	too few single f.	onp.	1.0545				
					too many duos	offp.	1.2292
					(too few duos	onp.	0.5374)
	too few accumulat.	offp.	2.682*		too many accumulat.	offp.	1.0999
	too many accumulat.	onp.	1.4603*		too few accumulat.	onp.	1.8879*
					too many accumulat.	junct.	0.8417

more faeces can be found on path. This holds both for conspicuous and not conspicuous objects. The same effect of faeces accumulations at dens bears on the interaction of Conspicuous Object and Number present for a given level of Path (significant only for data set I). Too many accumulations were found on conspicuous objects on paths.

Based on the analyses of data set II (excluding dens), I suggest that foxes follow two kinds of rules, which I term locational and functional strategies. A locational strategy tells the fox where exactly to drop the faeces, given its current position. A functional strategy governs the fox's over-riding goals, irrespective of its current position. From the results of the log linear model I hypothesise two locational strategies (Figure 5.35):

(1) If the animal is off a fox trail, probability of detection is low. Thus, to improve detection probability, the first action rule is 'select a conspicuous object'. An occasional alternative is "select another faeces" - two faeces together would represent a formidable conspicuous object itself!

(2) If the animal is on a fox trail, probability of detection is high, thus it is more important to maximize the encounter rate, and so the action rule is 'select a site with no other faeces present'.

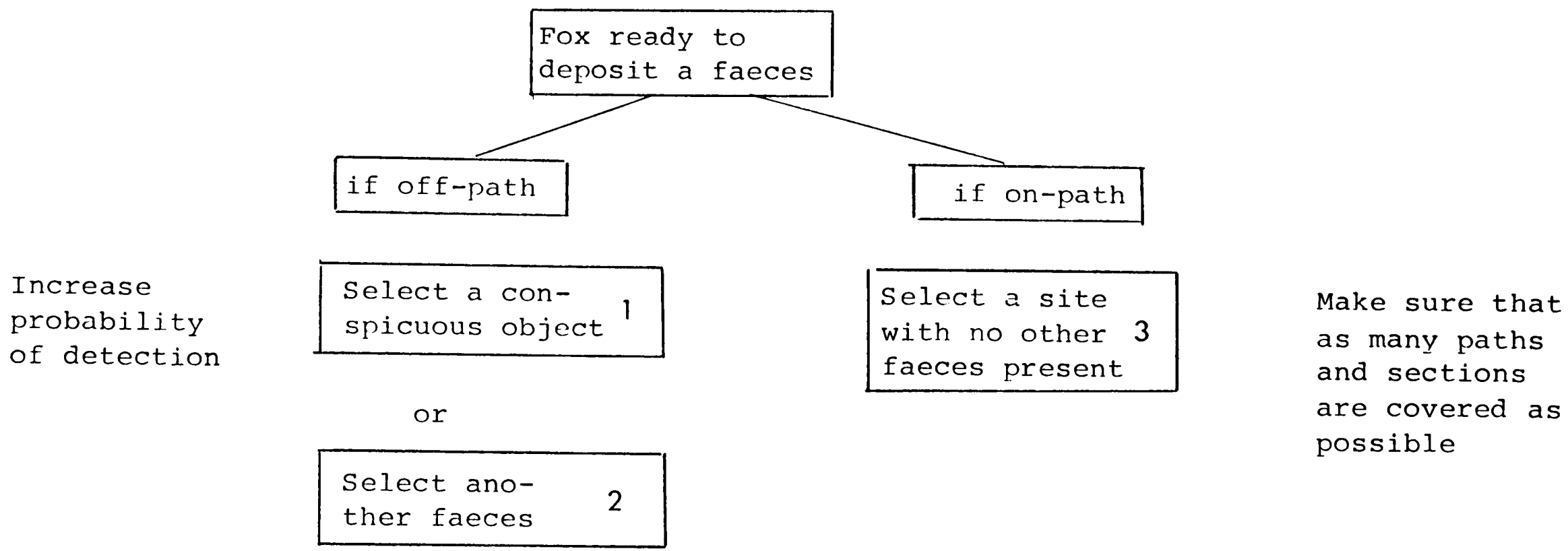
Two basic functional strategies reflect the conditions for maximizing information transmission. Foxes should position their faeces to increase:

(1) Probability of encounter by an appropriate recipient (the majority of faeces are on trails and are spread along them, but some are also sited off paths).

(2) Probability of detection (less of a problem if faeces are on trails, but off trails, careful placement improves odour diffusion and visual detection).

In summary, then, foxes seem to place their faeces more often than expected by chance in such a fashion that information transmission is

Fig. 5.35 Rules for deposition of fox faeces as derived from the log-linear models.



1 too many single faeces off-path are found on conspicuous objects

2 too many duos and accumulations off-path are found not on conspicuous objects

3 too few duos and accumulations occur on path, regardless of presence or absence of a conspicuous object

improved.

5.5.3.2. Discussion

Two aspects remain to be discussed. Firstly, how does sampling affect the results, and secondly, what functions could marking with faeces serve?

Two kinds of sampling bias are possible. First, errors may stem from the different sampling regimes underlying data sets I and II. I conclude that this risk is negligible because (i) the ratio of sites with conspicuous to not conspicuous objects is very similar for both data sets. (ii) a large proportion of faeces from data set II were collected during systematic searches, albeit primarily for other purposes. Second, systematic errors can occur. For instance, faeces on conspicuous objects are by definition more likely to be detected. However, we were highly experienced and diligent in this task, so errors should be minimized and consistent.

One limitation of this kind of analysis is that it does not consider the scent-marking behaviour of individuals. Studies on wolves have shown that different individuals may show different scent-marking behaviour off and on trails; so do individuals of different social status (Macdonald 1985). Thus, the pattern of faeces deposition as evidenced by the log-linear models may combine the results of different types of foxes behaving in different ways. However, although this possibility limits the level of detail of interpretation, it may not necessarily change much of the basic pattern.

Faeces may persist for weeks or even months at a site, so there is potential for long-term information. Short-term information is communicated by urination and glandular secretions in a variety of contexts (Macdonald 1979b, 1985), including territorial marking and 'book-keeping' (Henry 1977). I suggest that faeces serve possible three communicative functions.

Firstly, they are a good visual and olfactory beacon for anal gland secretion. Studies on the chemical nature of anal gland secretion have shown that a considerable proportion consists of volatile fatty acids (Macdonald 1985). Some of these may be highly volatile, but others can be expected to belong to the group of low volatile high lipid secretions that should release odours only slowly (cf. Gorman et al. 1984). Secondly, faeces could serve as aides memoires. For example, some foxes detected and exposed the release mechanism of traps and invariably placed a dropping on the trap. Perhaps these faeces warned themselves and other foxes of the danger. Thirdly, faeces may have a possible function associated with territorial or at least range advertisement. Token urination remains olfactorally and visually conspicuous for a shorter time than faeces. There are some indications that foxes are able to individually identify scents set by different conspecifics (Macdonald 1985). If faeces together with anal sac secretion etc. can provide clues to the identification of the individual that deposited them, an intruder that meets the owner of the area will recognise it by matching the scent-marks against the scent of the encountered animal (matching hypothesis Gosling 1982, Gorman et al. 1984). Several studies show both empirically and theoretically that contests between owners and intruders imply an asymmetry of roles that helps to avoid an escalation into long and costly fights (detrimental to both participants), if both individuals are aware of the other's status (Leimar & Enqvist 1984, Maynard Smith & Parker 1976, Hammerstein 1981, Hammerstein & Parker 1982, Maynard Smith 1982). Thus, an owner who advertises his status, for instance by means of scent-marking, conveys to a contestant information on role identification and plays an evolutionarily stable strategy that involves little fighting and minimizes the risk of losing a contest.

5.6. Habitat composition of and resource use in ranges.

This section presents a first summary of the interrelations between resource presence (via habitat availability) and resource use as evidenced by the diet and the habitat composition of the ranges. Habitat composition of the ranges is presented in Table 5.27. The categories used throughout this section are:

GRASSLAND: habitat types 5, 6, 46.

ARABLE: habitat types 28, 29, 30.

WOODLAND: all woodlands except 37, deciduous woodland.

SHRUB: scrub (10), bracken (35), hedges (36, 44)

HUMAN: habitat types 1, 2, 3, 23, 47.

P+DW: pasture plus deciduous woodland.

The latter category was identified as one resource unit due to the high abundance of earthworms in pasture and deciduous woodland. At least for badger ranges, they occur in a complementary fashion: with little deciduous woodland much pature is present and vice versa (Table 5.31). Hence I believe it is justified to use them as one unit.

5.6.1. Observed and expected proportions of habitats per group range.

Most badger and fox ranges comprise a habitat composition significantly different from the composition of the study area (Table 5.28), indicating that perhaps active selection for or against certain habitats may take place. Habitats occur over a wide range of proportions ranging from a fraction of a hectare up to 70 hectare (P+DW, Table 5.29).

Table 5.27 Sizes and habitat composition of group ranges in Wytham. Only major habitat categories used in subsequent analyses are listed; thus the totals (ha) exceed the sum of the listed categories, and the percent values bot add up to 100 %.

a) Fox group ranges

	GRASS-LAND	ARABLE	WOOD-LAND	SHRUB	HUMAN	PAST. +D.W.	TOTAL
(1) ABSOLUTE VALUES IN HECTARE							
F9	5.389	4.472	–	1.250	2.695	2.694	22.500
F3	–	–	9.695	0.056	–	22.333	33.500
F11	0.528	14.000	0.250	1.778	2.528	23.417	46.000
F8	0.250	1.667	2.222	2.666	4.754	31.111	51.500
F1	1.000	19.695	0.306	2.194	2.889	24.555	56.500
F7	8.305	24.444	–	2.916	1.500	31.056	71.500
F5	6.250	5.528	18.278	3.583	2.222	27.808	83.000
F6	0.944	24.639	16.361	2.722	–	39.972	85.500
F4	15.167	48.806	–	2.834	12.582	9.056	92.000
F2	1.631	16.250	0.389	5.806	0.944	69.306	104.000
(2) RELATIVE VALUES IN PERCENT							
F9	23.95	17.65	–	5.56	11.98	11.98	71.12
F3	–	–	28.94	0.17	–	66.66	95.77
F11	1.15	30.44	0.54	3.86	4.35	50.91	91.25
F8	0.49	3.24	4.32	5.17	9.22	60.41	82.85
F1	6.12	34.86	0.55	3.88	5.11	43.46	93.98
F7	11.62	34.19	–	4.08	2.10	34.44	86.43
F5	7.53	6.66	22.02	4.32	2.68	42.61	85.82
F6	1.10	28.80	19.29	3.18	–	46.75	99.03
F4	16.48	53.05	–	3.08	13.68	9.84	96.13
F2	1.55	15.62	0.37	5.58	0.91	66.64	90.67

b) Badger group ranges

(1) ABSOLUTE VALUES IN HECTARE							
B10	1.056	2.361	9.223	0.139	–	9.139	22.361
B1	0.862	27.250	–	0.306	0.222	13.194	42.667
B5	2.472	6.861	9.722	4.056	–	25.250	48.611
B4	–	25.694	10.833	0.111	–	18.805	56.000
B2	1.472	48.750	–	0.972	0.166	14.583	67.583
B3	0.056	28.945	5.028	5.000	0.333	34.027	75.306
(2) RELATIVE VALUES IN PERCENT							
B10	4.72	10.56	41.24	0.62	–	40.37	97.51
B1	2.02	64.37	–	0.72	0.52	30.92	98.55
B5	5.09	14.11	20.00	8.34	–	51.94	99.48
B4	–	45.88	19.35	0.20	–	33.58	99.01
B2	2.18	73.93	–	1.47	0.25	21.58	99.41
B3	0.07	38.44	6.68	6.64	0.44	45.18	97.45

Table 5.28 Comparison of observed and expected habitat composition of ranges. Expected proportions were derived from the proportion each habitat occupies in the study area.

a) Foxes

Group	G value	df	significance
F1	6.807	5	n.s.
F2	18.464	5	< .005
F3	14.366	2	< .001
F4	42.086	4	< .001
F5	21.966	5	< .001
F6	10.662	4	< .05
F7	2.579	4	n.s.
F8	30.819	5	< .001
F9	35.027	4	< .001
F11	10.166	5	n.s.

b) badgers

B1	25.070	4	< .001
B2	36.227	4	< .001
B3	13.008	5	< .025
B4	16.845	3	< .001
B5	12.461	4	< .025
B10	39.105	4	< .001

Table 5.29 Analysis of differences between habitats a) in the proportion they occupy in fox and badger ranges, b) the variability of this proportion.

a) are differences in the sizes different habitat types occupy in fox and badger ranges significant ?

Kruskal-Wallis one-way analysis of variance, df= 5.

Badger group ranges:	H (adj) = 22.452	p < 0.001 (hectares)
	H (adj) = 23.526	p < 0.001 (% values)
Fox group ranges :	H (adj) = 24.121	p < 0.001 (hectares)
	H (adj) = 26.0	p < 0.001 (% values)

In both species, differences between habitats are significant. The largest section in a fox or a badger group range is, on average, occupied by PASTURE+DECIDUOUS WOODLAND.

b) are differences in the variability of the proportion each habitat occupies in a range significant ?

Kruskal-Wallis one-way analysis of variance, df = 5:

Badger group ranges :	H (adj) = 12.51	p < 0.05 (hectares)
Badger group ranges :	H (adj) = 13.52	p < 0.025 (% values)
Fox group ranges :	H (adj) = 13.30	p < 0.025 (hectares)
Fox group ranges :	H (adj) = 16.85	p < 0.005 (%values)

(Evaluation Table 5.30)

5.6.2. Dispersion of habitats composition between ranges.

Not only are absolute or relative proportions of habitats different from each other but habitats also vary significantly in the degree of which their contribution to a range changes from one range to another (Table 5.29). For badgers, habitats that are present in relative constant proportions (ie. little inter-group variability) are especially P+DW (% values, Table 5.30), but also several of the other habitat types, if ha values are considered (Table 5.30). These however, occur with more variability in relative proportions. In foxes, little variability occurs mainly for P+DW but also for shrub. As Table 5.31 shows, this is due to the steady increase of the proportion of shrub and D+PW with range size (see also Fig. 5.36-37). Human habitations vary considerably in their contribution to the range, but nevertheless seem to be partly responsible for the delineation of range boundaries ! This difference in variability perhaps reflects the different relationships of the productivity of habitats in relation to their size. While a large field of pasture contains more earthworms, and a longer hedge more birds, a compost heap may be equally 'productive' whether it occurs in a large or a small garden.

5.6.3. Habitat composition and range size.

The relationship between the key habitats identified in the preceding section and range size is illustrated in Fig. 5.36 and Fig. 5.37 (also Table 5.31). While it is no surprise that habitats constituting the bulk of the landscape (such as arable fields) will increase in contribution with range size, small habitats , e.g. shrub, cannot necessarily be expected to grow in the same proportions. P+DW grows with range size in absolute terms, but

Table 5.30 Multiple comparison of habitats with different variability in the proportion they occupy group ranges (only significant differences listed)

Habitat with large variab.	Habitat with small variab.	actual value	critical value	significance
1. Badgers: HECTARES				
HUMAN	GRASSLAND	11.17	10.71	< 0.05
SHRUB	ARABLE	12.33	10.71	< 0.05
HUMAN	ARABLE	18.00	17.76	< 0.002
HUMAN	WOODLAND	12.83	10.71	< 0.05
HUMAN	PAST.+D.W.	16.33	15.89	< 0.005
2. Badgers: %-VALUES				
GRASSLAND	PAST.+D.W.	10.5	10.47	< 0.05
HUMAN	ARABLE	15.17	14.09	< 0.01
WOODLAND	PAST.+D.W.	13.50	12.59	< 0.02
SHRUB	PAST.+D.W.	12.50	10.47	< 0.05
HUMAN	PAST.+D.W.	20.33	18.69	< 0.001
3. FOXES : HECTARES				
GRASSLAND	SHRUB	16.67	16.21	< 0.02
GRASSLAND	PAST.+D.W.	15.11	13.54	< 0.05
WOODLAND	SHRUB	21.78	19.83	< 0.005
WOODLAND	HUMAN	13.67	13.54	< 0.05
WOODLAND	PAST.+D.W.	20.22	19.83	< 0.005
4. FOXES : %-VALUES				
GRASSLAND	SHRUB	16.67	15.47	< 0.02
GRASSLAND	PAST.+D.W.	18.33	17.25	< 0.01
WOODLAND	ARABLE	15.44	12.92	< 0.05
WOODLAND	SHRUB	22.33	21.01	< 0.002
WOODLAND	PAST.+D.W.	24.00	22.54	< 0.001
HUMAN	SHRUB	14.44	12.92	< 0.005
HUMAN	PAST.+D.W.	16.11	15.47	< 0.02

Table 5.31 Analysis of dependencies of the proportion of a habitat in fox and badger group ranges on range size and the presence of other habitats in the range.

a) are there significant relationships between proportions of different habitats ?

(i) correlation of GRASSLAND and WOODLAND (%-Values)

Badger group ranges : rho = -0.886, df=6, $p < 0.01$
Fox group ranges : rho = -0.27 df=10, n.s.

(ii) correlation of pasture and deciduous woodland (%values), a priori expectaction is a negative correlation :

Badger group ranges : rho = -0.776 df=6 $p < 0.05$
Fox group ranges : rho = 0.006 df=10 n.s.

b) relationship of proportion of habitats to fox group range sizes (a priori expectation is a positive correlation)

SHRUB vs range size (ha) : rho = 0.879, df = 10, $p < 0.002$

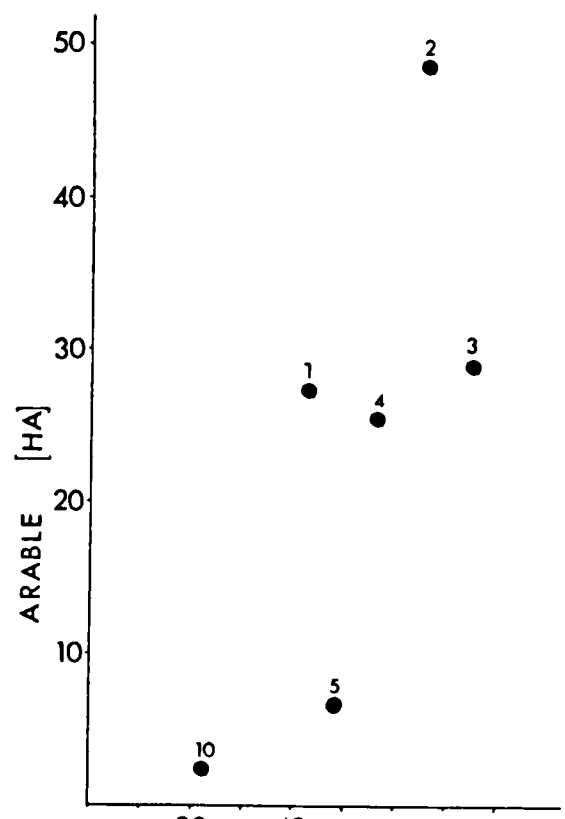
The proportion of shrub increases with range size.

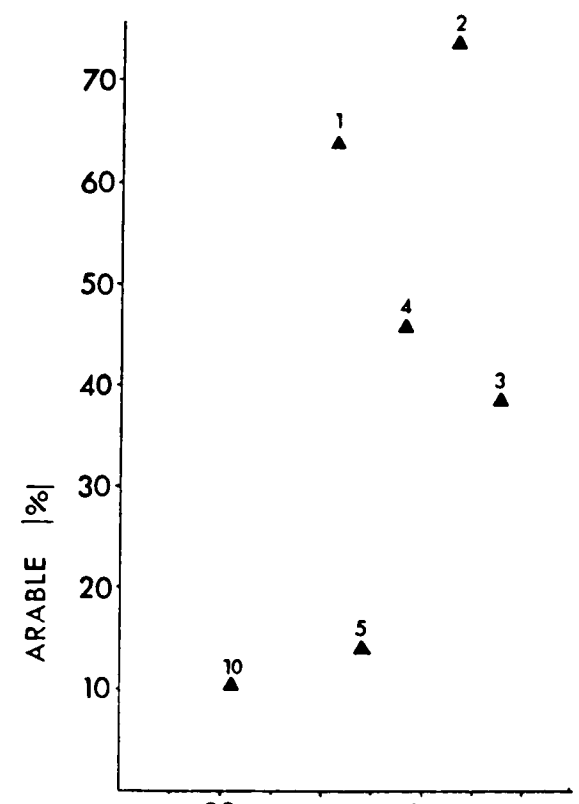
PAST.+D.W. (ha) : rho = 0.576 df = 10 $p < 0.05$

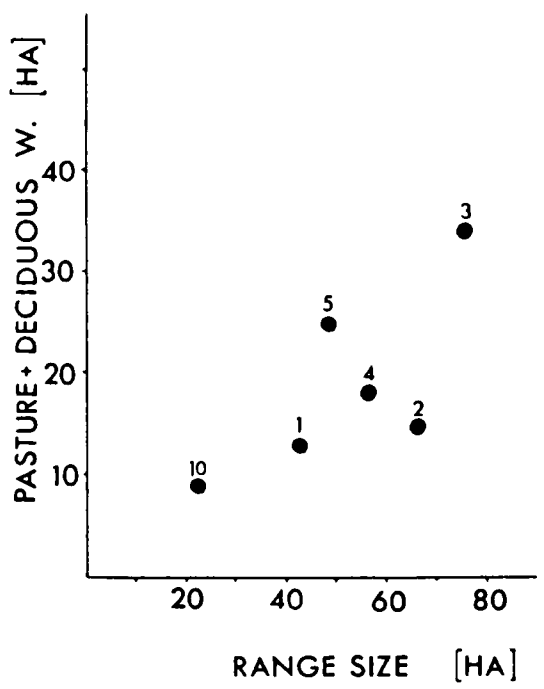
The proportion of deciduous woodland and pasture increases with range size.

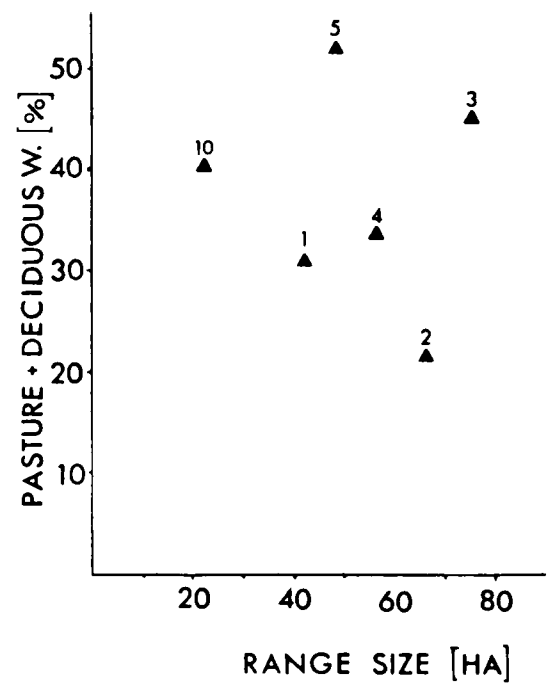
Fig. 5.36–5.37

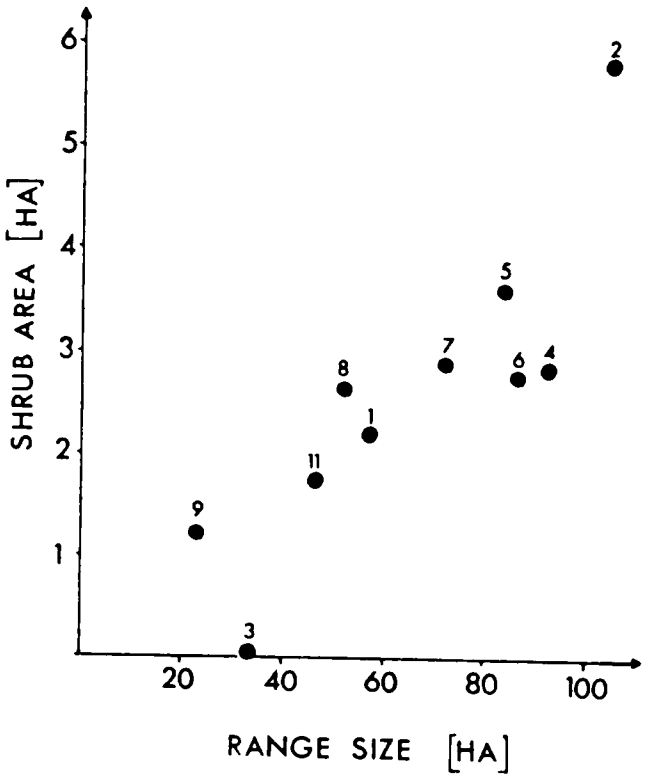
Area and proportion of habitats in relation to (5.36) badger and (5.37) fox group ranges

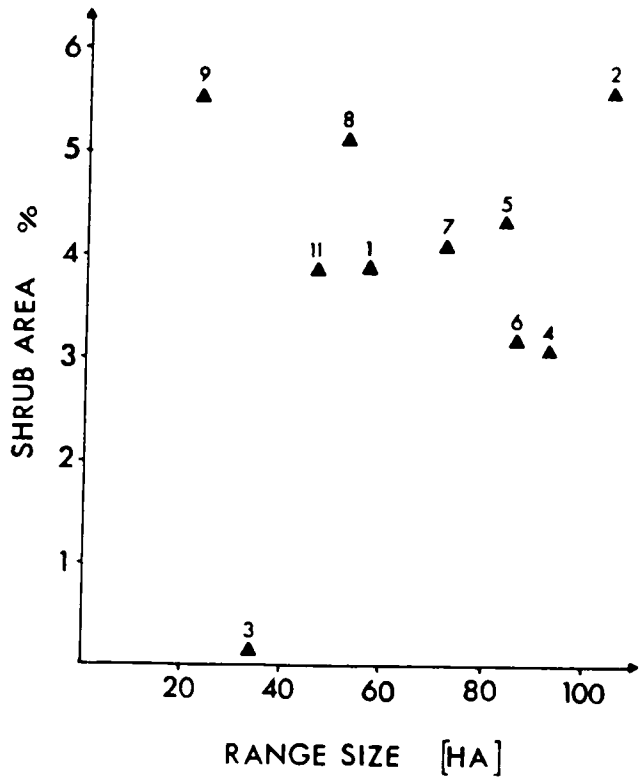

ARABLE [HA]
50
40
30
20
10
2
1
3
4
5
10
20
40
60
80
RANGE SIZE [HA]

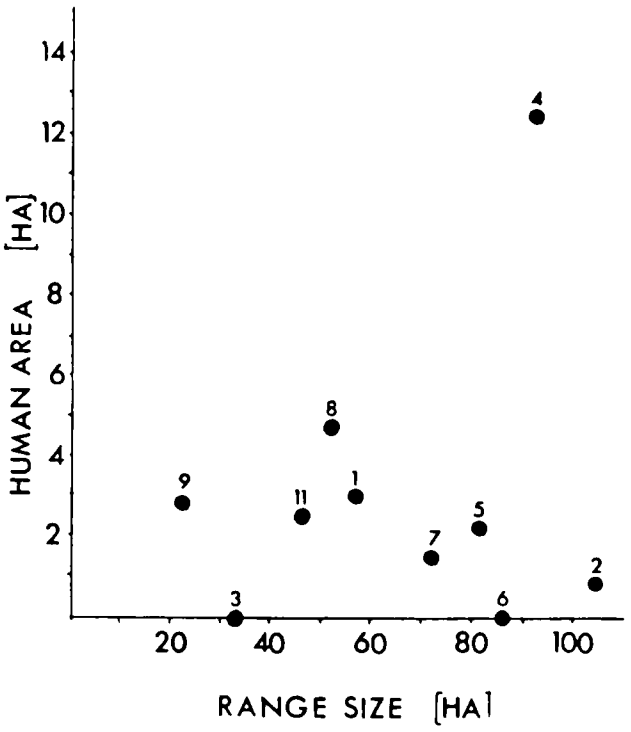

ARABLE [%]
70
60
50
40
30
20
10
2
1
4
3
5
10
20
40
60
80
RANGE SIZE [HA]

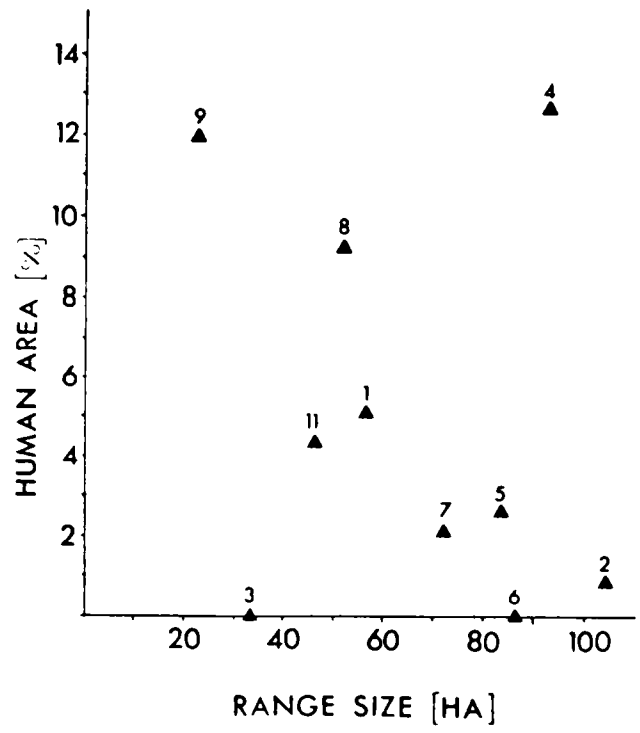

PASTURE + DECIDUOUS W. [HA]
40
30
20
10
3
5
4
1
2
10
20
40
60
80
RANGE SIZE [HA]

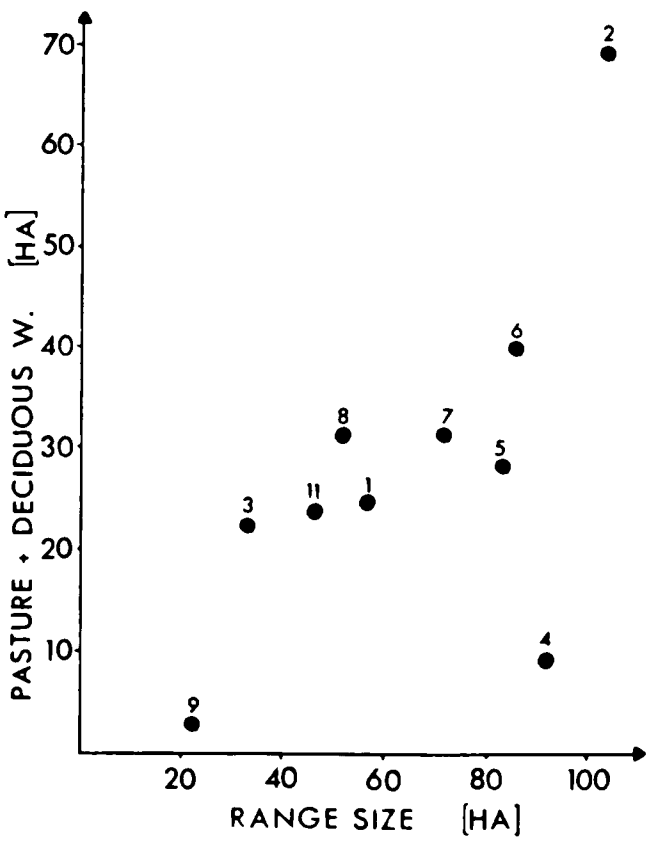

PASTURE + DECIDUOUS W. [%]
50
40
30
20
10
5
3
10
4
1
2
20
40
60
80
RANGE SIZE [HA]

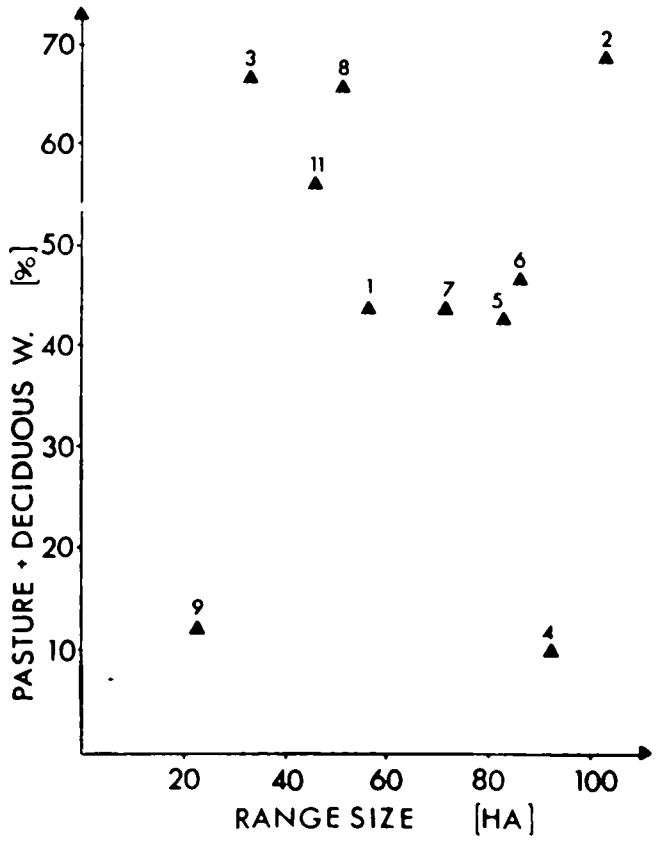

SHRUB AREA [HA]
RANGE SIZE [HA]


SHRUB AREA %
RANGE SIZE [HA]


HUMAN AREA [HA]
RANGE SIZE [HA]


HUMAN AREA [%]
RANGE SIZE [HA]


PASTURE + DECIDUOUS W. [HA]
RANGE SIZE [HA]


PASTURE + DECIDUOUS W. [%]
RANGE SIZE [HA]

occupies a relative constant proportion.

5.6.4. Habitat composition of individual ranges within the same group.

The results presented so far constitute mean values per group range. Consideration of individual ranges within broadly the same framework should indicate to what extent group range composition mirrors individual choice. While the distinction between members of badger groups is not tidy (Table 5.32), and the ranges of individual badgers sometimes do and sometimes do not show a similar composition, it is clear that there are large differences in fox groups. These differences may be partly an artefact of sample size (well tracked females vs. little tracked males in Ranges F6 and F7). The results from the HOMEFARM group show, however, some consistent, intersexual differences in habitat composition of ranges. Reasons for sex-specific differences will be discussed in Chapter 6.

5.6.5. Habitat composition and resource use of group ranges.

Group ranges of foxes and badgers are easily, and reliably distinguished by their habitat composition. The Stepwise Discriminant Function Analysis (SDFA) whose results are reported in Table 5.34, indicates that the proportion of P+DW and HUMAN are the key habitats that suffice to distinguish the species. Foxes have on average a much higher proportion of human habitation than badgers while their proportion of P+DW is similar; here again foxes occupy more P+DW. This apparent contradiction with the finding that the badgers, not the foxes specialize in earthworms, can easily be resolved, if individual ranges are considered: badger group ranges contain large areas of wheat fields that are underrepresented in use by

Table 5.32 Comparison of the habitat composition (relative, ie. percent values) of individual ranges within groups.

Group	Members	G	df	significance	data select.
	(1) BADGERS				
B1	GEORGE,SARA	13.699	4	< 0.01	intensive
		5.912	4	n.s.	15 min
B2	ALI,NANI,WILF	7.97	8	n.s.	intensive
		7.714	8	n.s.	15 min
B4	JO,PEACEFUL,VICIOUS	46.18	4	< 0.001	15 min
	(2) FOXES				
F1	GASPER,KOBUK, BRAMBLE,PODGE	35.808	15	< 0.001*	15 min
	the two males vs the two females	16.94	5	< 0.005*	
	the males: G vs K	8.797	5	n.s.	
	the females: B vs P	9.803	5	n.s.	
F6	OLDMAHOG, BOOTS	11.531	3	< 0.01	15 min
F7	PINTOOTH,RABBITS	21.452	4	< 0.001	15 min

* adjusted alpha level of significance = 0.015

Table 5.33 Comparison of range size parameters of foxes and badgers.

a) Differences in range sizes between foxes and badgers ?

(i) INDIVIDUAL RANGES: fixes selected at 15 min intervals, radio locations only;

Mann-Whitney U = 66.5, n=9, m=13, $p < 0.02$

Individual fox ranges are larger than individual badger ranges.

(ii) GROUP RANGES: fixes selected at 15 min intervals, radio locations only (foxes); combination of tracking and bait marking results (badgers);

Mann-Whitney U = 41, n=6, m=10, n.s.

Group ranges are equally large in foxes and badgers.

b) Differences in the variation of range sizes between foxes and badgers ?

Levene's Test, followed by Mann-Whitney U-test:

(i) INDIVIDUAL RANGES: fixes selected at 15 min intervals, radio locations only:

Mann-Whitney U = 72.5, n=9, m=13, $p < 0.05$

Range sizes of individual foxes are more variable than those of badgers

(ii) GROUP RANGES: fixes selected at 15 min intervals, radio locations only (foxes); combination of tracking and bait marking results (badgers)

Mann-Whitney U = 41, n=6, m=10, n.s.

Range sizes of group ranges are equal in variability for foxes and badgers.

Table 5.34 Results of Stepwise Discriminant Analysis of differences in habitat composition (relative values) of fox and badger group ranges. Analysis was run using program BMDP7M, with option FORCE = 0, and the critical F-value for entering habitat categories set at the default value of 4.0.

STEP 1: inclusion of habitat category HUMAN

U statistic (Wilks' lambda) = 0.721, df= 1,14
approximate F statistic = 5.425
tolerance = 1.000

STEP 2: inclusion of habitat category PASTURE+DECIDUOUS WOODLAND

U statistic (Wilks' lambda) = 0.451, df= 2,13
approximate F statistic = 7.897
tolerance = 0.507

Final F-matrix: Fox vs Badger = 7.897, df = 2, 13, p < 0.01

Classification functions:

GROUP = VARIABLE	FOX	BADGER
HUMAN	1.51133	0.77631
PASTURE+D.W.	0.39645	0.25284
CONSTANT	-13.24915	-5.48208

	Classification matrix			jackknifed classification		
GROUP	PERCENT CORRECT	NO OF CASES CLASSIFIED INTO GROUP		PERCENT CORRECT	NO OF CASES CLASSIFIED INTO GROUP	
		FOX	BADGER		FOX	BADGER
FOX	90.0	9	1	80.0	8	2
BADGER	100.0	0	6	83.3	1	6
TOTAL	93.7	9	7	81.2	9	7

badgers (Chapter 6).

Table 5.35 presents the results of Spearman rank correlations of habitat proportions and occurrence of certain prey items in the diet. For both foxes and badgers there is, despite the small sample sizes (n=6 for for foxes and badgers), a significant correlation with the proportion of P+DW present. For badgers, this is illustrated in Fig. 5.38. Mixed plantations are used by badgers to consume tree fruits, and deciduous plantations to devour other invertebrates. Here, the fine differentiation of woodland types into separate habitat categories is post hoc justified by the patterns of resource use by badgers. Rabbit consumption by foxes correlates with presence of long grassland. Since long grassland occurs only in small proportions per range, it may not be an indicator of increased population density of rabbits. Instead, long grassland is probably used as a convenient structure for successful stalking of unsuspecting rabbits sitting in a neighbouring habitat. A similar interpretation can be derived from the analysis of movement patterns in Chapter 6.

5.6.6. Discussion.

In Chapter 4 it was shown that - despite broad similarities - there are interesting differences in the diet of foxes and badgers which are best compatible with the suggestion that foxes react in an opportunistic fashion to resource presence, while badgers concentrate on earthworms as their main energy source. No differences could be found in the average size, or the variability of size of group ranges (Table 5.33). Such differences might have been expected, since the diet of foxes changes considerably from range to range and hence an adaptation of range size to the local conditions seems prudent. These differences are indeed found, when individual ranges are considered: not only are individual fox ranges on average larger than

Table 5.35 Rank correlations of proportion of a habitat type (in hectares or as a relative proportion) and dietary spectrum (estimated dry weight) of fox and badger group ranges. Only significant correlations listed.
38 = deciduous plantations;
24 = marsh land
7+37 = pasture + deciduous woodland
40 = mixed plantations
29 = summer cereals
5 = long grass
* = $p < 0.05$; ** = $p < 0.01$ *** = $p < 0.001$

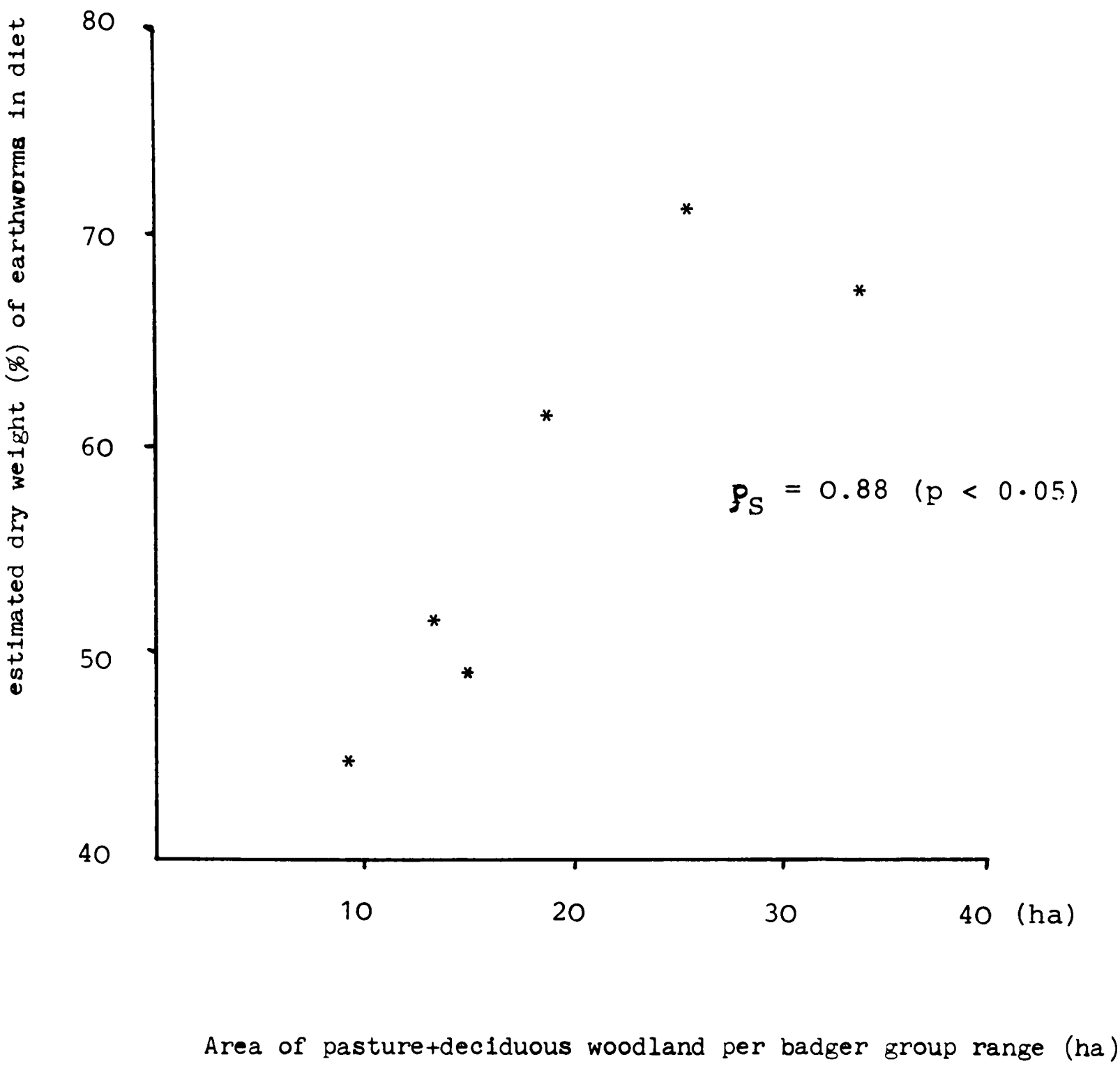
1. Badgers

HABITAT:	38	24 (%)	7+37(ha)	40 (%)	29 (%)
Invertebrates	0.92*				
Rabbits		-0.83*			
Earthworms			0.88*		
Grass	0.94*			0.94*	
Cereals					0.83*
Tree fruits	0.94*			0.94*	

2. Foxes

HABITAT:	7 (%)	7 (ha)	23	5 (%)	5 (ha)	7+37 (%)
	***	**	*			
Invertebrates	-1.	0.94	-0.81			
Fruits				-0.83*		
Birds	-0.88*					
Rabbits				0.88*	0.94**	-0.83*
Earthworms				-0.88*		0.83*

Fig. 5.38 Correlation of proportion of earthworms in the diet of badger group ranges and proportion of pasture and deciduous woodland per group range.



individual badger ranges (Table 5.33), but size also varies to a greater extent. This is due to the fact that the ranges actually utilized by an individual badger may constitute only a proportion of the total range (Chapter 6). One possible interpretation of this difference between range sizes of individuals and groups in badgers may be a 'fail-safe' mechanism: for most of the time only a fraction of the group range is required to feed a badger. However, under bad conditions, additional areas may be required to satisfy the range inhabitants. Therefore, group ranges should contain a safety margin and hence be larger than individual ranges. Then range maintenance will also be cheaper and more efficient than with large changes - modest changes of range boundaries are more efficient and less likely to lead to escalated conflicts between neighbours (Section 5.4).

The investigation of habitat composition in relation to resource use and range configuration permits to draw some conclusions about 'key' habitats. Pasture and deciduous woodland together are essential habitats for badgers. Further evidence for this is presented in the analysis of movements in Chapter 6. Range configuration can, in some cases at least, be explained as a result of the dispersion of pasture areas (Fig 5.30-33). These are results entirely compatible with the resource dispersion hypothesis, which predicts that range size should be determined by the dispersion of food patches. In Chapter 7, I shall discuss this problem again and conclude that RDH is certainly consistent with the resource setup in Wytham, while an additional factor, defense of resources, is likely to play a decisive role in the formation of groups.

Due to their more varied feeding habits, foxes present a more complicated picture. Human housing constitutes one key habitat, since the dispersion of human housing influences the delineation of range boundaries. Pasture + Deciduous Woodland form a second key resource unit evidenced by their constant representation in the group ranges. A third group of

important habitats is summarized by SHRUB; these are small, but very diverse habitats (bracken, hedges, scrubs with grass layers) known to harbour a large variety of interesting prey items.

6. Patterns of range utilization

6.1. Methods

6.2. Patterns of space use

6.2.1. One week with PODGE in the breeding season

6.2.2. Range use by OLDMAHOG

6.2.3. Range use by other foxes

6.2.4. Range use within the HOMEFARM fox group

6.2.5. Range use by badgers

6.2.6. Direction preferences in local movements

6.2.7. Conclusions

6.3. Simultaneous movements within the UPPER FOLLIES badger group

6.3.1. Coordination of movements

6.3.2. Renewal periods and interference pressure

6.4. Habitat utilization

6.4.1. Habitat preferences

6.4.2. Habitat characteristics and resource levels in visited cells

6.4.3. Intensity of use in relation to resource density

6.4.4. Patterns of visits to different habitats

6. Patterns of range utilization

In the previous chapter I looked at the spatial configuration and the size of badger and fox home ranges and correlated them with the presence of habitats and resources. These analyses provide preliminary insights of the importance of certain areas to the animals. To gain a deeper understanding of these results we have to explore in detail the utilization of the animals' ranges. In this chapter I first look at the picture of range usage that emerges from the accumulation of many nights' data. I shall then investigate what kind of movement patterns in a given night are responsible for the overall picture of range utilization.

6.1. Methods

Data from radio tracking were used to analyse movement patterns. For foxes, complete nights of intensive tracking were available only for a minority of individuals. Therefore the number of locations ('fixes') per area unit was used as a measure of the intensity of use of the area. Fixes were selected by program ICELLH according to the 15 minutes independence interval criterion (Chapter 5, Appendix 4), and summed over each area unit. For some foxes, and most of the badgers, two measures of the intensity of use were derived from nights of intensive radio tracking: (i) number of visits (NOV) and (ii) duration of stay (DOS) per area unit. For complete nights of radio-tracking, program TRANSIT (adapted from Doncaster (1985)) calculated arrival and departure times for each area unit, by splitting the elapsed time between two successive locations in different areas and assigning half to each area. The error of this approximation is likely to be small, since - due to the intensive tracking efforts - locations were

rarely more than 5 minutes apart. Therefore, the maximum possible error, the difference between the actual and calculated time of 'crossing the border', was reduced to 2-3 minutes which turns out to be unimportant in the context of this analysis. Program CELTIM used the calculated arrival and departure times and compiled the number of visits and the total duration of stay (in hours) per area unit. Output from program CELTIM was then used for a variety of analyses described below.

Two kinds of area units were used: (i) 'Natura' patches delineated on the habitat map and (ii) a systematic 50 by 50 metre quadratic grid which eliminated effects due to varying sizes of habitat patches (see 6.4.). Where analyses relied heavily on actual departure times and time intervals between successive visits to the same cell, cell size was varied (25, 50 and 100 m) to explore the effects of choice of cell size on the patterns of use.

Scaling of space use, patterns of space use and the effects of the spatial location of a site on its intensity of use by an animal ('spatial dependence') were investigated by spatial autocorrelation functions. Appendices 5, 6 and 7 describe the problem of spatial dependence and solutions to it, explain the parameters important for the investigation of scaling in space, introduce two measures of spatial autocorrelation (Moran's I and Geary's c), and finally explain how to interpret spatial correlograms and spatial models and the results of fitting models to the data. Computation of spatial autocorrelations were performed by program AUTCOR using the algorithms listed in Appendix 7. For foxes, the number of fixes per 50 m cell, selected according to the 15 min independence interval criterion, was employed as a measure of the intensity of use. For badgers, I used the measures derived from records of intensive radio- tracking as described above.

Possible interference between the movements of group members was investigated for one badger group, the UPPER FOLLIES range B2. Here, I was

reasonably certain that all group members had been tagged (Chapter 5). Locations of all three tagged animals, the females ALI and NANI and the male WILF, were recorded simultaneously. This was possible since all individuals spent almost all of their time in one small valley. I recorded simultaneous locations at fixed intervals of 15 minutes from the beginning to the end of the night for a period of seven consecutive nights in October 1983. In the middle of October, foraging activities are expected to soar since badgers have to accumulate reserves for the inactive periods in winter and for lactation in spring. Therefore I assumed that the majority of movements involved foraging. Activity at the sett mainly involves cleaning nest chambers and decorating them with fresh hay and leaves, and was consequently excluded from the analysis as were periods of rest or inactivity. Programs were written to process the data through the following stages of analysis:

(1) Program PRAEP associated each location with the appropriate cell number, depending on the chosen size (25, 50 or 100 m).

(2) Program HAUPT computed distances between pairs of animals at successive locations and compiled times of visits and identity of visitor for each cell.

(3) Program ZAEHL identified whether given pairs of animals moved closer or further to each other between successive locations, and compiled a summary for all three possible pairs (ALI-NANI, NANI-WILF, ALI-WILF). Distance changes were tested for random arrangement with the runs test for trends (Sokal & Rohlf (1981)) by considering increases (withdrawals) and decreases (approaches) in distance and excluding instances when separations did not change (= 12% of all cases).

(4) Program VISIT calculated (i) the number of visits by each individual to each cell, (ii) the total number of visits by all three badgers to each cell, (iii) the mean duration of visit of each individual per cell, and (iv) the average revisit interval of each individual per cell. Several

successive locations of an individual in the same cell were treated as one visit.

(5) Program ZELLE3 used the output of programs HAUPT and VISIT to calculate single and average revisit intervals (renewal periods) per cell by pooling the movements of all three individuals. Renewal periods were computed separately for (a) cases in which a cell was visited twice in succession by the same individual, and (b) cases in which successive visitors were different individuals. Revisit intervals were calculated as 'mean' estimates. For each location, the individual was assumed to start its visit at the time of taking the fix and finish the visit just before the next location. For example, an individual located in cell A at 21.00 hours, in cell B at 21.15 and in cell A again at 21.30 would be accorded a revisit interval of 15 minutes. However, reality could substantially vary around this estimate: the animal might have left cell A at 21.14, arrived at cell B at 21.15 and re-entered cell A at 21.16 yielding the minimum revisit interval of 2 minutes, or it could have left cell A at 21.01, stayed in cell B until 21.29 to return to cell A at 21.30, yielding the maximum revisit interval of 28 minutes. Given a sufficient sample size, the 'true' revisit intervals would be expected to be normally distributed between the two possible extremes.

The analysis of habitat preferences was based on 50 m grid cells. The habitat composition of grid cells was identified by applying the same procedure as described in Chapter 2 and 5 and Appendix 3. An estimate of habitat diversity per grid cell was taken simply as the number of different habitats represented in a cell (program TRACKHAB). Earthworm biomass per cell was estimated by multiplying the proportion that each habitat occupied in a cell with a factor as listed in Table 6.1 (program TCHANGE). Those cells within the aea of habitat recording (Chapter 2) were also tagged with the scores of the first four axes of the detrended correspondence analysis

Table 6.1 Allocation of worm biomasses per area unit to different habitats

Habitat	Number	Biomass g m	Source (Table 3.1)
Grassland	5	23.0	this study
Pasture	7	97.1	Kruuk's study
Winter cereals	28	48.2	Kruuk's study
Summer cereals	29	48.2	Kruuk's study
Deciduous woodland	37	83.7	this study, mean value of both soil categories
Deciduous plantations	38	38.1	this study, plantation on clay (deciduous pl. are mostly confined to this soil)
Beechwood	39	12.3	Cuendet's study, mean value of both soil categories
Mixed plantations	40	27.8	this study, mean of both soil categories (typical distribution for this habitat)
Coniferous plantations	41	17.5	this study, plantation on rendzina, since mostly confined to this soil category

All other habitats were scored as 0 and not considered for analysis, since no information on worm biomasses available. Data from Kruuk's study were preferred for some habitats, since his sample sizes were larger.

Figures 6. 1-6.28. Range use by foxes

Each fox comprises 4 figures on 2 sheets

Fig x.a:

Three-dimensional plot of intensity of use of range plotted on a 100 m grid, produced by program GINOPLOT using the GINO graphics package available on the VAX 11/780. Coordinate 0,0 is the southwest corner of an area. The z-axis represents number of fixes per area unit. Scale of the z-axis remains identical for all sections of the graph, ie. a perspective reduction of cells in the background is excluded. Note that (for simplicity and uniformity) all plots are on 100 by 100 m cells, while the spatial analysis was undertaken for 50 by 50 cells. However, some of the ranges were too large to fit in a 30 by 30 units grid of 50 by 50 m for graphical illustration

Fig. x.b

Contour plot of intensity of use of range, again evaluated on a 100 m grid, produced by program GINOPLOT. Data set identical as for Fig. x.a. Equal levels of Utilization Intensity (UI) are delineated by a contour line. Black areas are the result of contour lines sitting so close to each other that resolution of single lines becomes impossible. White areas surrounded by black areas represent plateaux where the UI is higher than the top contour level chosen. Below is a list of contour step size and the number of fixes at white area plateau level:

Fox	Fig. Numbers	Contour step (Number of fixes per cell)	Plateau
Bramble	6.1 - 6.2	1.0	15
Elke	6.3 - 6.4	1.0	15
Gasper	6.5 - 6.6	2.05	40
Grizzle	6.7 - 6.8	0.64	10
Kali	6.9 - 6.10	1.26	25
Kboom	6.11 - 6.12	1.0	15
Konuk	6.13 - 6.14	2.05	40
Lio	6.15 - 6.16	1.36	20
Oldmahog	6.17 - 6.18	1.0	20
Oldsabre	6.19 - 6.20	0.44	5
Pintooth	6.21 - 6.22	1.0	20
Podge	6.23 - 6.24	2.05	40
Surprise	6.25 - 6.26	1.26	25
Taru	6.27 - 6.28	1.0	15

Figures 6. 1-6.28 (Cont.)

Fig. x+1.a:

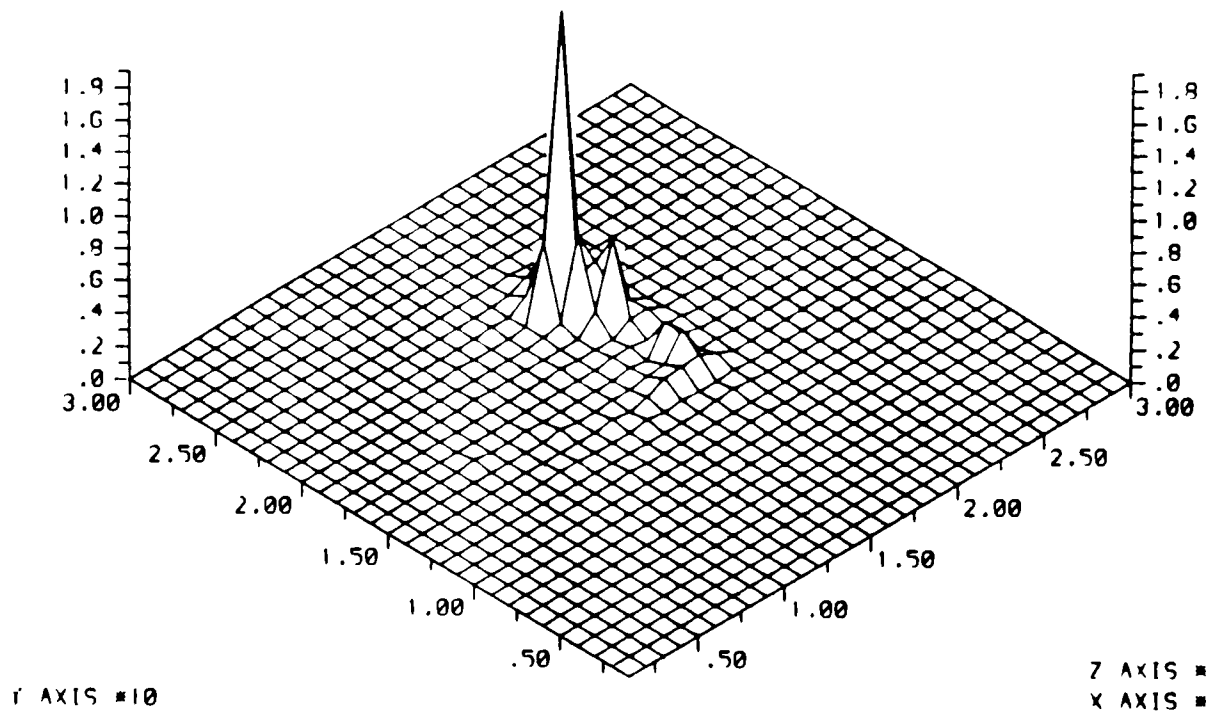
Results of fitting the spatial models 1 to 5 (see 6.2.2. and Appendices 5-7) to UI data. The weighing function along the x-axis represents the number of the model; the higher the number, the more weight is attached to pairs of cells at a large distance. The y-axis represents the results, plotted as spatial autocorrelation coefficients (SACs), Moran's I and Geary's c. Plotting symbols for the SAC are

SAC	SAC significantly different from expected mean (null hypothesis rejected)	SAC corresponding to expected mean value (null hypothesis confirmed)
Moran's I	filled circles	stars
Geary's c	filled squares	zeros with a dot

Fig. x+1.b:

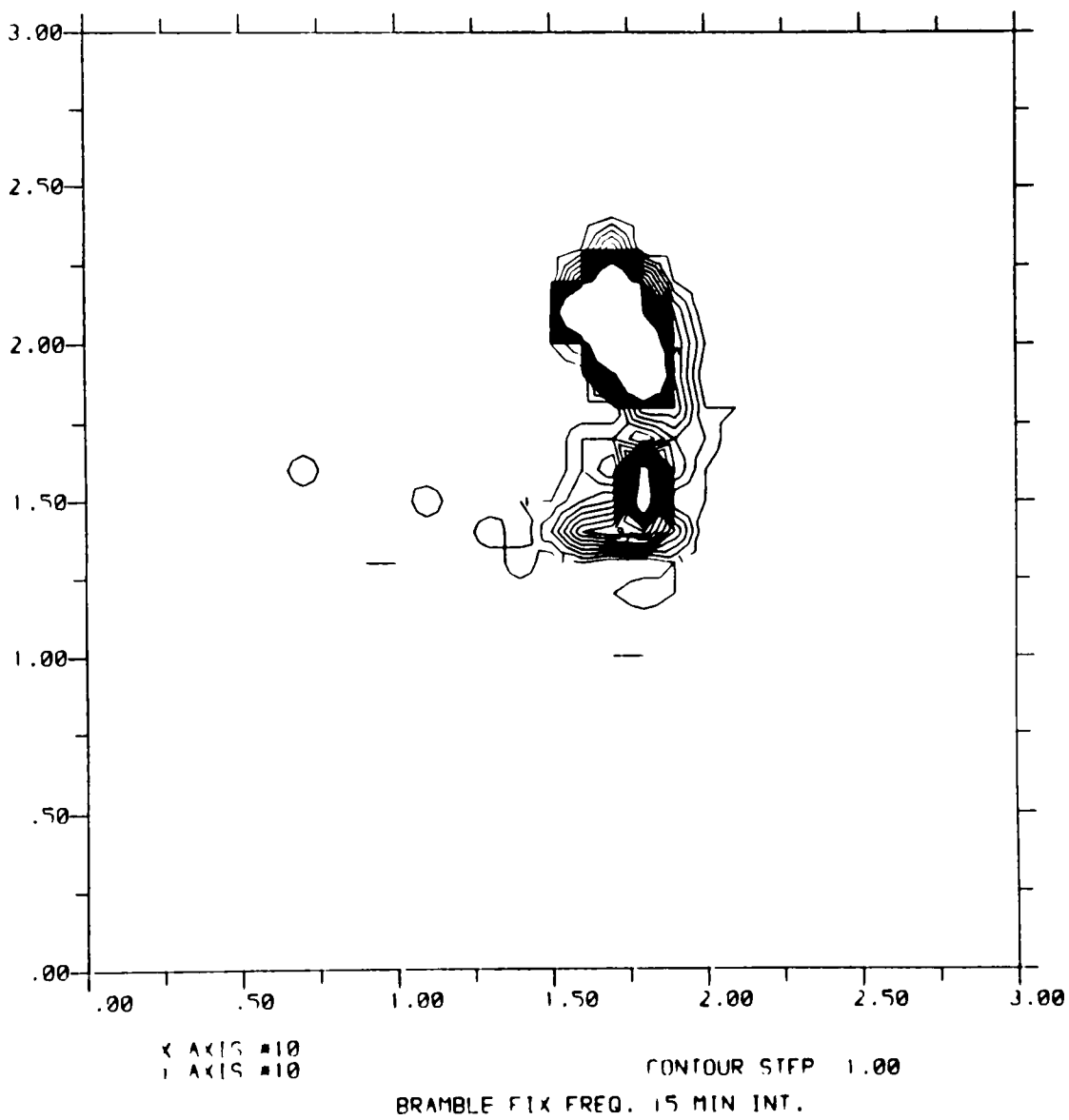
Spatial correlograms of UI data, using Moran's I as SAC. For a detailed explanation, see text or Appendix 5.
Filled circles: SAC significantly different from the expected mean (null hypothesis rejected)
Stars: SAC cannot be distinguished from the expected mean (null hypothesis confirmed)

All "significant" results refer to a probability of 0.05

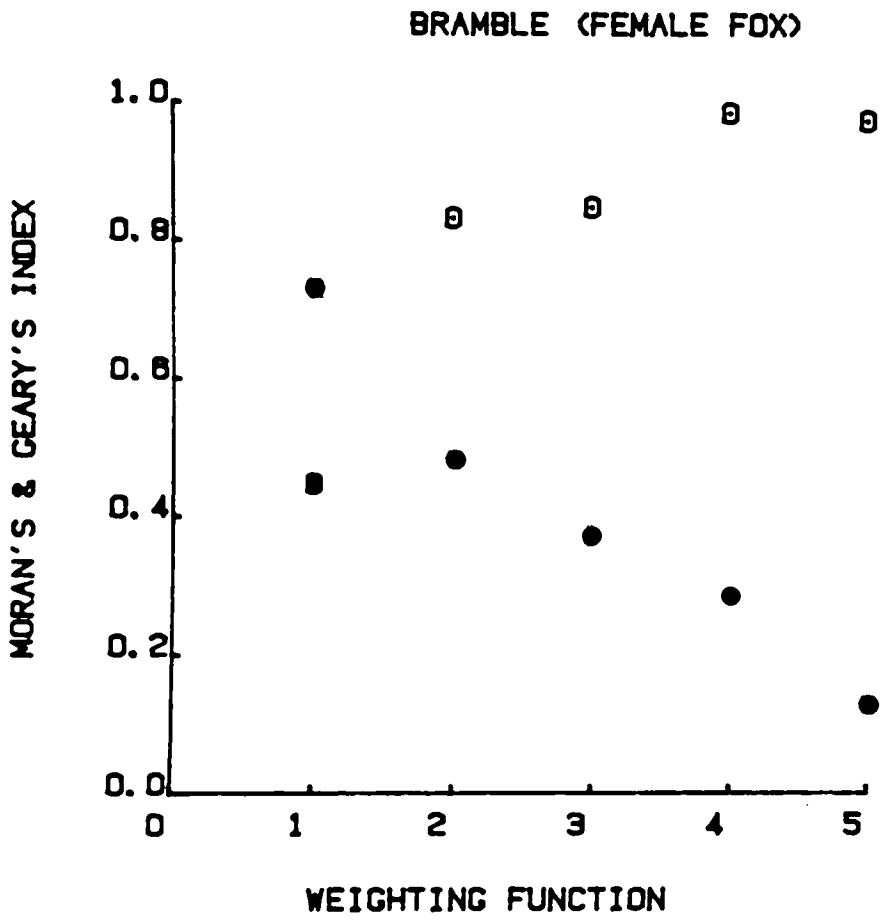


BRAMBLE FIX FREQ. 15 MIN INT.

6-1a.



6-1b.



6-2a

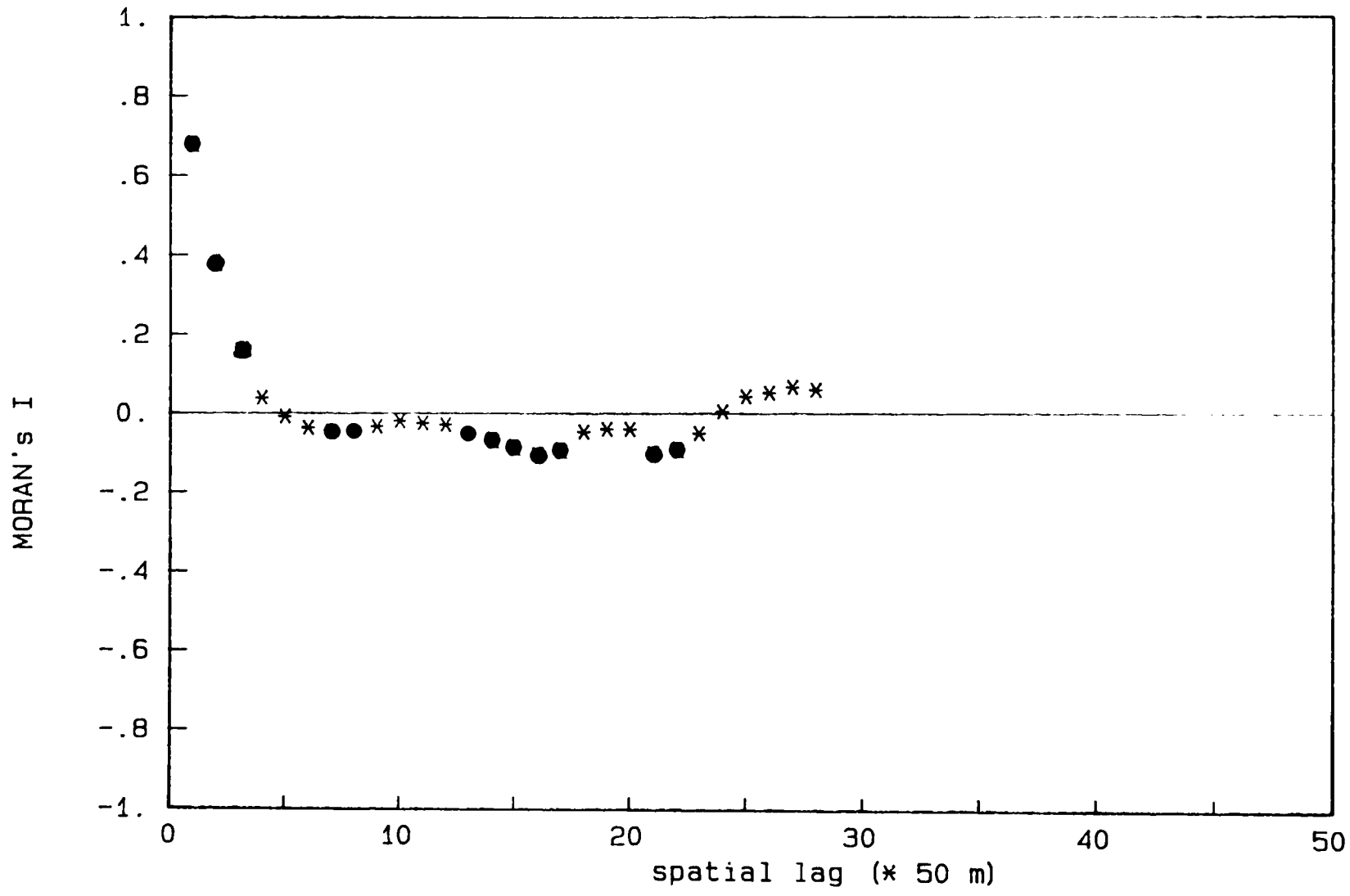
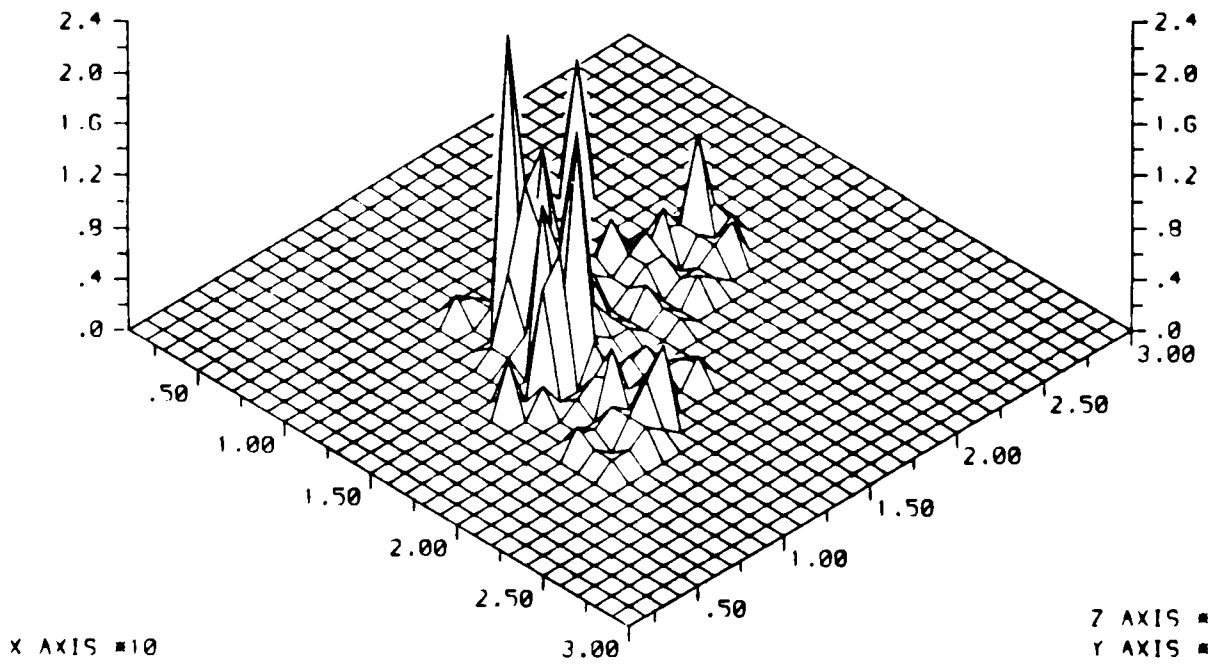


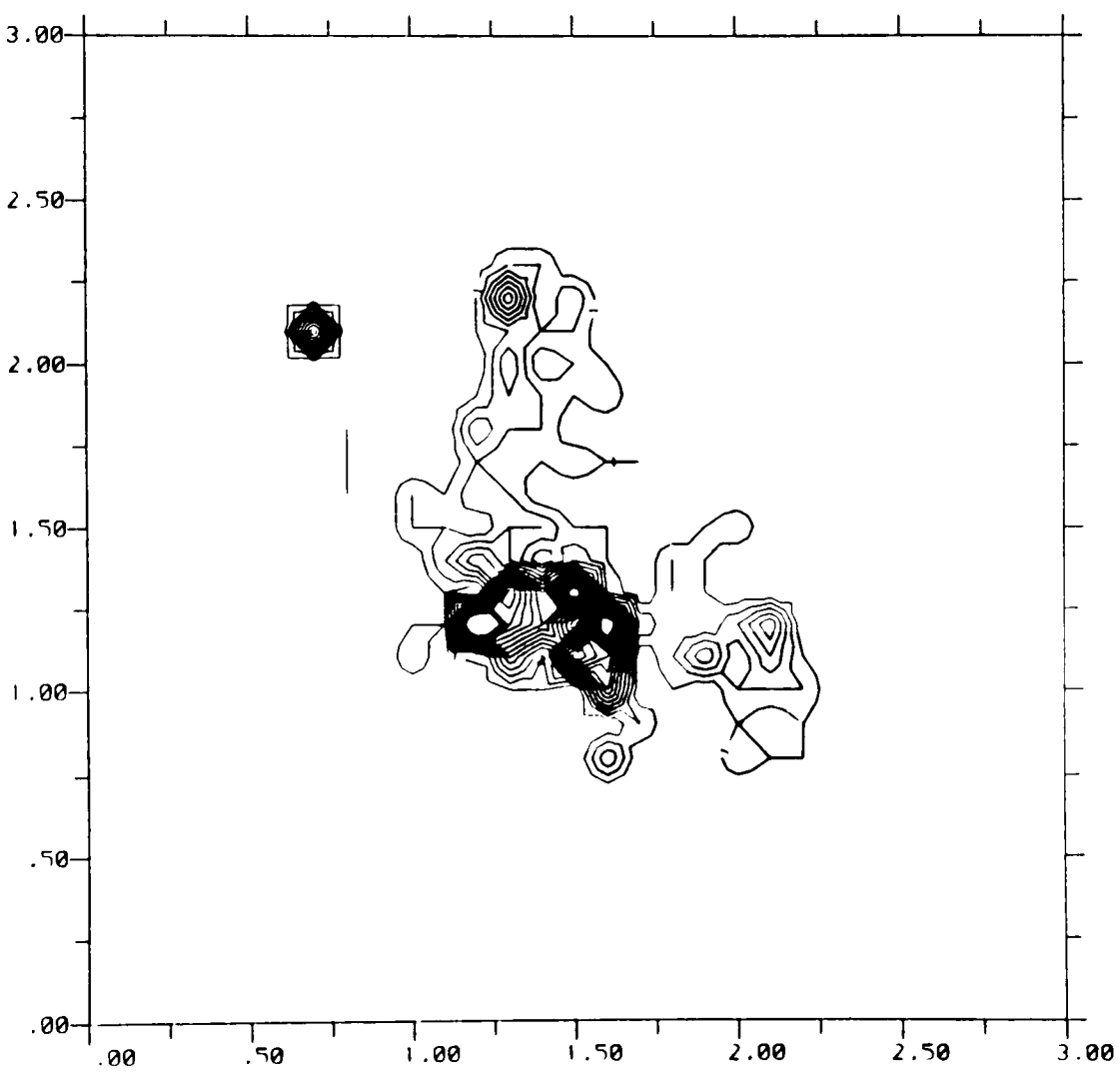
Fig. Correlogram of the spatial autocorrelation function using MORAN's I as correlation coefficient. BRAMBLE, 15 min data

6-2b.



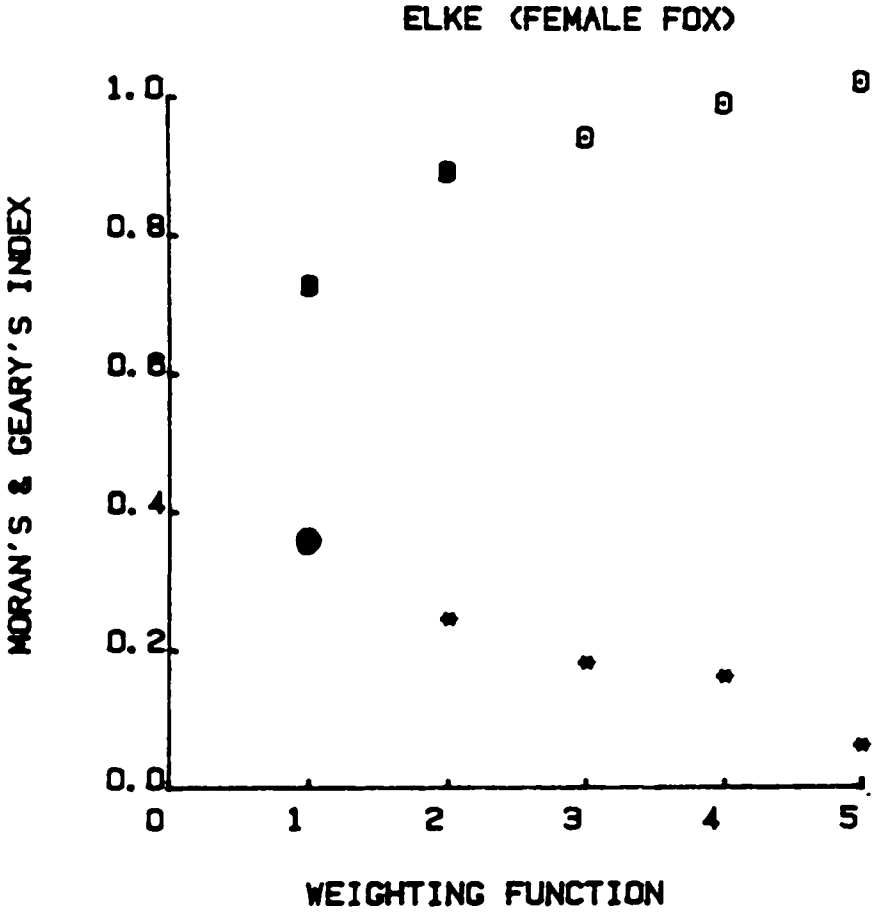
FLKE FIX FREQ. 15 MIN INT.

6-3a



FLKE FIX FREQ. 15 MIN INT.

6-3b



6-4a

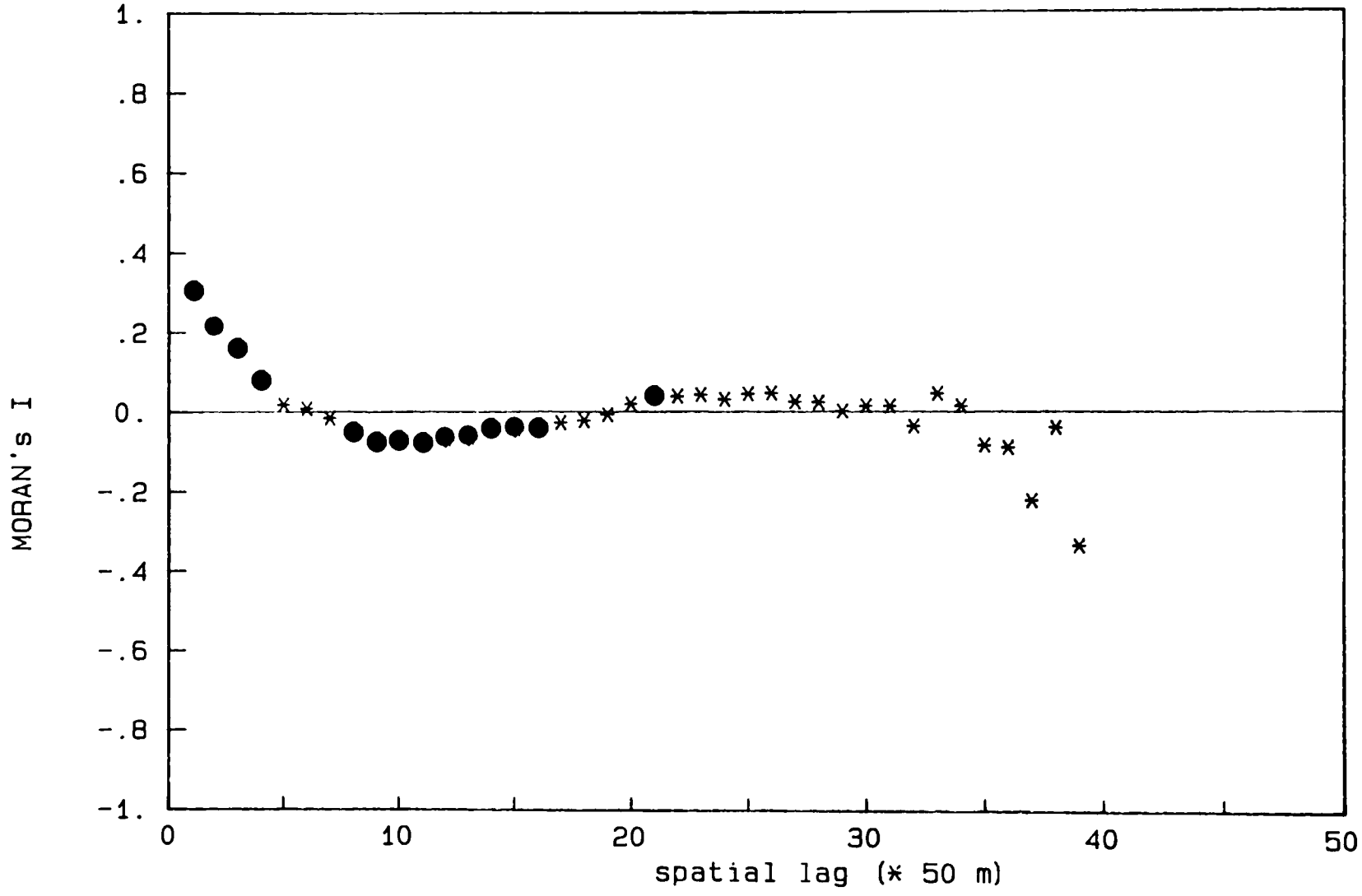
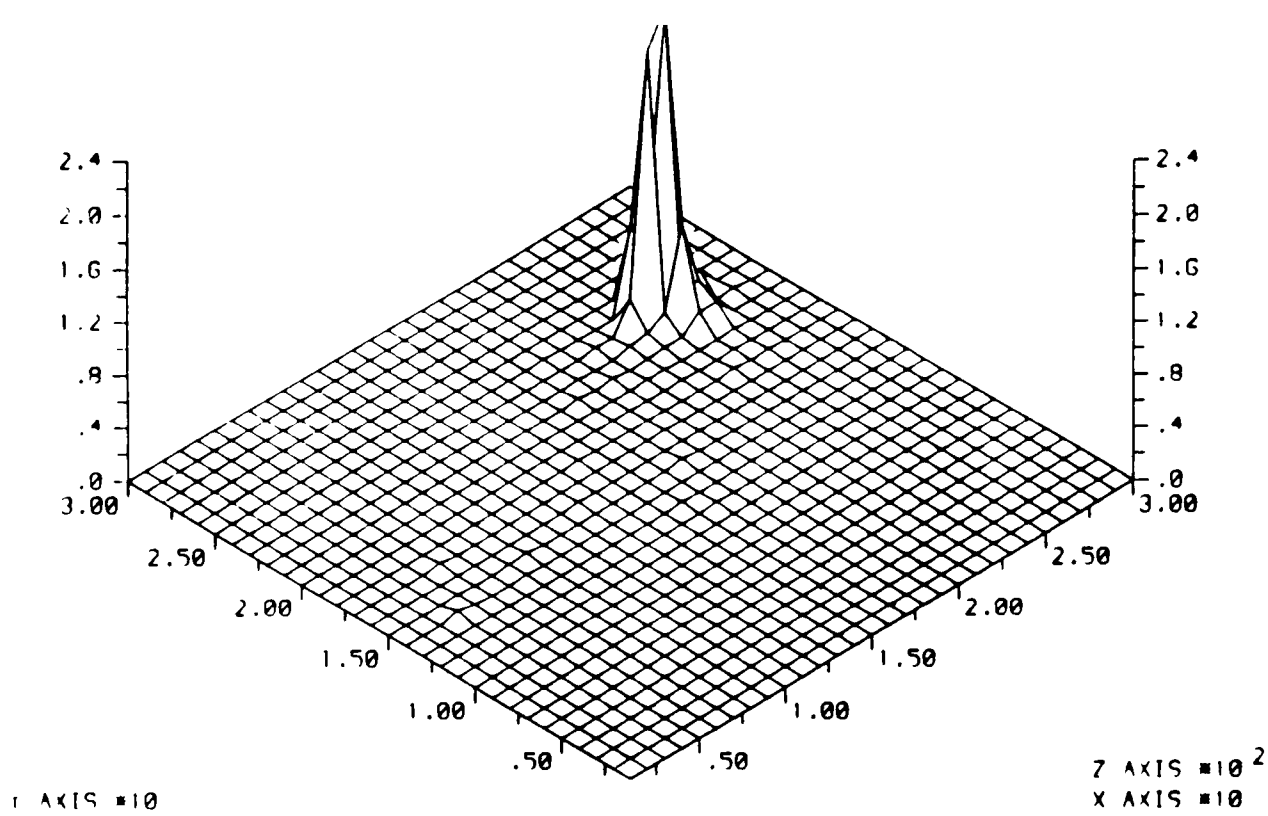


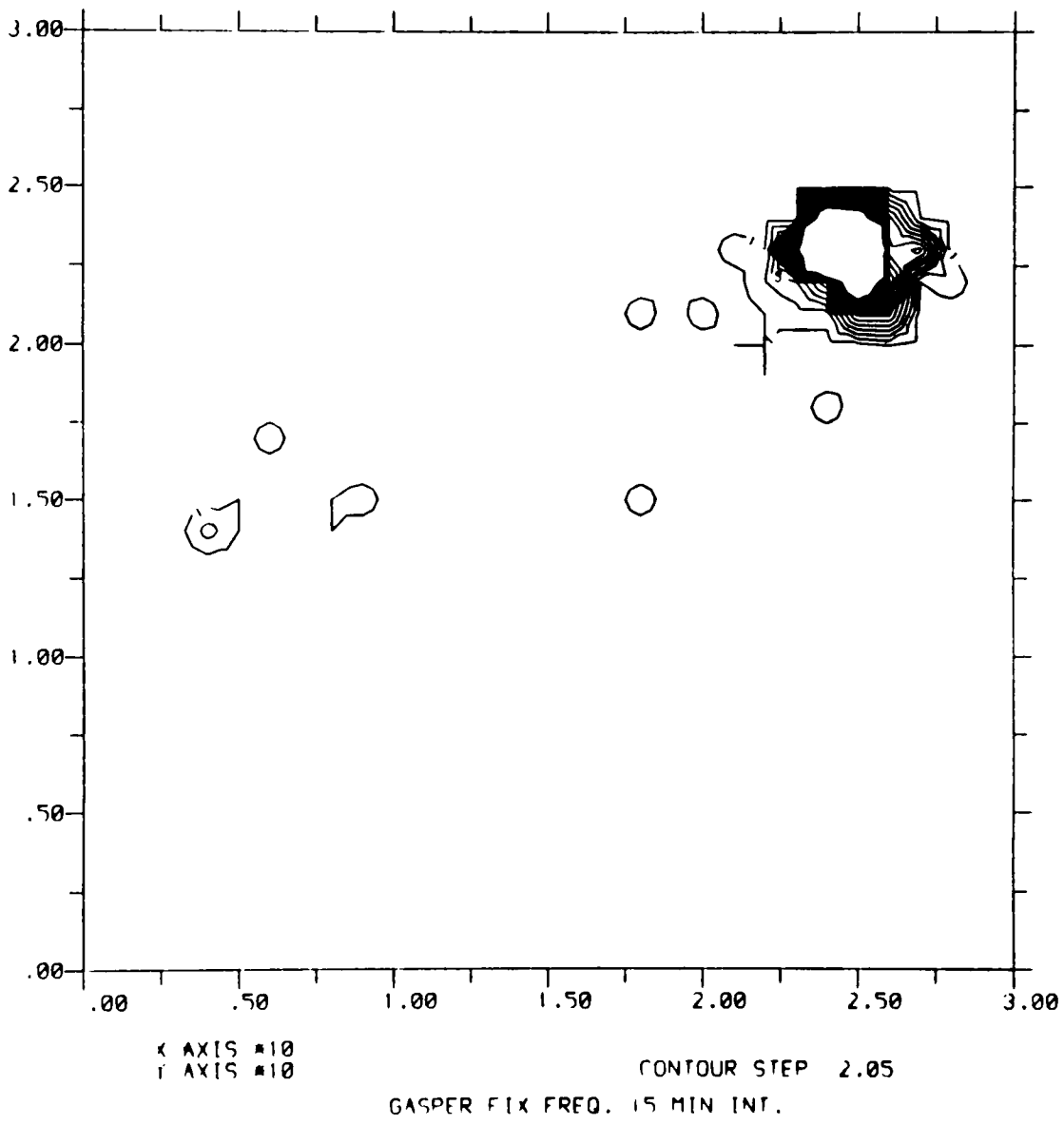
Fig. Correlogram of the spatial autocorrelation function using MORAN's I as correlation coefficient. ELKE, 15 min data

6-4b



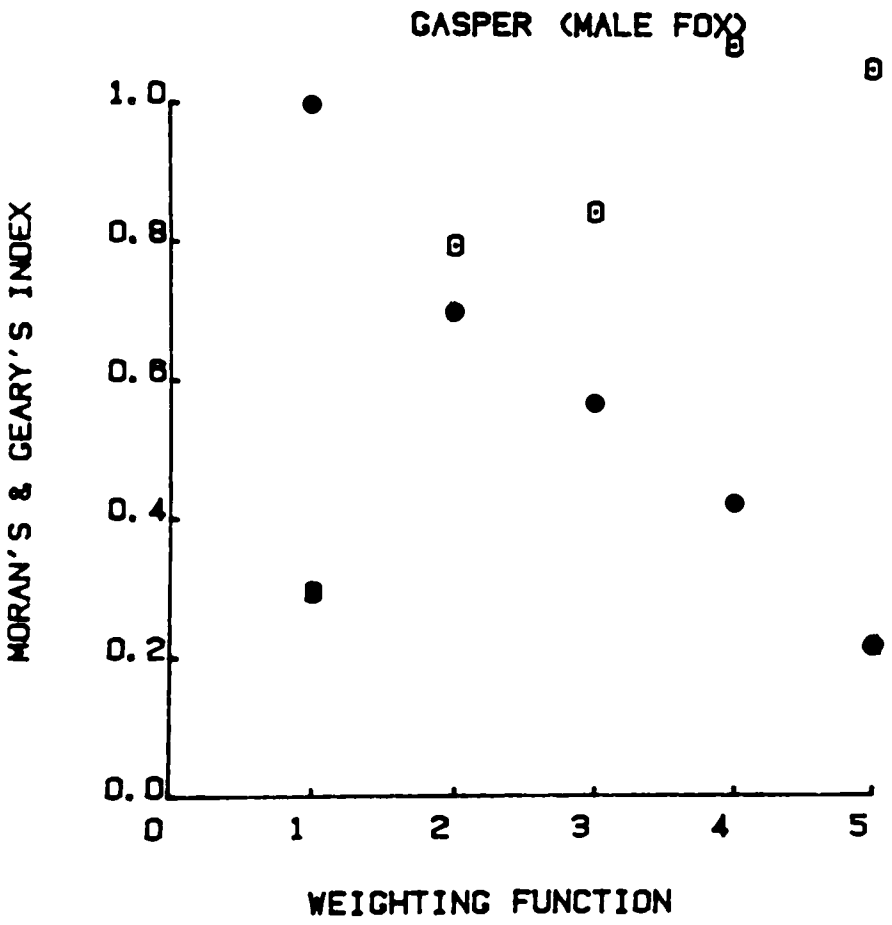
GASPER FIX FREQ. 15 MIN INT.

6-5a



GASPER FIX FREQ. 15 MIN INT.

6-5b



6-6a

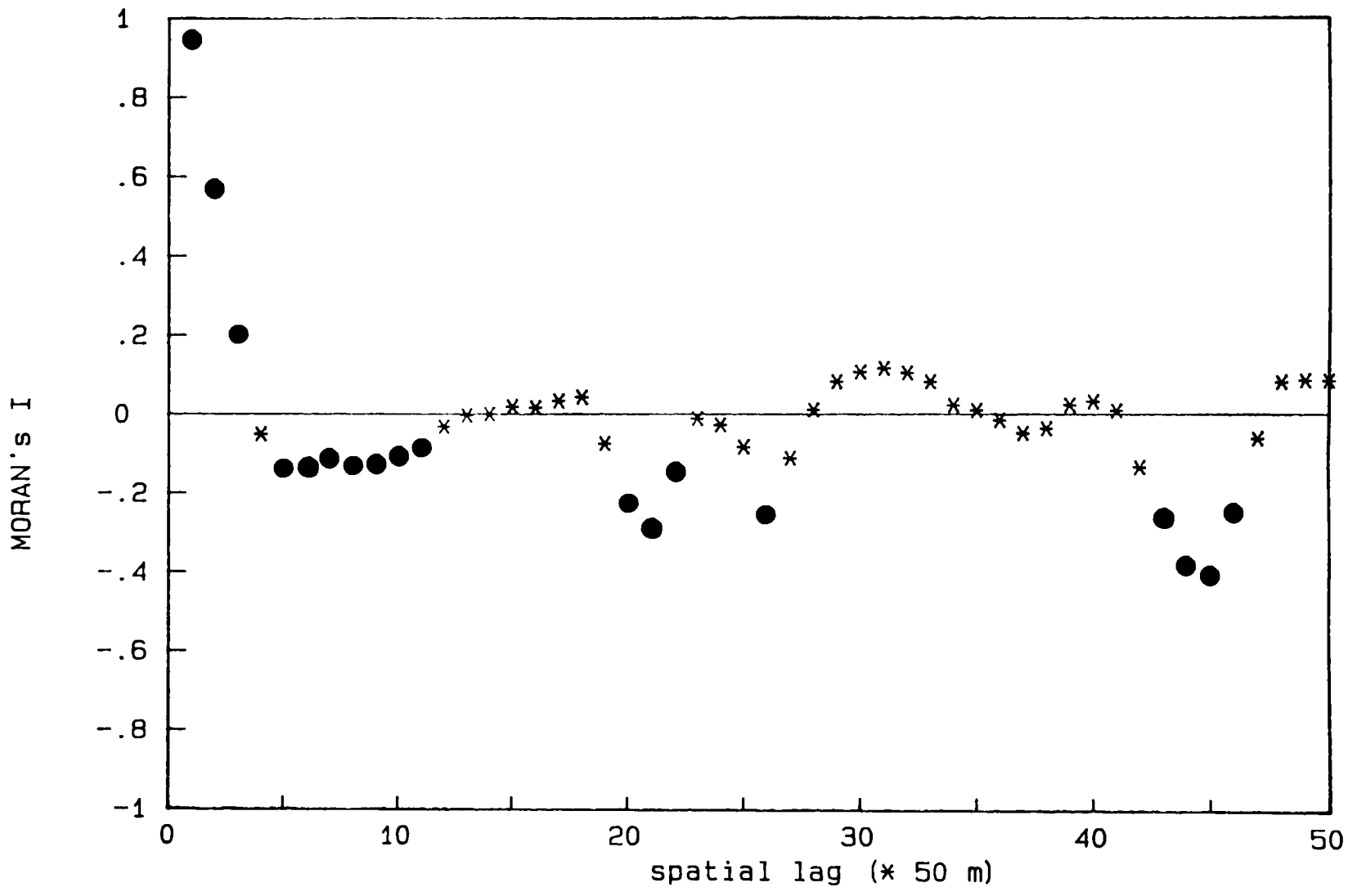
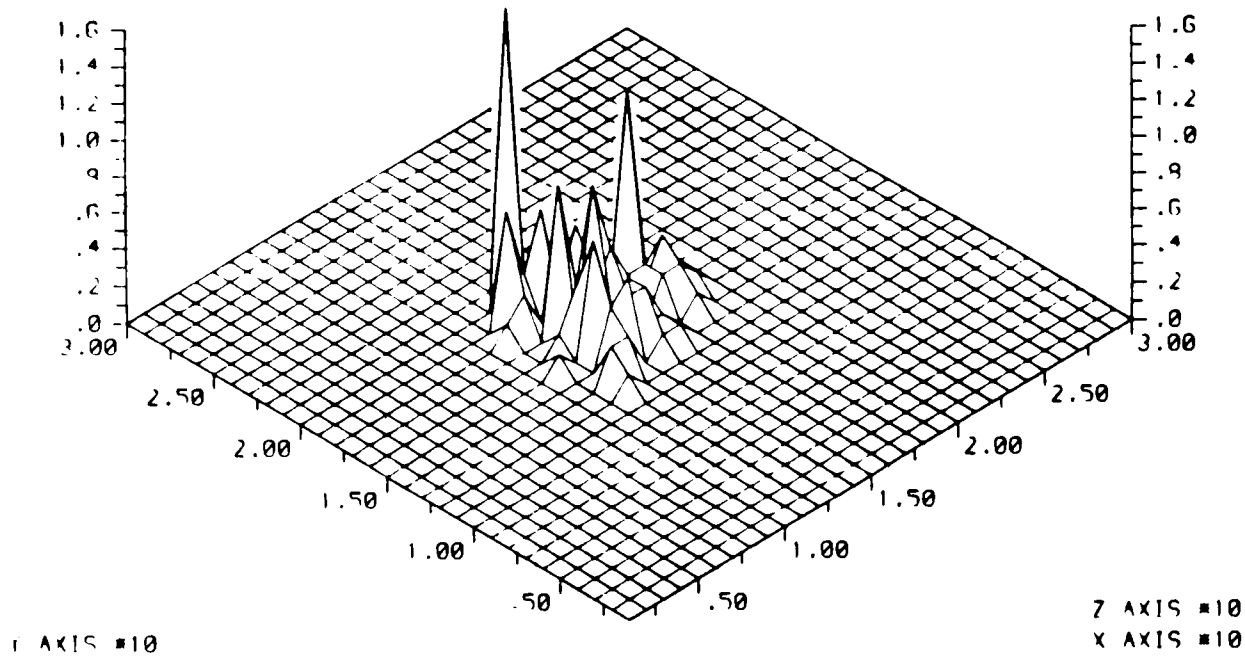


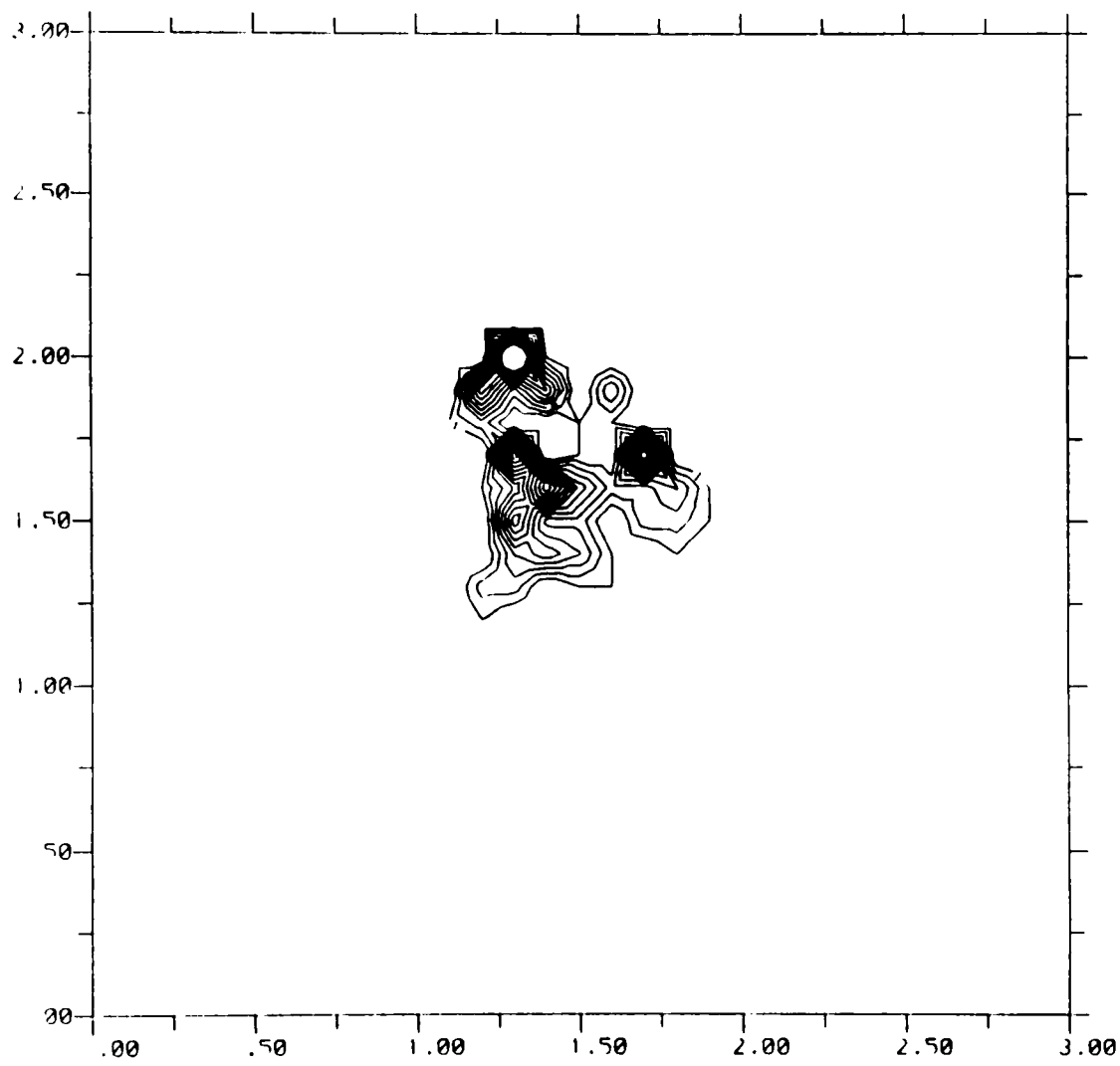
Fig. Correlogram of the spatial autocorrelation function using MORAN's I as correlation coefficient. GASPER, 15 min data

6-6b.



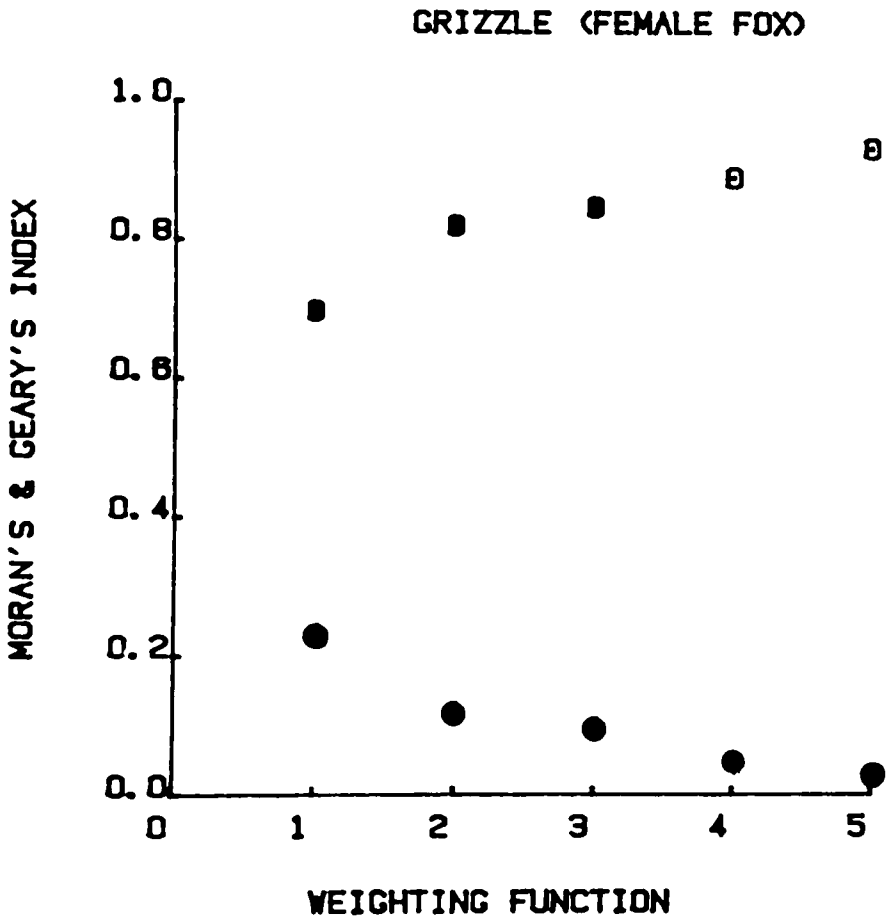
GRIZZLE FIX FREQ. 15 MIN INT.

6-7a



GRIZZLE FIX FREQ. 15 MIN INT.

6-7b



6-8a

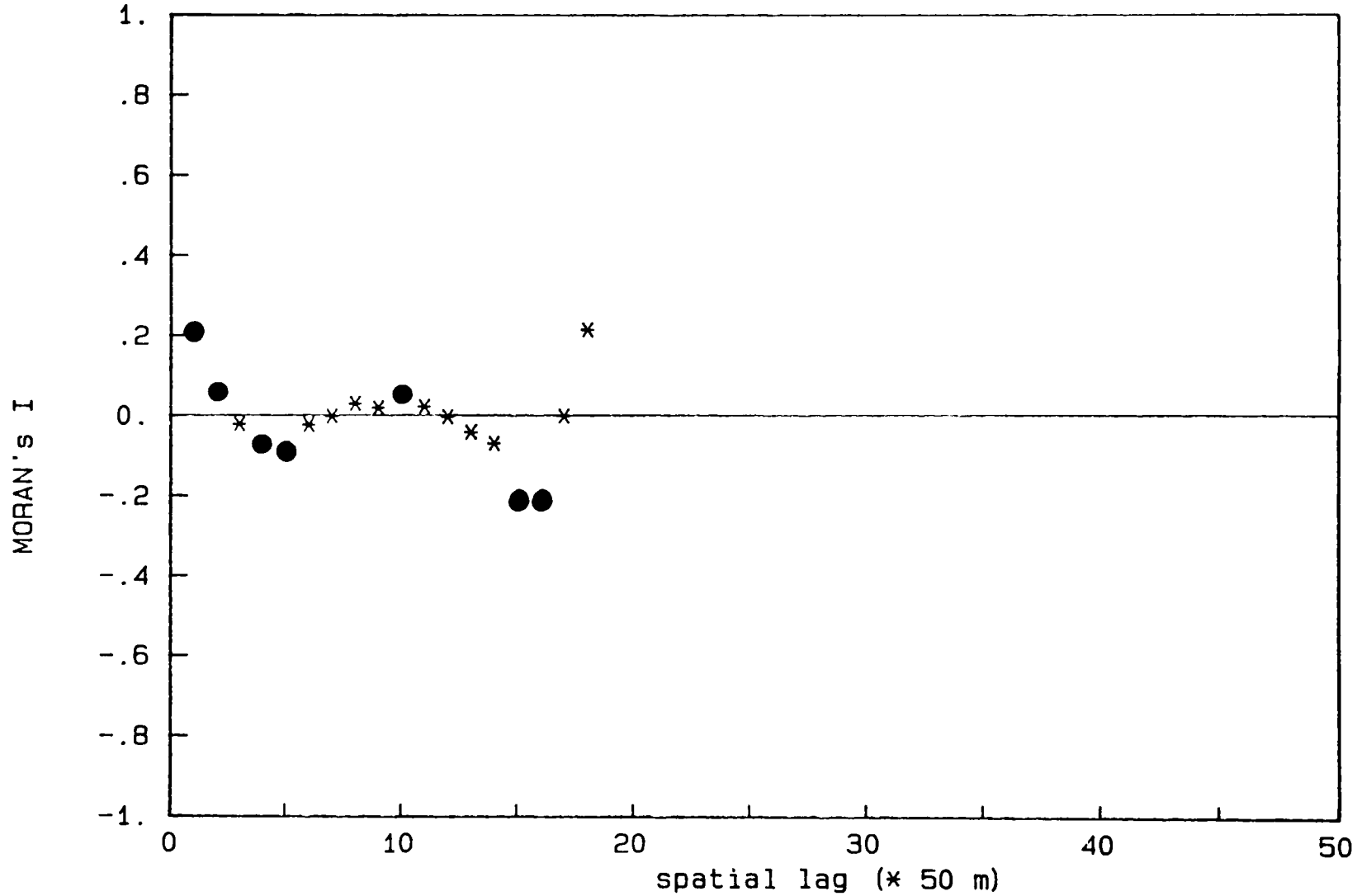
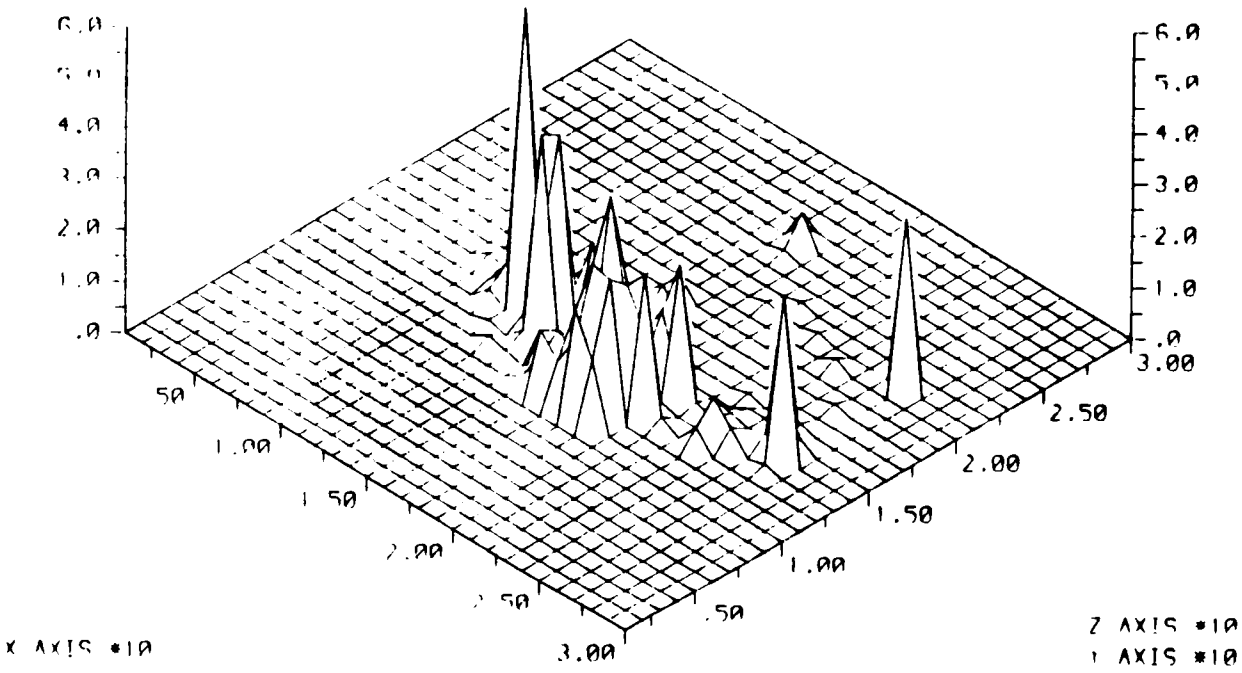


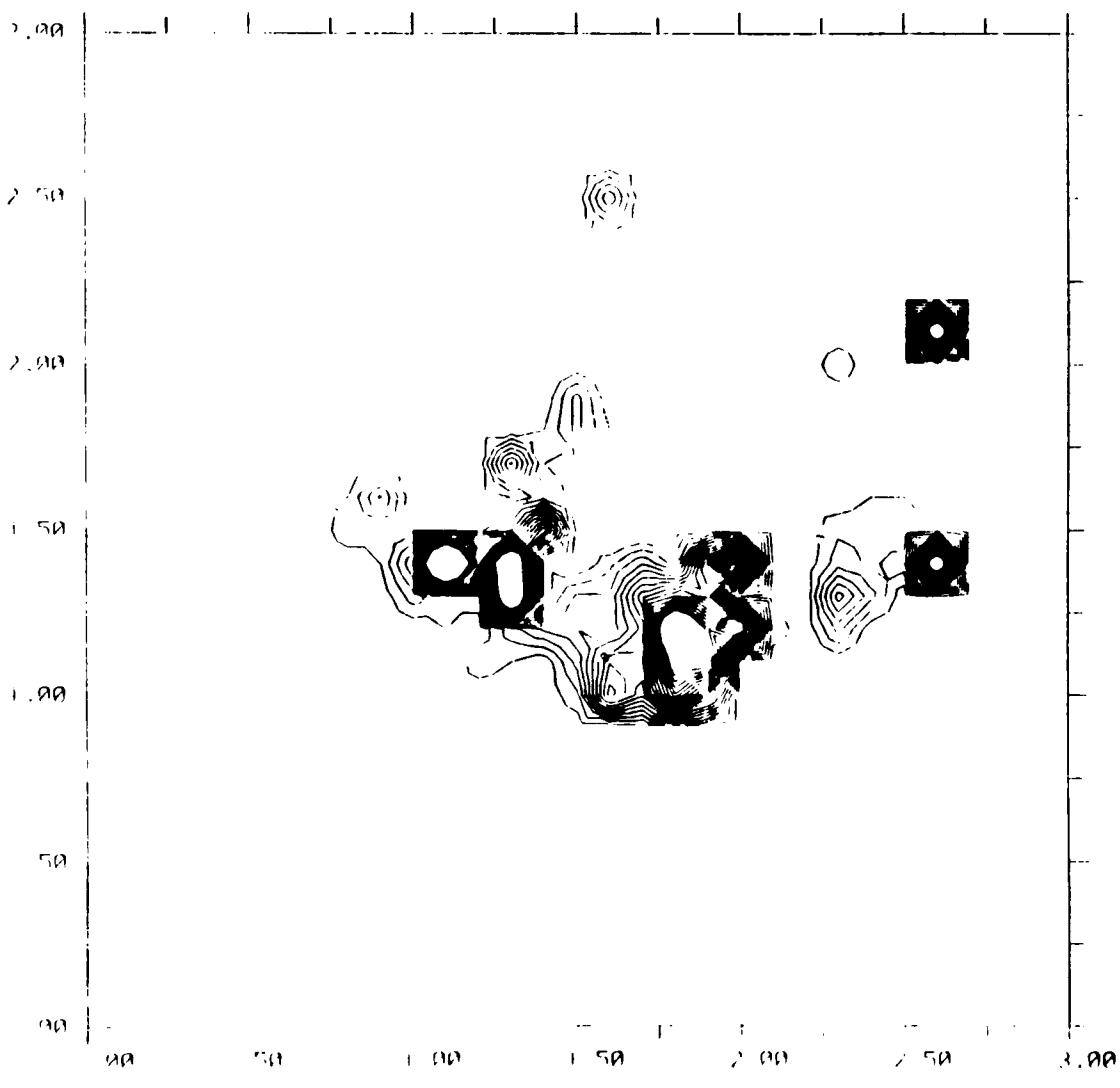
Fig. Correlogram of the spatial autocorrelation function using MORAN's I as correlation coefficient. GRIZZLE, 15 min data

6-8b



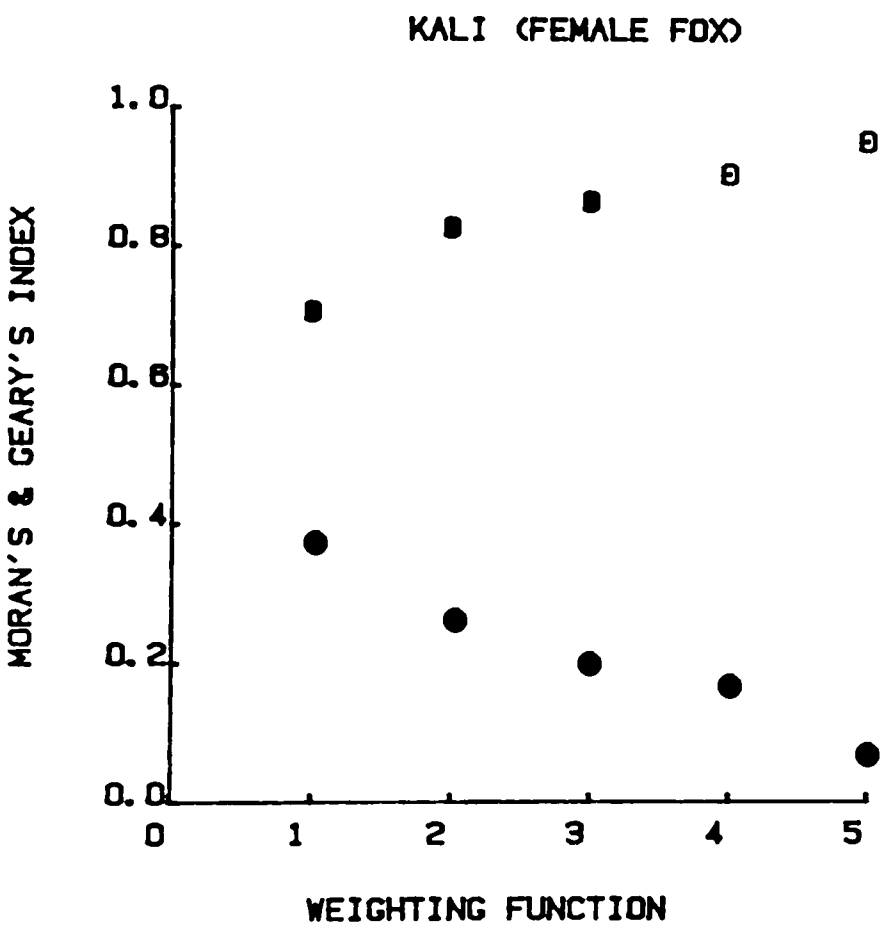
KALI FIX FREQ. 15 MIN INT.

6-9a



KALI FIX FREQ. 15 MIN INT.

6-9b



6-10a

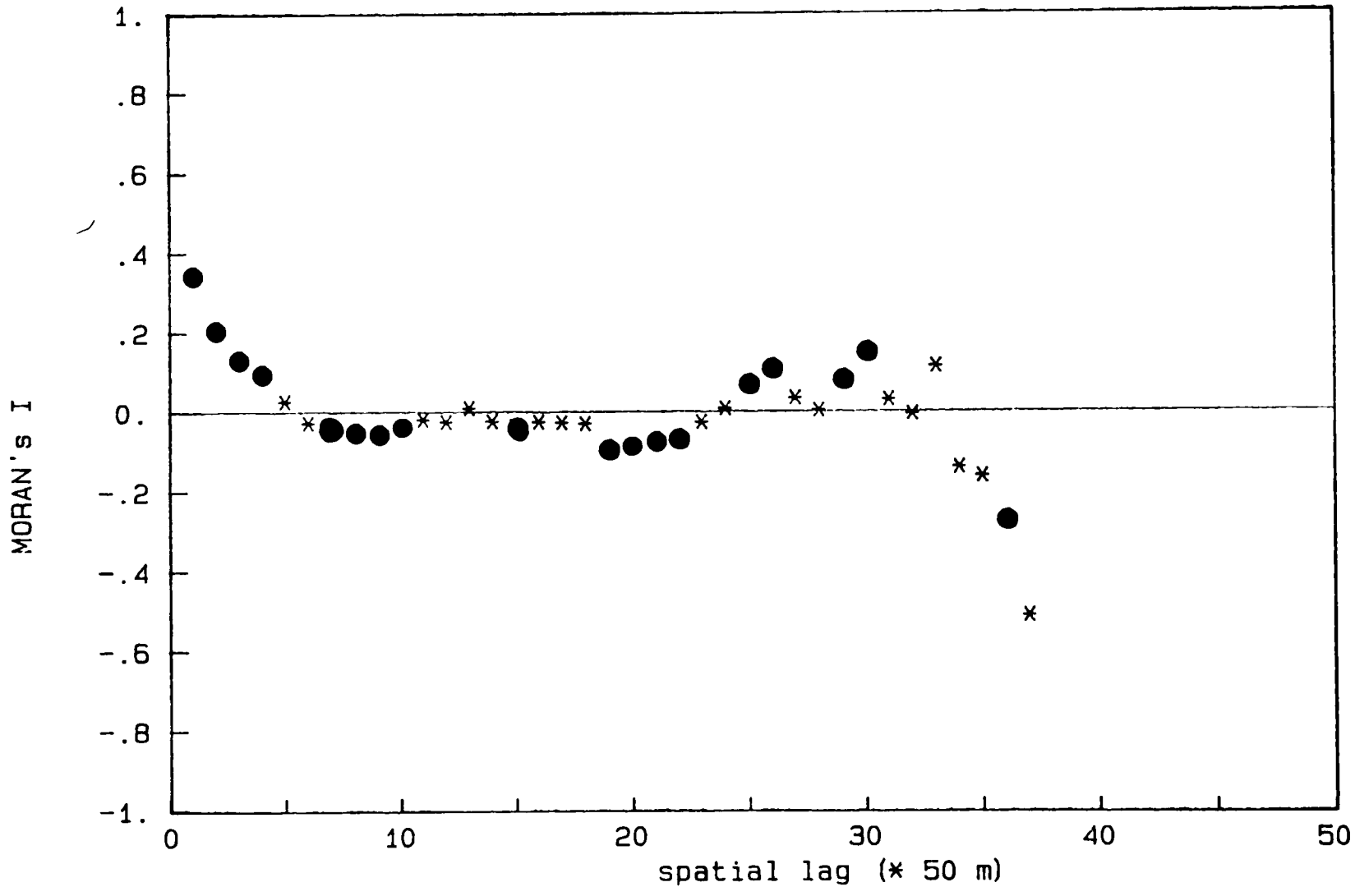
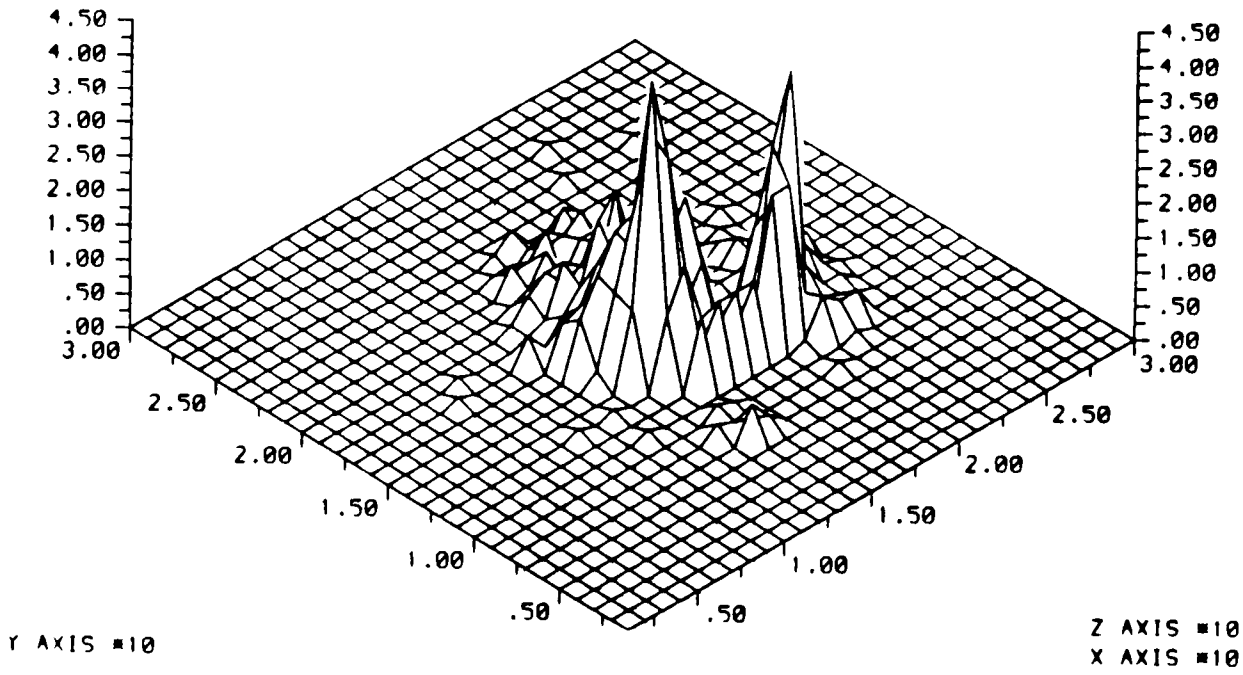


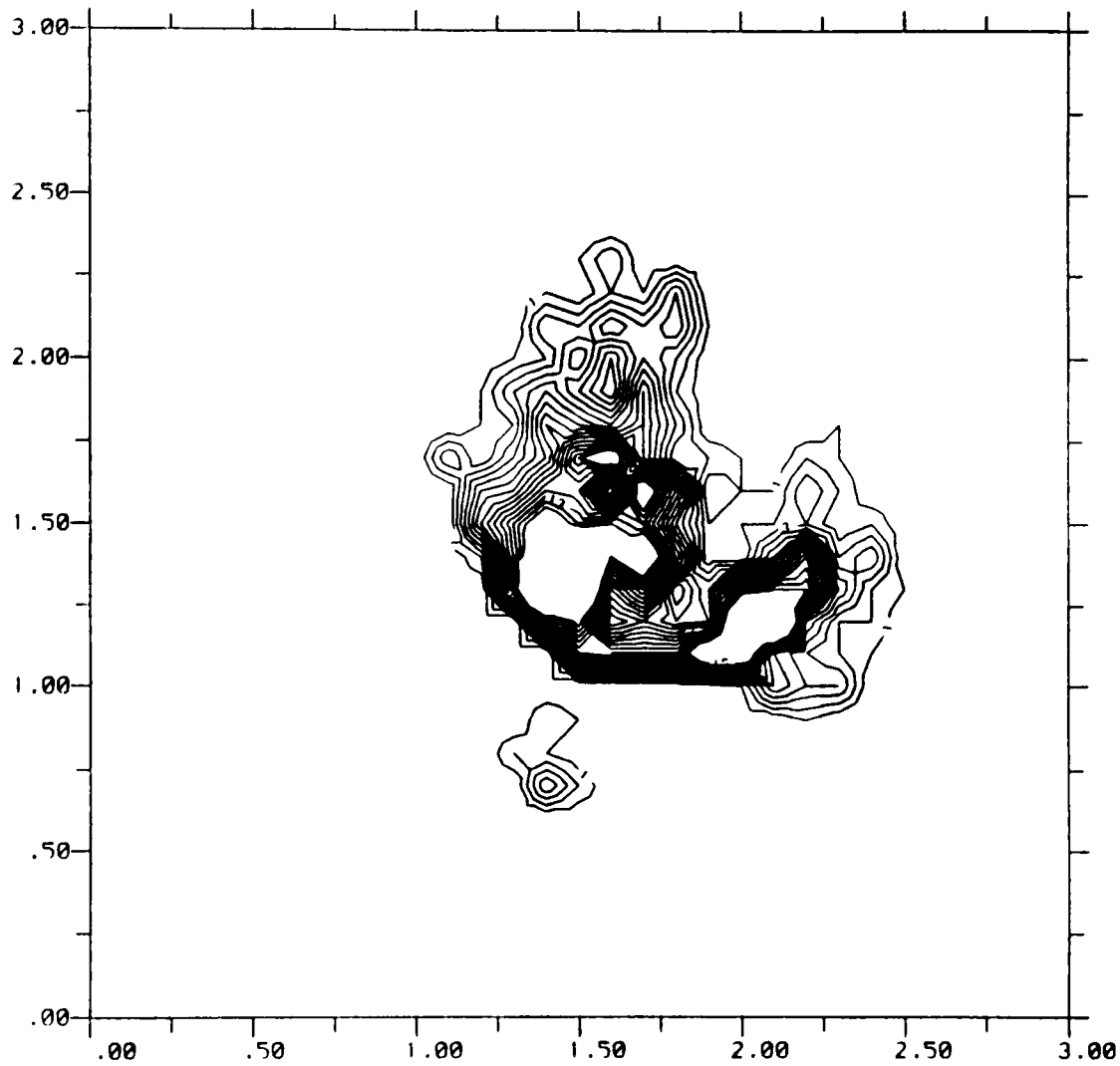
Fig. Correlogram of the spatial autocorrelation function using MORAN's I as correlation coefficient. KALI, 15 min data

6-10b



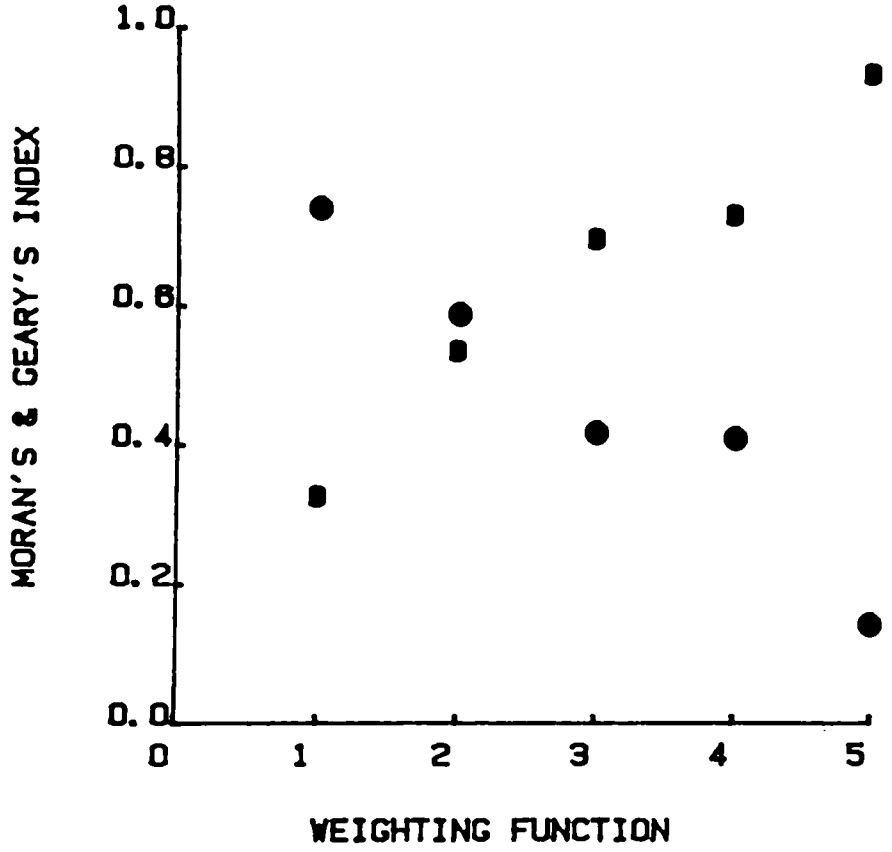
KBOOM FIX FREQ. 15 MIN INT.

6-11a



KBOOM FIX FREQ. 15 MIN INT.

6-11 b



6-12a

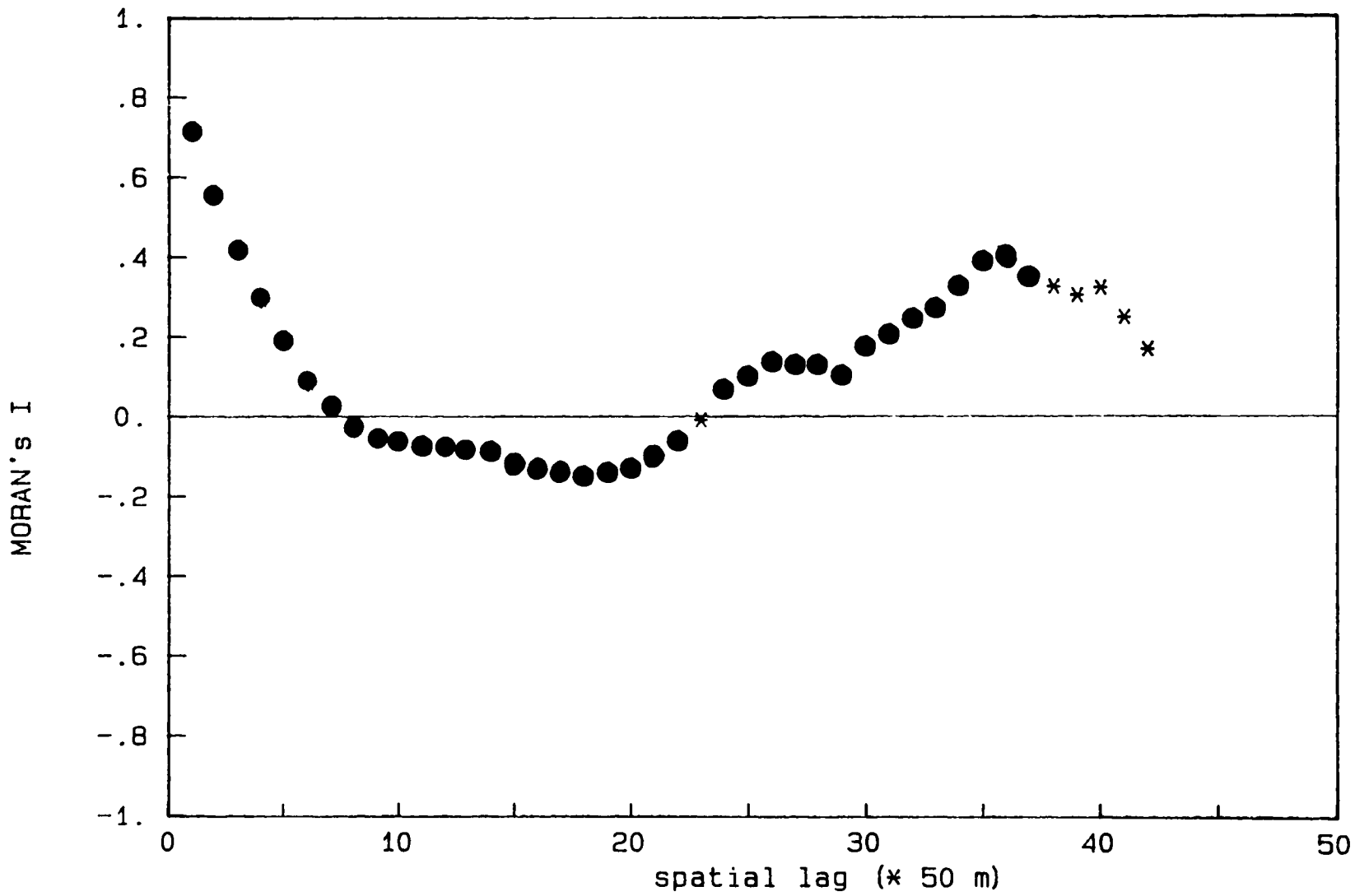
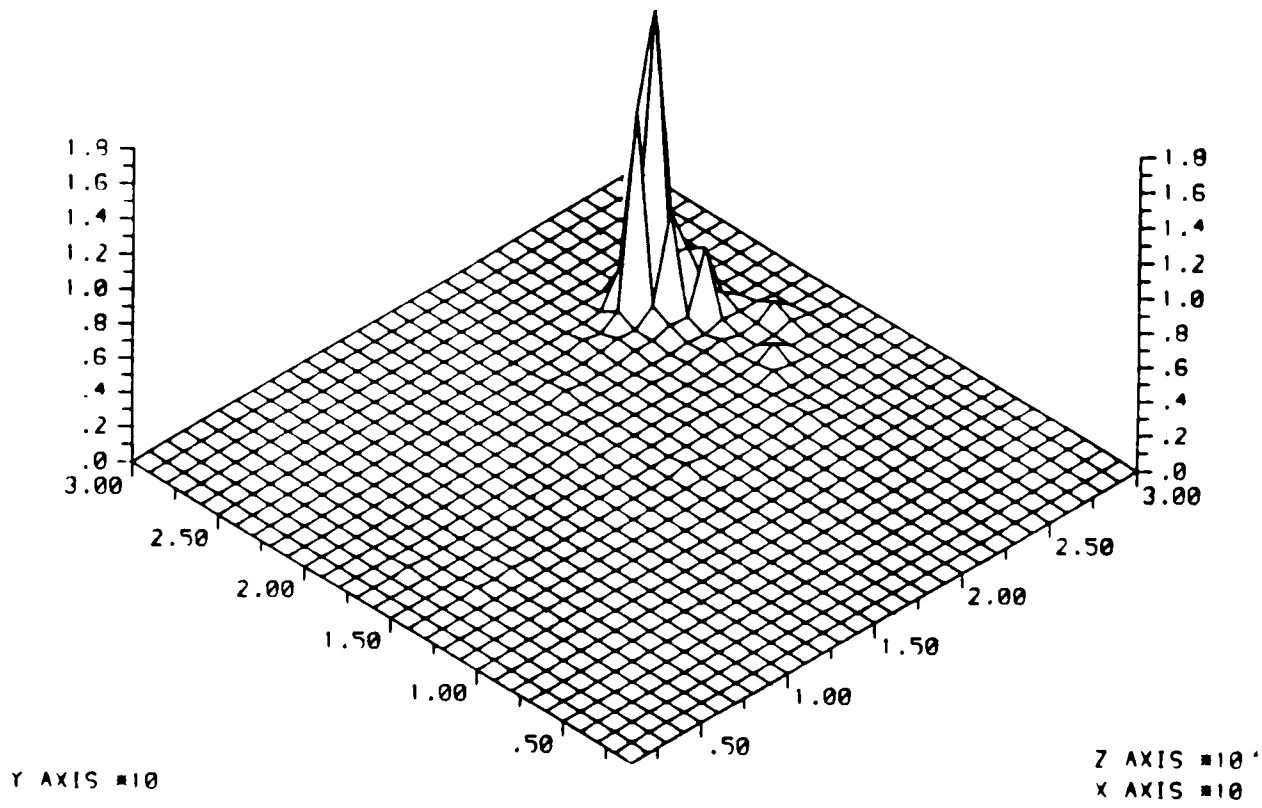


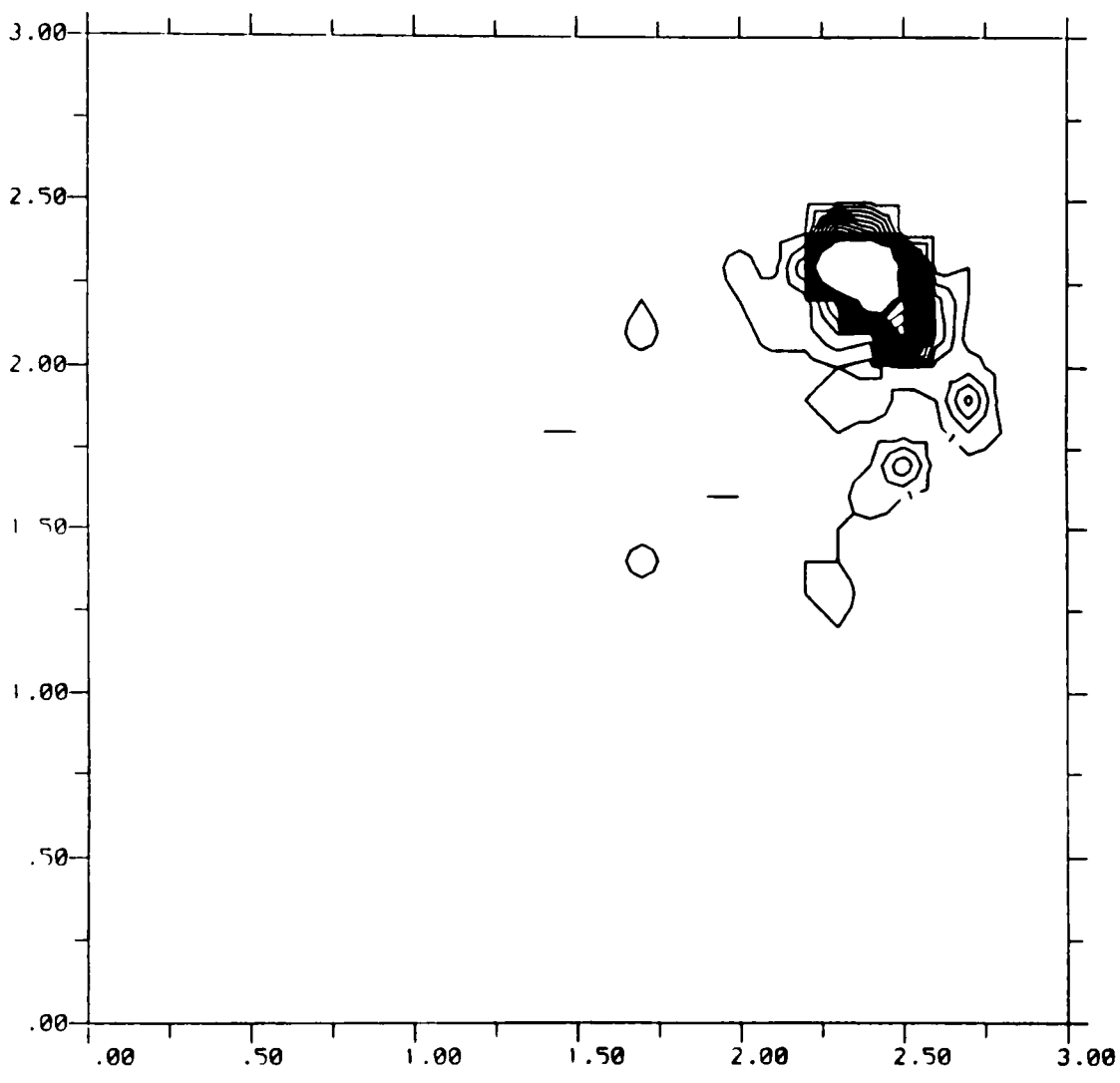
Fig. Correlogram of the spatial autocorrelation function using MORAN's I as correlation coefficient. KBOOM, 15 min data

6-12b



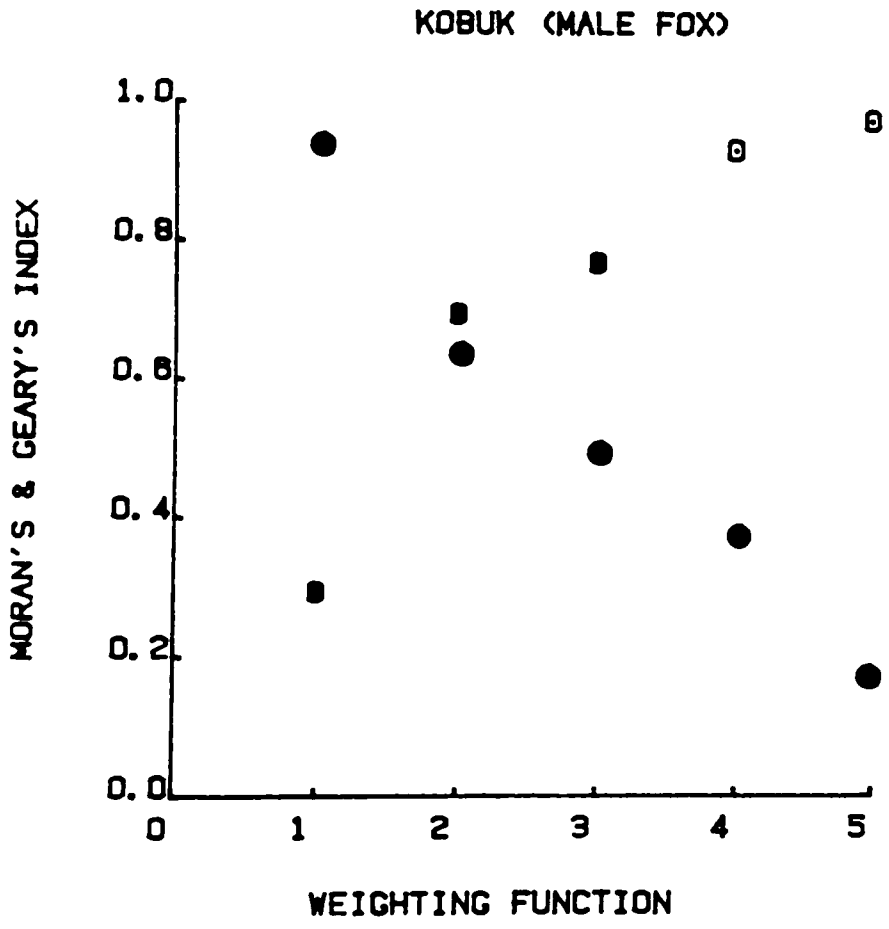
KOBUK FIX FREQ. 15 MIN INT.

6-13a



KOBUK FIX FREQ. 15 MIN INT.

6-13b



6-14a

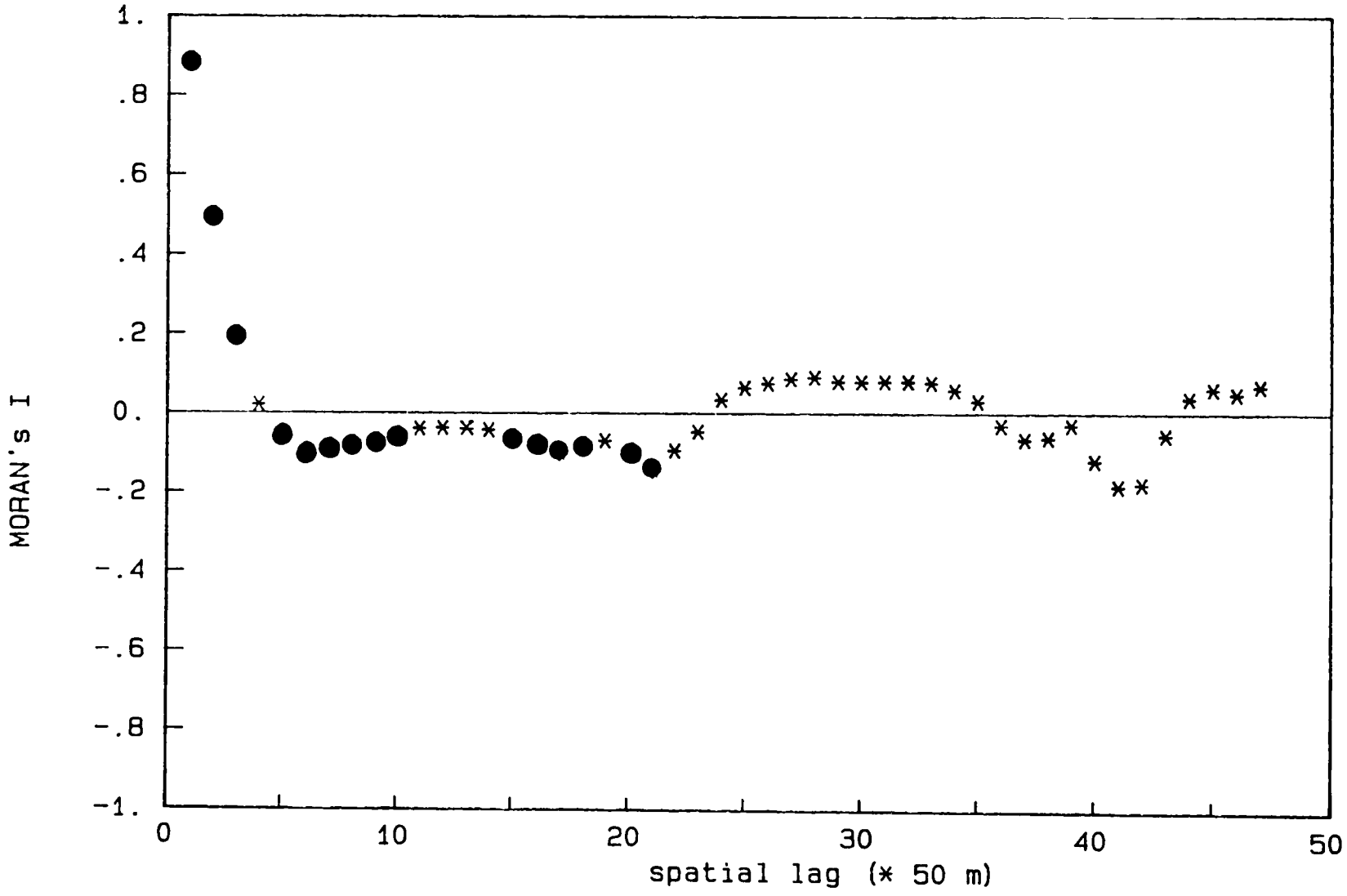
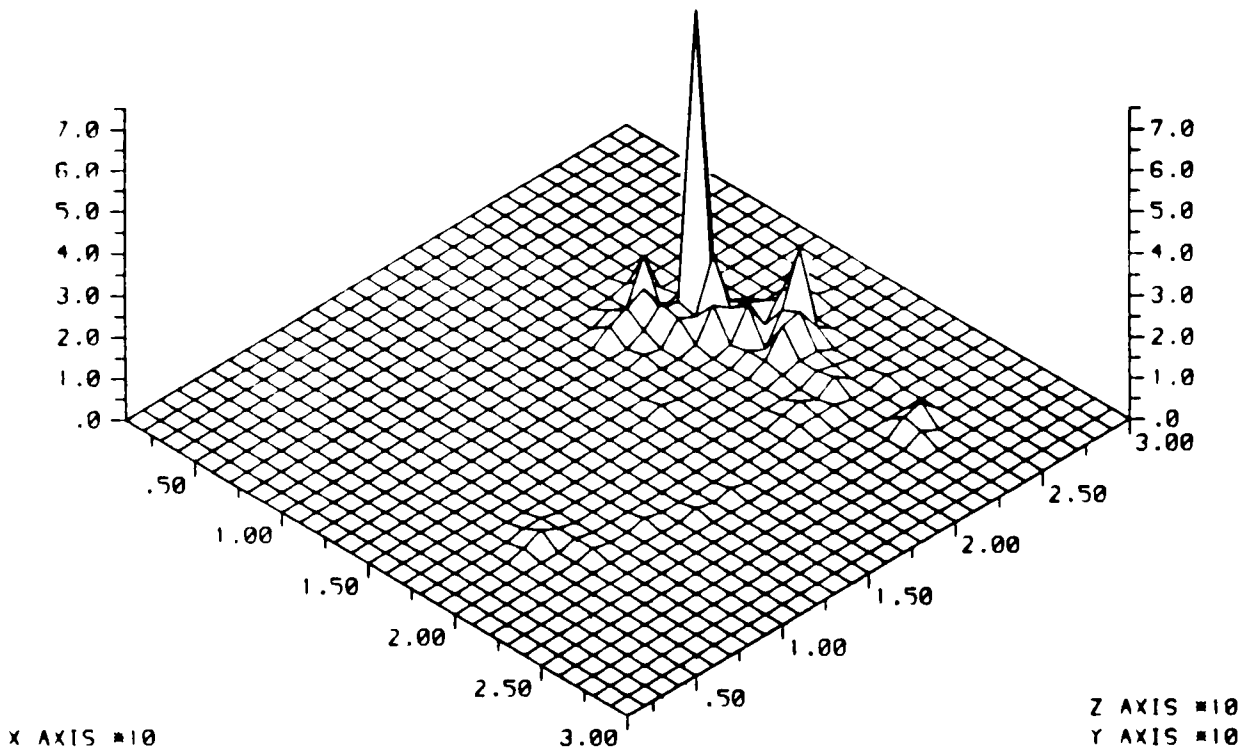


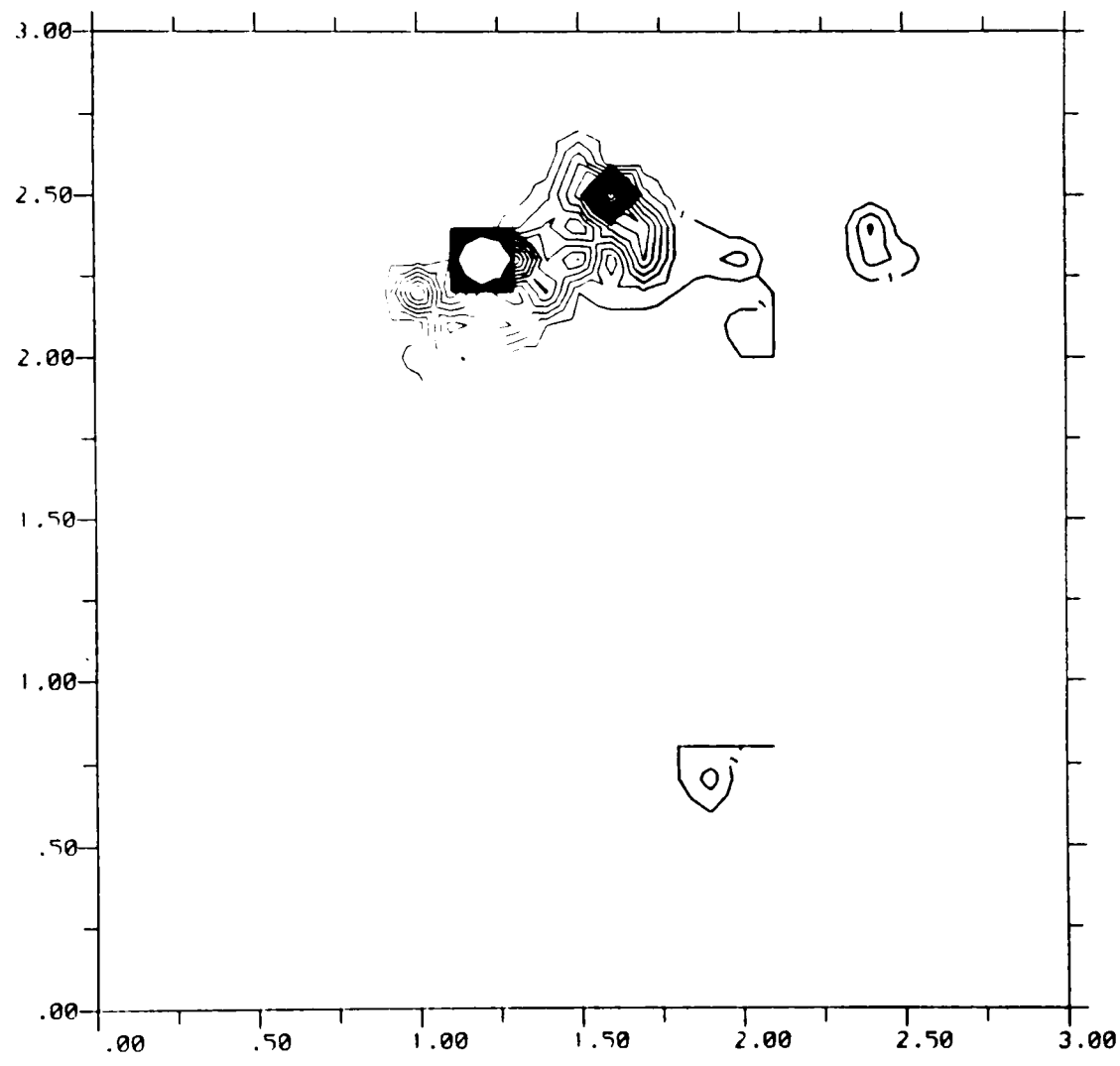
Fig. Correlogram of the spatial autocorrelation function using MORAN's I as correlation coefficient. KOBUK, 15 min data

6-14b



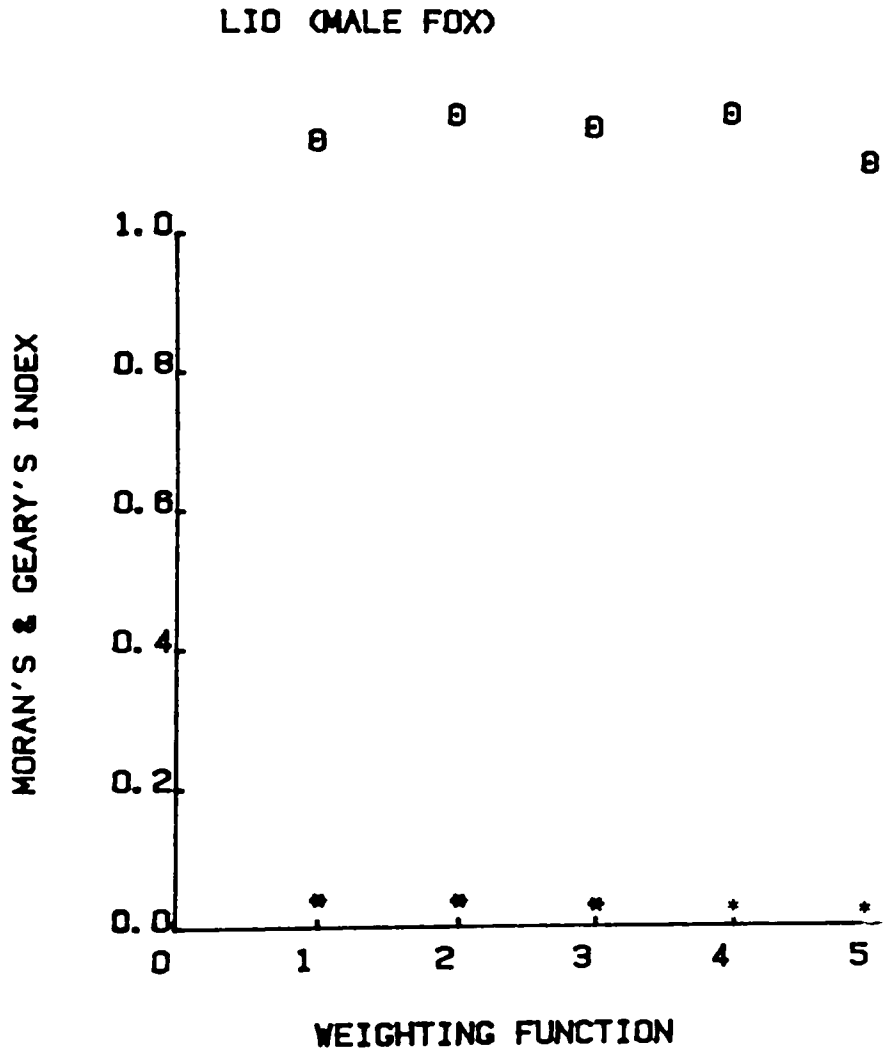
LIO FIX FREQ. 15 MIN INT.

6-15a



LIO FIX FREQ. 15 MIN INT.

6-15b



6-16a

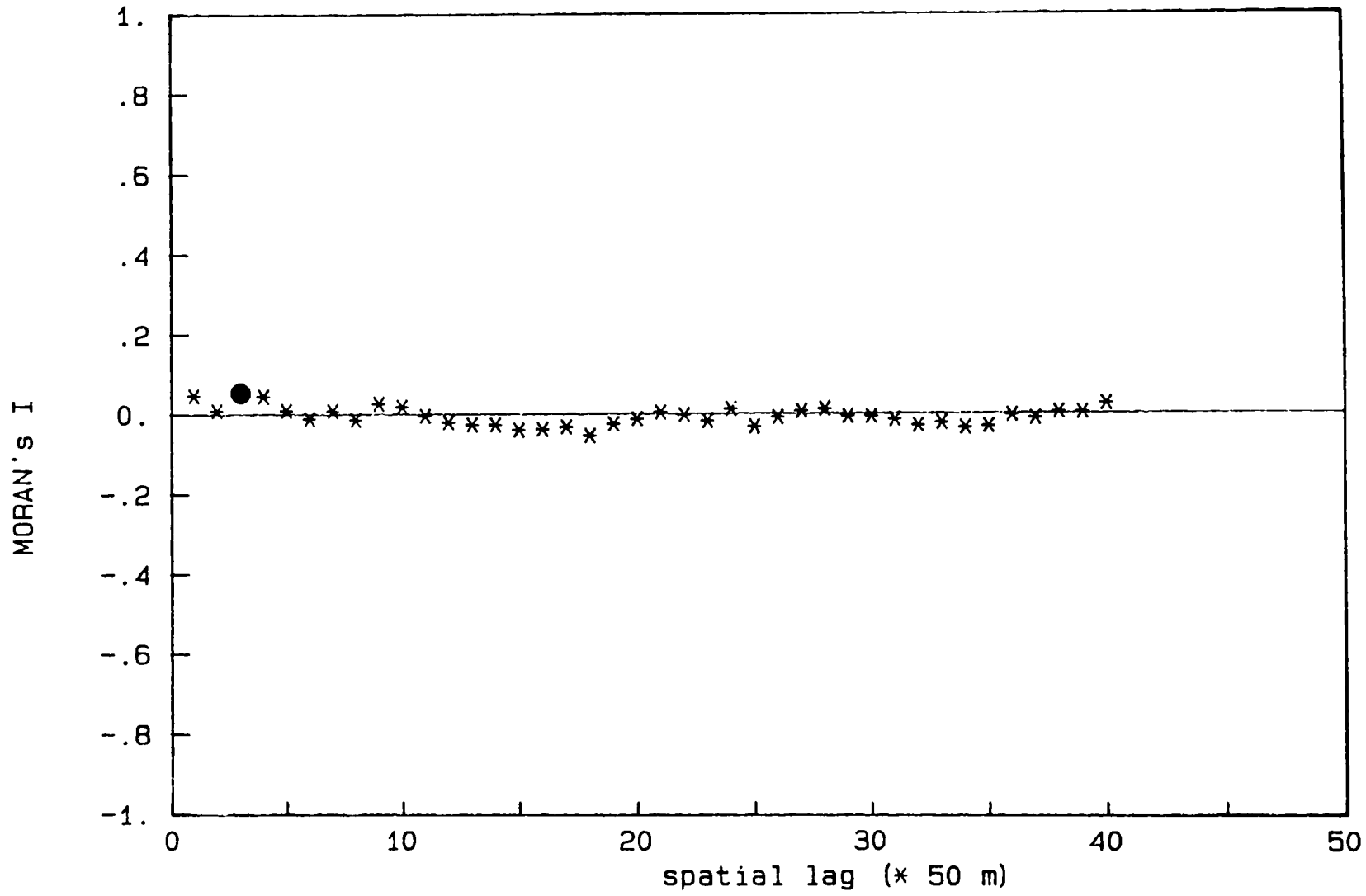
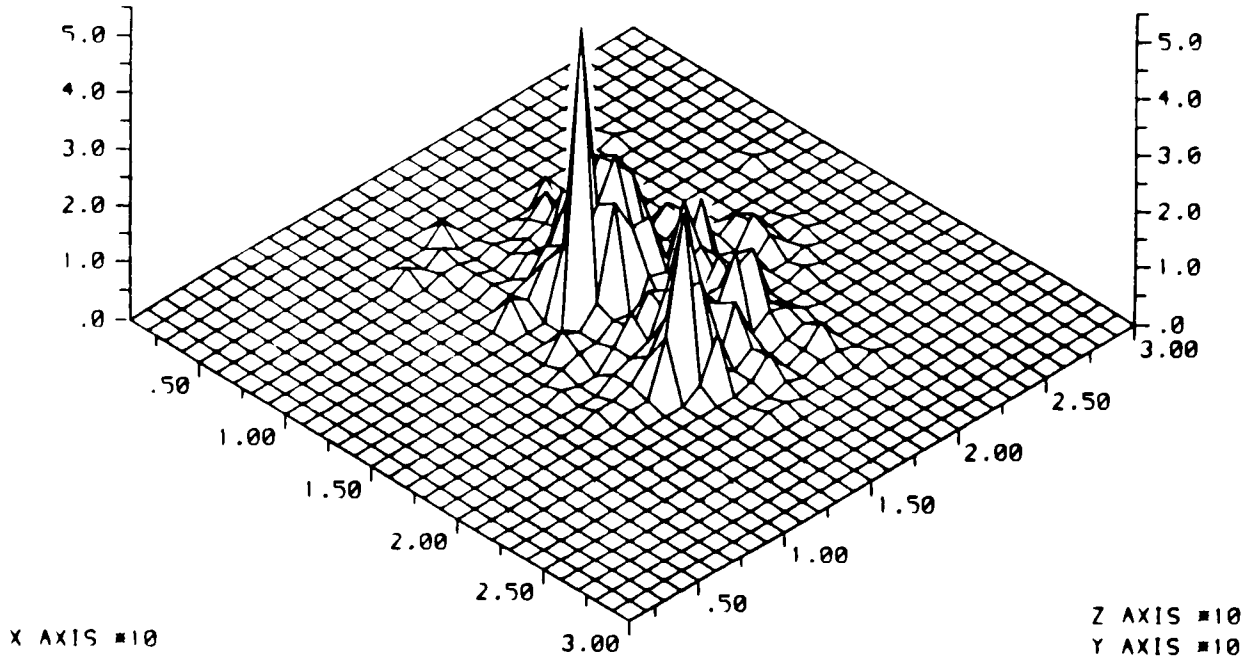


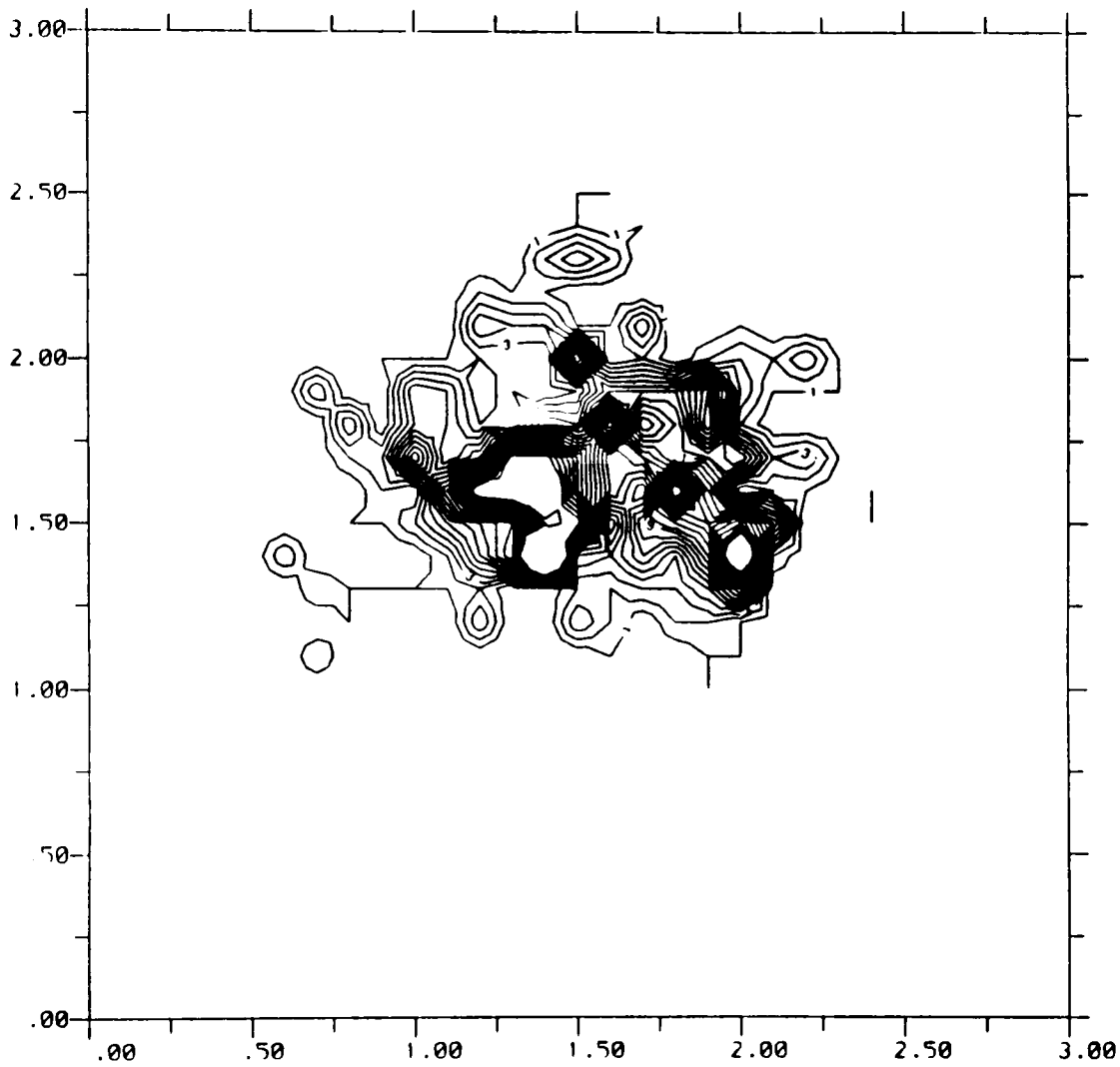
Fig. Correlogram of the spatial autocorrelation function using MORAN's I as correlation coefficient. LIO, 15 min data

6-16b



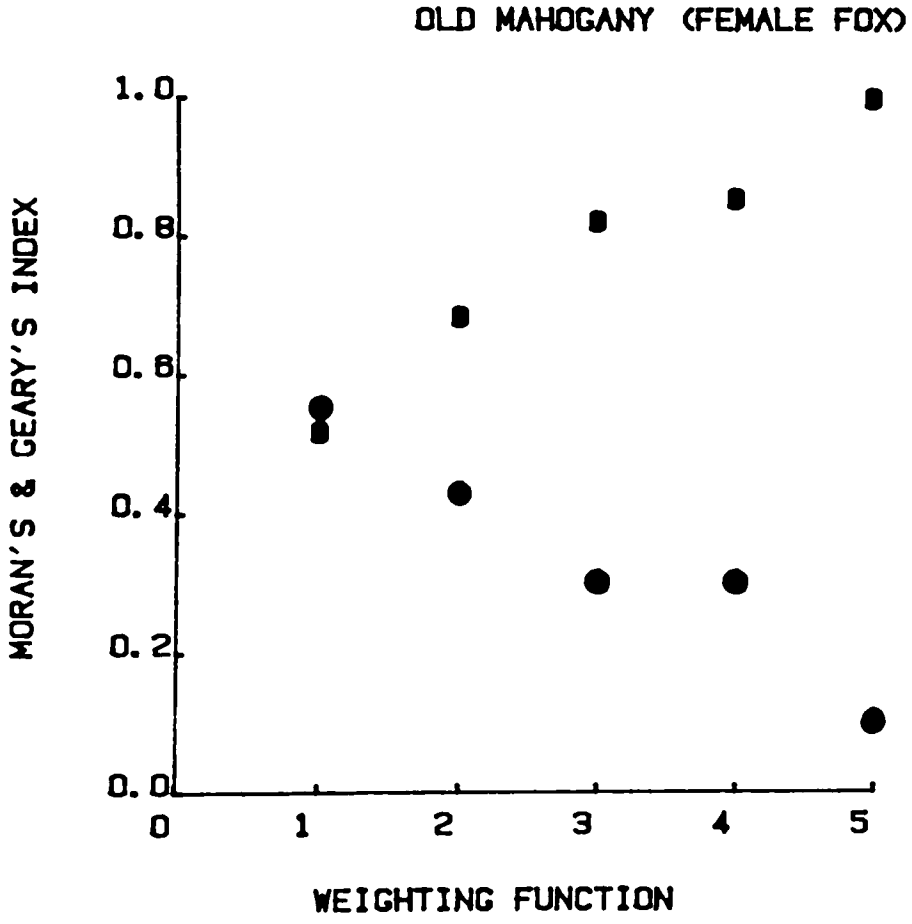
OLD MAHOG FIX FREQ 15 MIN INT

6-17a



OLD MAHOG FIX FREQ 15 MIN INT

6-17b



6-18 a

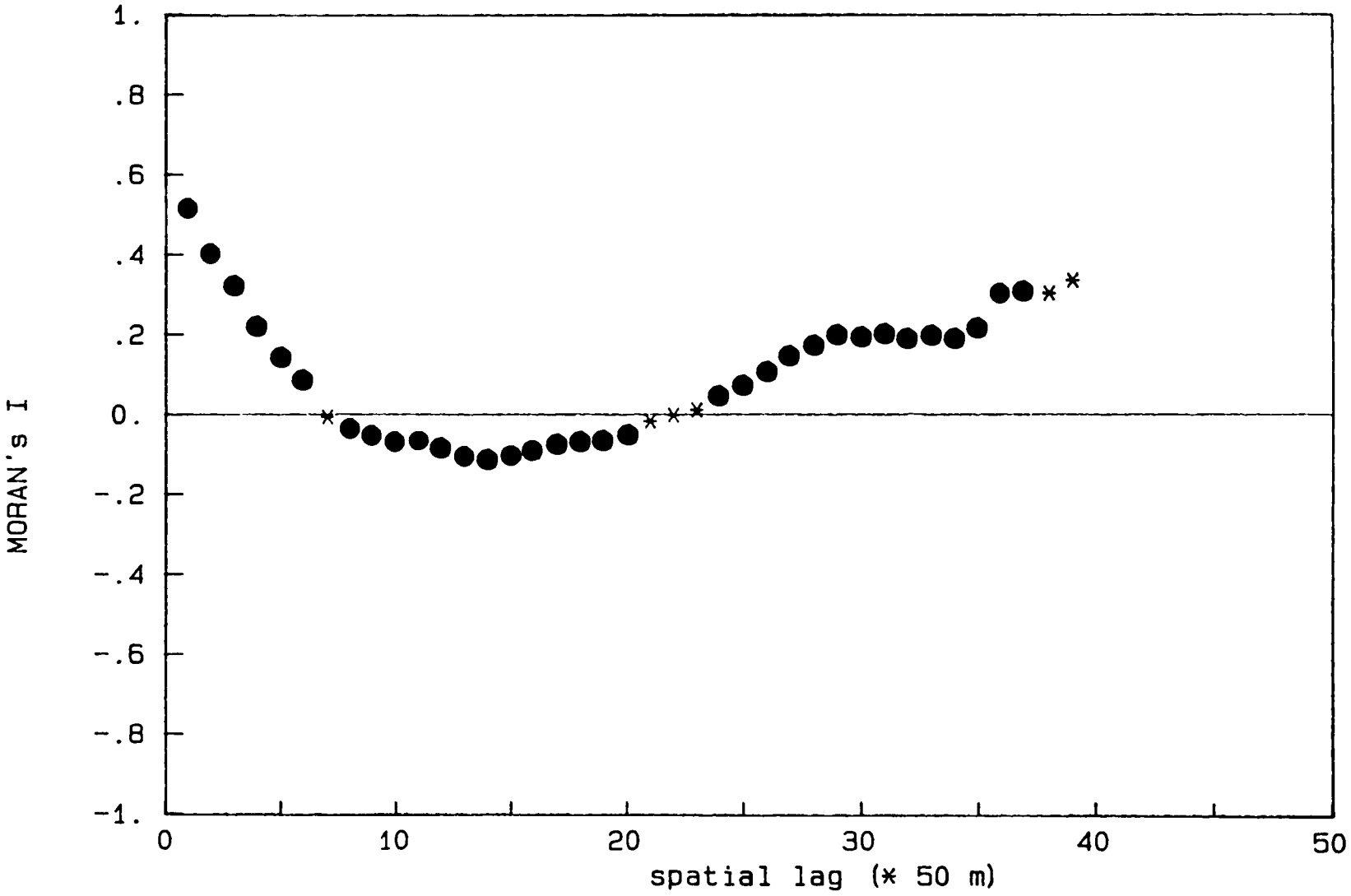
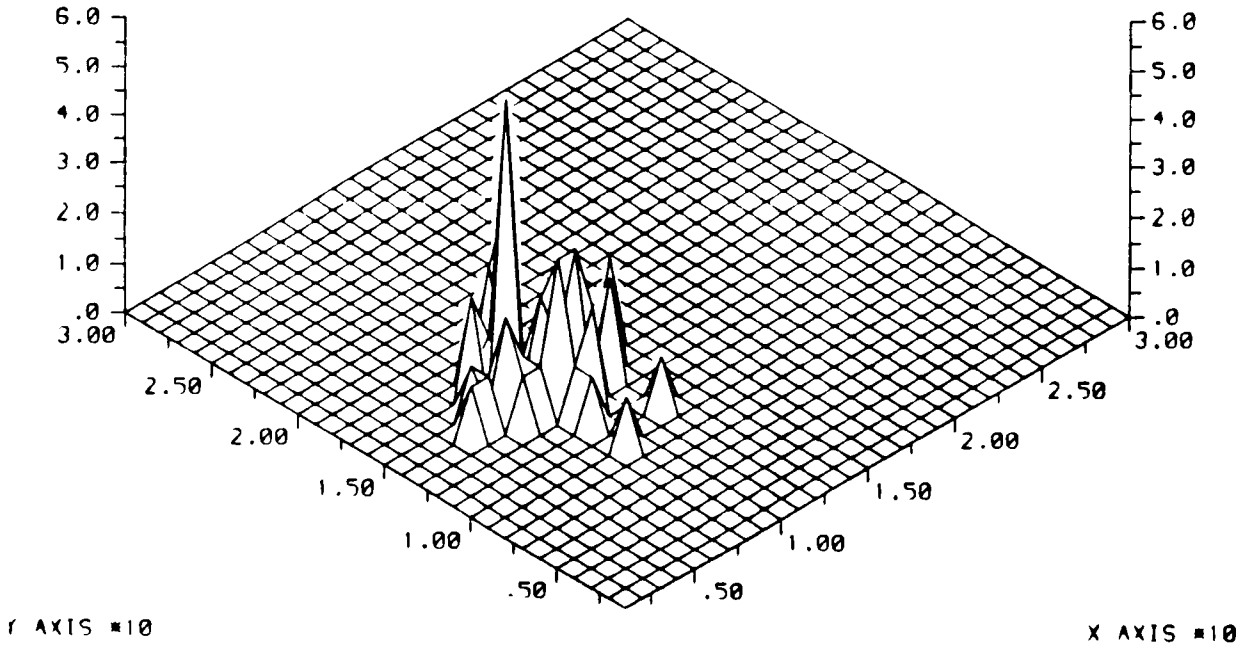


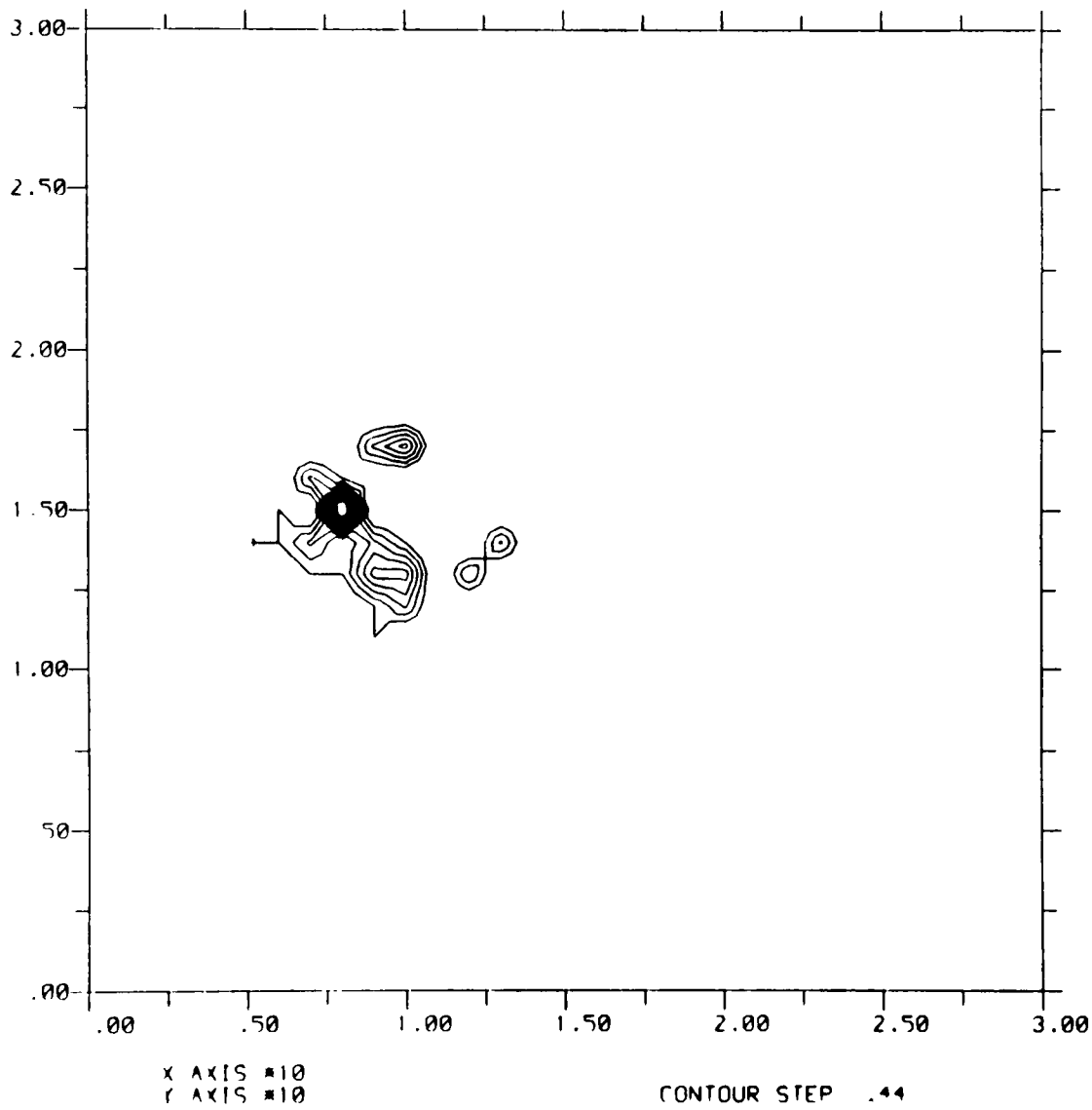
Fig. Correlogram of the spatial autocorrelation function using MORAN's I as correlation coefficient. OLDMAHOGANY, 15 min data

6-18b



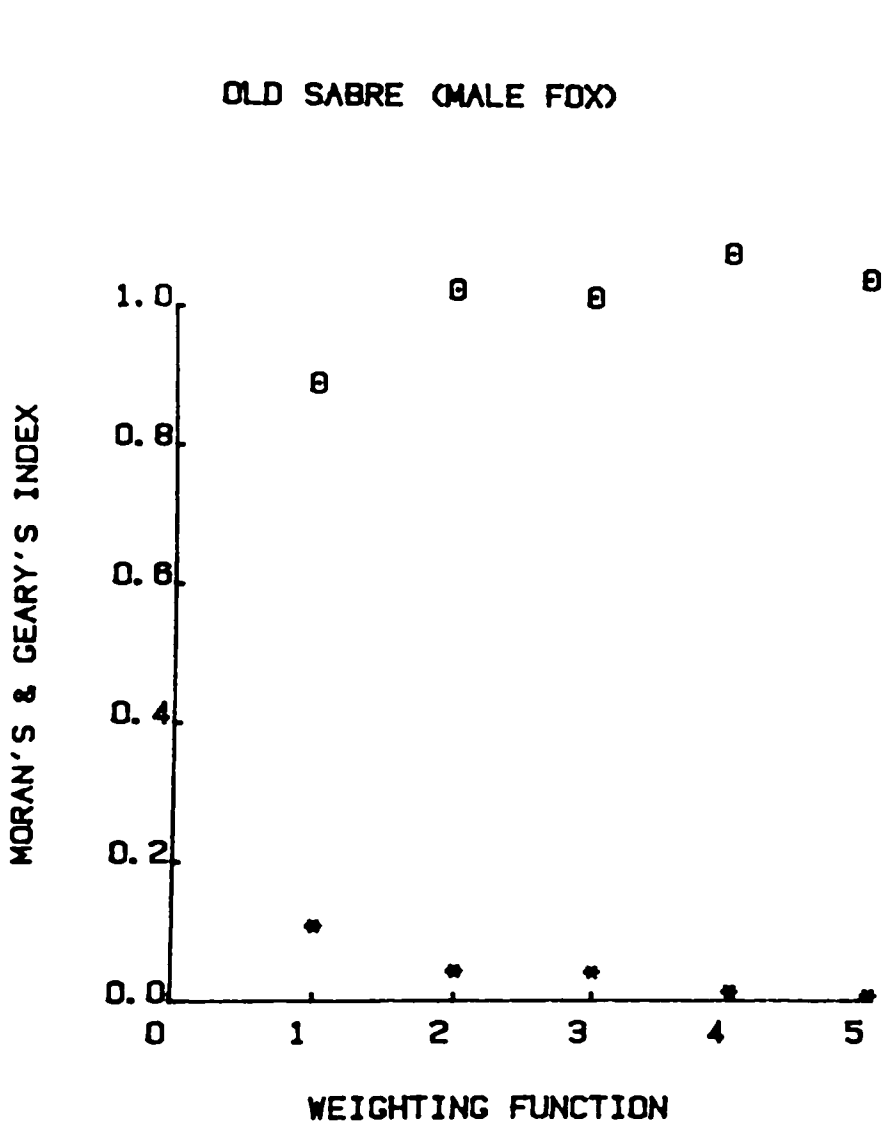
OLD SABRE FIX FREQ 15 MIN INT.

6-19a



OLD SABRE FIX FREQ 15 MIN INT.

6-19b



6-20a

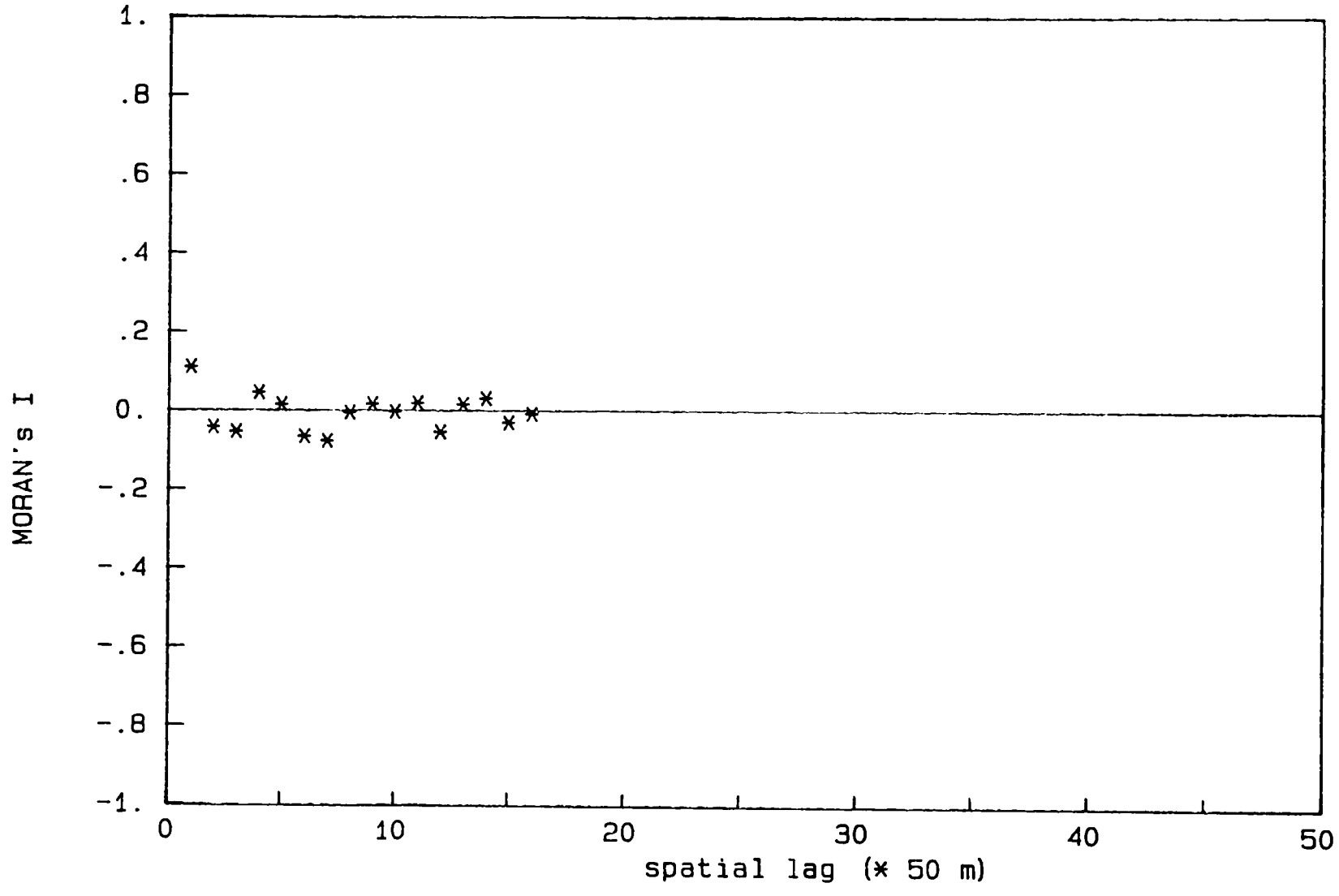
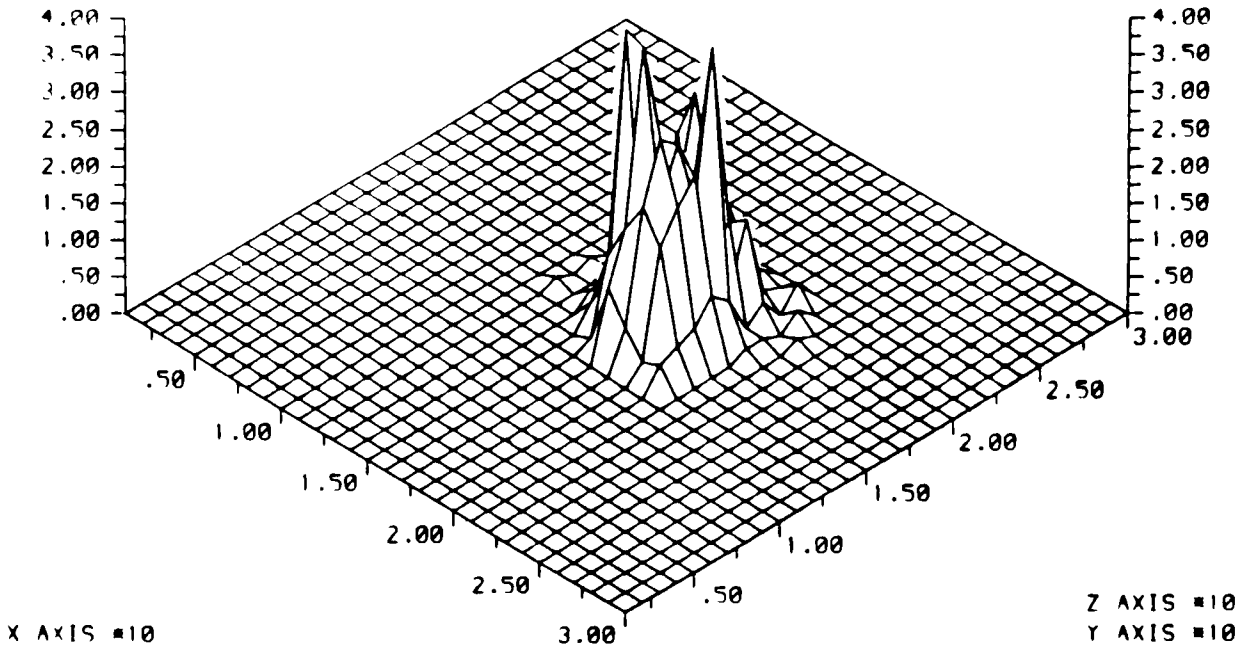


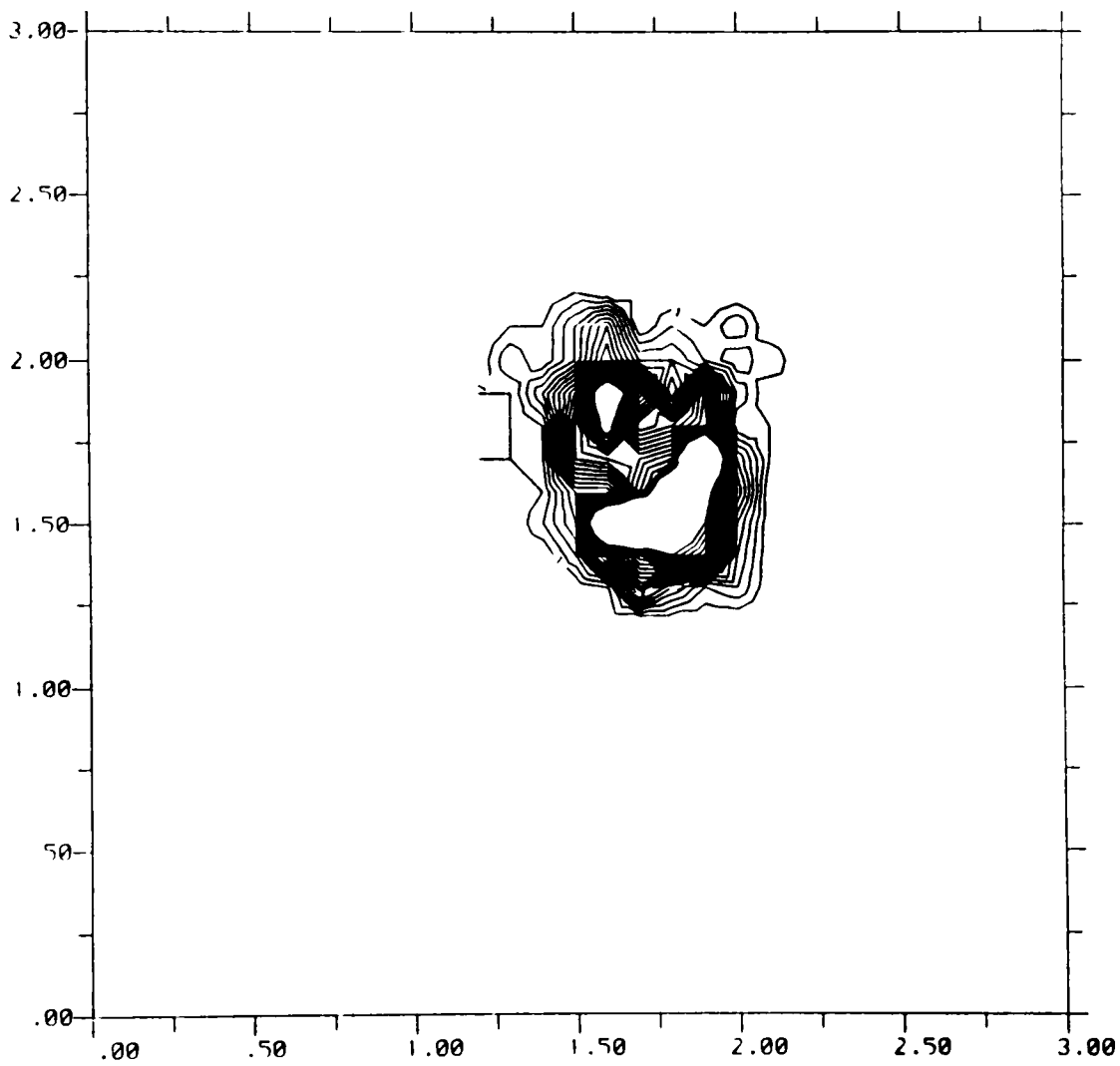
Fig. Correlogram of the spatial autocorrelation function using MORAN's I as correlation coefficient. OLDSABRE, 15 min data

6-20b



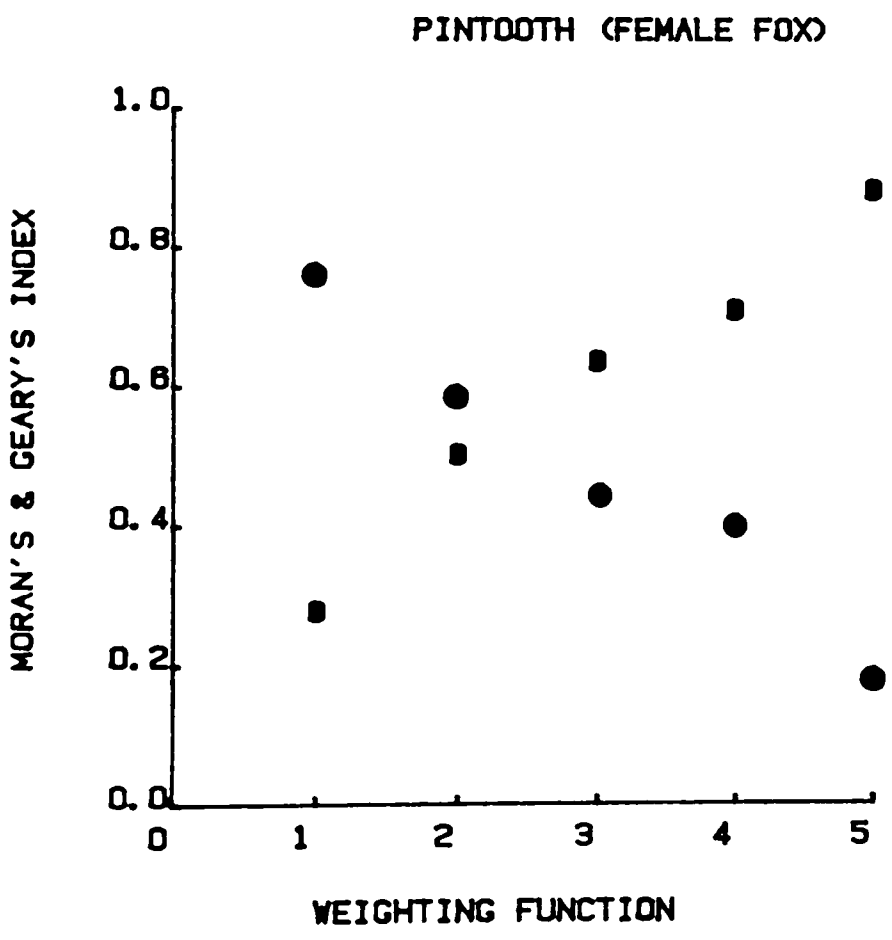
PINTOOTH FIX FREQ IS MIN INT.

6-21a



PINTOOTH FIX FREQ IS MIN INT.

6-21b.



6-22a

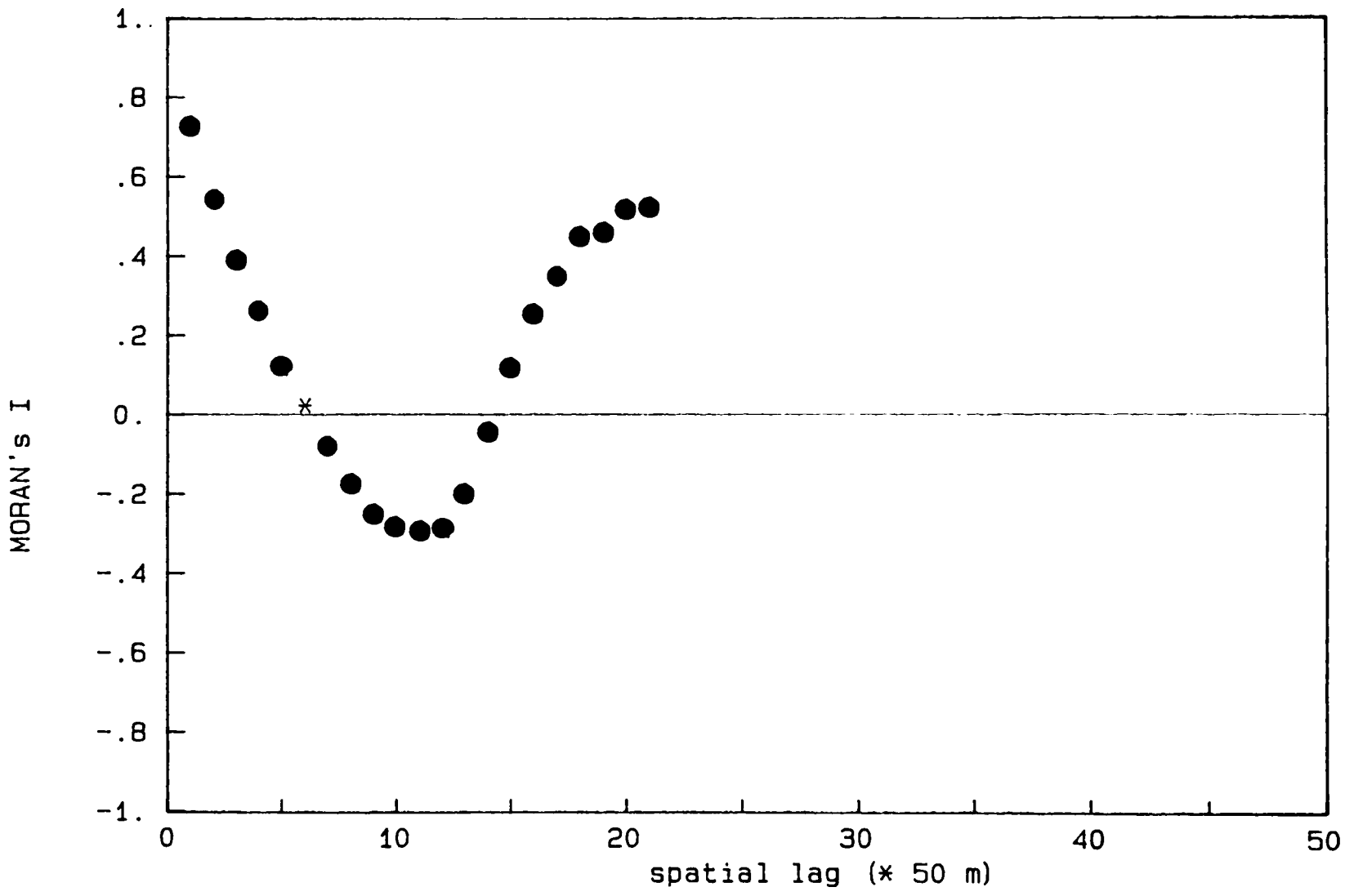
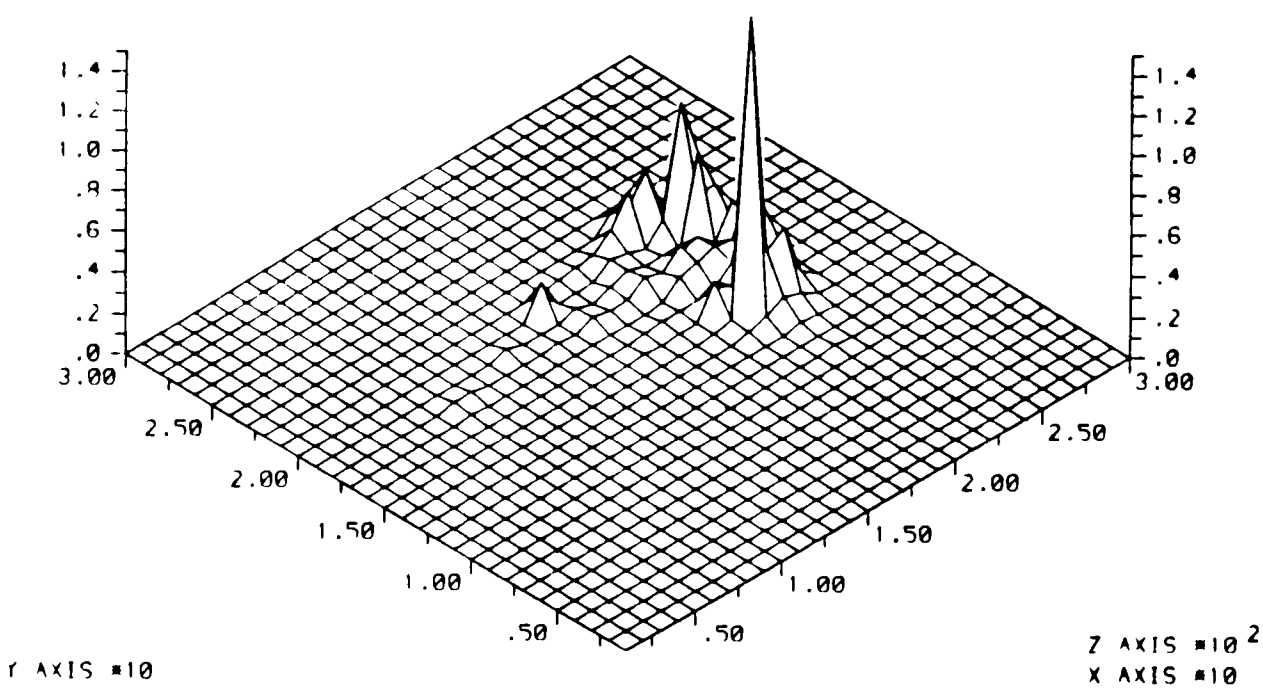


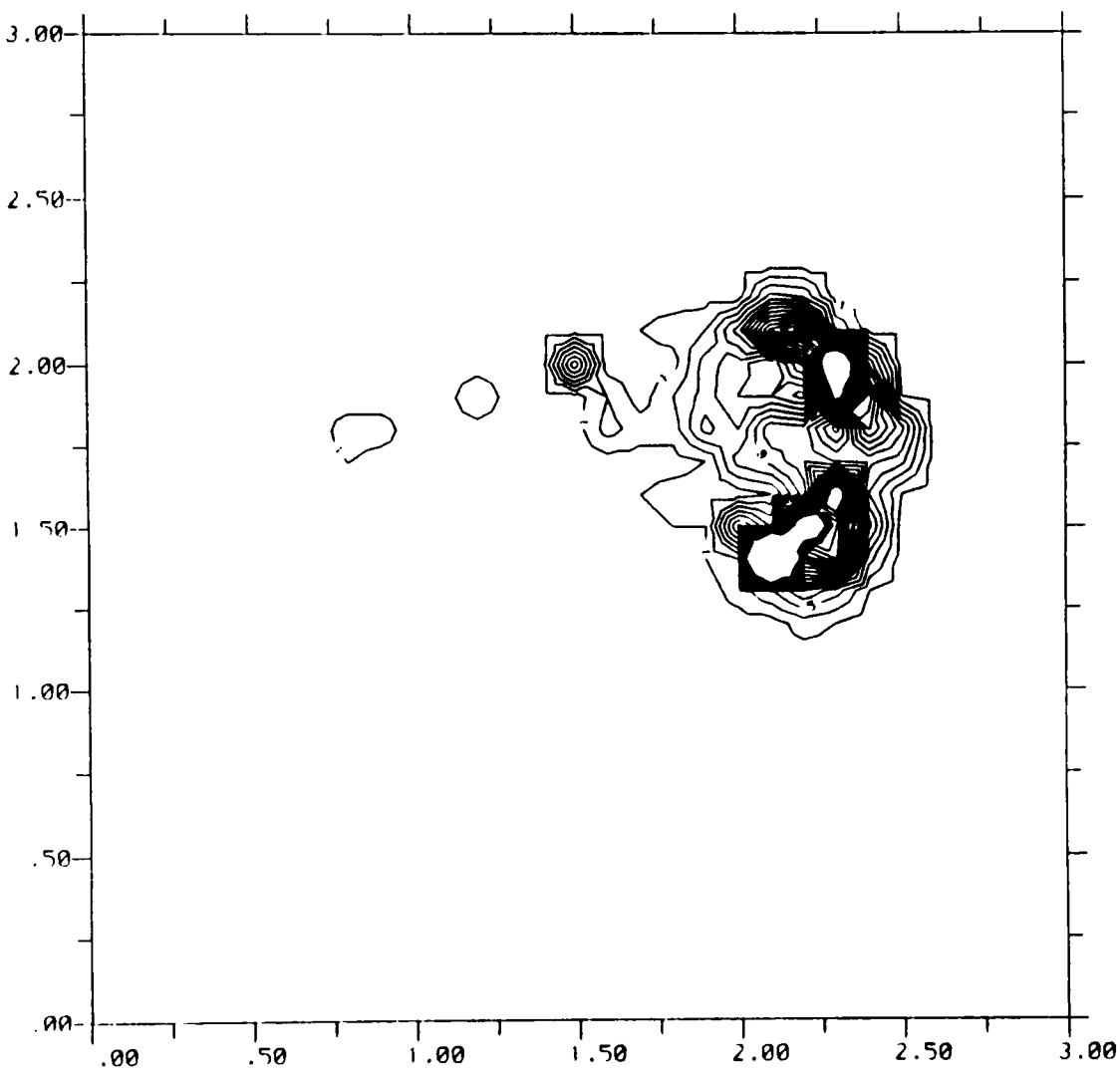
Fig. Correlogram of the spatial autocorrelation function using MORAN's I as correlation coefficient. PINTOOTH, 15 min data

6-22b



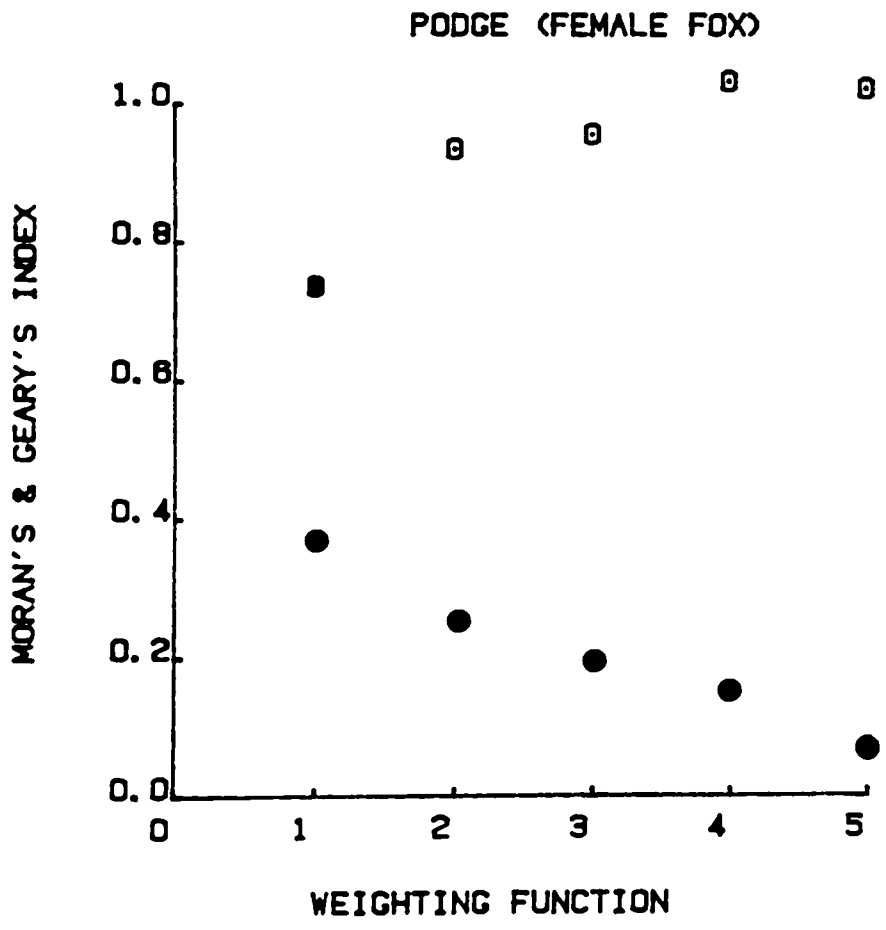
PODGE FIX FREQ 15 MIN INT

6-23a



PODGE FIX FREQ 15 MIN INT

6-23b.



6-24a

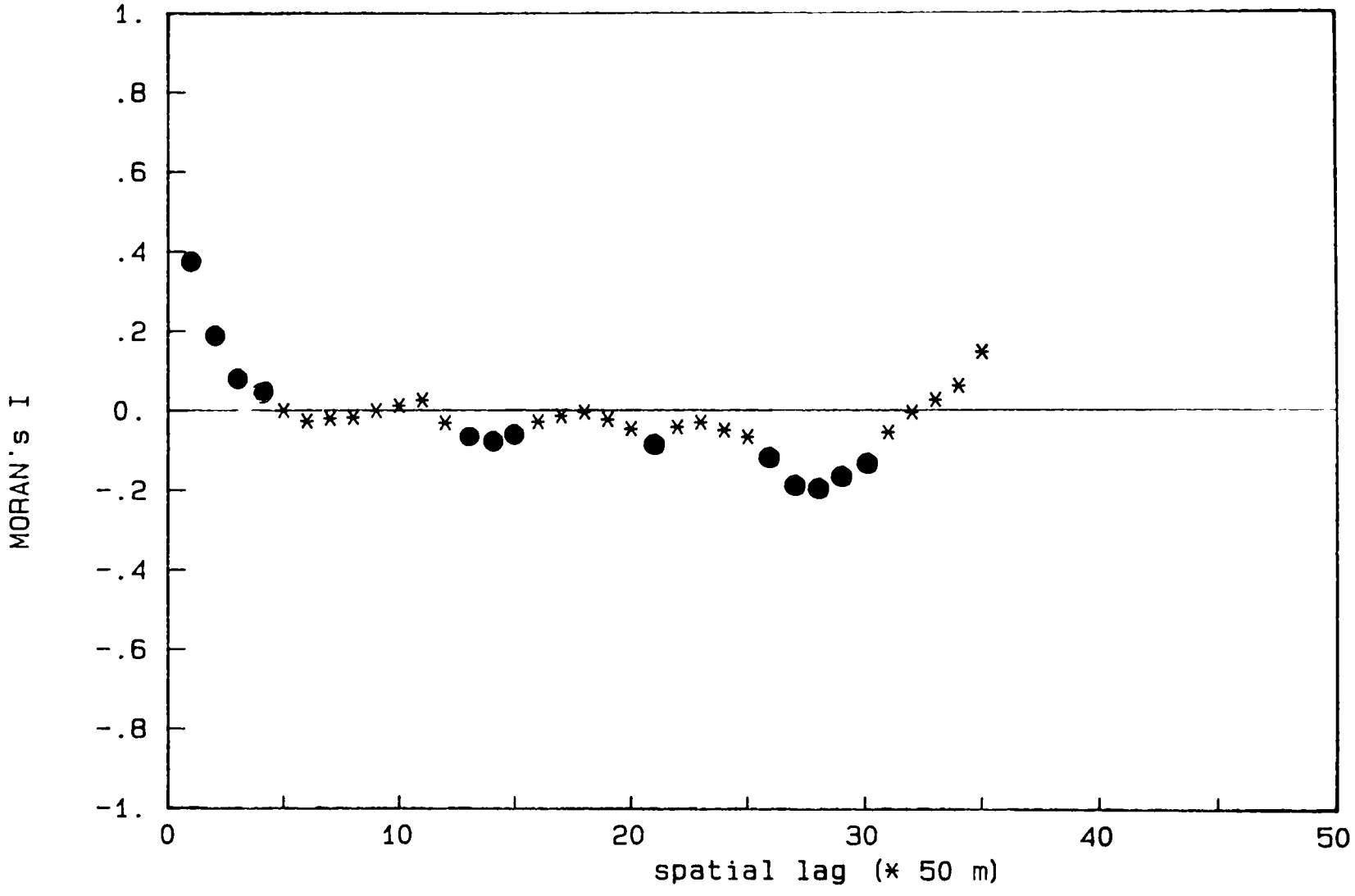
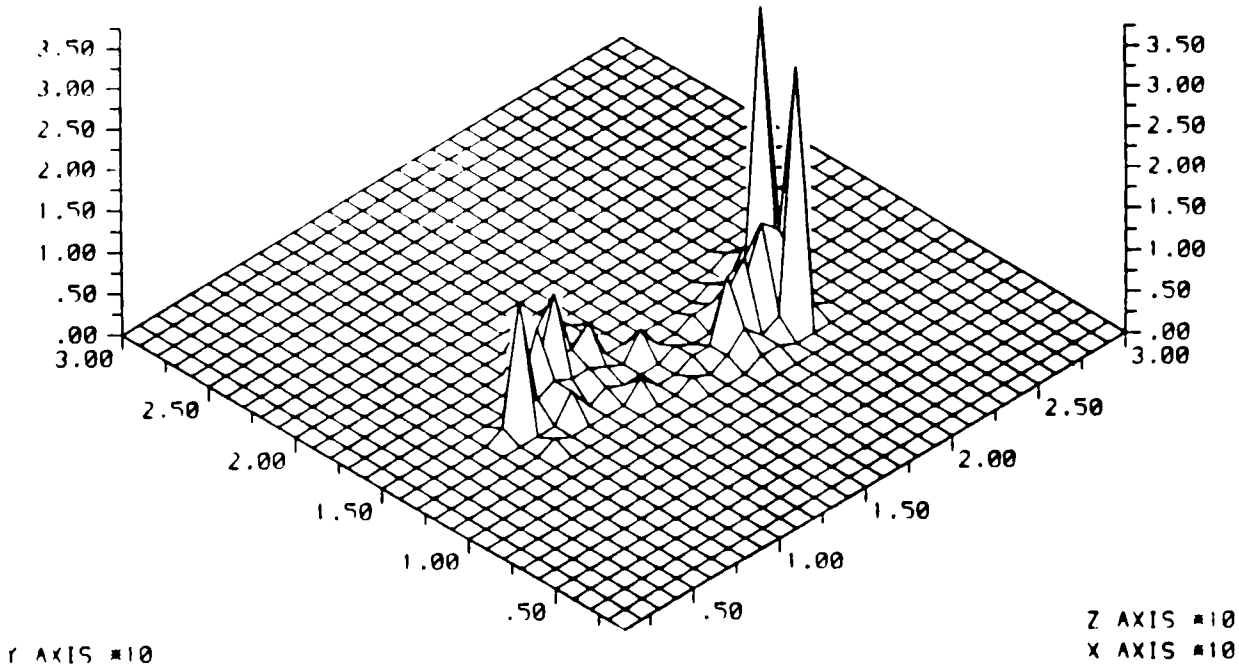


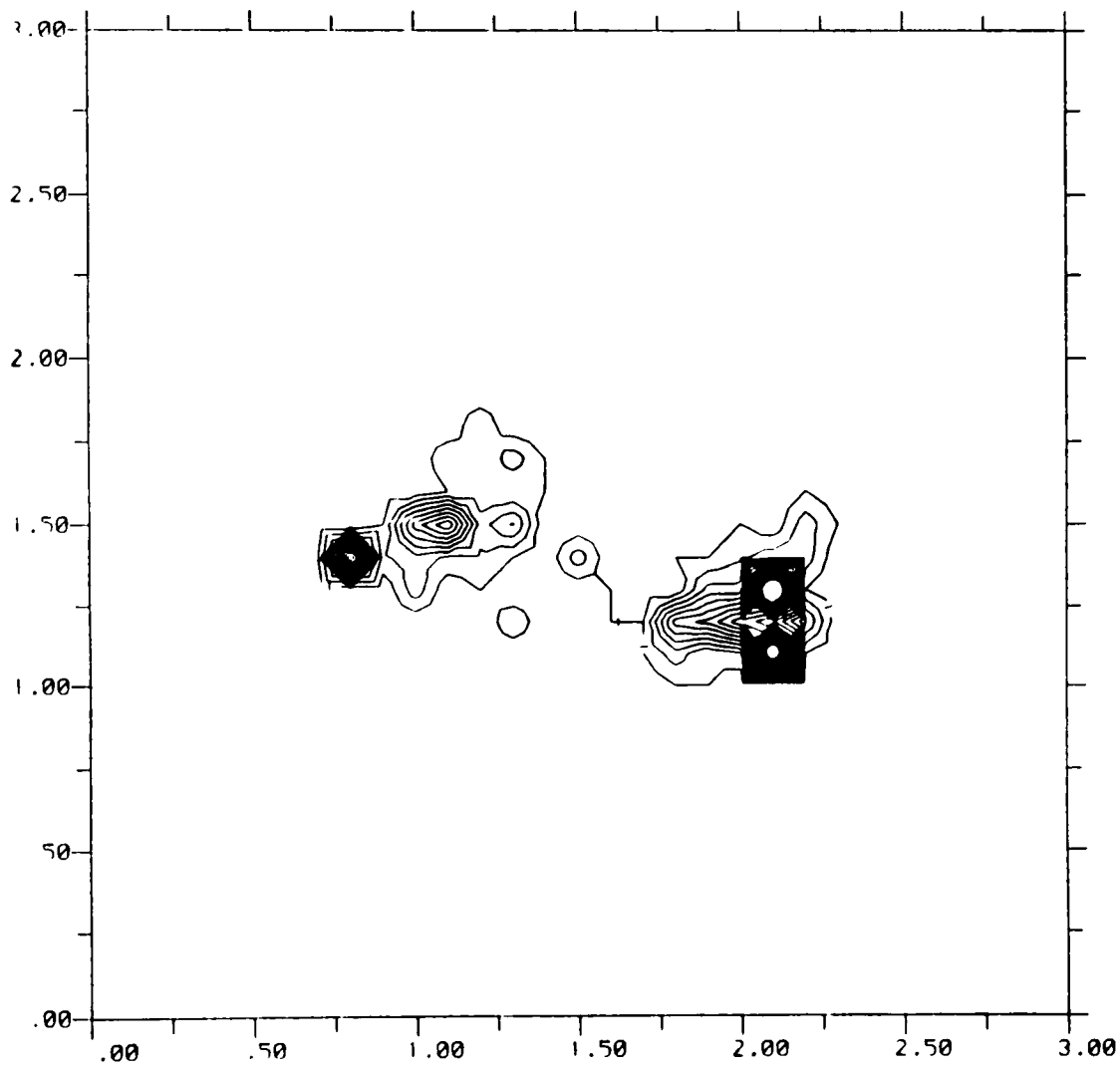
Fig. Correlogram of the spatial autocorrelation function using MORAN's I as correlation coefficient. PODGE, 15 min data

6-24b



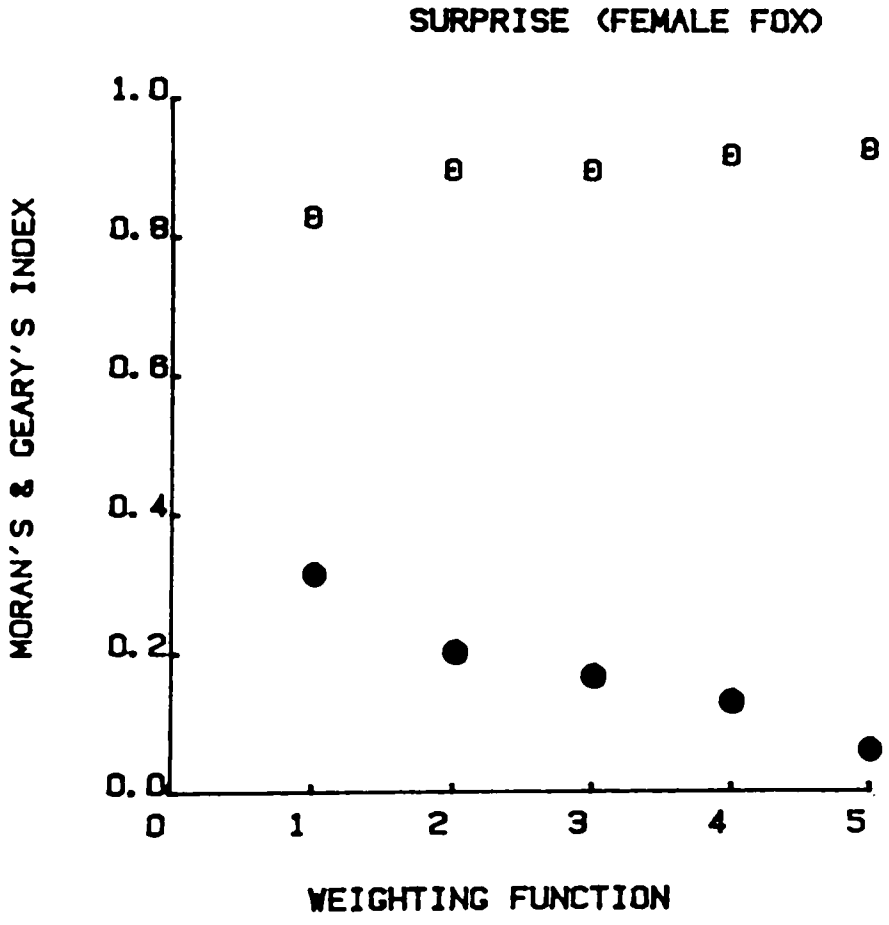
SURPRISE FIX FREQ 15 MIN INT

6-25a



SURPRISE FIX FREQ 15 MIN INT

6-25b



6-26a

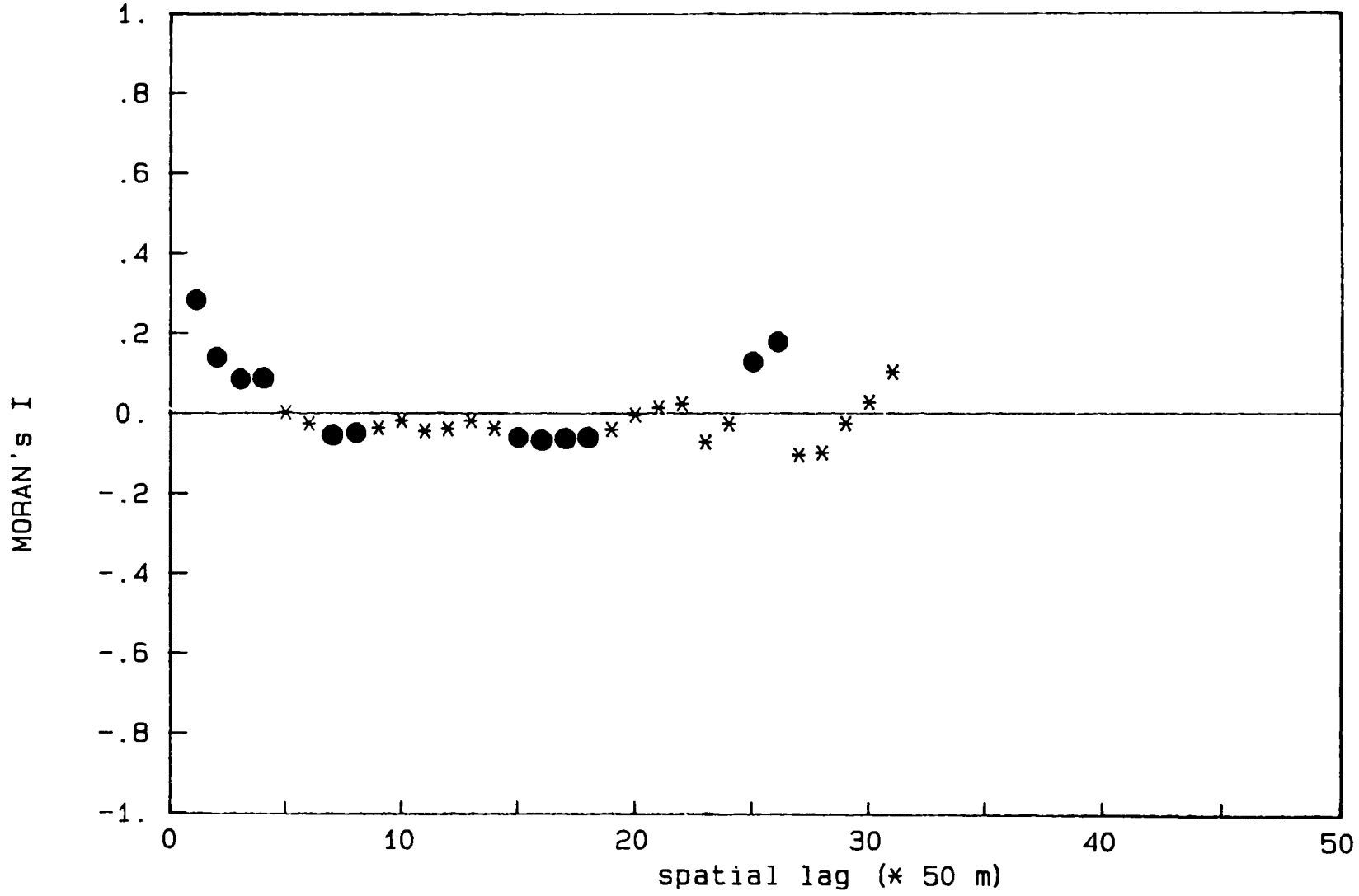
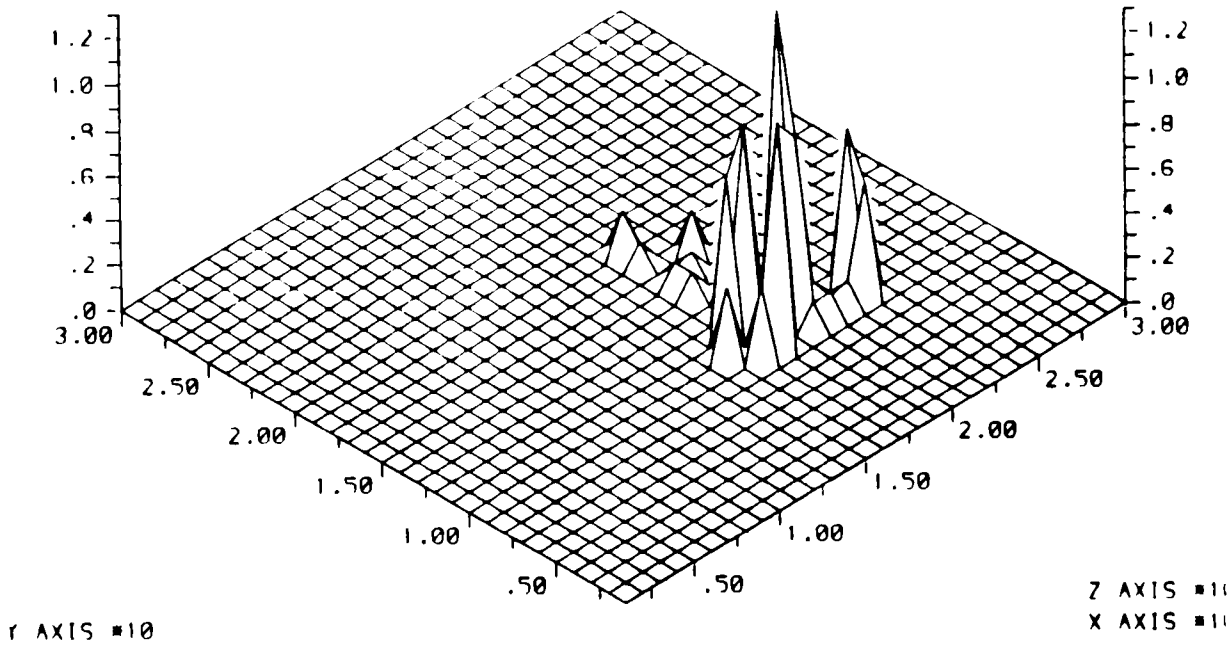


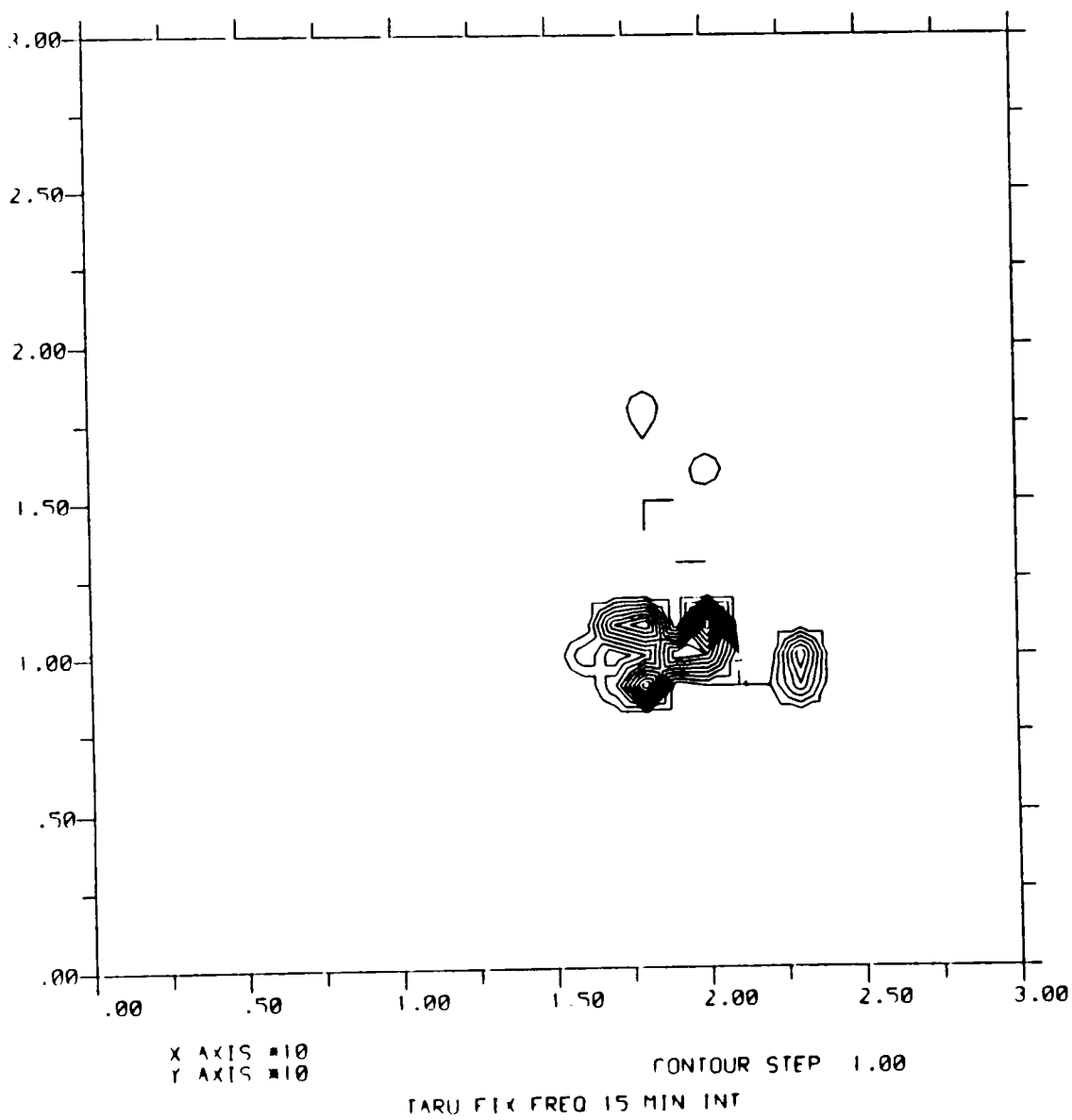
Fig. Correlogram of the spatial autocorrelation function using MORAN's I as correlation coefficient. SURPRISE, 15 min data

6-26b



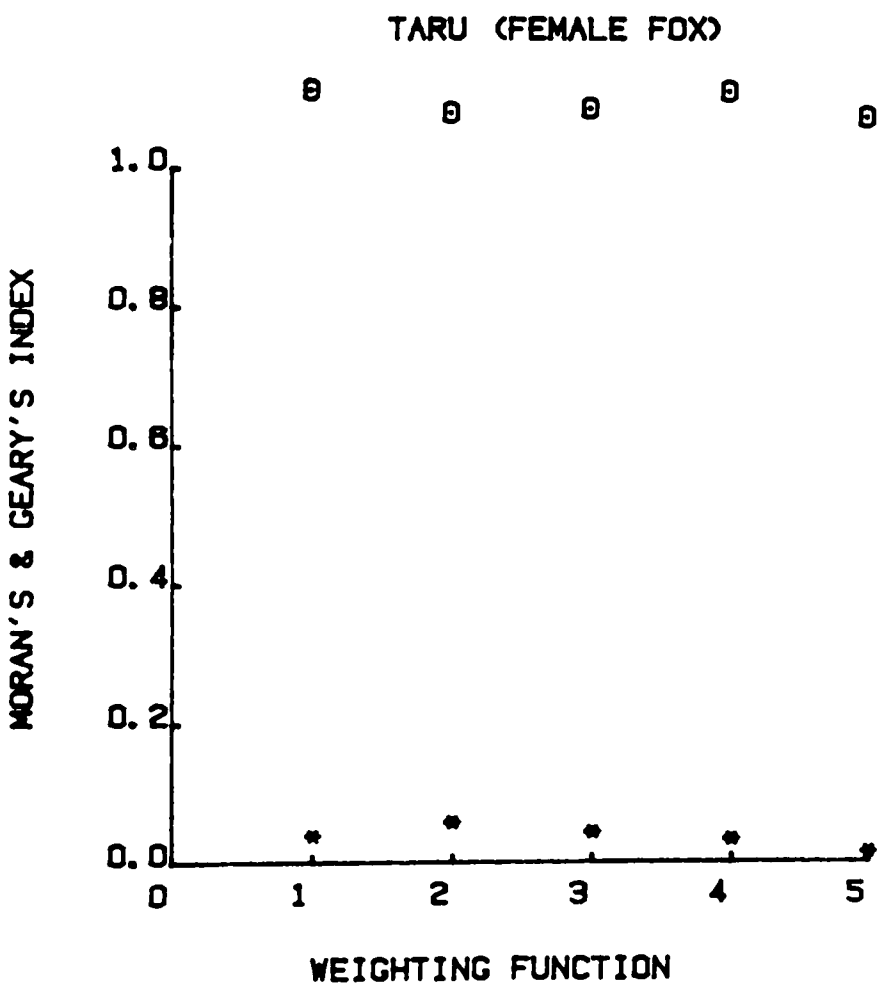
TARU FIX FREQ 15 MIN INT

6-27a



TARU FIX FREQ 15 MIN INT

6-27b



6-28a

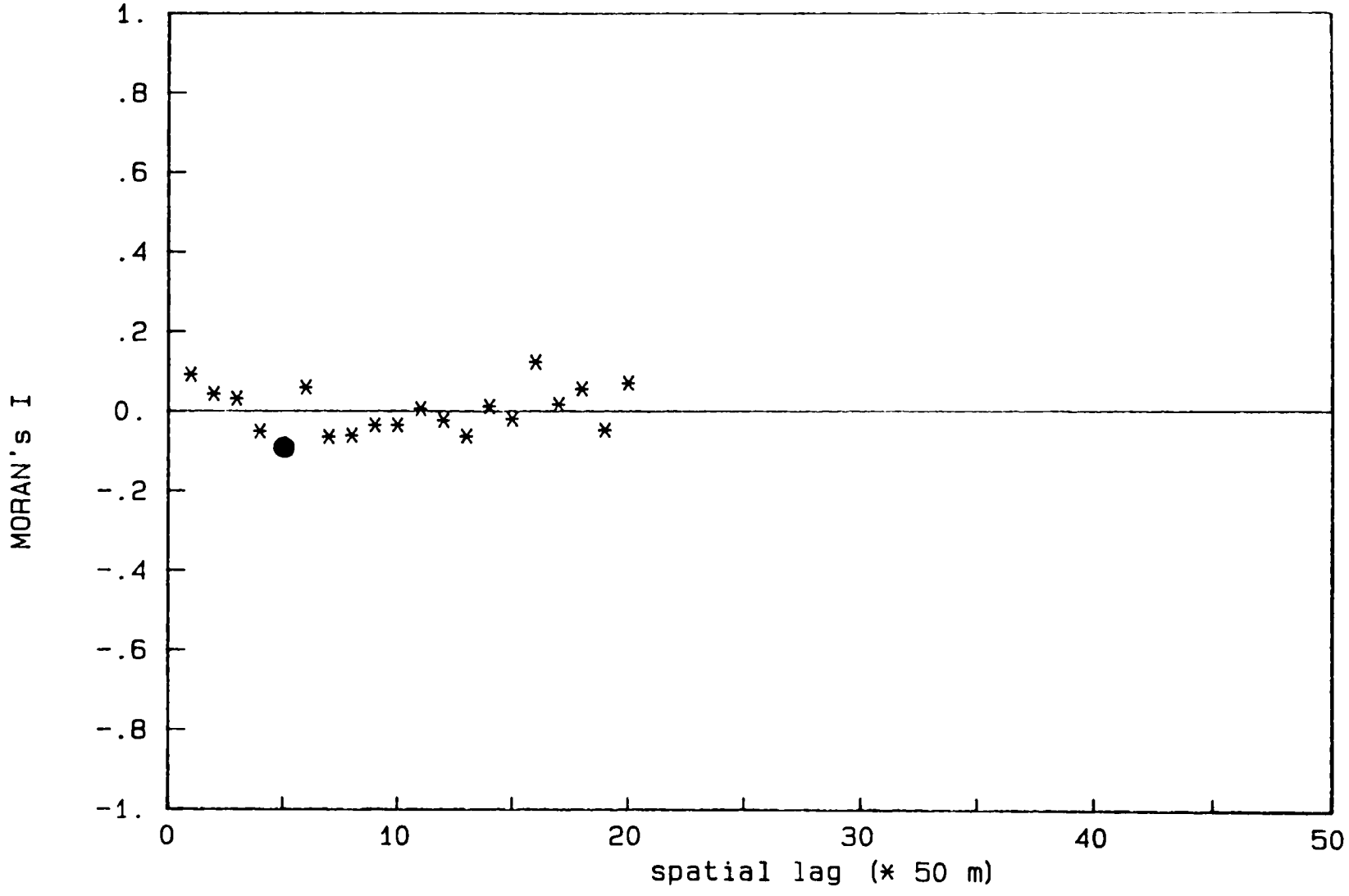
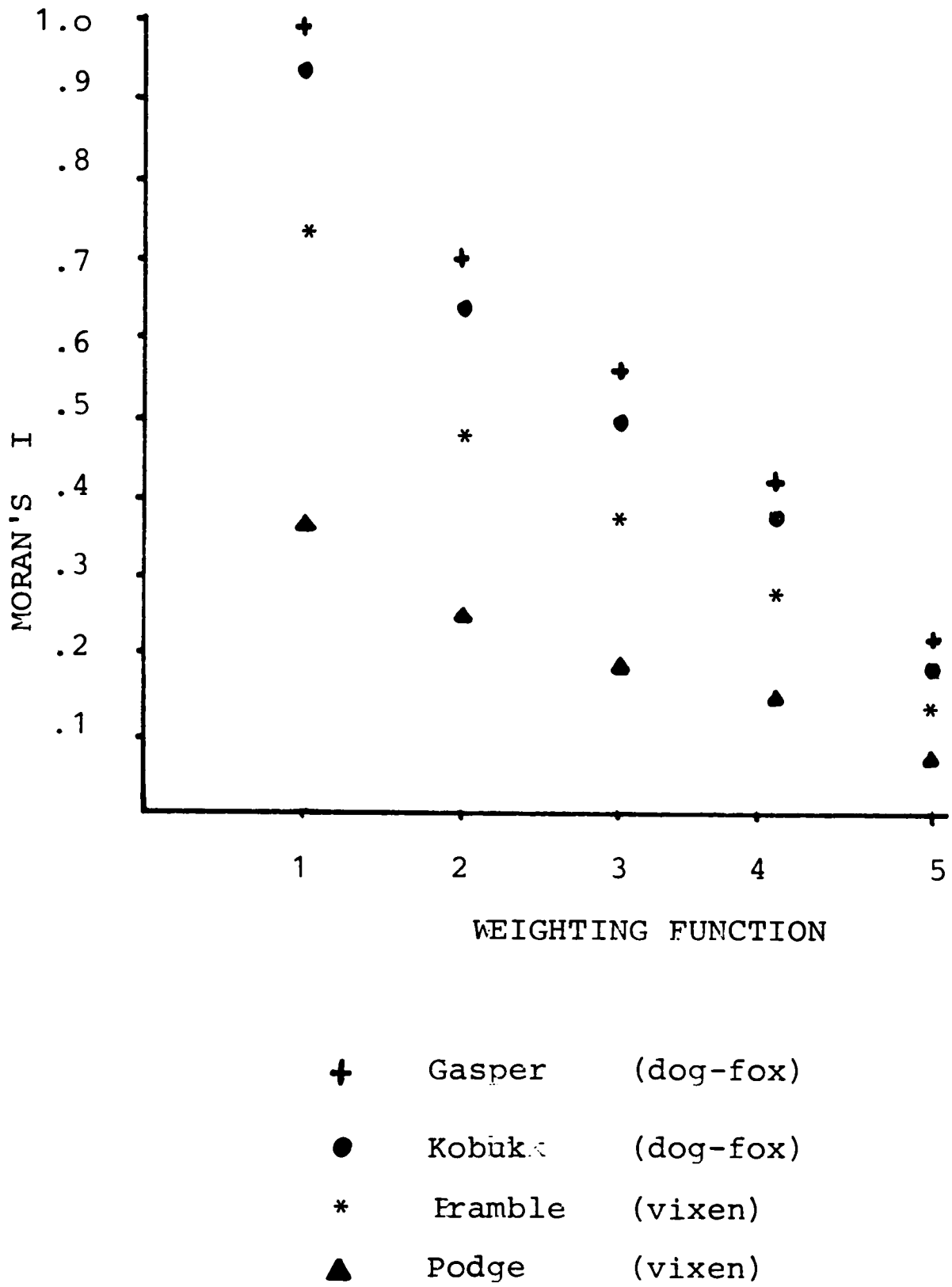


Fig. Correlogram of the spatial autocorrelation function using MORAN's I as correlation coefficient. TARU, 15 min data

6-28b

Fig. 6.29. Results of fitting the spatial models 1 to 5 (see 6.2.2. and Appendices 5-7 for a detailed explanation) to the observed range utilization intensity, evaluated on a 5o by 5o m grid, of the four members of the HOMEFARM fox group.



x-axis: the weighting function represents the number of the model; the higher the number, the more weight is attached to pairs of cells at a large distance

y-axis: the results of fitting the models to the data expressed as Moran's spatial autocorrelation coefficient. All plotted spatial autocorrelation coefficients are significantly different from the expected mean at $p < 0{\cdot}001$

Fig. 6.30–6.50. Range use by badgers

Each badger comprises at least 4 figures on 2 sheets, some 6 figures on three sheets

Fig. x.a: 3D plot of intensity of use of range as measured by the frequency of visits to 50 by 50 m cells, produced by program GINOPLOT. Coordinate 0,0 is the southwest corner of an area. Other details identical to plots of fox ranges.

Fig. x.b: 3D plot of intensity of use of range as measured by the duration of stay (in hours) per 50 by 50 m cells, produced by program GINOPLOT. Coordinate 0,0 is the southwest corner of an area. Other details identical to plots of fox ranges.

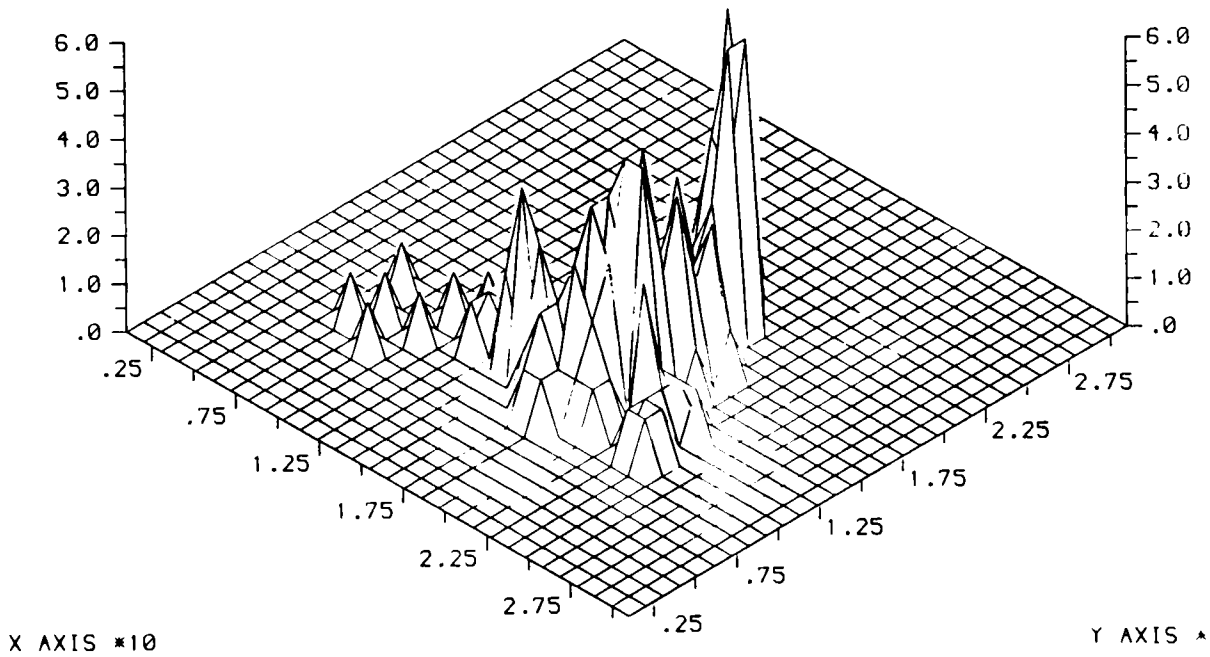
Fig. x+1.a, x+1.b; or x+1.a, x+2.a: Spatial correlograms of UI data, using Moran's I as spatial autocorrelation coefficient. For a detailed explanation see text or Appendix 5. Symbols as for fox ranges.

If present, Fig. x+1.b & x+2.b: Results of fitting spatial models 1 to 5 (see 6.2.2. and Appendices 5–7) to UI data. Plots identical to fox plots, except for part of the symbols:

SAC	SAC significantly different from the expected mean (null	SAC corresponding to the expected mean (null hypothesis confirmed)
Moran's I	filled circles	stars
Geary's c	encircled plus	plus

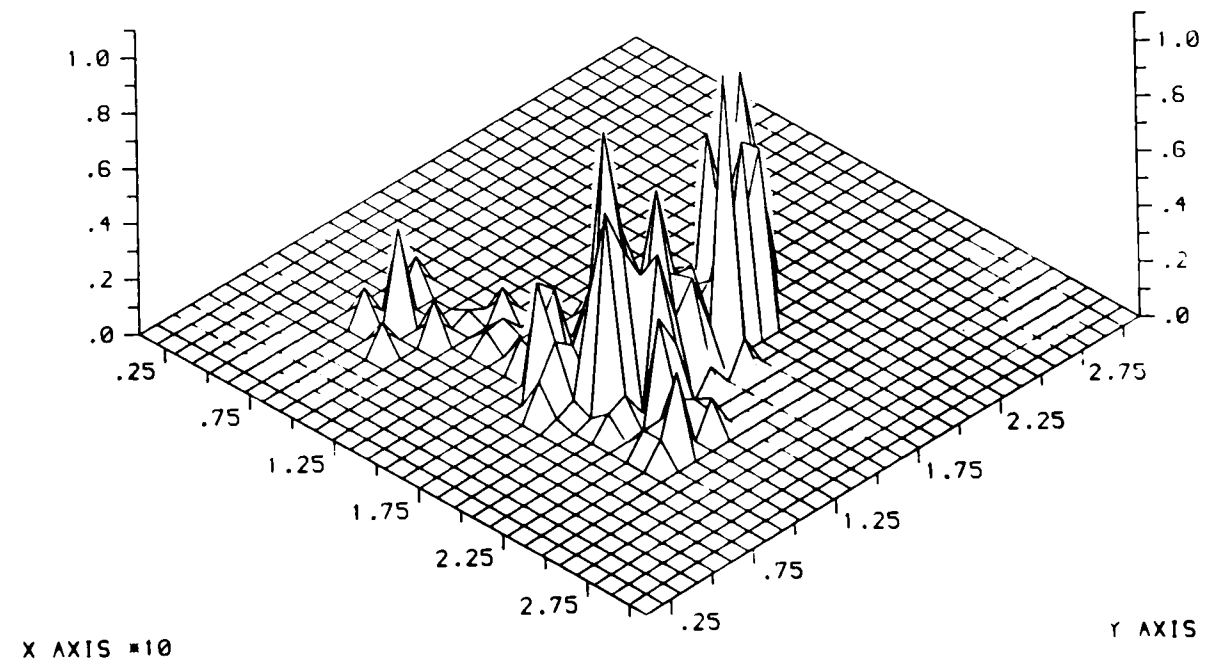
Results of the fitting procedure were not plotted for all individuals, since most turned out to be insignificant. An example of such insignificant results are, however, shown for badgers ALI and NANI. Below is a list of plots for each individual badger.

Badger	3D plots	correlogram	models
George	6.30 a+b	6.31 a+b	-
Helen	6.32 a+b	6.33 a+b	-
Sara	6.34 a+b	6.35a, 6.36a	6.35b, 6.36b
Ali	6.37 a+b	6.38a, 6.39a	6.38b, 6.39b
Nani	6.40 a+b	6.41a, 6.42a	6.41b, 6.42b
Wilf	6.43 a+b	6.44a, 6.45a	6.44b, 6.45b
Peaceful	6.46 a+b	6.47a, 6.48a	6.47b, 6.48b
Vicious	6.49 a+b	6.50 a+b	



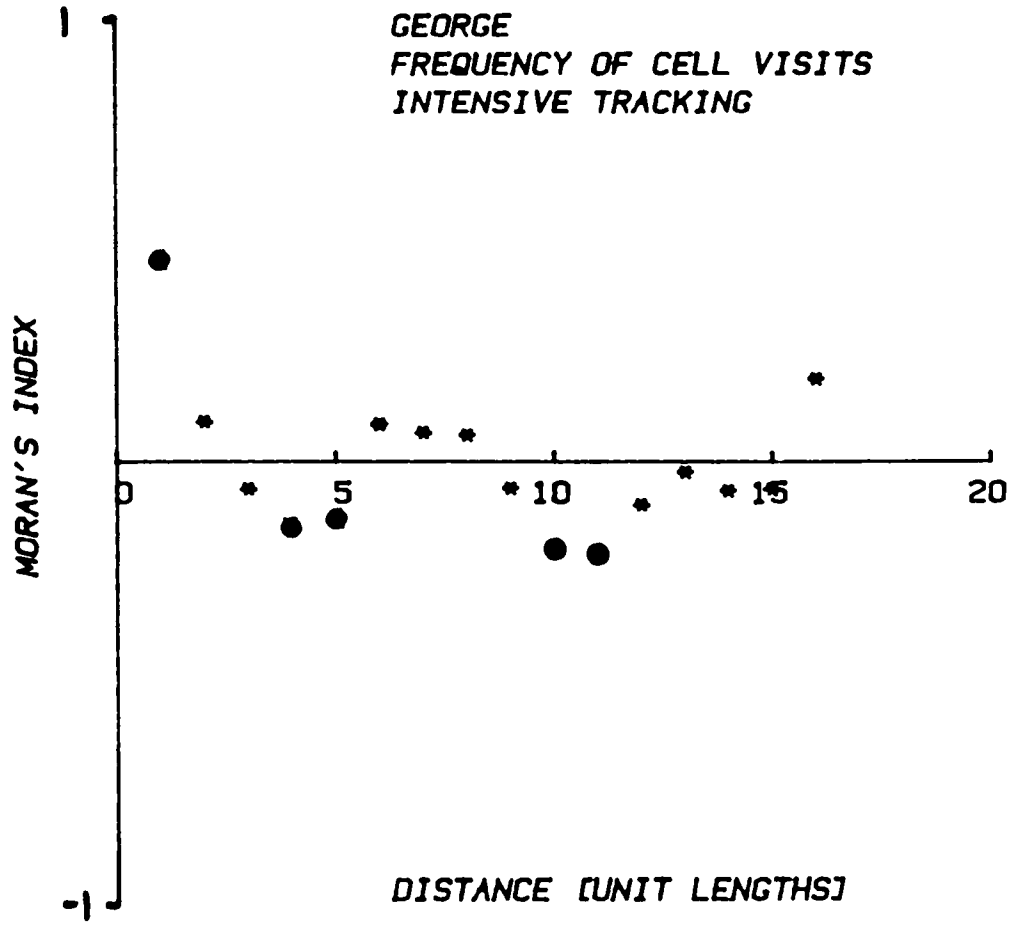
GEORGE : FREQUENCY OF CELL VISITS (INT.T

6-30a

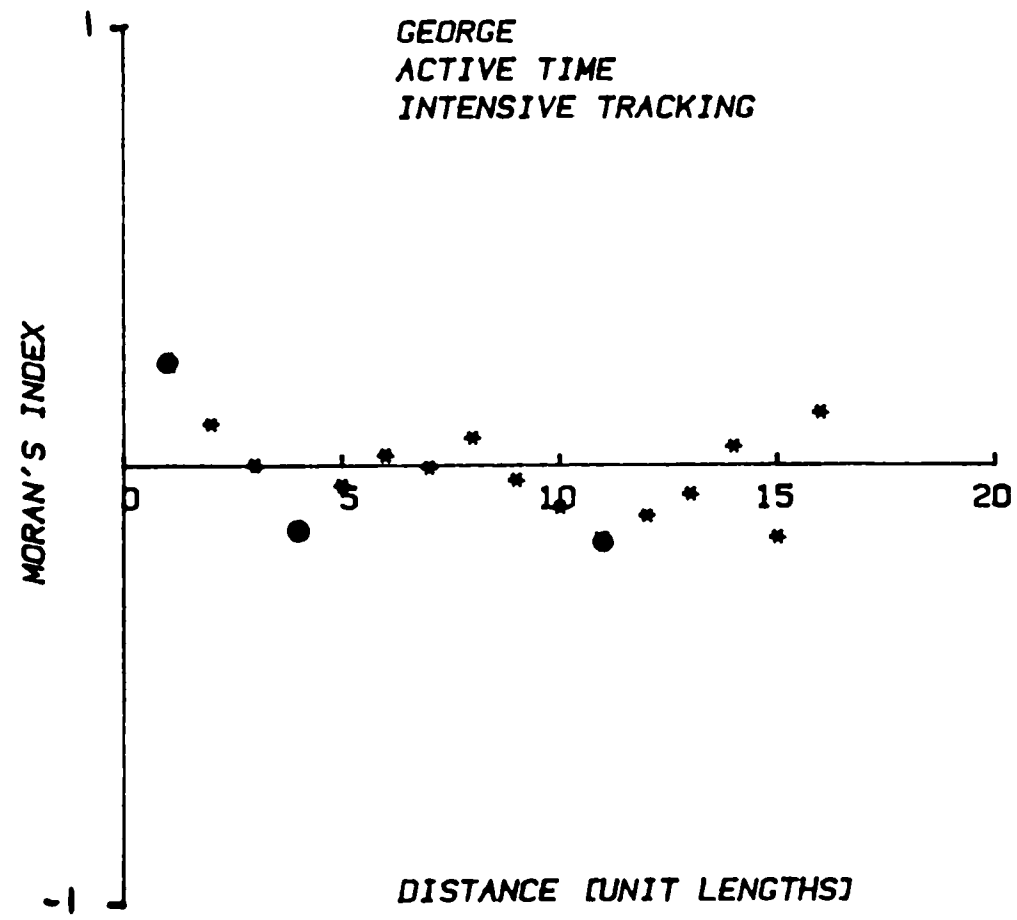


GEORGE : ACTIVE TIME (INTENSIVE TRACKING

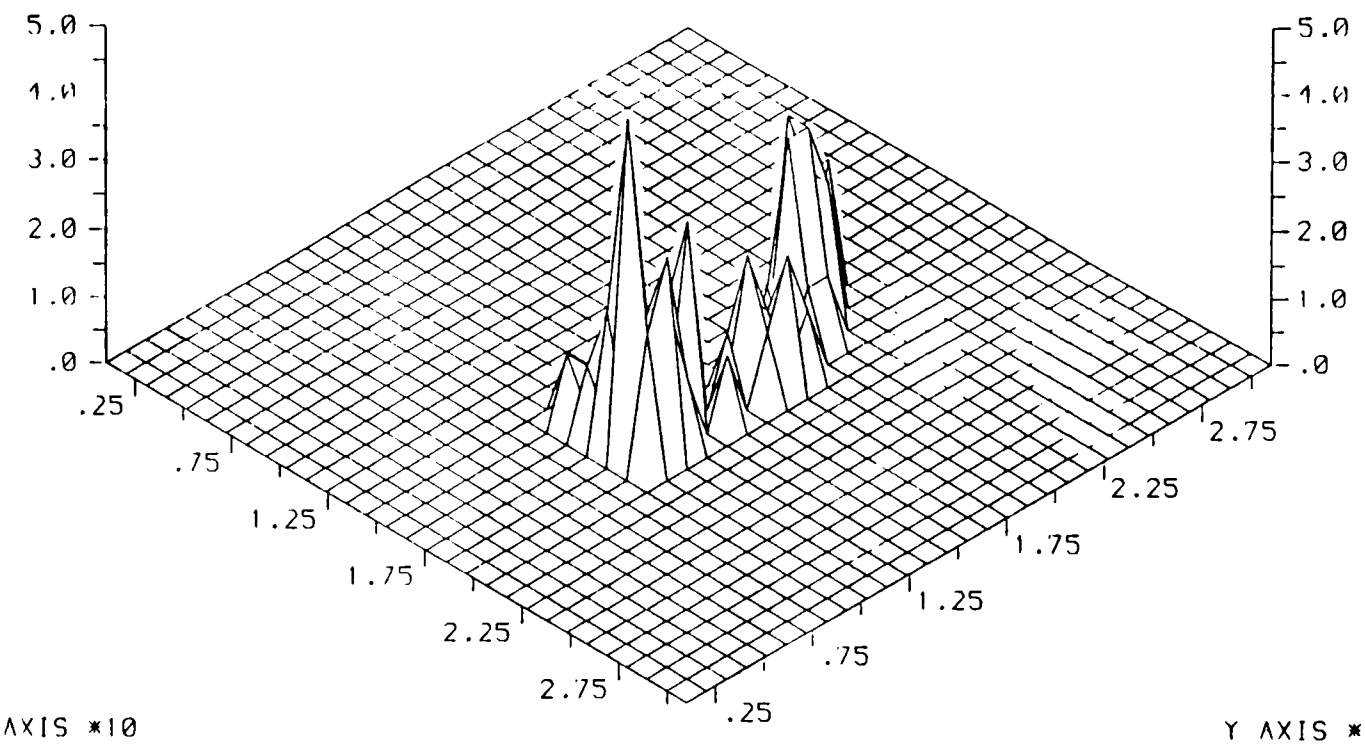
6-30b


GEORGE
FREQUENCY OF CELL VISITS
INTENSIVE TRACKING
MORAN'S INDEX
1
-1
0
5
10
15
20
DISTANCE [UNIT LENGTHS]

6-31a

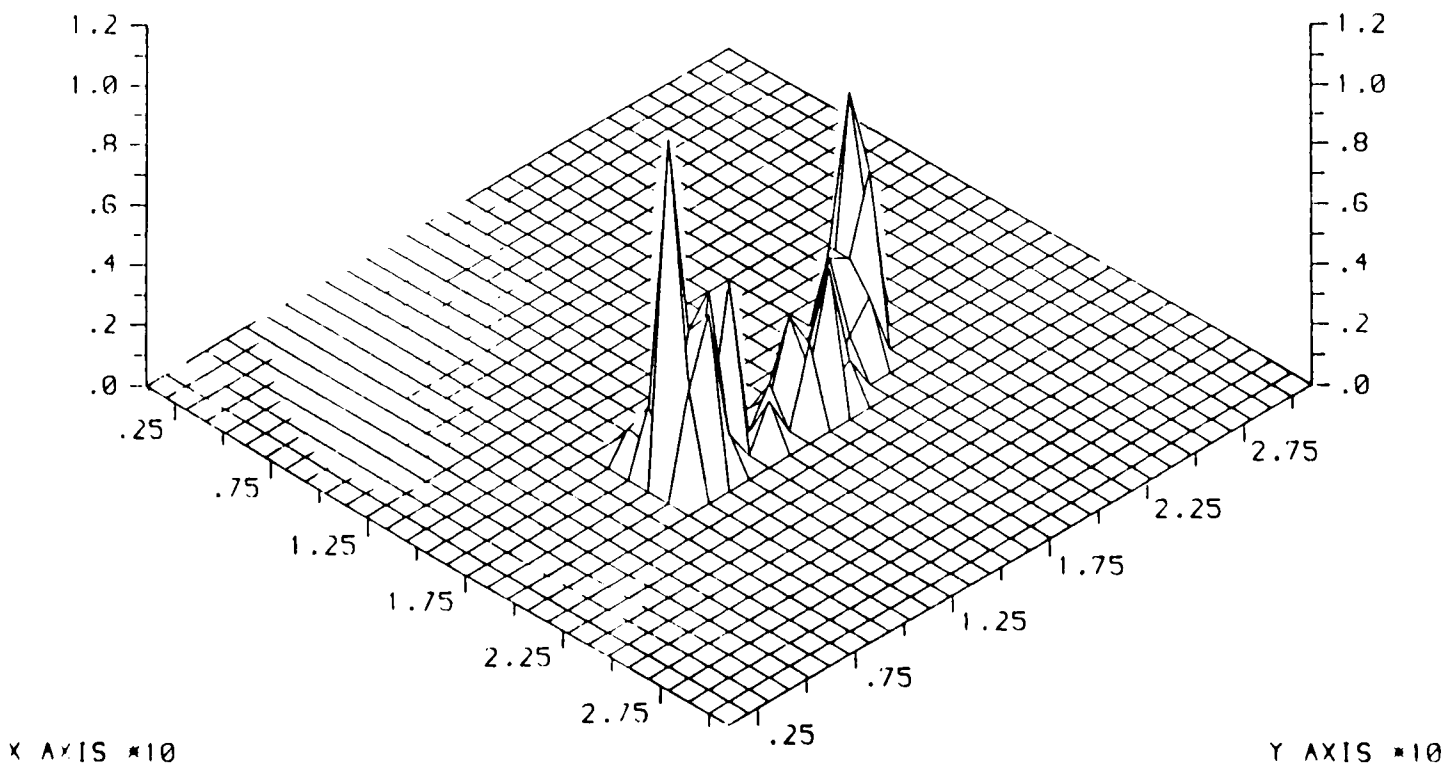

GEORGE
ACTIVE TIME
INTENSIVE TRACKING
MORAN'S INDEX
1
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5
10
15
20
DISTANCE [UNIT LENGTHS]

6-31b



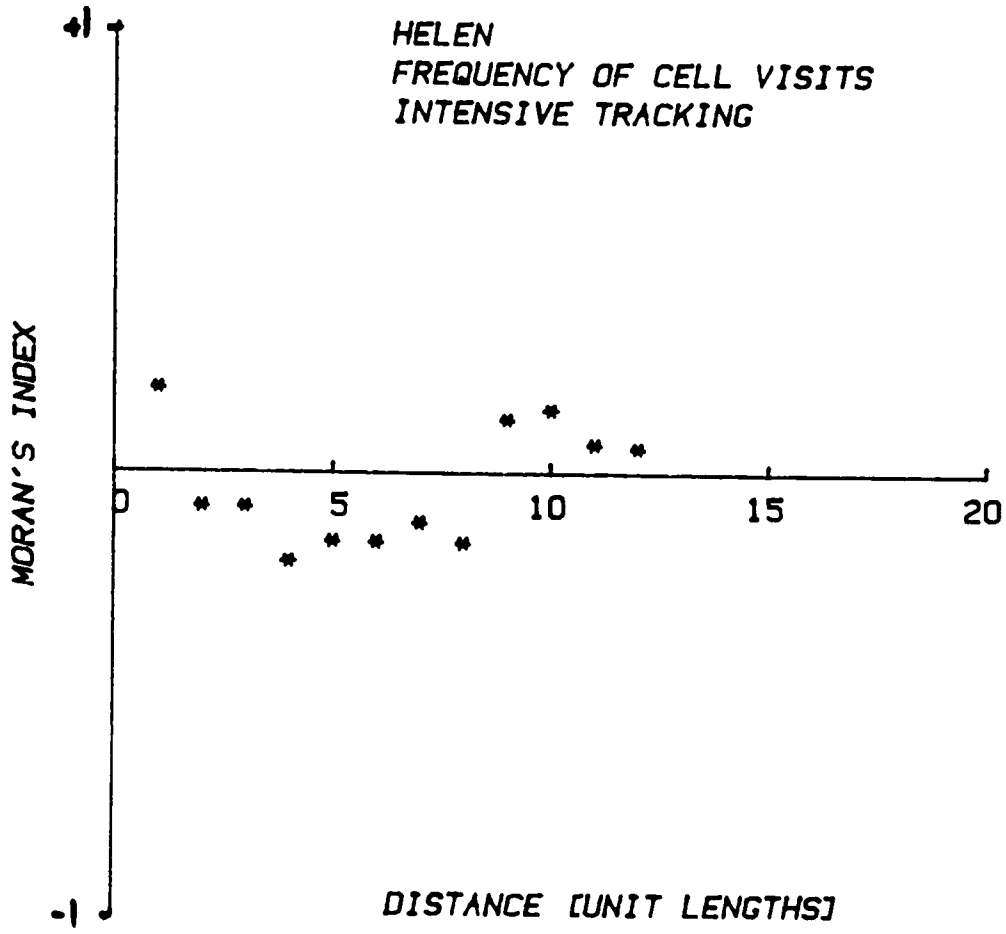
HELEN : FREQUENCY OF CELL VISITS (INT.TR

6-32a

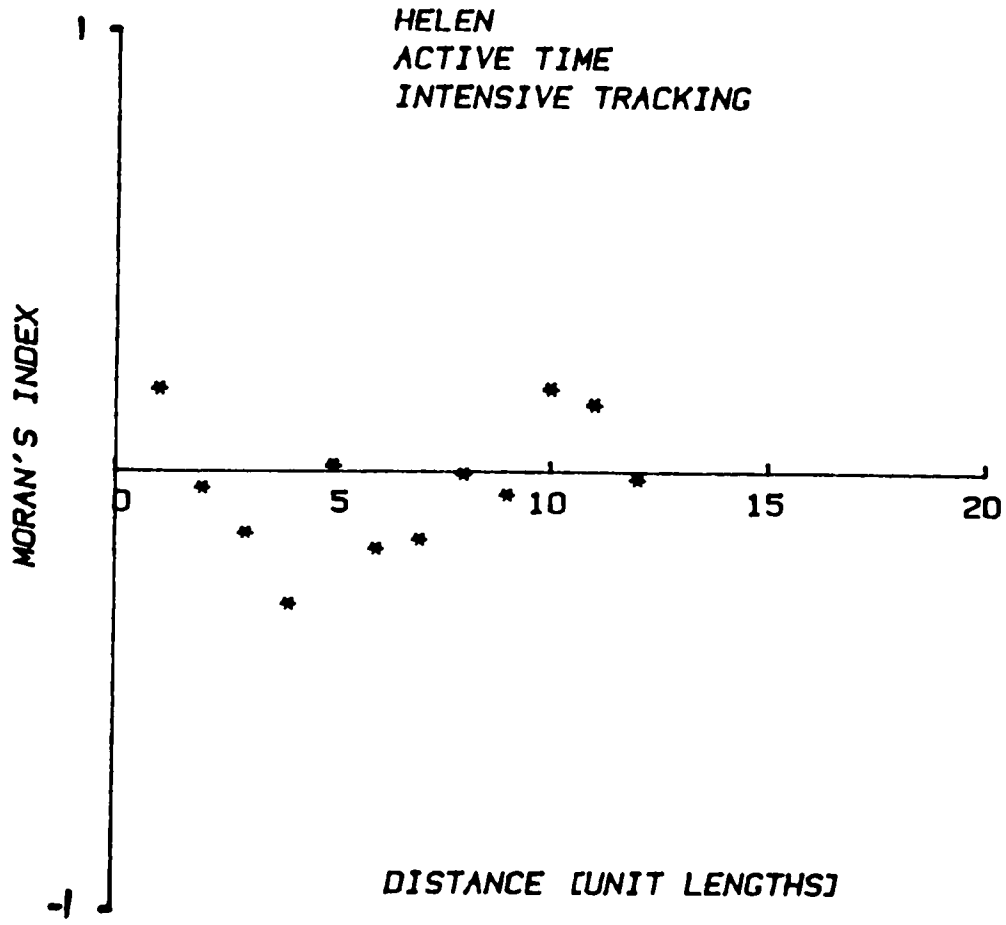


HELEN : ACTIVE TIME (INTENSIVE TRACKING)

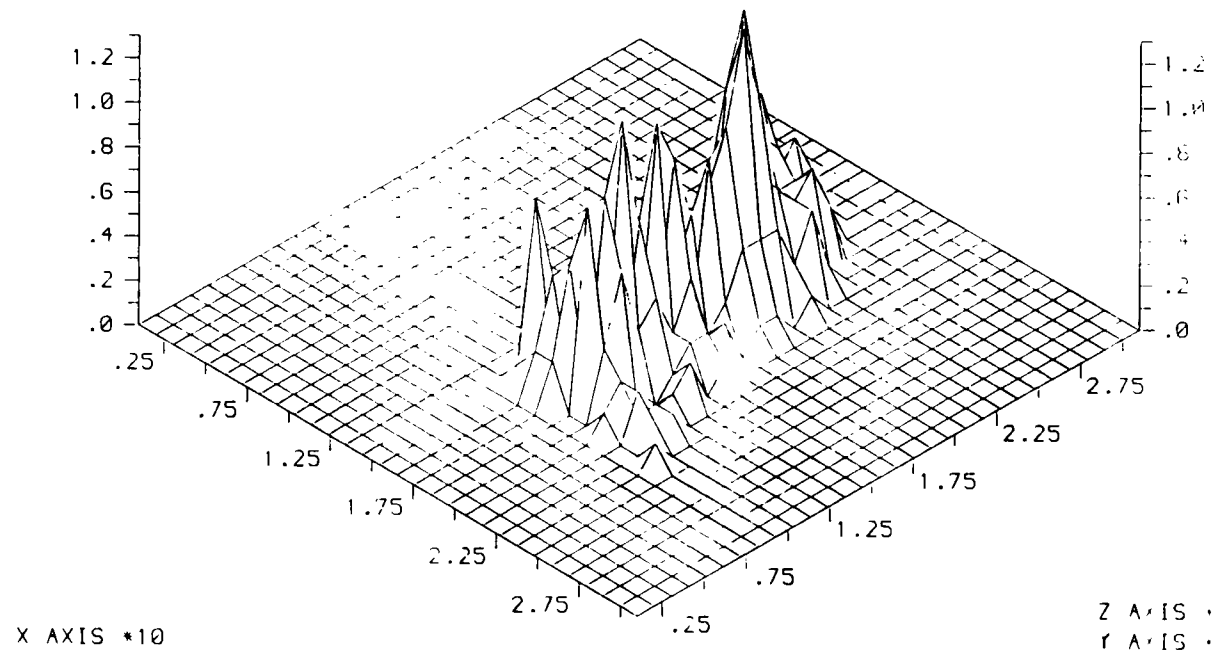
6-32b


+1
HELEN
FREQUENCY OF CELL VISITS
INTENSIVE TRACKING
MORAN'S INDEX
0
5
10
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-1
DISTANCE [UNIT LENGTHS]

6-33a

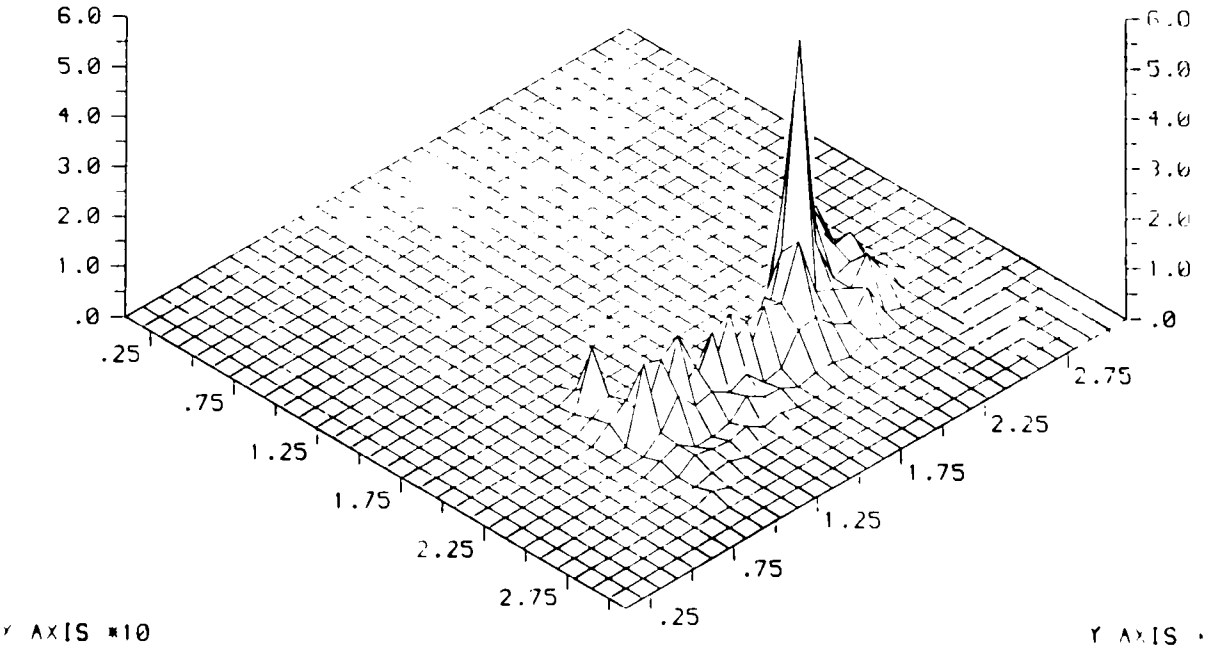

1
HELEN
ACTIVE TIME
INTENSIVE TRACKING
MORAN'S INDEX
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10
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-1
DISTANCE [UNIT LENGTHS]

6-33b



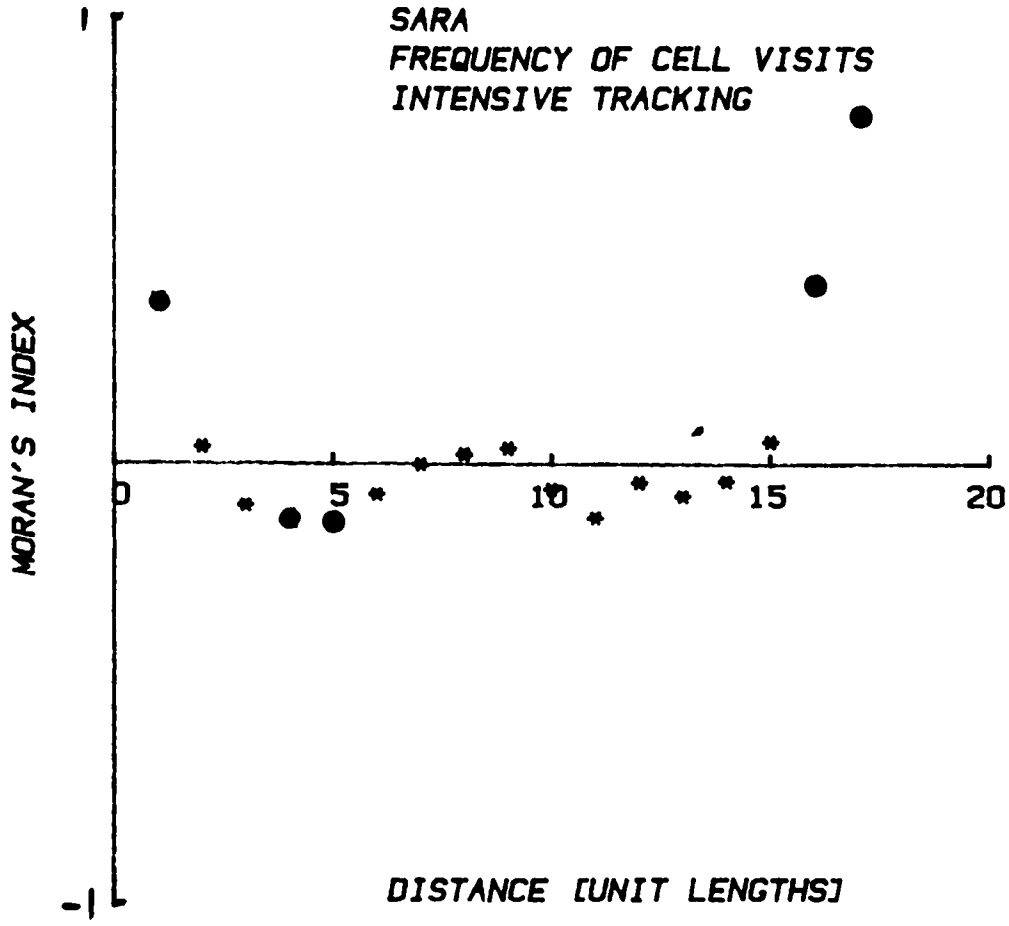
SARA : FREQUENCY OF CELL VISITS (INT. TR

6-34a

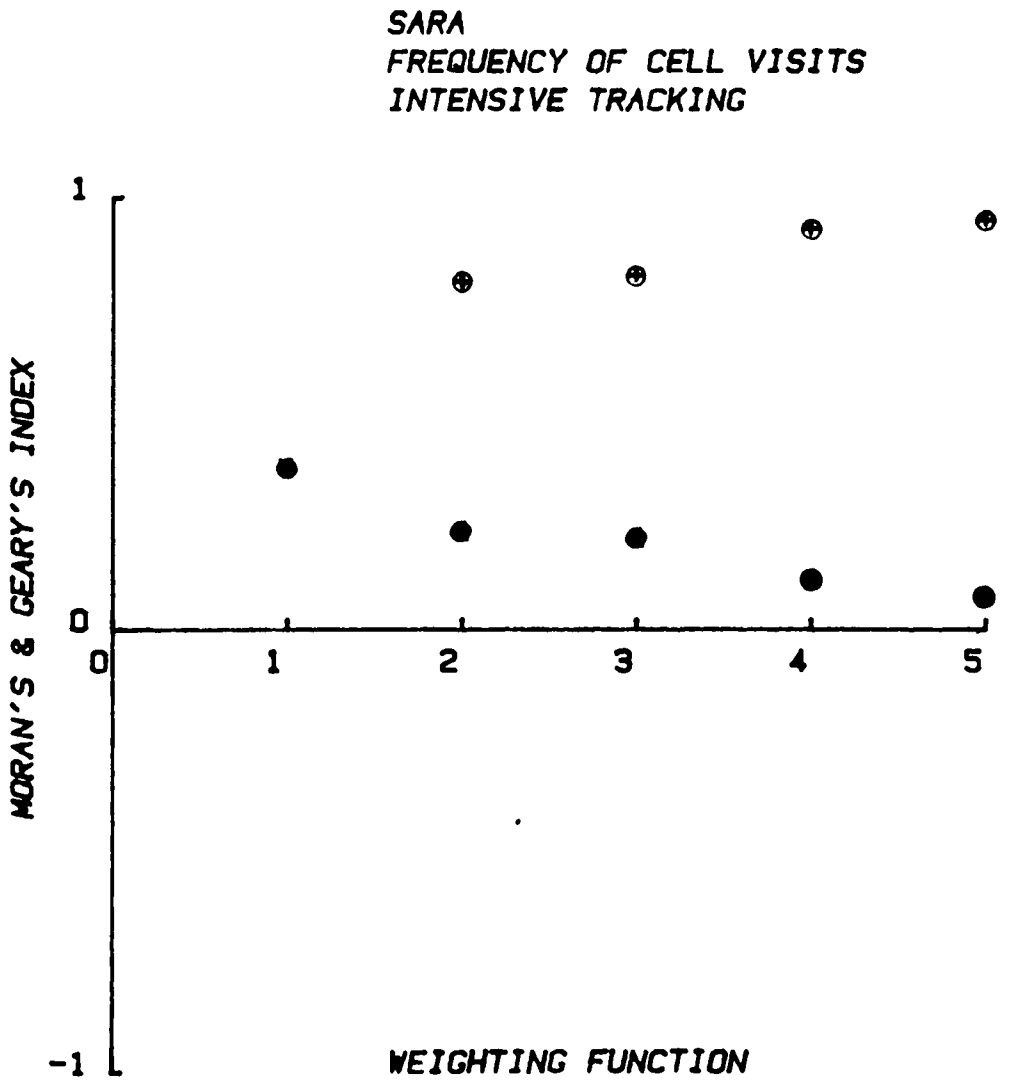


SARA : ACTIVE TIME (INTENSIVE TRACKING)

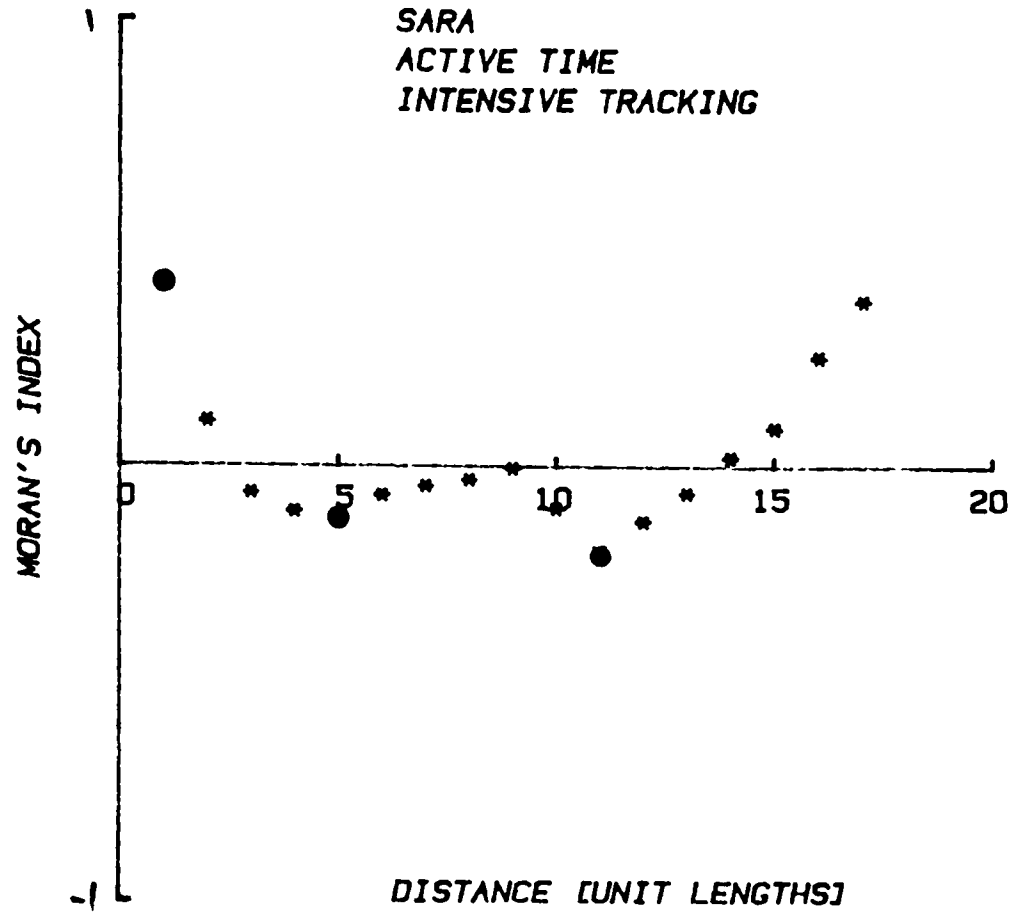
6-34b


SARA
FREQUENCY OF CELL VISITS
INTENSIVE TRACKING
MORAN'S INDEX
1
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DISTANCE [UNIT LENGTHS]

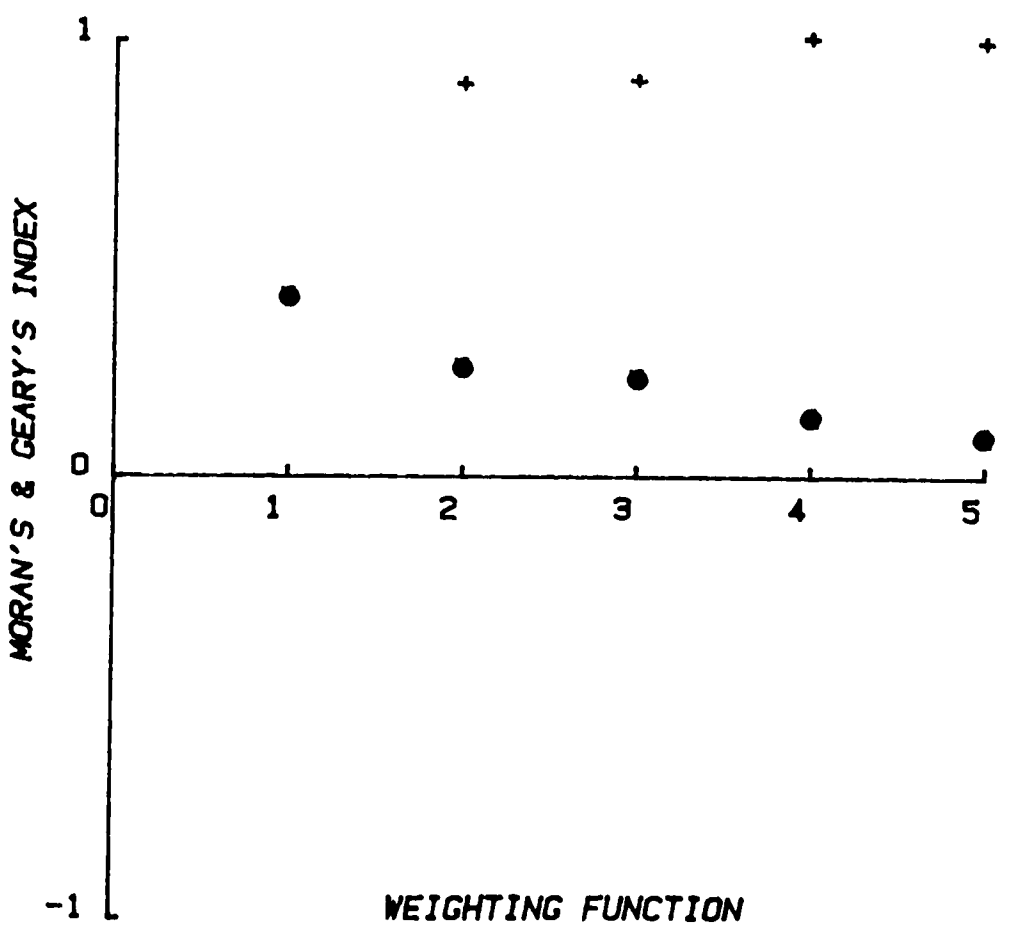
6-35a


SARA
FREQUENCY OF CELL VISITS
INTENSIVE TRACKING
MORAN'S & GEARY'S INDEX
1
0
-1
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WEIGHTING FUNCTION

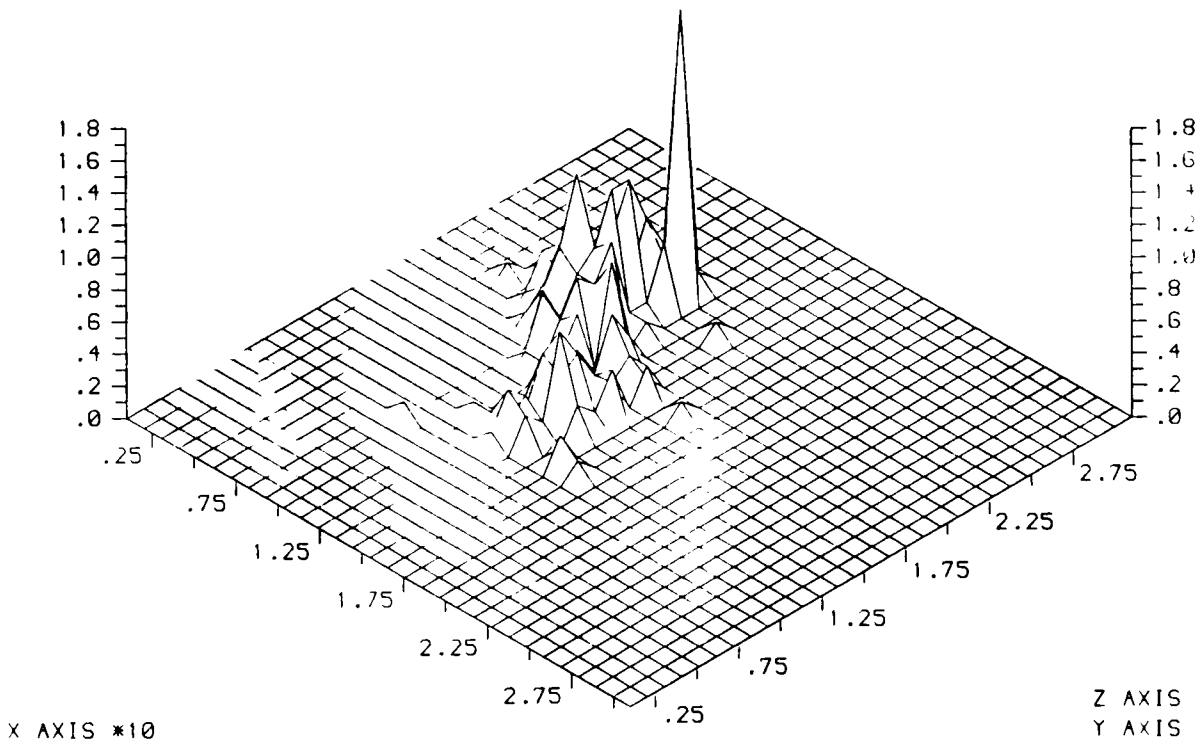
6-35b


SARA
ACTIVE TIME
INTENSIVE TRACKING
MORAN'S INDEX
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DISTANCE [UNIT LENGTHS]

6-36a

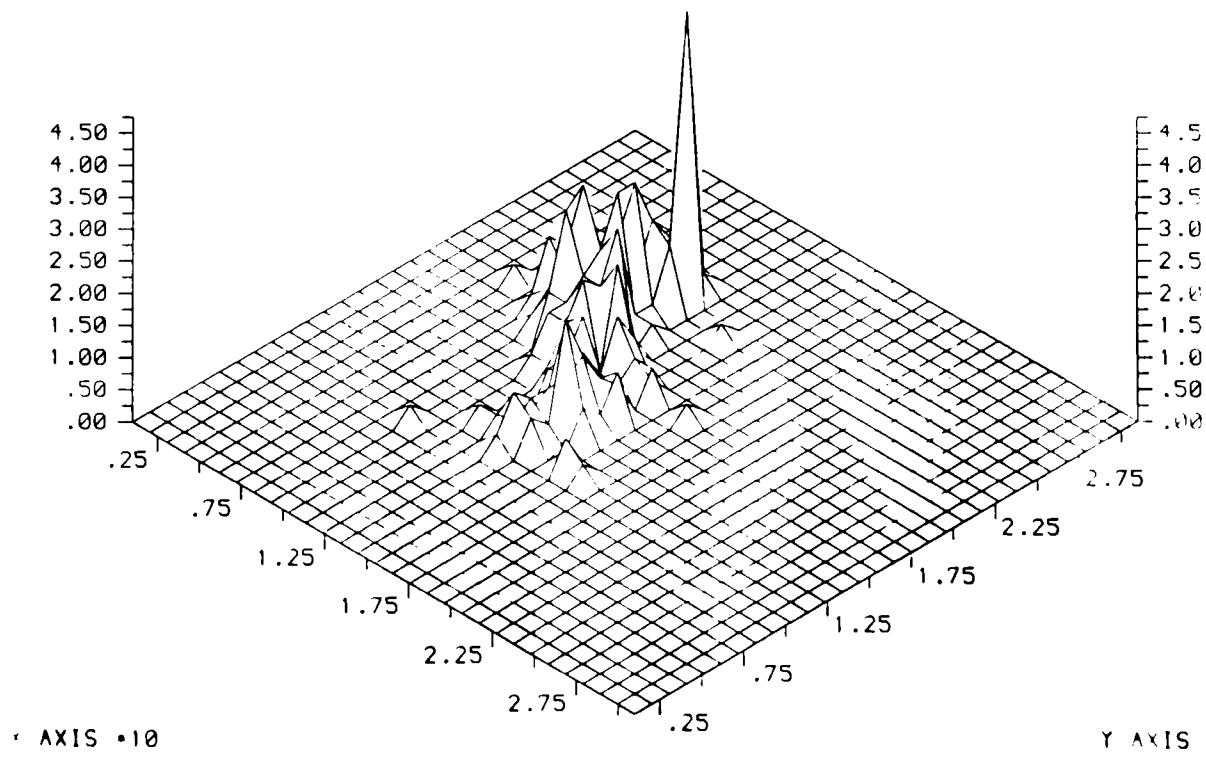

SARA
ACTIVE TIME
INTENSIVE TRACKING
MORAN'S & GEARY'S INDEX
1
0
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1
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3
4
5
WEIGHTING FUNCTION

6-36b



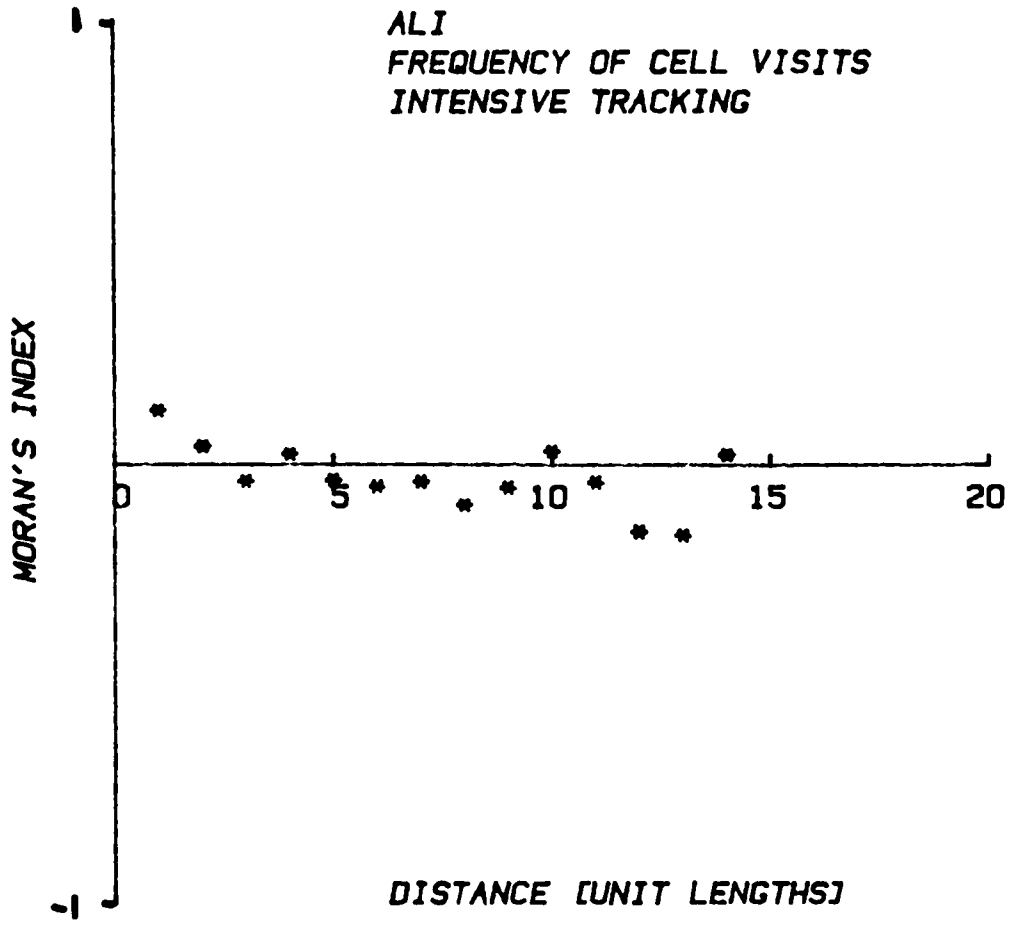
ALI : FREQUENCY OF CELL VISITS (INT. TRA

6-37a

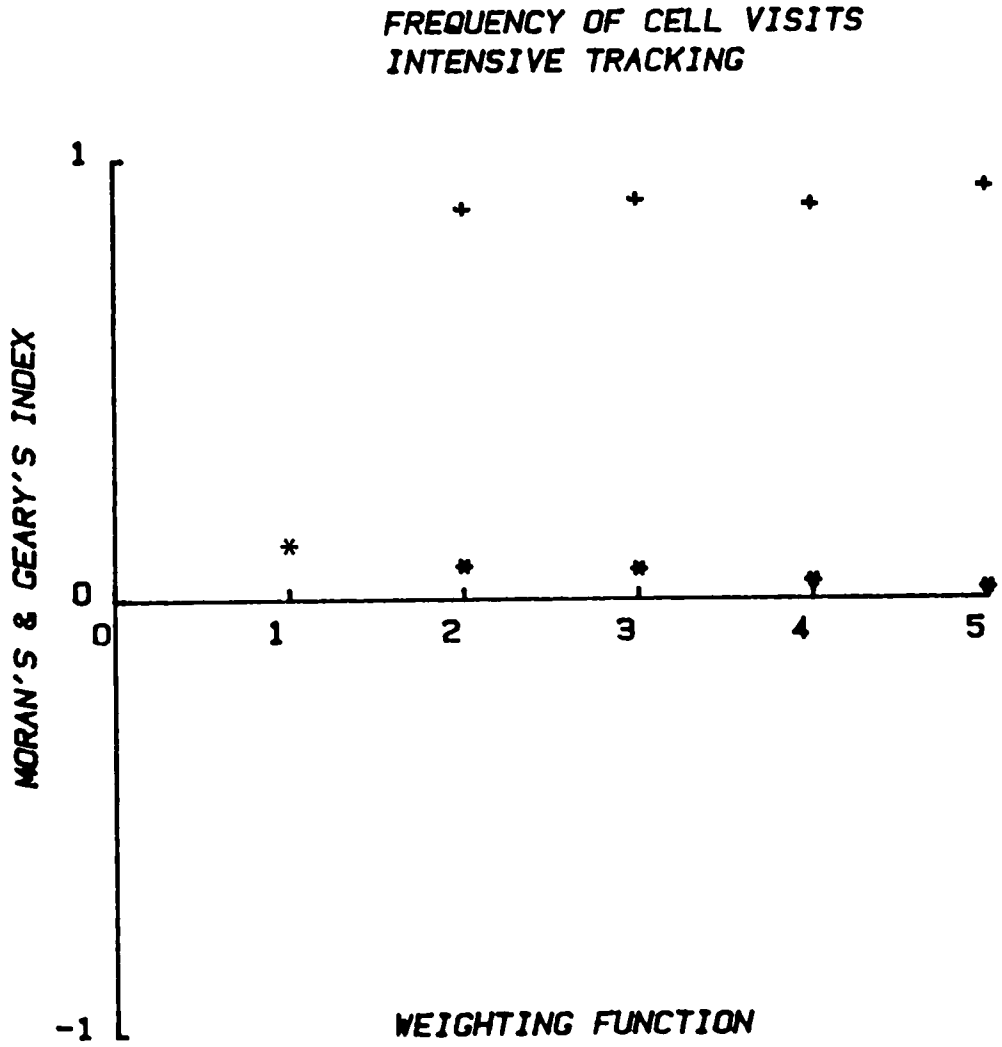


ALI : ACTIVE TIME (INTENSIVE TRACKING)

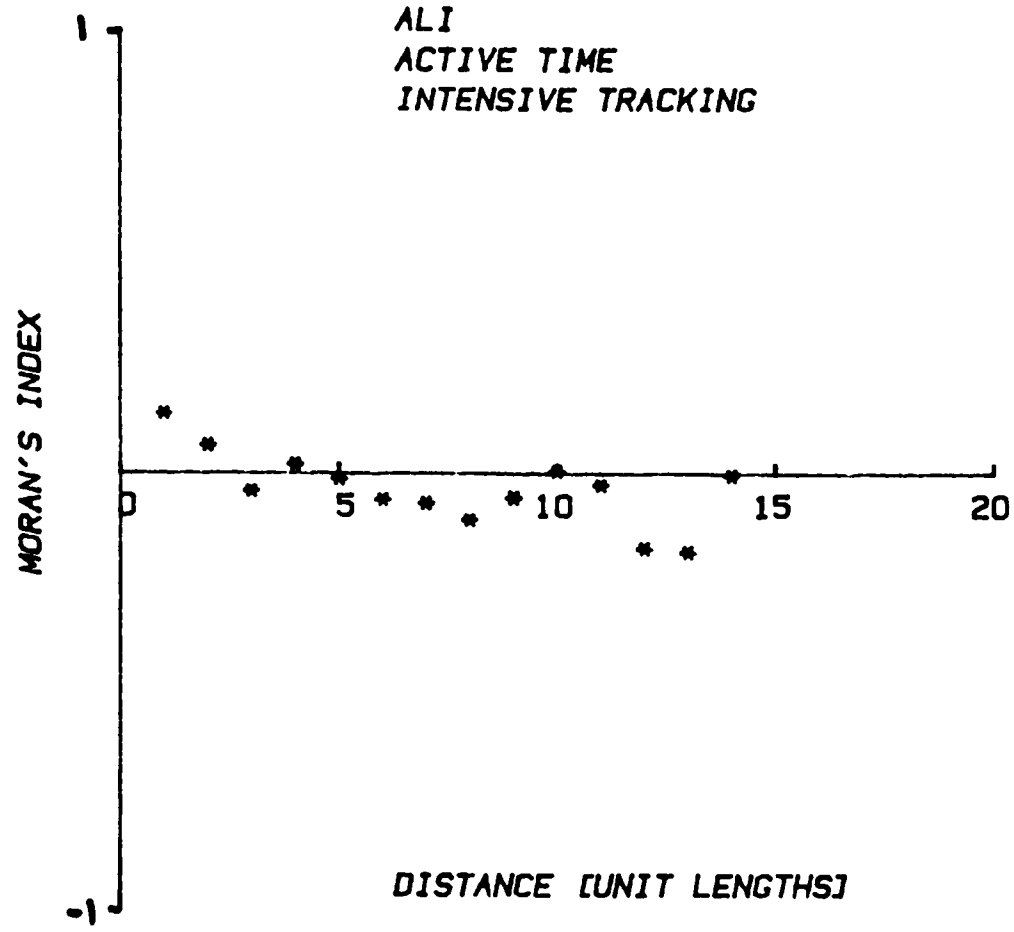
6-37b


ALI
FREQUENCY OF CELL VISITS
INTENSIVE TRACKING
MORAN'S INDEX
1
-1
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20
DISTANCE [UNIT LENGTHS]

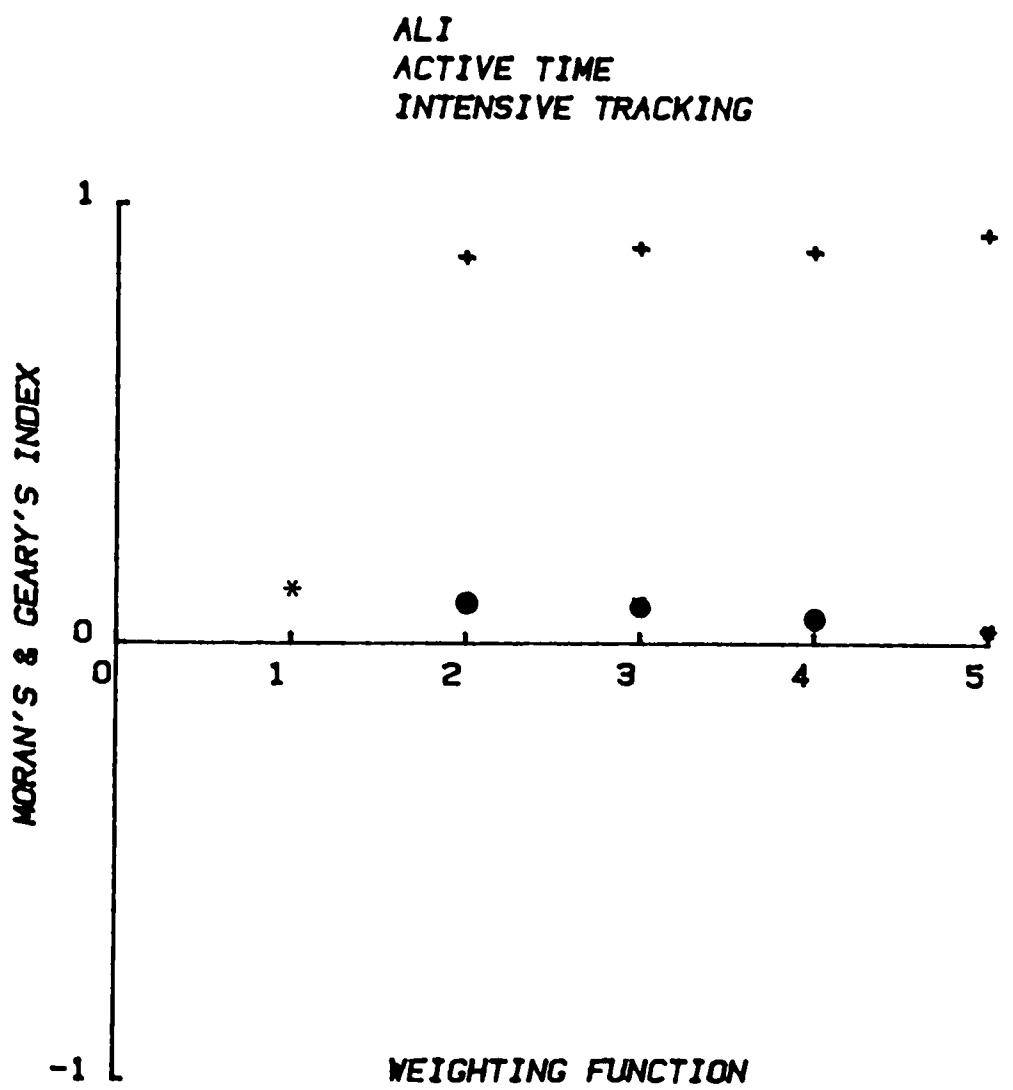
6-38a


ALI
FREQUENCY OF CELL VISITS
INTENSIVE TRACKING
MORAN'S & GEARY'S INDEX
1
0
-1
0
1
2
3
4
5
WEIGHTING FUNCTION

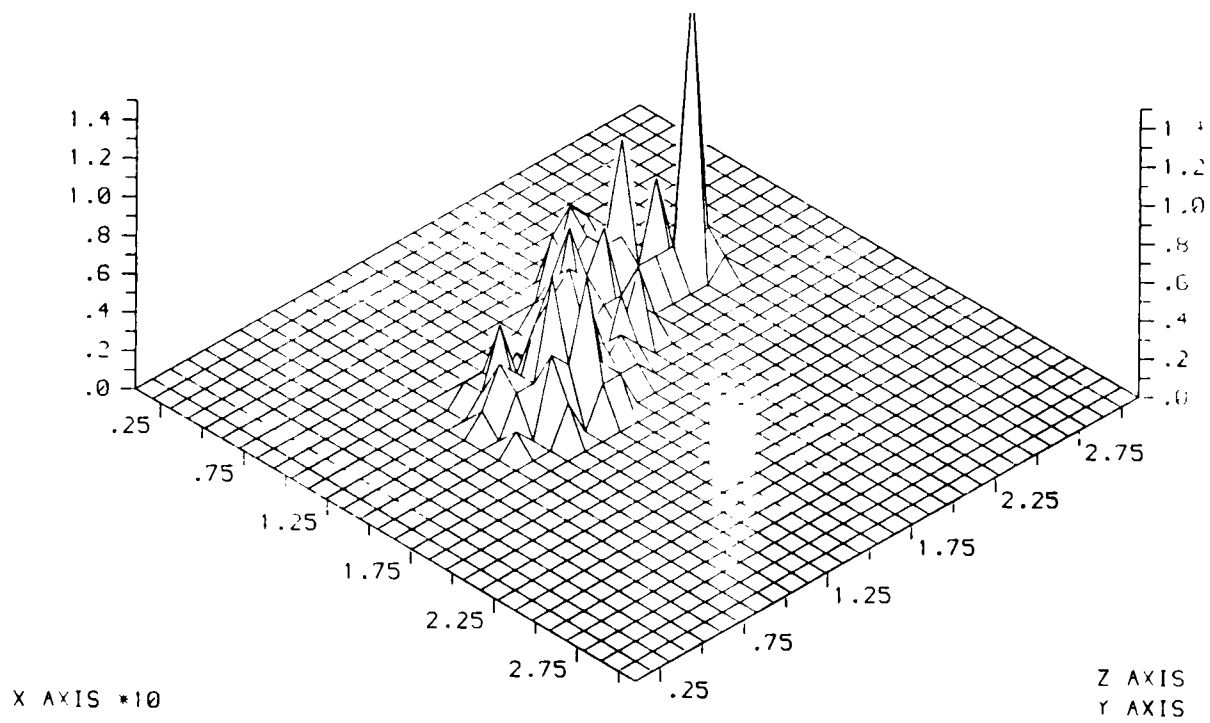
6-38b


ALI
ACTIVE TIME
INTENSIVE TRACKING
MORAN'S INDEX
1
-1
0
5
10
15
20
DISTANCE [UNIT LENGTHS]

6-39a

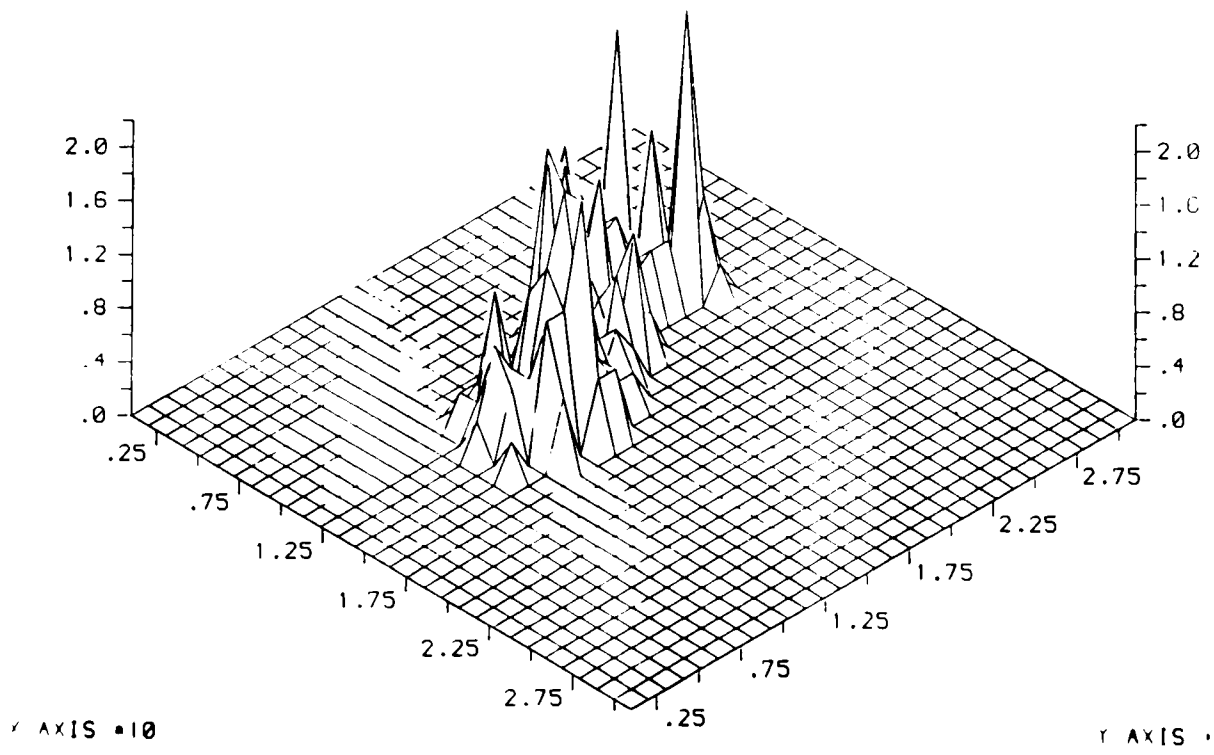

ALI
ACTIVE TIME
INTENSIVE TRACKING
MORAN'S & GEARY'S INDEX
1
0
-1
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1
2
3
4
5
WEIGHTING FUNCTION

6-39b



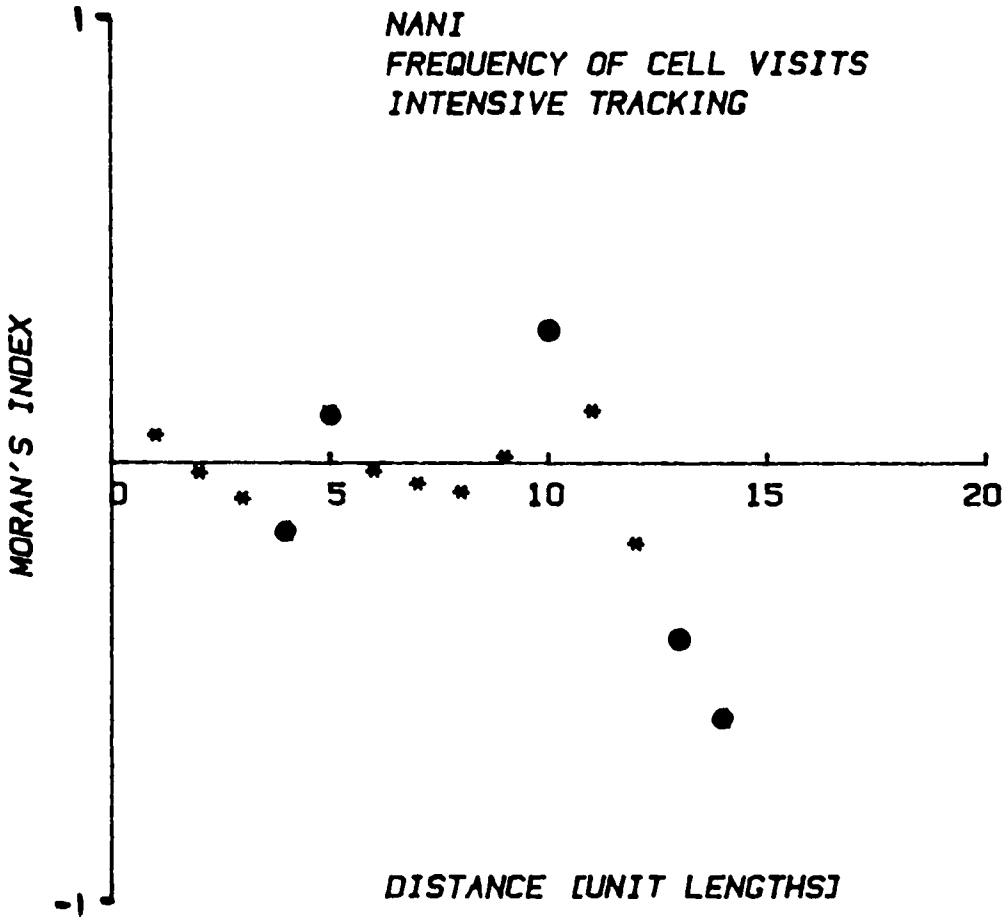
NANI : FREQUENCY OF CELL VISITS (INT.TRA

6-40 a

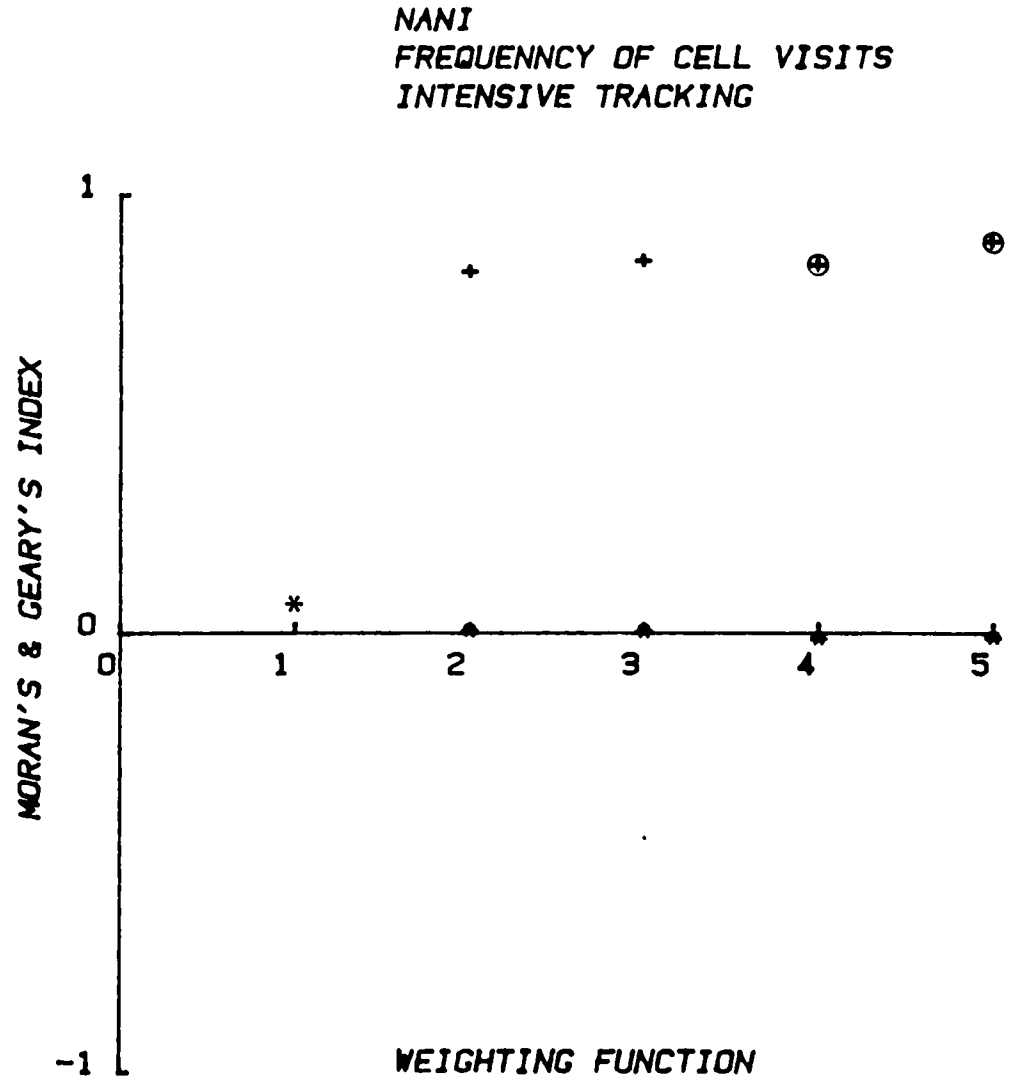


NANI : ACTIVE TIME (INTENSIVE TRACKING)

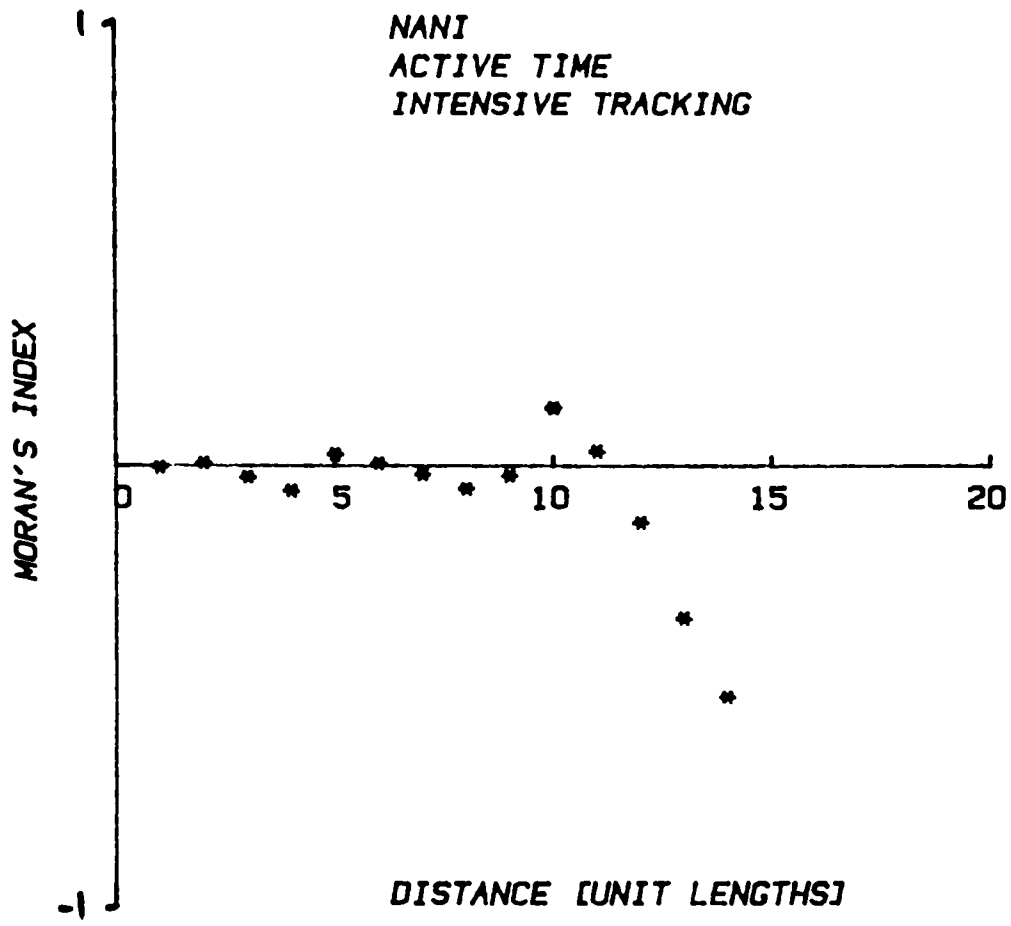
6-40 b


NANI
FREQUENCY OF CELL VISITS
INTENSIVE TRACKING
MORAN'S INDEX
1
-1
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5
10
15
20
DISTANCE [UNIT LENGTHS]

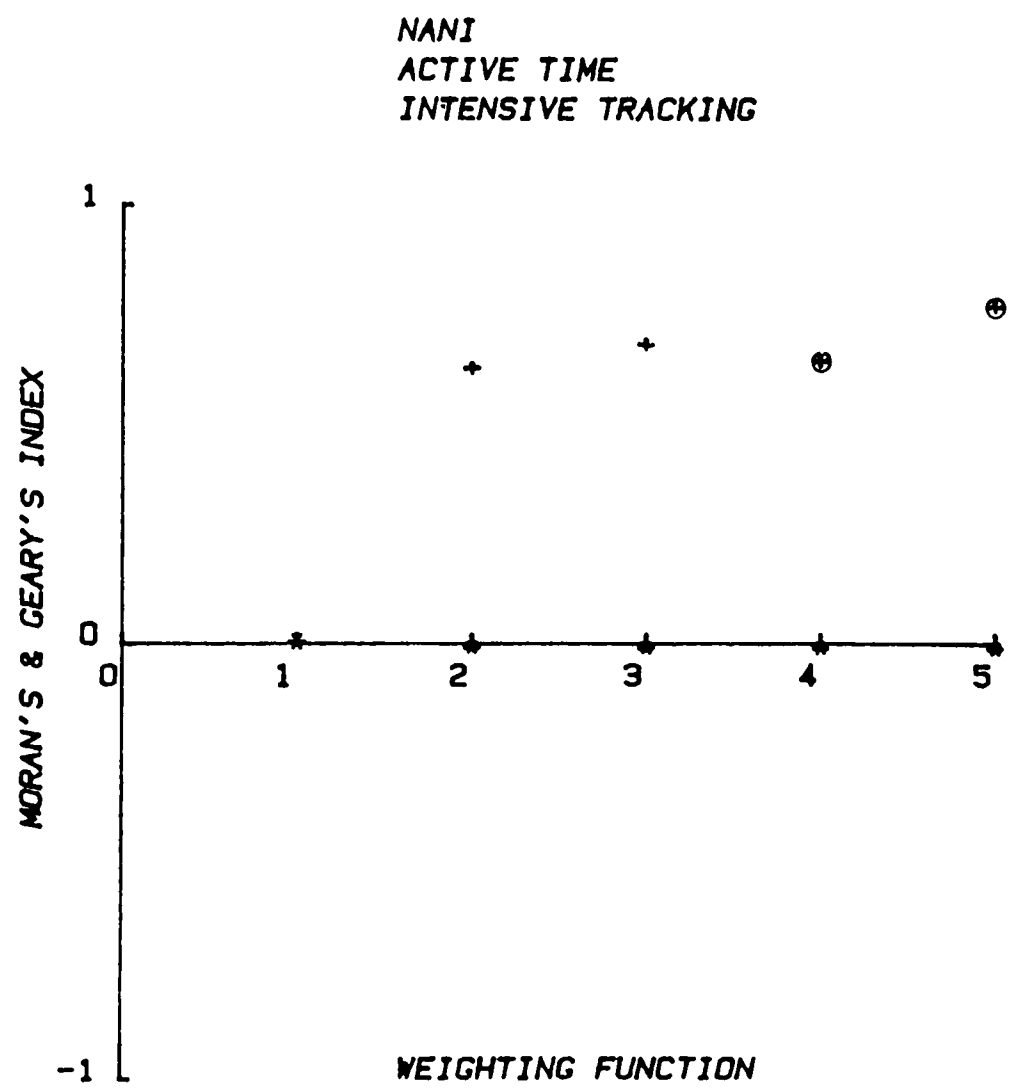
6-41e


NANI
FREQUENNCY OF CELL VISITS
INTENSIVE TRACKING
MORAN'S & GEARY'S INDEX
1
0
-1
0
1
2
3
4
5
WEIGHTING FUNCTION

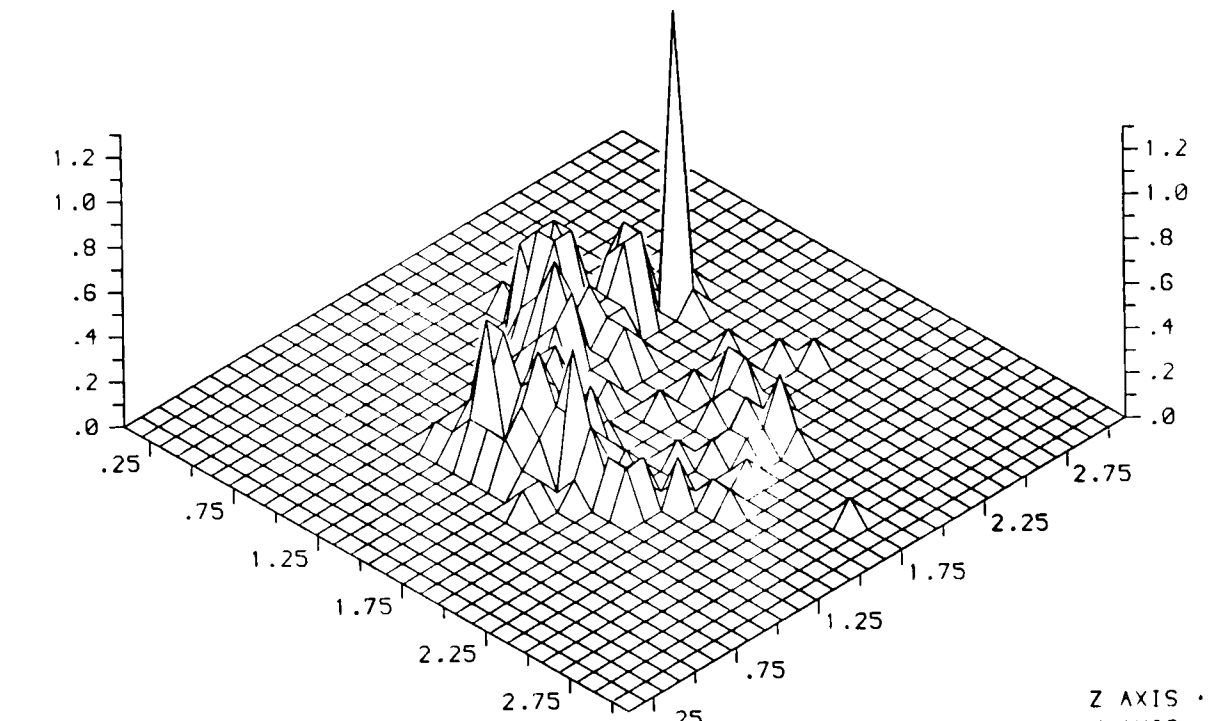
6-41b


NANI
ACTIVE TIME
INTENSIVE TRACKING
MORAN'S INDEX
1
-1
0
5
10
15
20
DISTANCE [UNIT LENGTHS]

6-42a

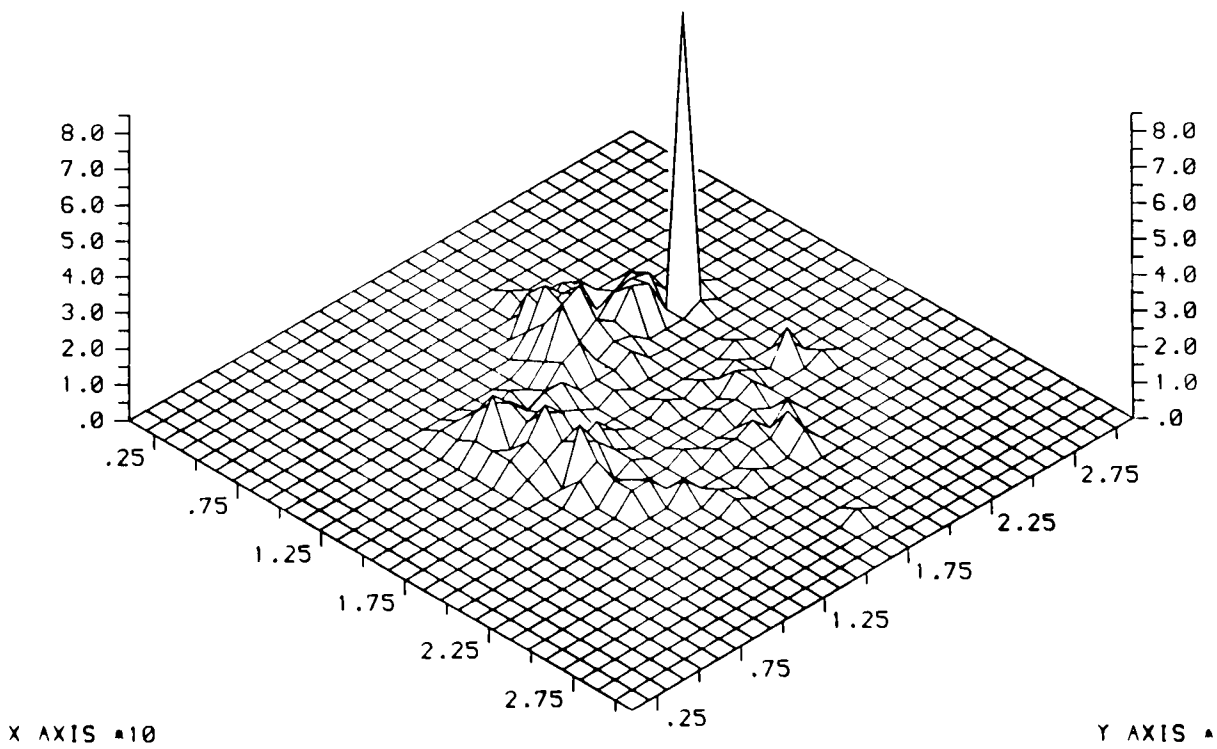

NANI
ACTIVE TIME
INTENSIVE TRACKING
MORAN'S & GEARY'S INDEX
1
0
-1
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1
2
3
4
5
WEIGHTING FUNCTION

6-42b



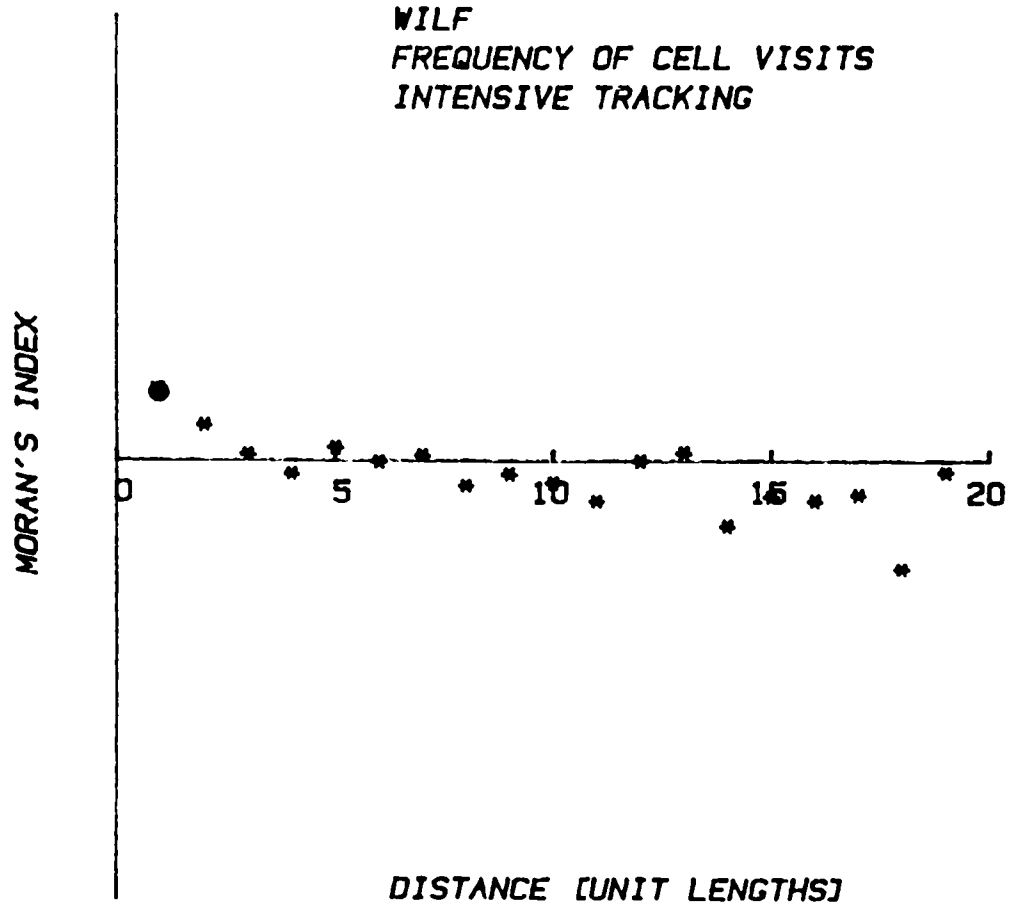
WILF : FREQUENCY OF CELL VISITS (INT. TR

6-43a

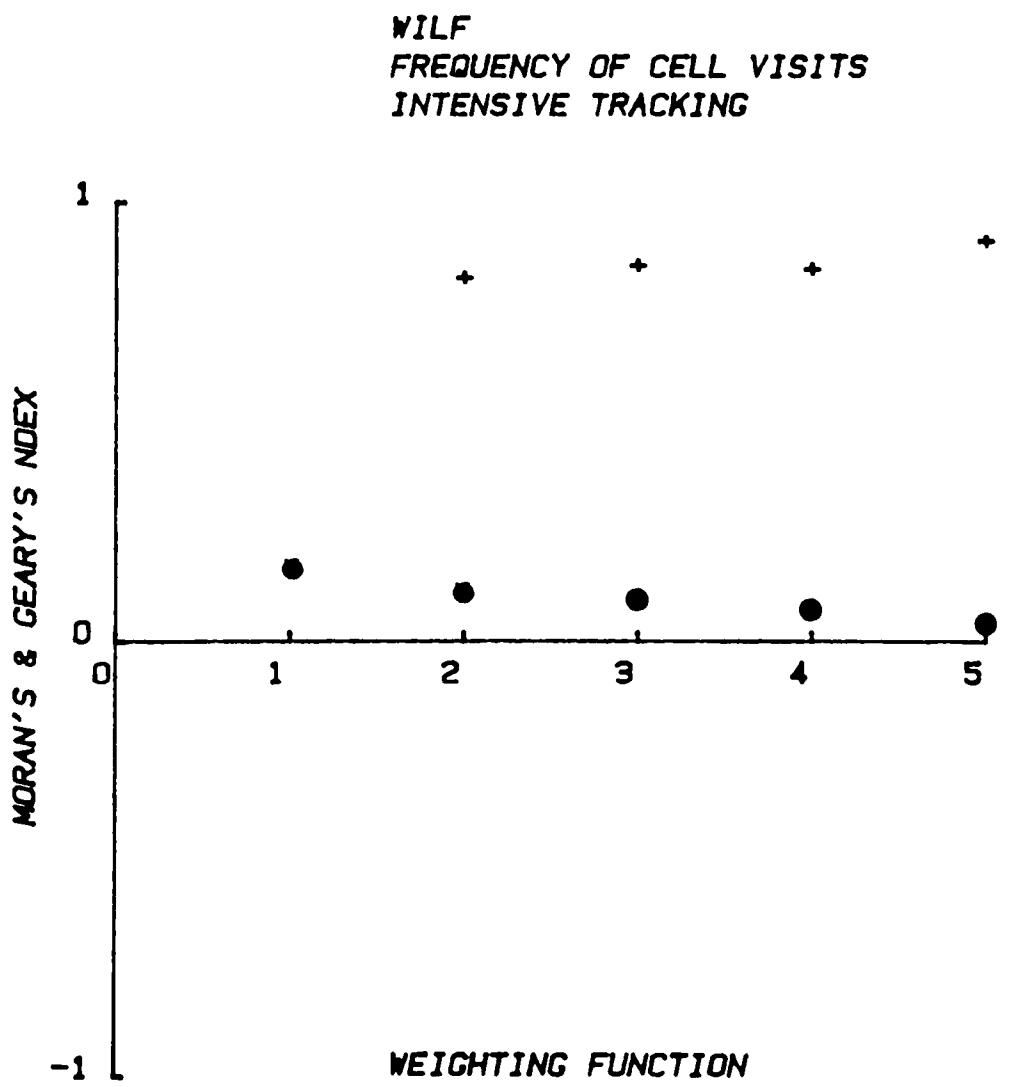


WILF : ACTIVE TIME (INTENSIVE TRACKING)

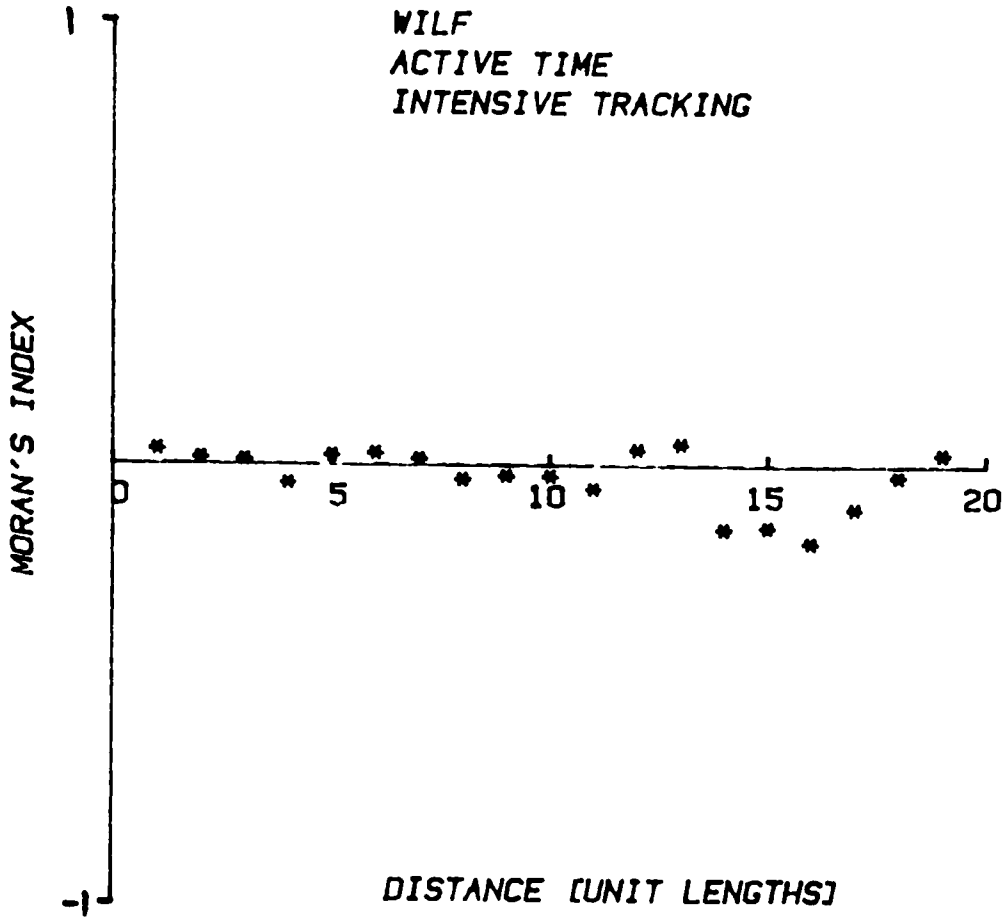
6-43b


WILF
FREQUENCY OF CELL VISITS
INTENSIVE TRACKING
MORAN'S INDEX
0
5
10
15
20
DISTANCE [UNIT LENGTHS]

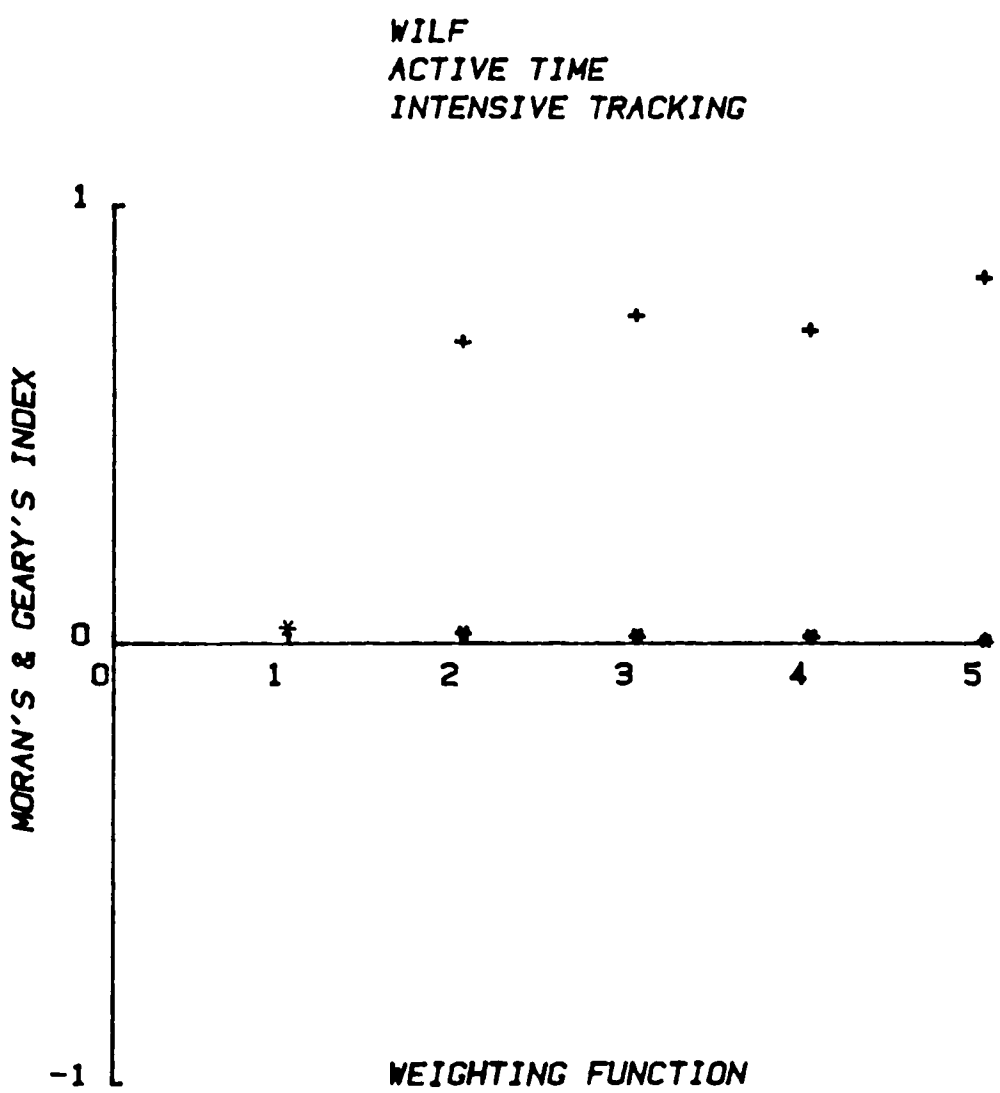
6-44a


WILF
FREQUENCY OF CELL VISITS
INTENSIVE TRACKING
MORAN'S & GEARY'S INDEX
1
0
-1
0
1
2
3
4
5
WEIGHTING FUNCTION

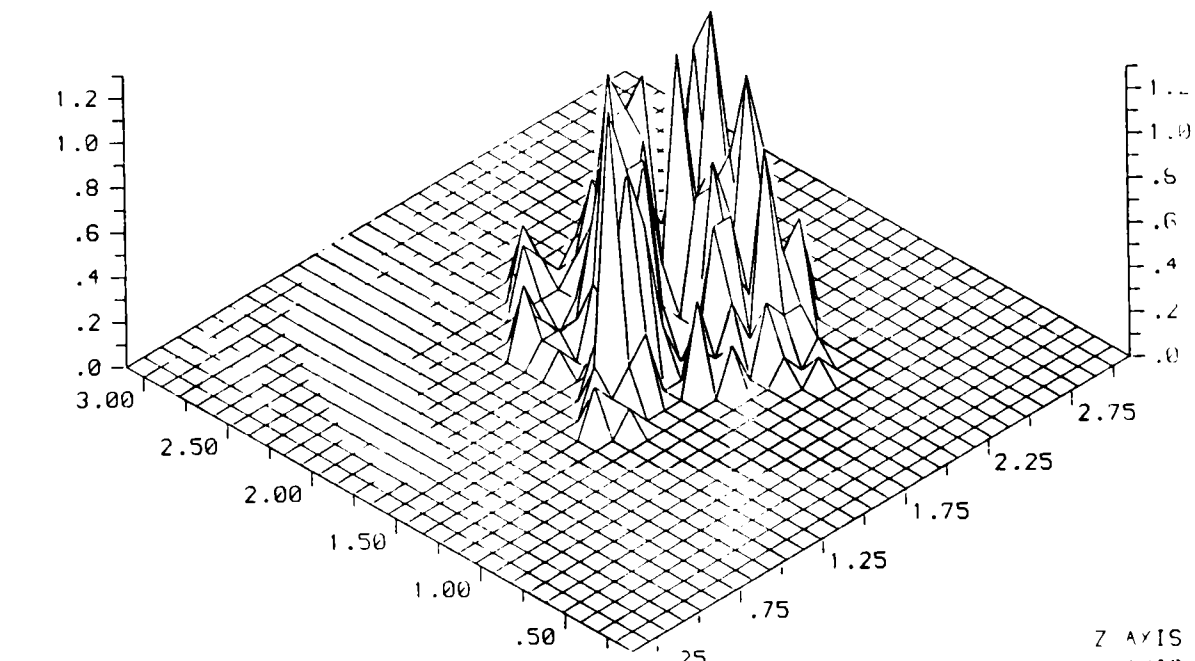
6-44b


WILF
ACTIVE TIME
INTENSIVE TRACKING
MORAN'S INDEX
1
-1
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5
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15
20
DISTANCE [UNIT LENGTHS]

6-45a

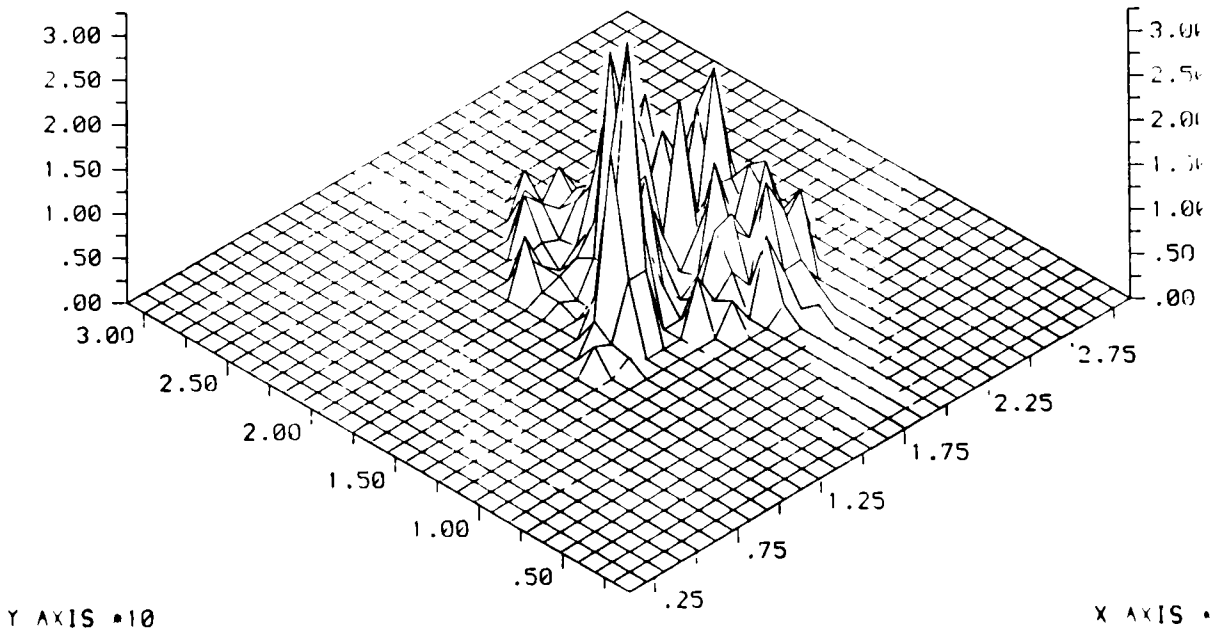

WILF
ACTIVE TIME
INTENSIVE TRACKING
MORAN'S & GEARY'S INDEX
1
0
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1
2
3
4
5
WEIGHTING FUNCTION

6-45b



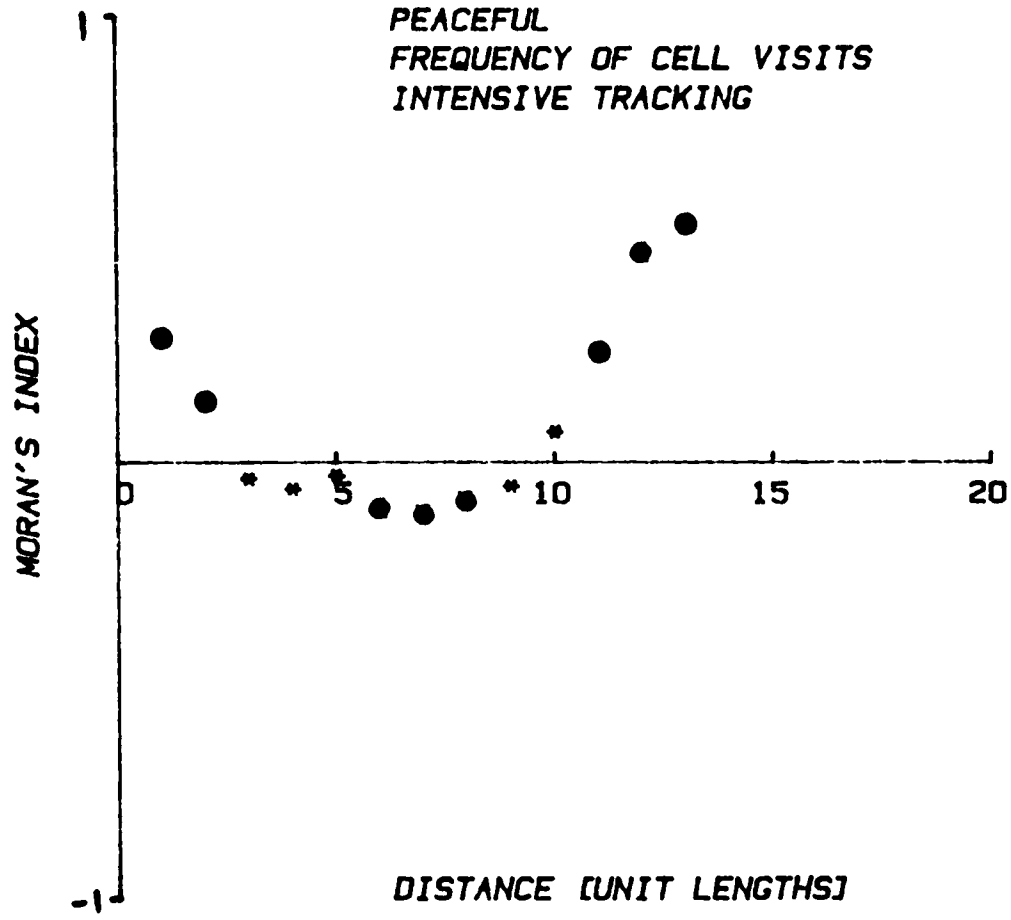
PEACEFUL : FREQUENCY OF CELL VISITS (INT

6-46 a

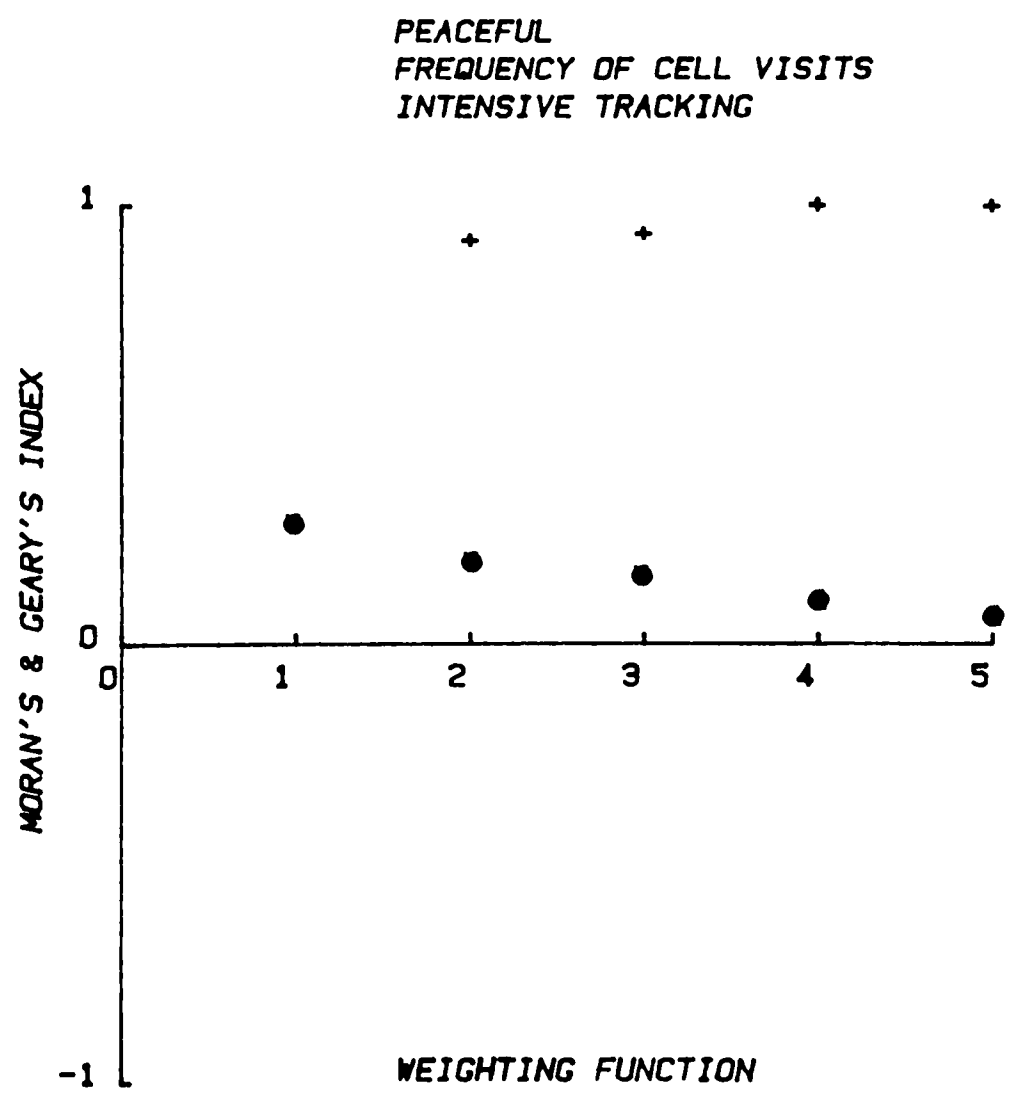


PEACEFUL : ACTIVE TIME (INTENSIVE TRACKI

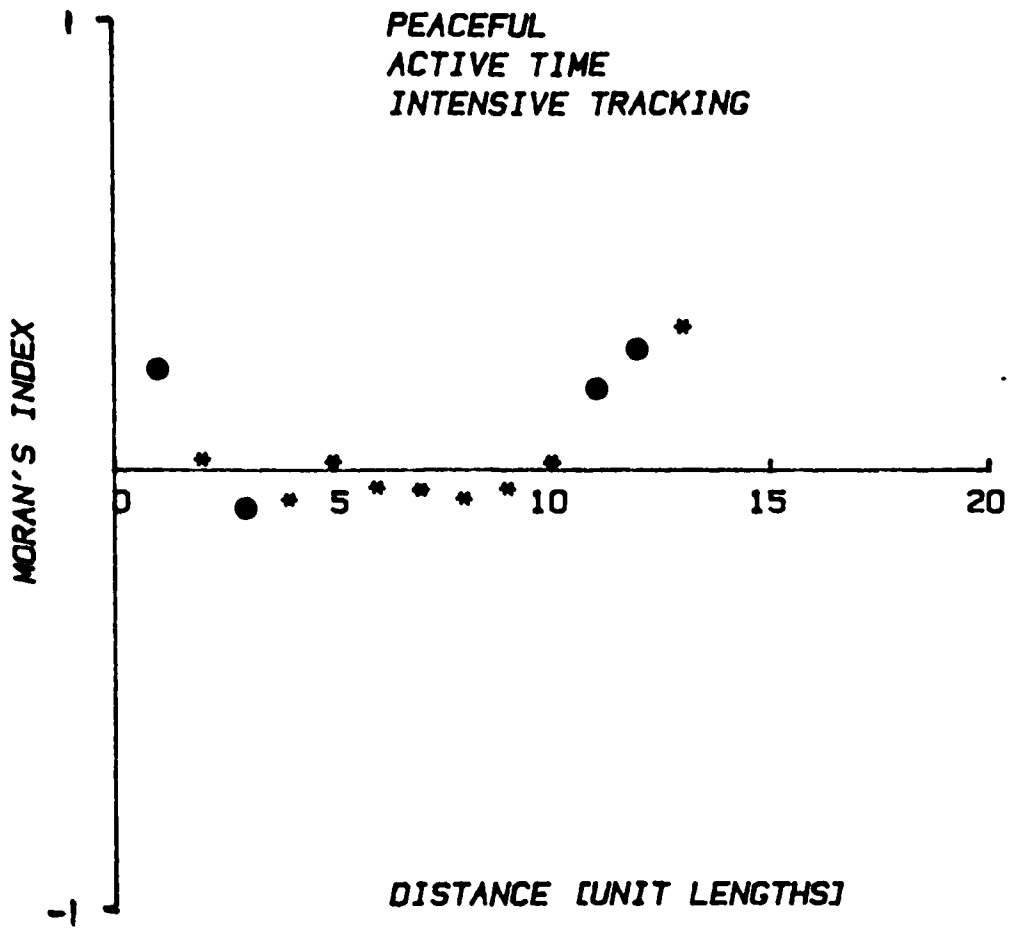
6-46 b


PEACEFUL
FREQUENCY OF CELL VISITS
INTENSIVE TRACKING
MORAN'S INDEX
1
-1
0
5
10
15
20
DISTANCE [UNIT LENGTHS]

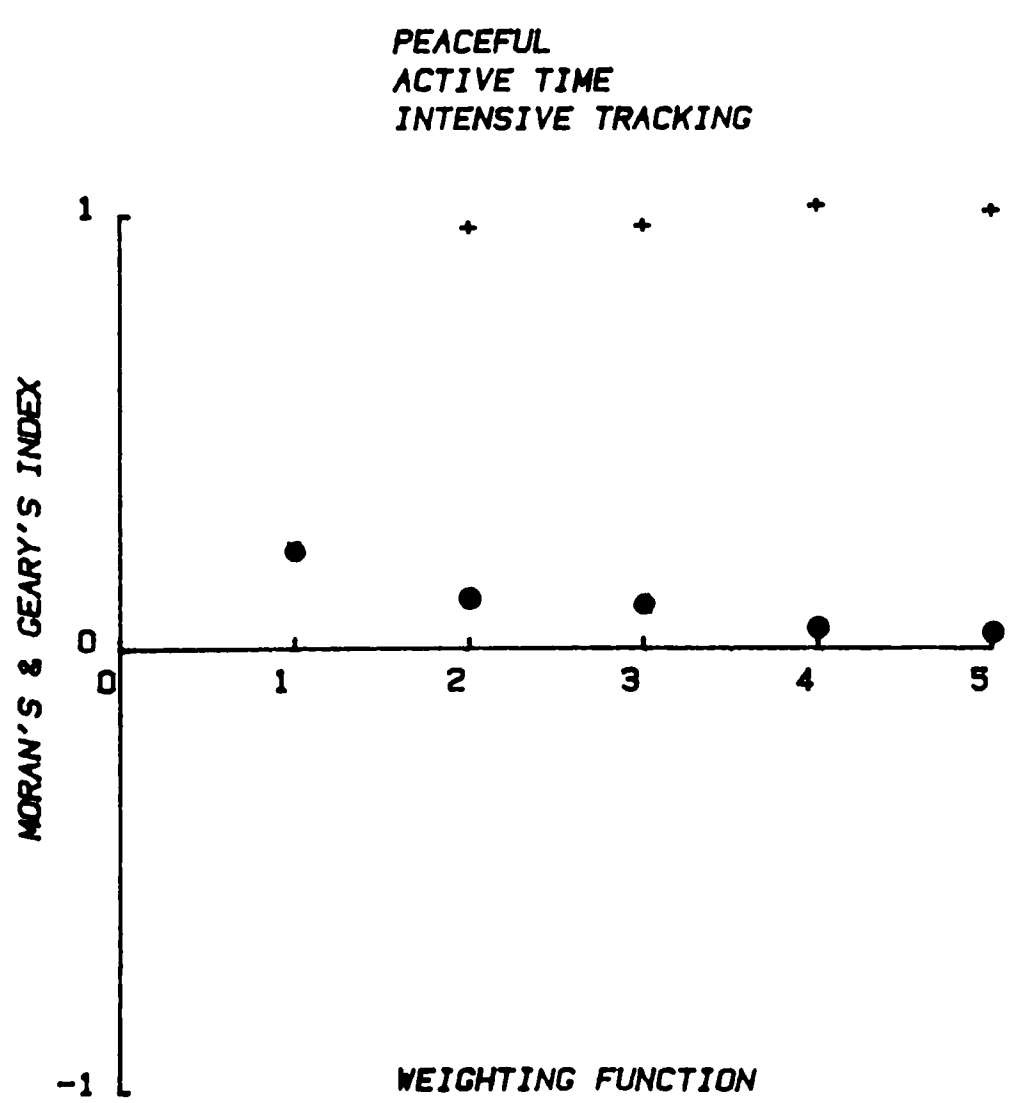
6-47a


PEACEFUL
FREQUENCY OF CELL VISITS
INTENSIVE TRACKING
MORAN'S & GEARY'S INDEX
1
0
-1
0
1
2
3
4
5
WEIGHTING FUNCTION

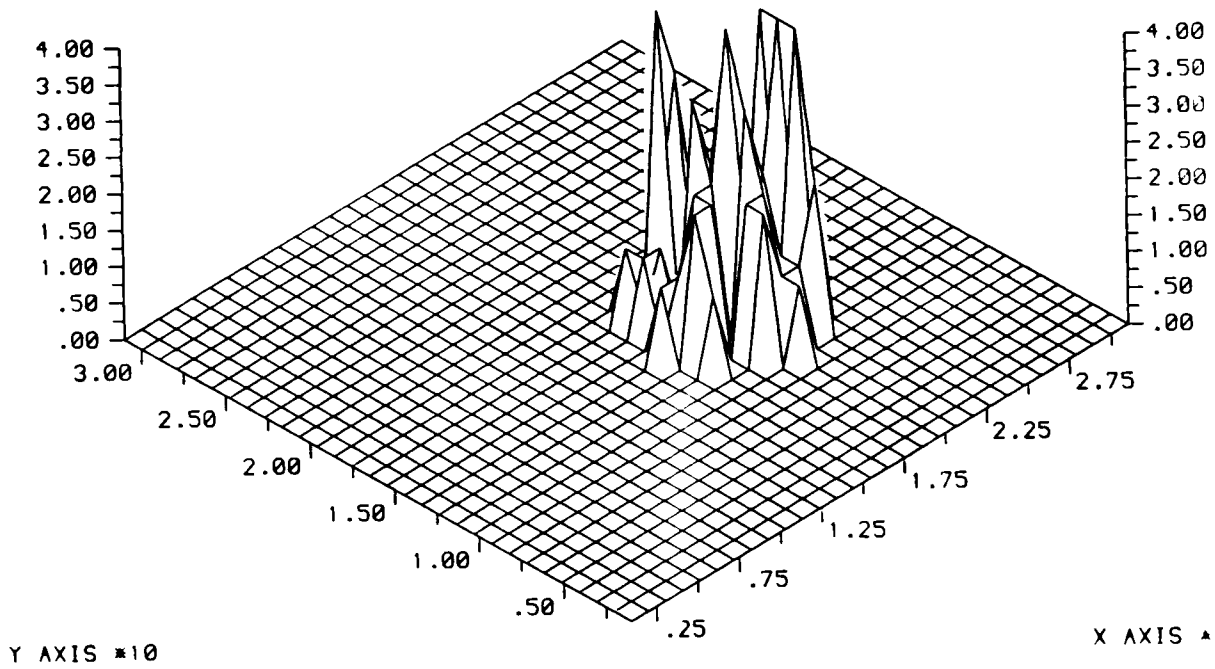
6-47b


PEACEFUL
ACTIVE TIME
INTENSIVE TRACKING
MORAN'S INDEX
1
-1
0
5
10
15
20
DISTANCE [UNIT LENGTHS]

6-48a

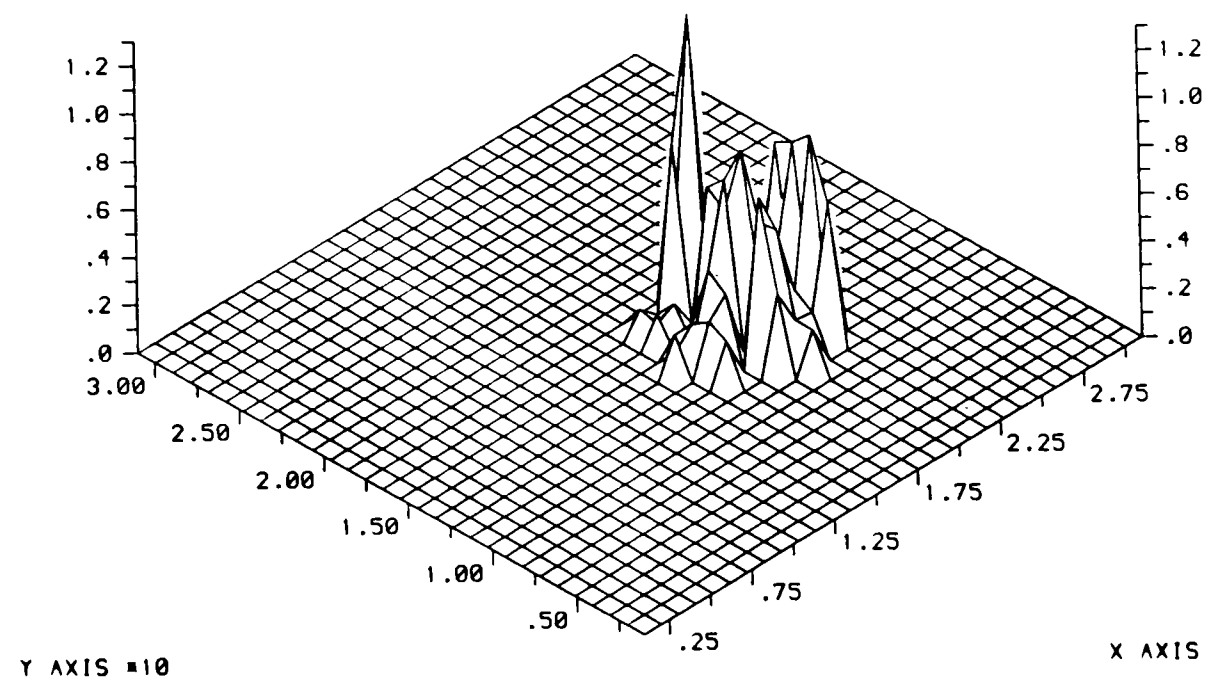

PEACEFUL
ACTIVE TIME
INTENSIVE TRACKING
MORAN'S & GEARY'S INDEX
1
0
-1
0
1
2
3
4
5
WEIGHTING FUNCTION

6-48b



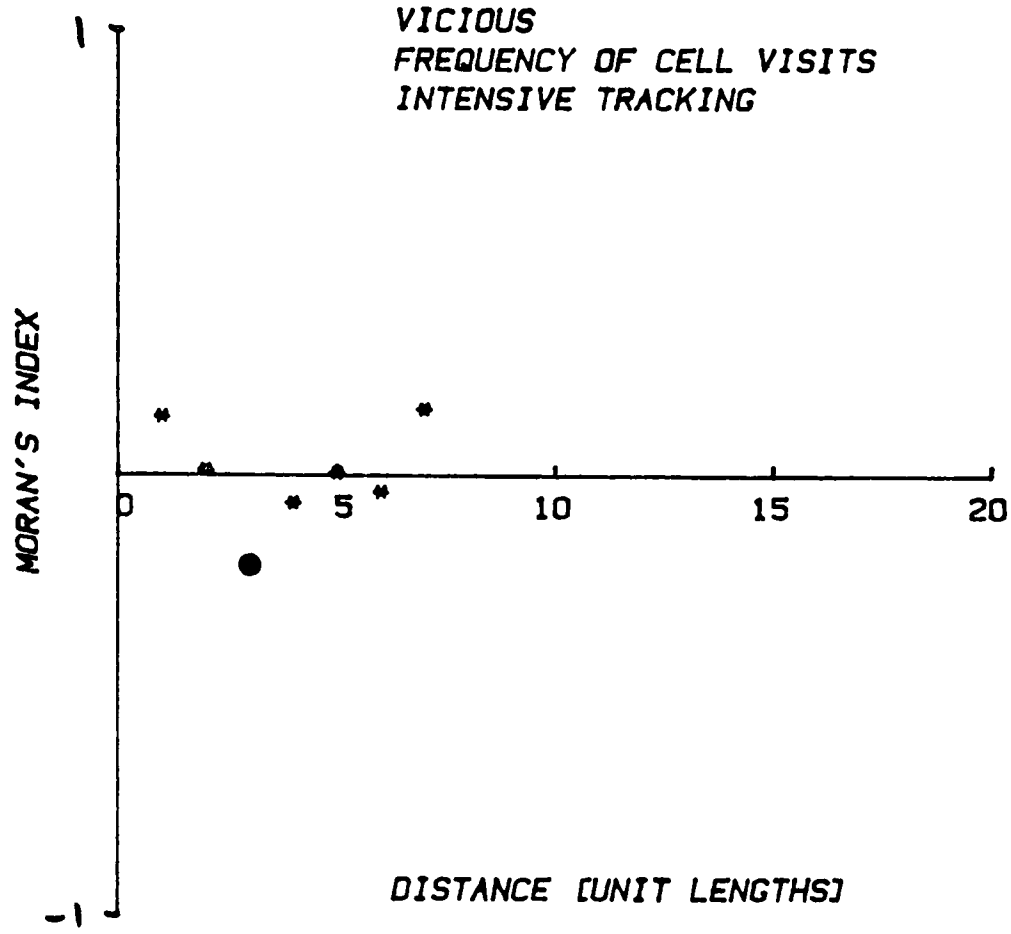
VICIOUS : FREQUENCY OF CELL VISITS (INT.

6-49 a

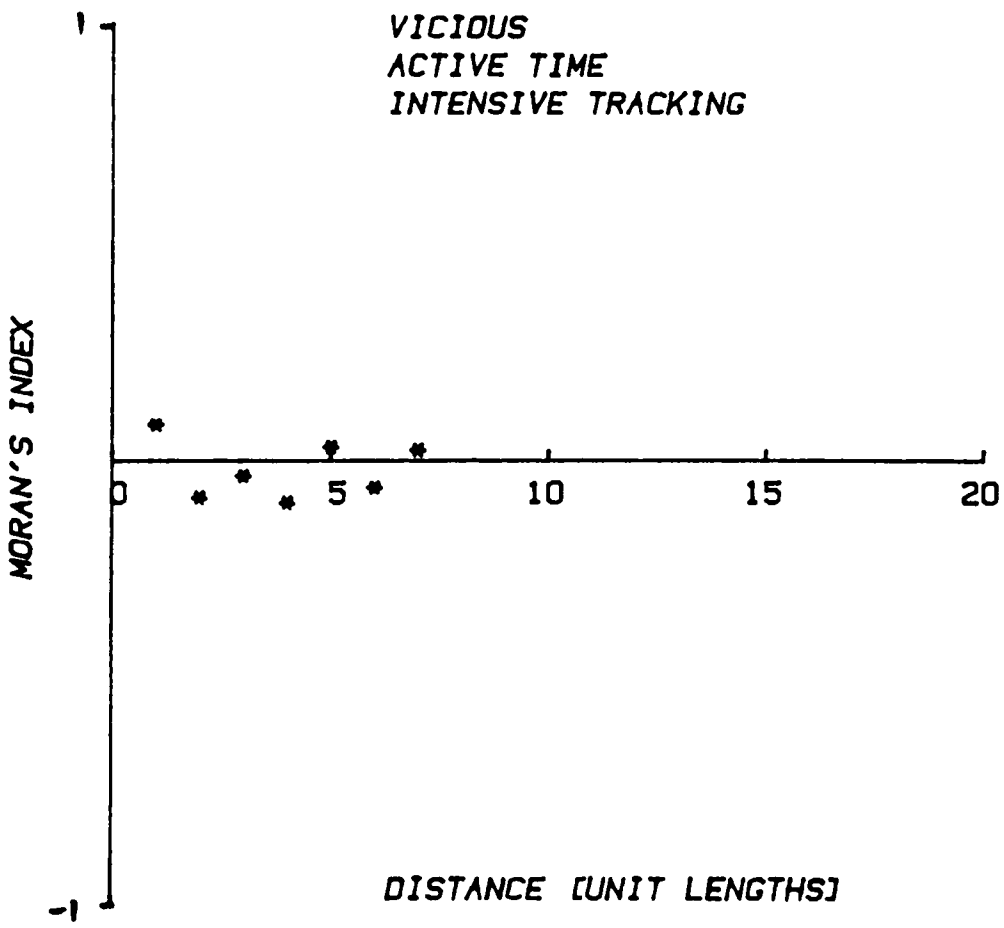


VICIOUS : ACTIVE TIME (INTENSIVE TRACKIN

6-49 b


VICIOUS
FREQUENCY OF CELL VISITS
INTENSIVE TRACKING
MORAN'S INDEX
1
-1
0
5
10
15
20
DISTANCE [UNIT LENGTHS]

6-50 a


VICIOUS
ACTIVE TIME
INTENSIVE TRACKING
MORAN'S INDEX
1
-1
0
5
10
15
20
DISTANCE [UNIT LENGTHS]

6-50 b

Figures 6.51-6.61. Range use by PODGE in the breeding season (04.05. 1982-12.05.1982)

Fig. 6.51-6.57a: Movements of PODGE in a given night. Each star represents a location. Lines connecting each location are the shortest paths between them. Note that the areas affected by these shortest connections are <u>not</u> considered in the analysis of range utilization, only the actual fixes! Movements are plotted on a section of the habitat map produced by program MAPITH (adapted and modified from Newdick (1983)); locations were plotted by program PLOT (Doncaster (1985)). Scale: 900 by 900 m.

Fig. 6.51-6.57b: 3D plots of duration of stay of PODGE in a given night, plotted on 50 by 50 m cells by program GINOPLOT and viewed from the southwest corner of the area. z-axis represents hours of stay. Other details identical to fox plots of Fig. 6.1-6.28.

Fig. 6.58 a+b: Summary 3D plots of (a) frequency of visits and (b) duration of stay for the entire week. Scales identical to previous 3D plots.

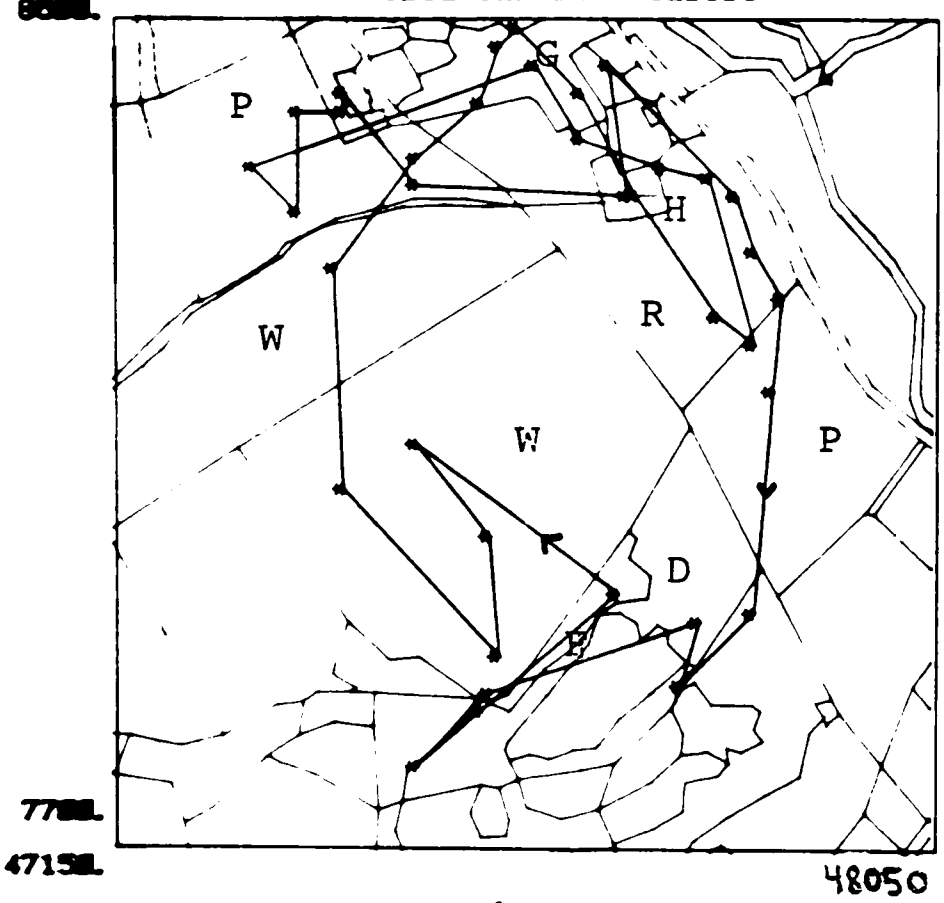
Fig. 6.59 a+b: Summary contour plots of (a) frequency of visits and (b) duration of stay for the entire week. See Figure captions of Fig. 6.1-6.28 for a more detailed explanation.

Fig. 6.60a, 6.61a: Spatial correlograms of range utilization for this week. Explanations and symbols identical as for Fig. 6.1-6.28.

Fig. 6.60b, 6.61b: Results of fitting the spatial models 1 to 5 (see 6.2.2., Appendix 5 and figure captions to Fig. 6.1-6.28 for a more detailed explanation) to utilization intensity data.
Filled circles: significant spatial autocorrelation coefficients (Moran's I) at p 0.05
Plusses: not significant spatial autocorrelation coefficients (Geary's c)

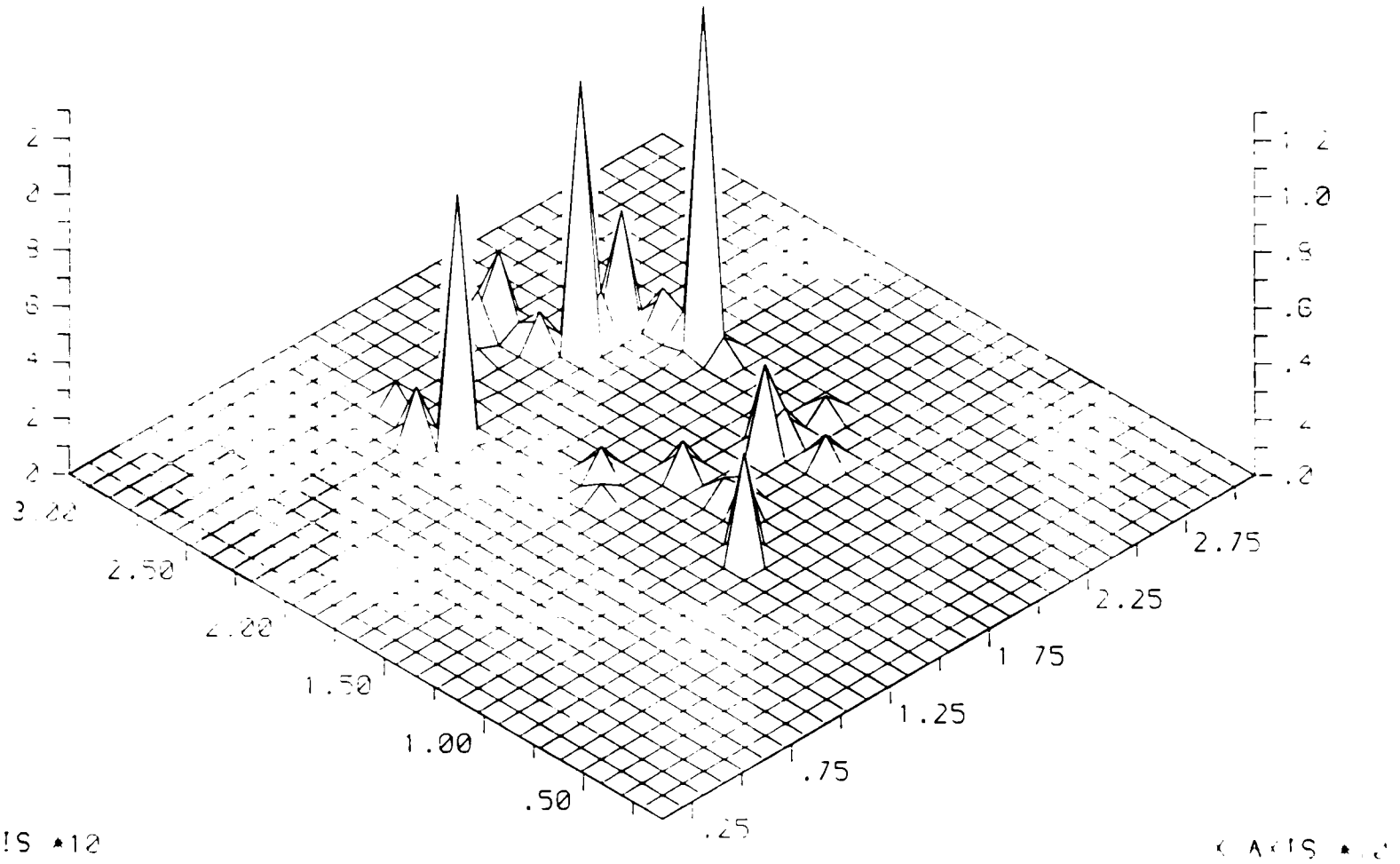
PODGE 820504 - 820505

TUESDAY



D = deciduous w.
F = fern (bracken)
G = Mrs. G.'s garden and adjacent woodl.
H = Home Farm
P = Pasture
R = Root crops
W = summer wheat

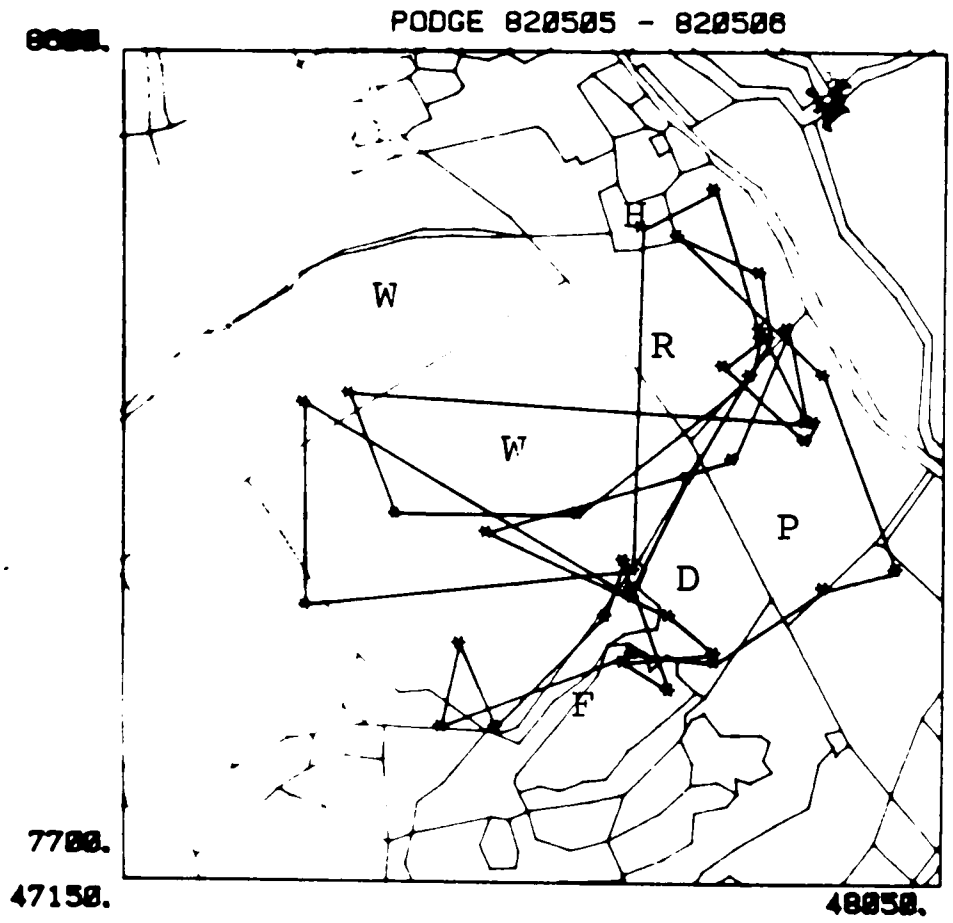
6-51a



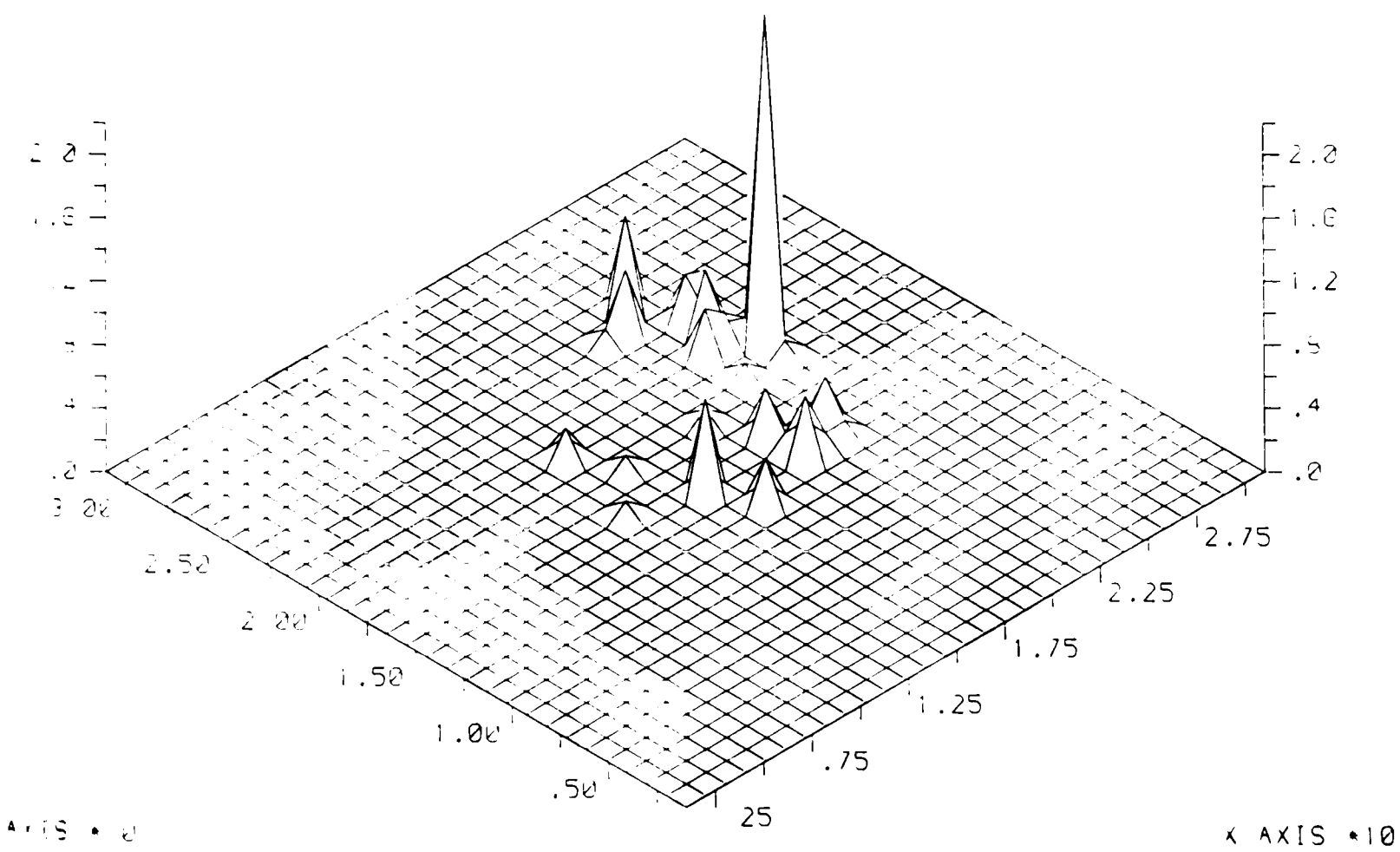
PODGE 84-05/05/82 ACTIVE TIME

6-51b

WEDNESDAY



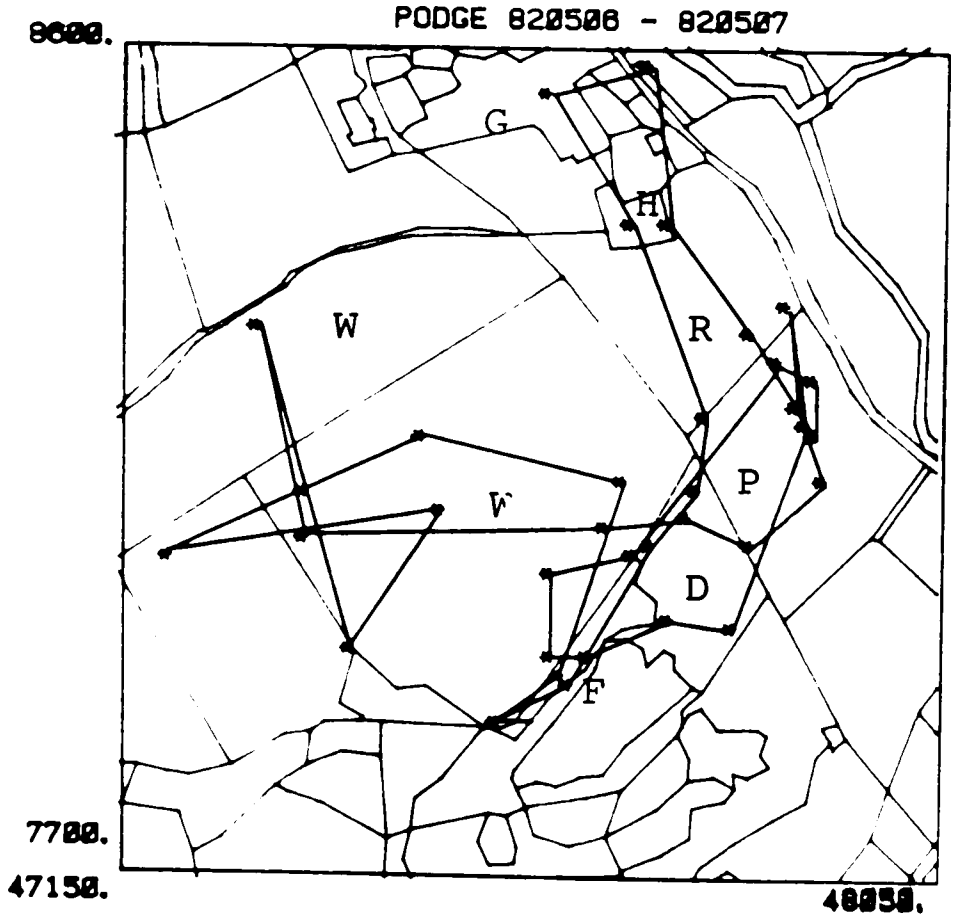
6-52a



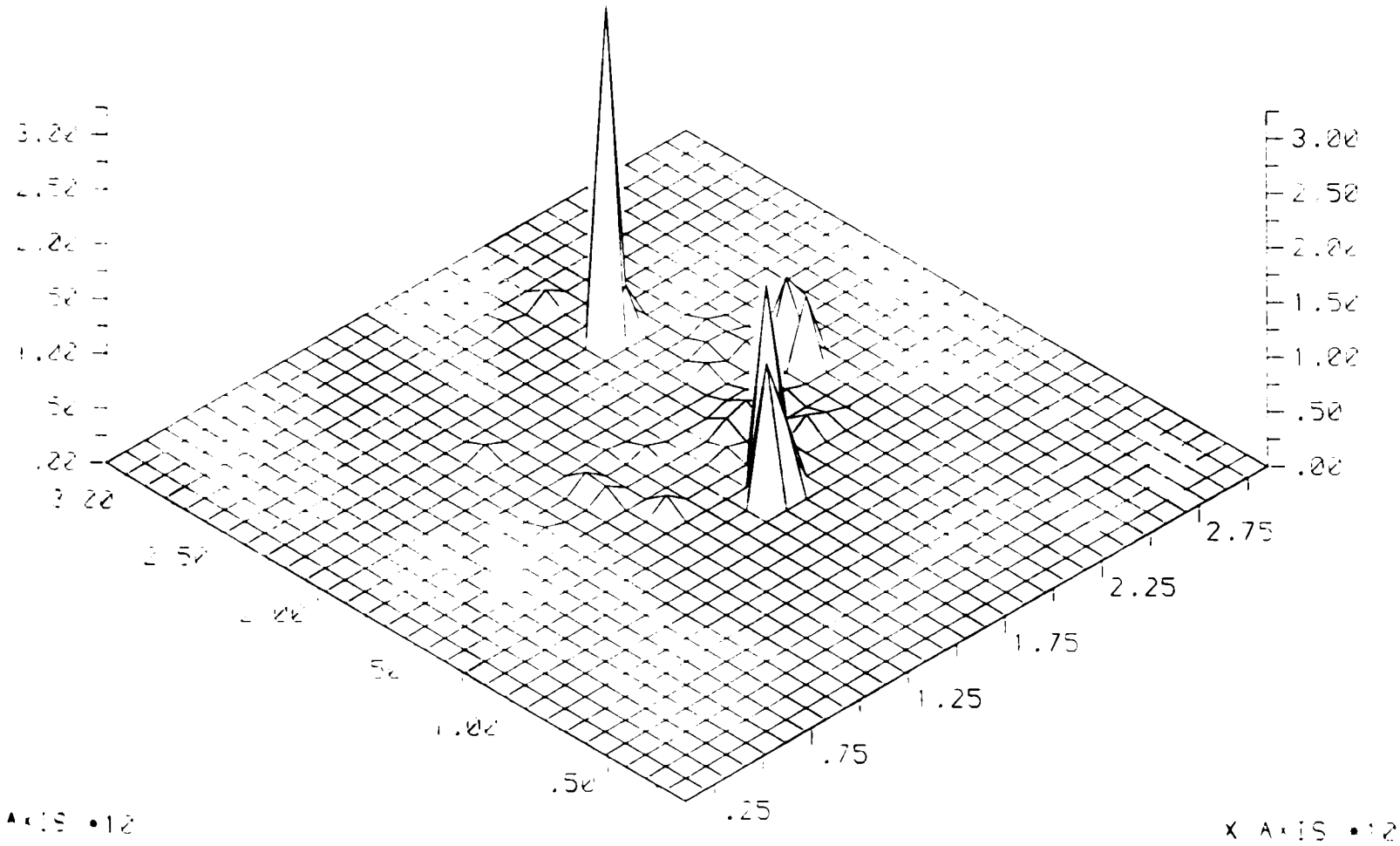
PODGE 05-06/05/82 ACTIVE TIME

6-52b

THURSDAY



6-53a

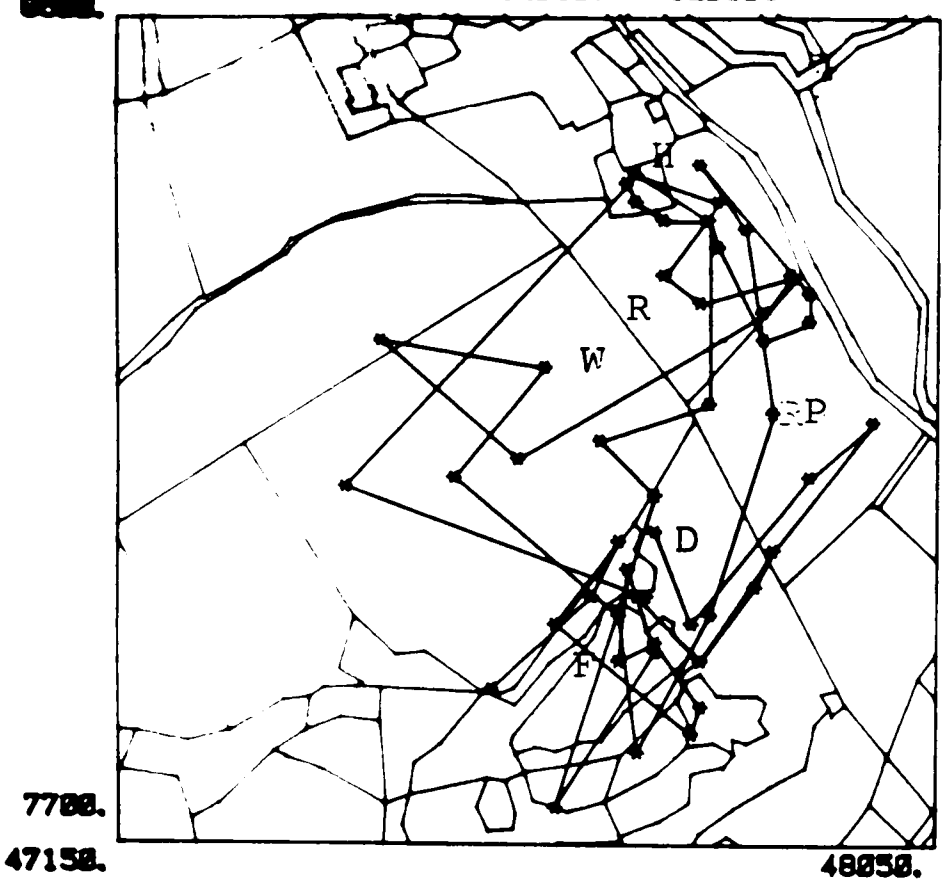


PODGE 06-07/05/82 ACTIVE TIME

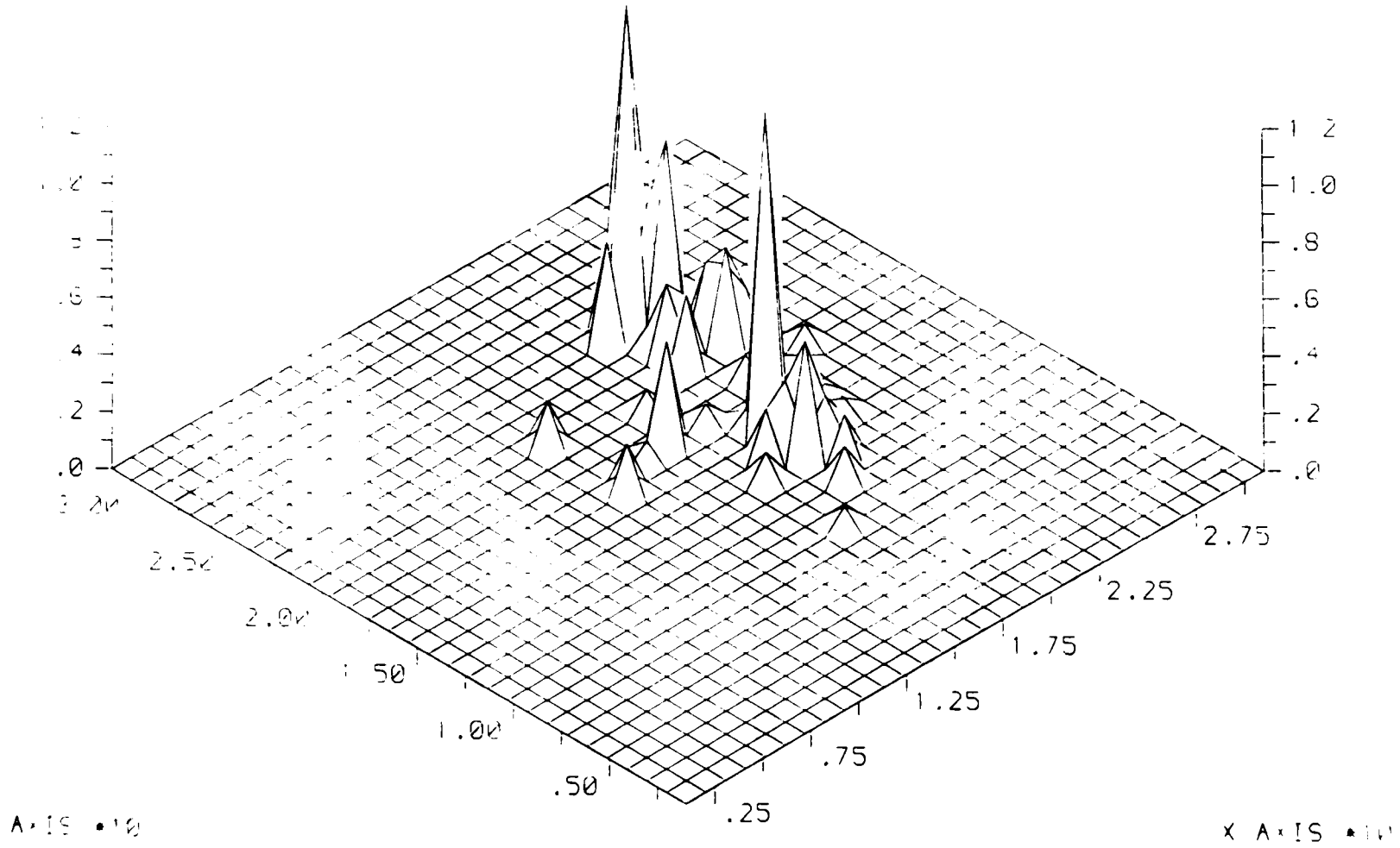
6-53b

FRIDAY

PODGE 820507 - 820508



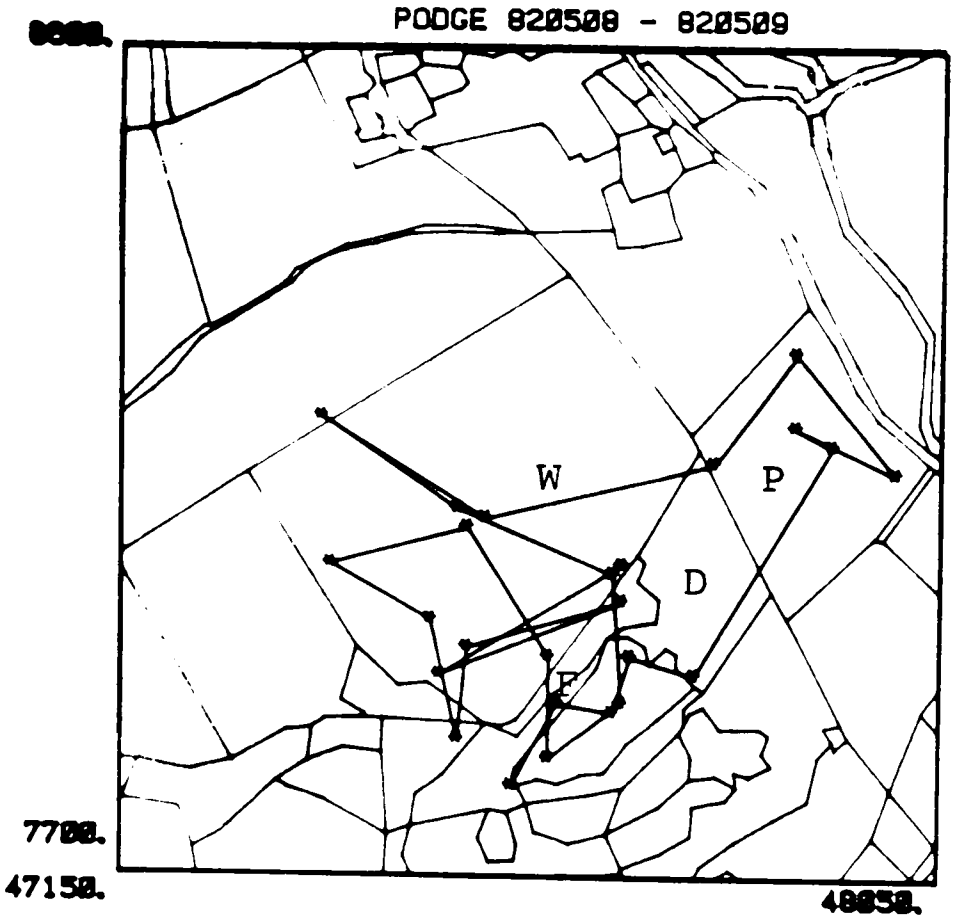
6-54a



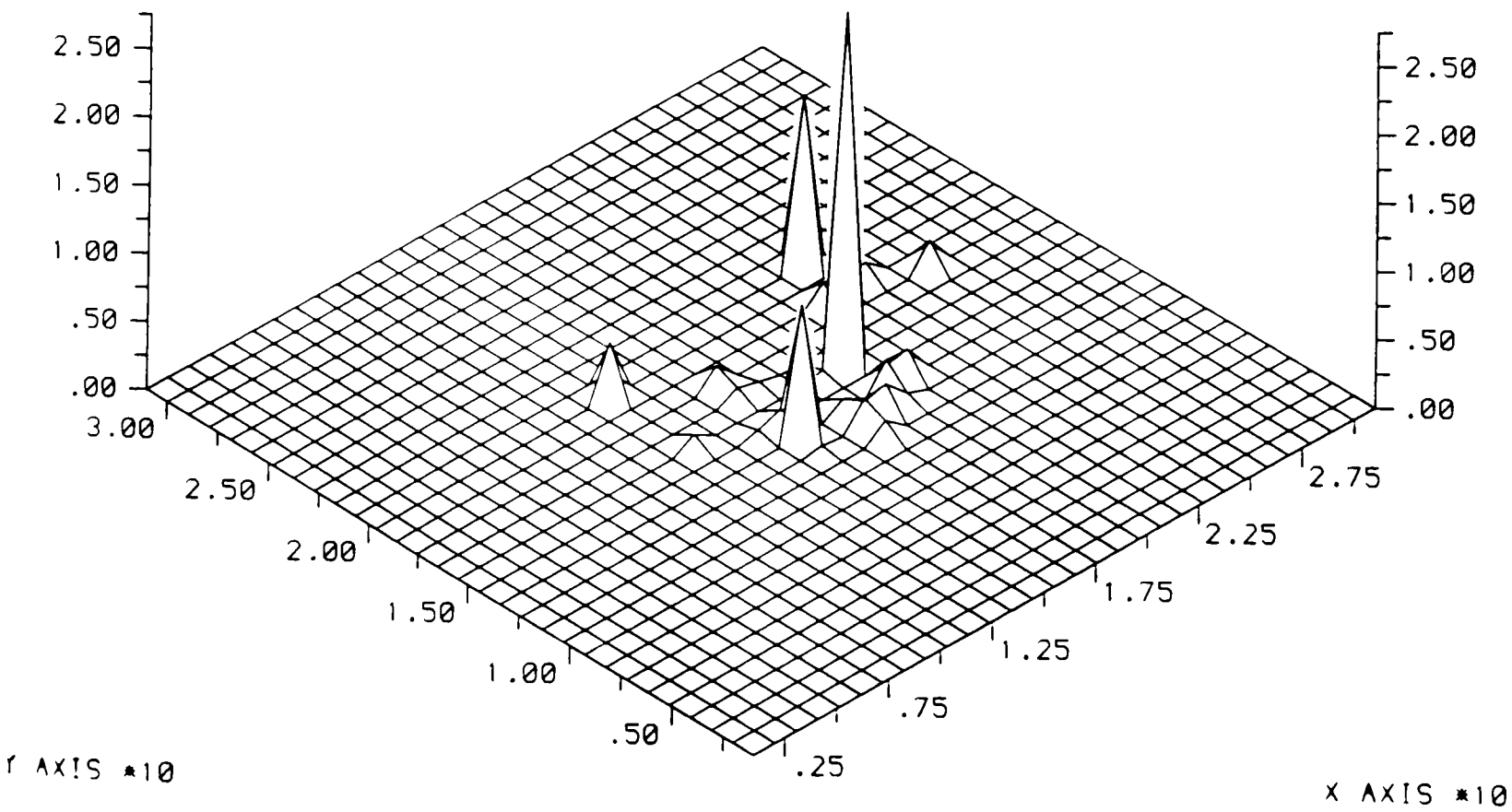
PODGE 07-08/05/82 ACTIVE TIME

6-54b

SATURDAY



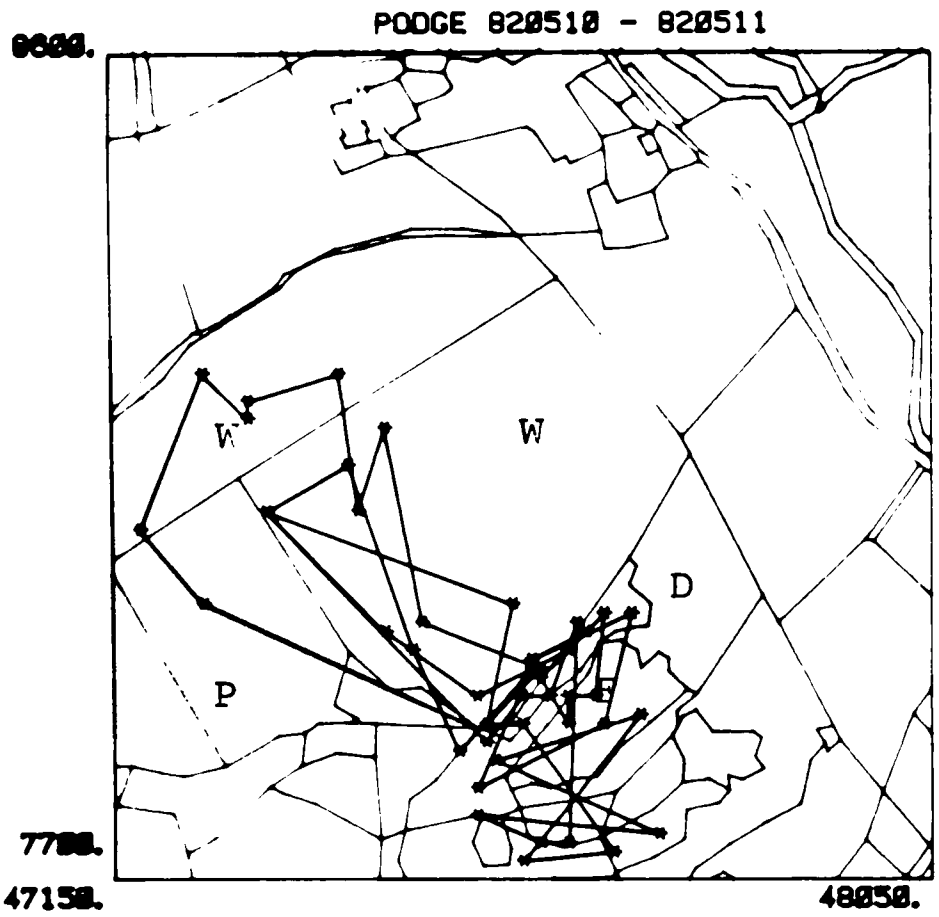
6-55a



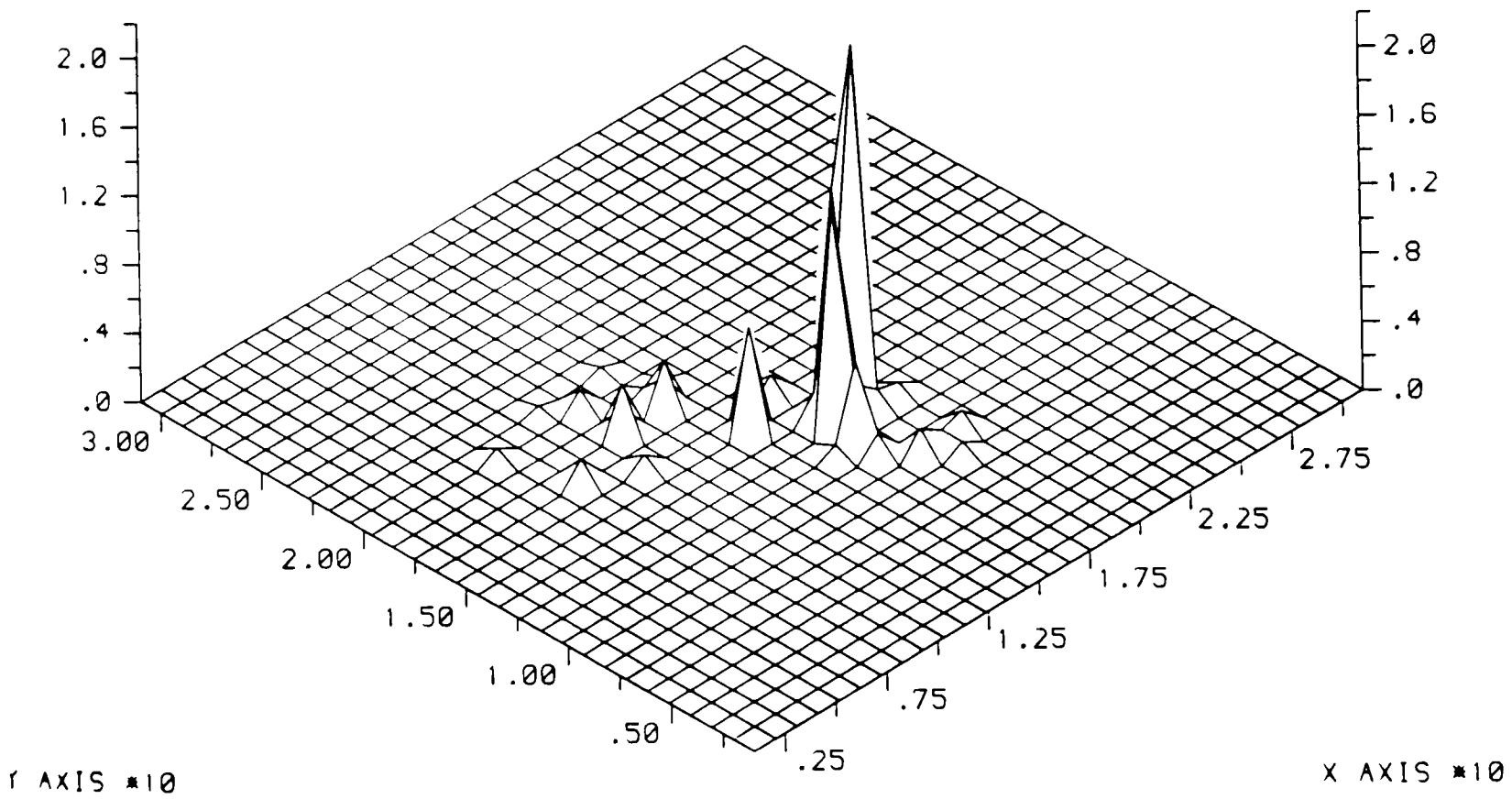
PODGE 08-09/05/82 ACTIVE TIME

6-55b

MONDAY



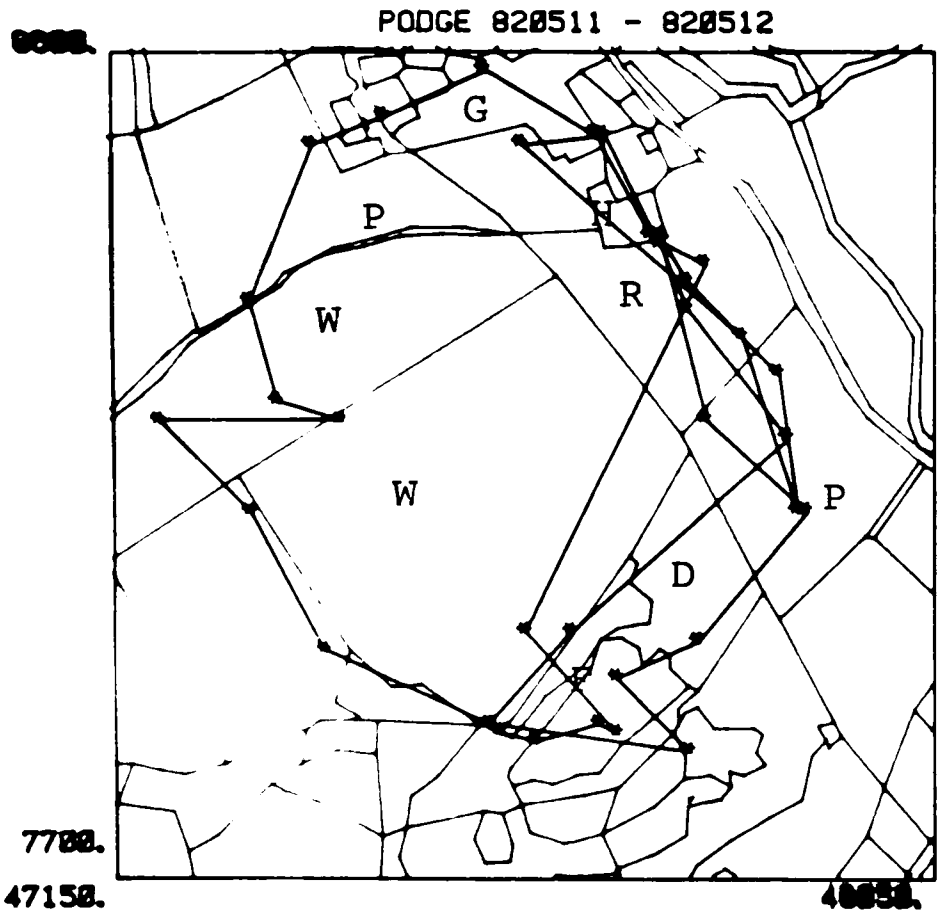
6-56 a



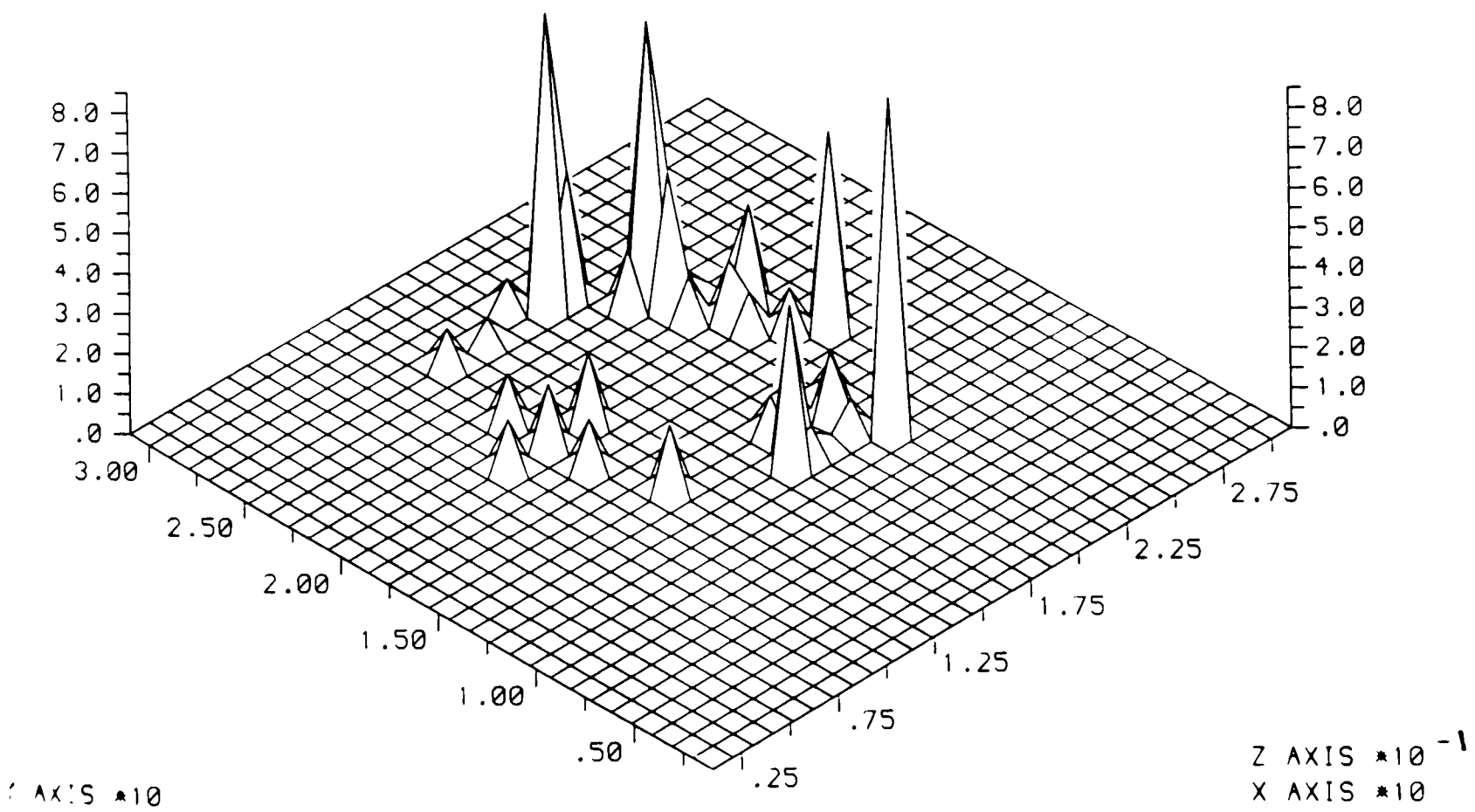
PODGE 10-11/05/82 ACTIVE TIME

6-56 b

TUESDAY

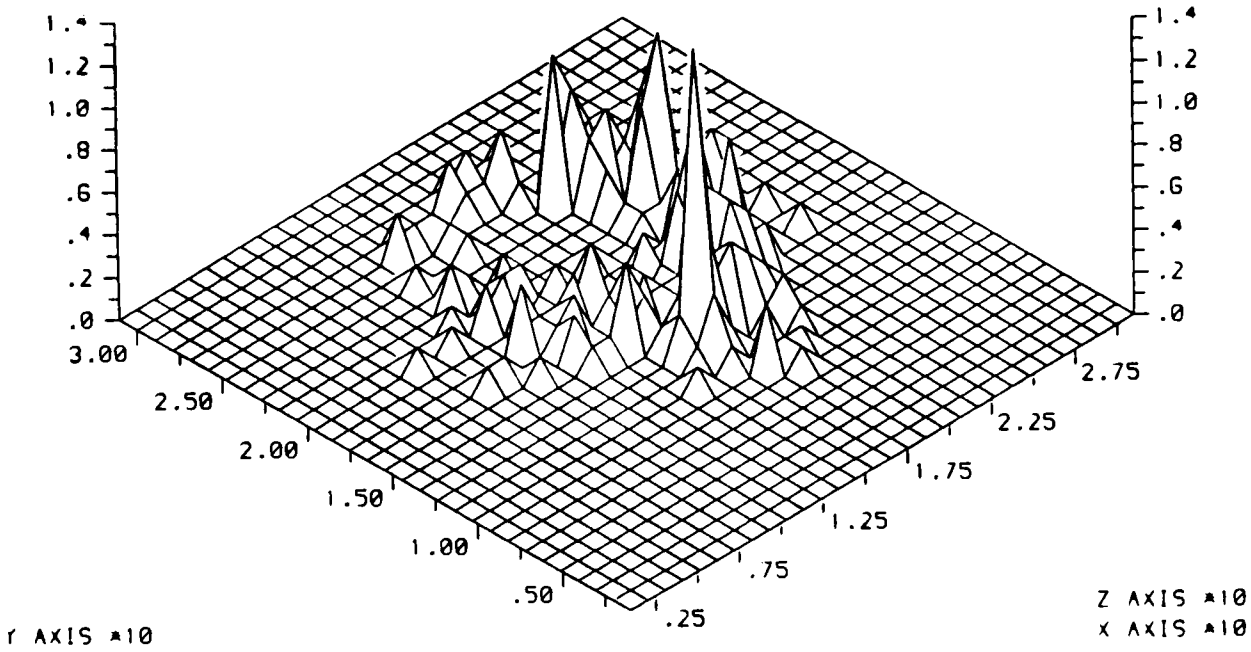


6-57a



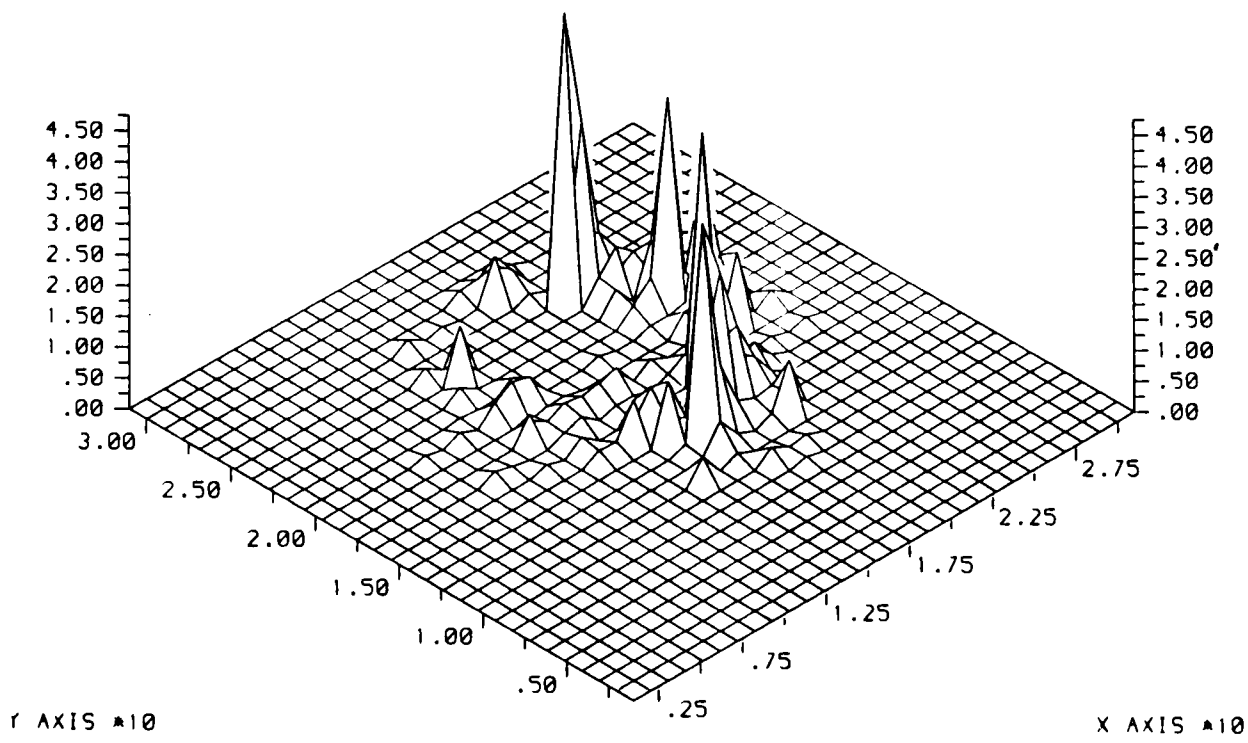
PODGE 11-12/05/82 ACTIVE TIME

6-57b



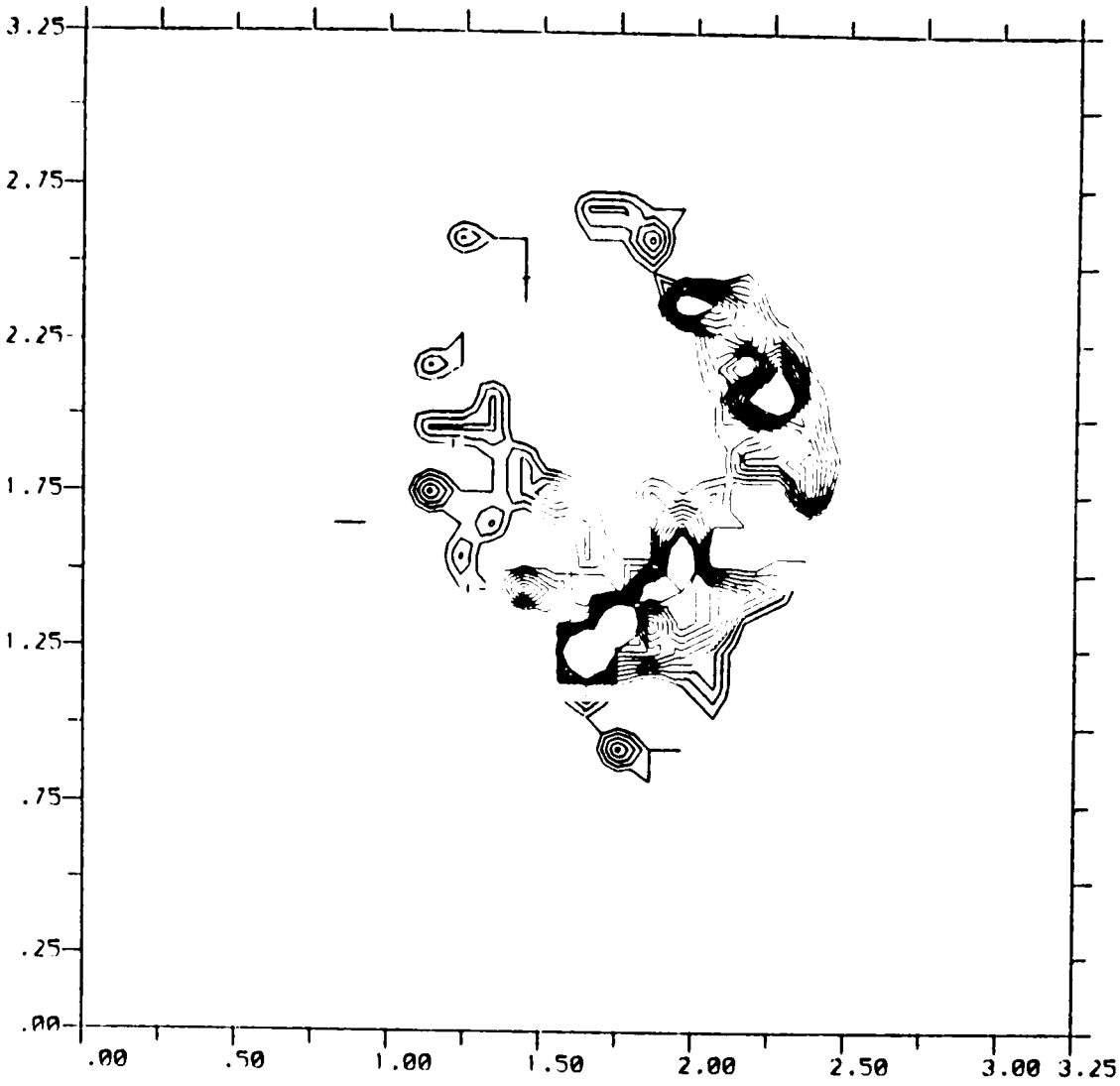
PODGE 04-12/05/82 FREQUENCY OF CELL VIS

6-58a

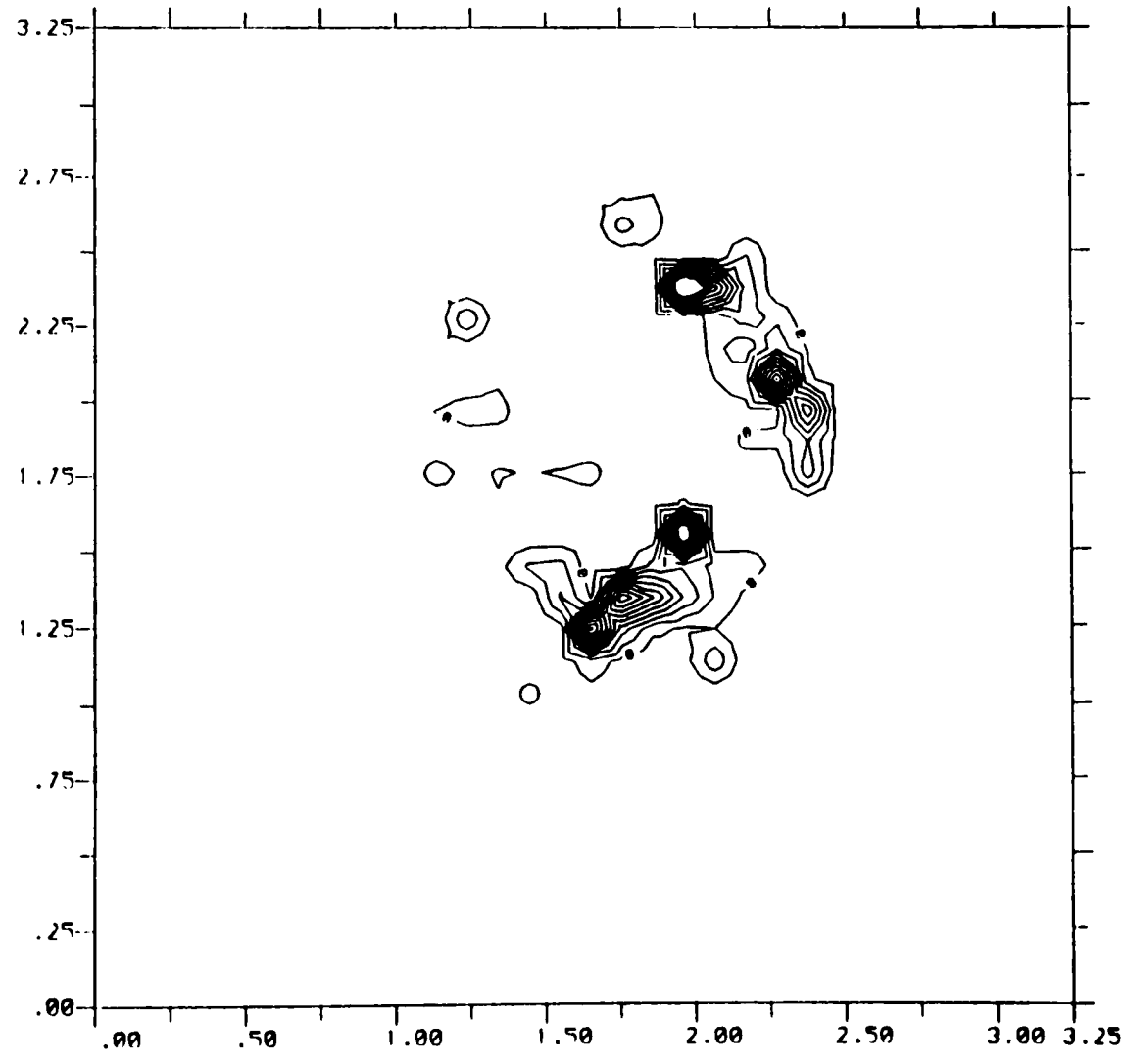


PODGE 04-12/05/82 ACTIVE TIME

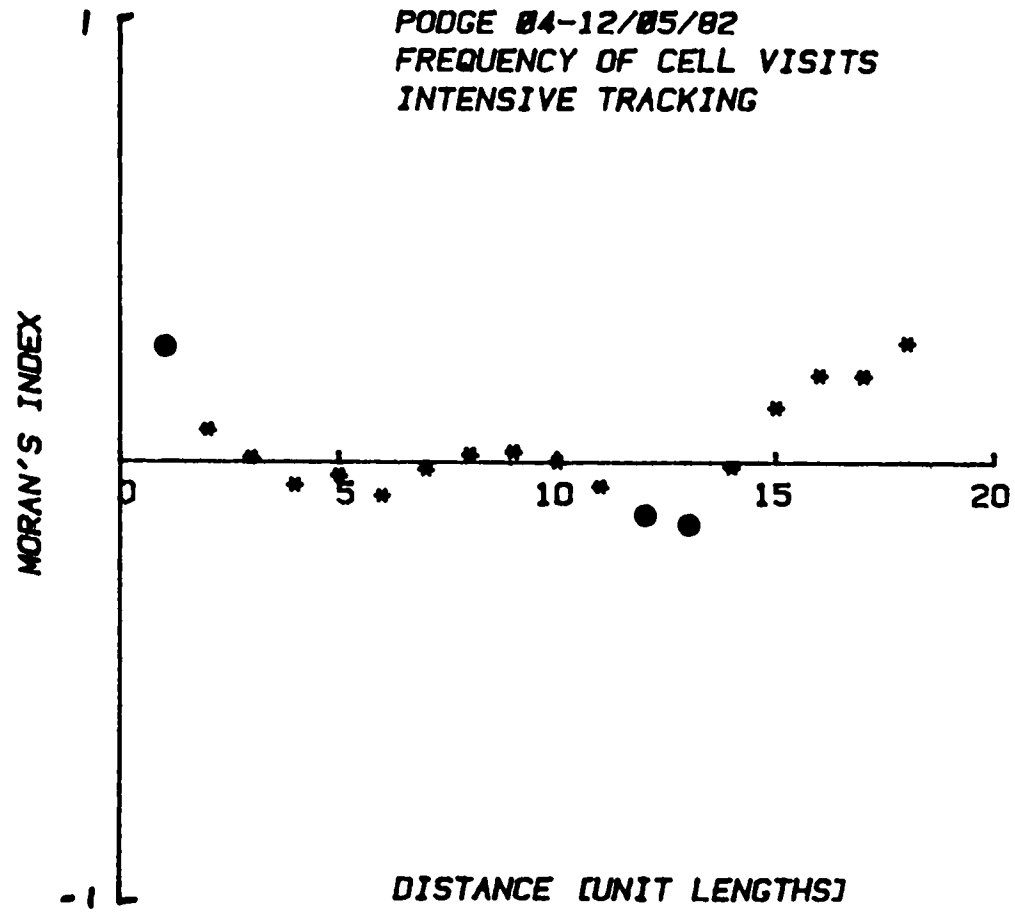
6-58b


3.25
2.75
2.25
1.75
1.25
.75
.25
.00
.00
.50
1.00
1.50
2.00
2.50
3.00
3.25
X AXIS *10
Y AXIS *10
CONTOUR STEP .44
PODGE 04-12/05/82 FREQUENCY OF CELL VIS

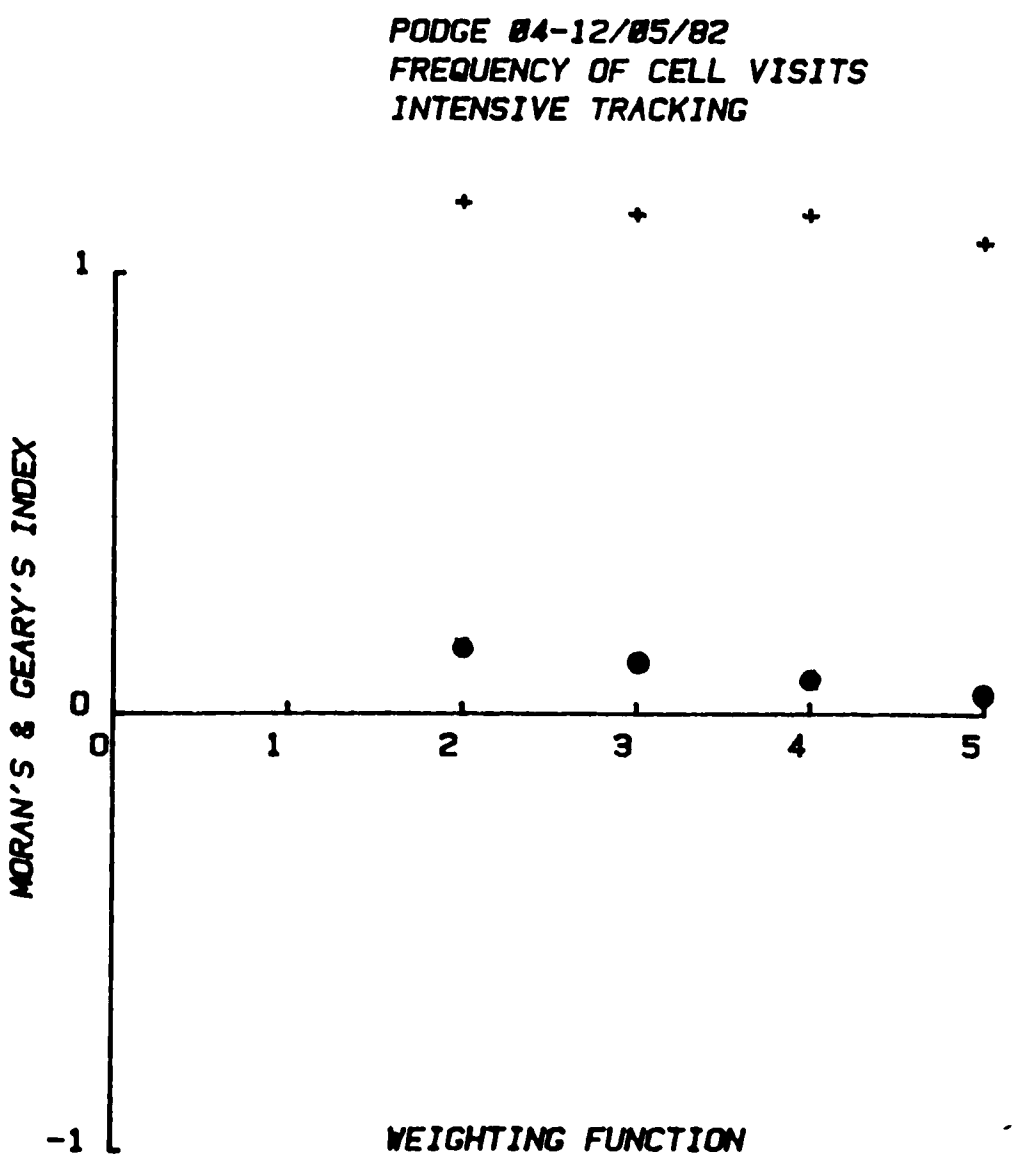
6-59a


3.25
2.75
2.25
1.75
1.25
.75
.25
.00
.00
.50
1.00
1.50
2.00
2.50
3.00
3.25
X AXIS *10
Y AXIS *10
CONTOUR STEP .33
PODGE 04-12/05/82 ACTIVE TIME

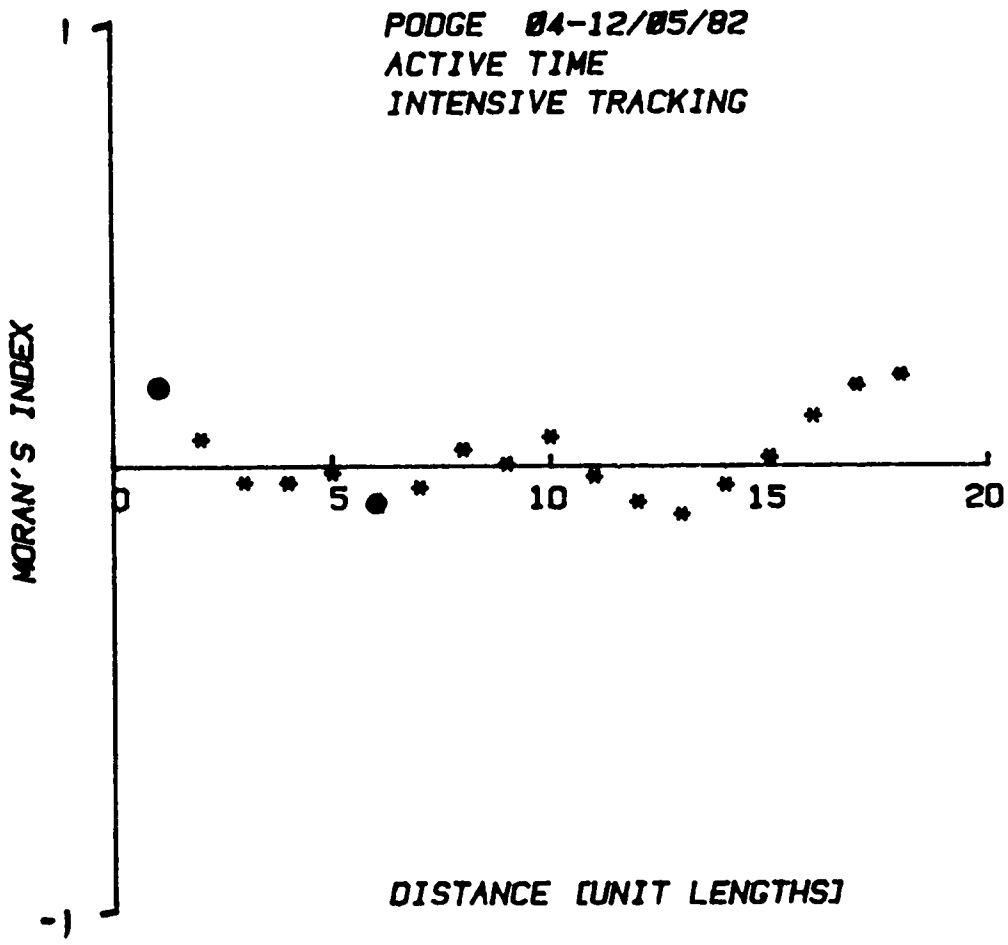
6-59b


PODGE 04-12/05/82
FREQUENCY OF CELL VISITS
INTENSIVE TRACKING
MORAN'S INDEX
1
-1
0
5
10
15
20
DISTANCE [UNIT LENGTHS]

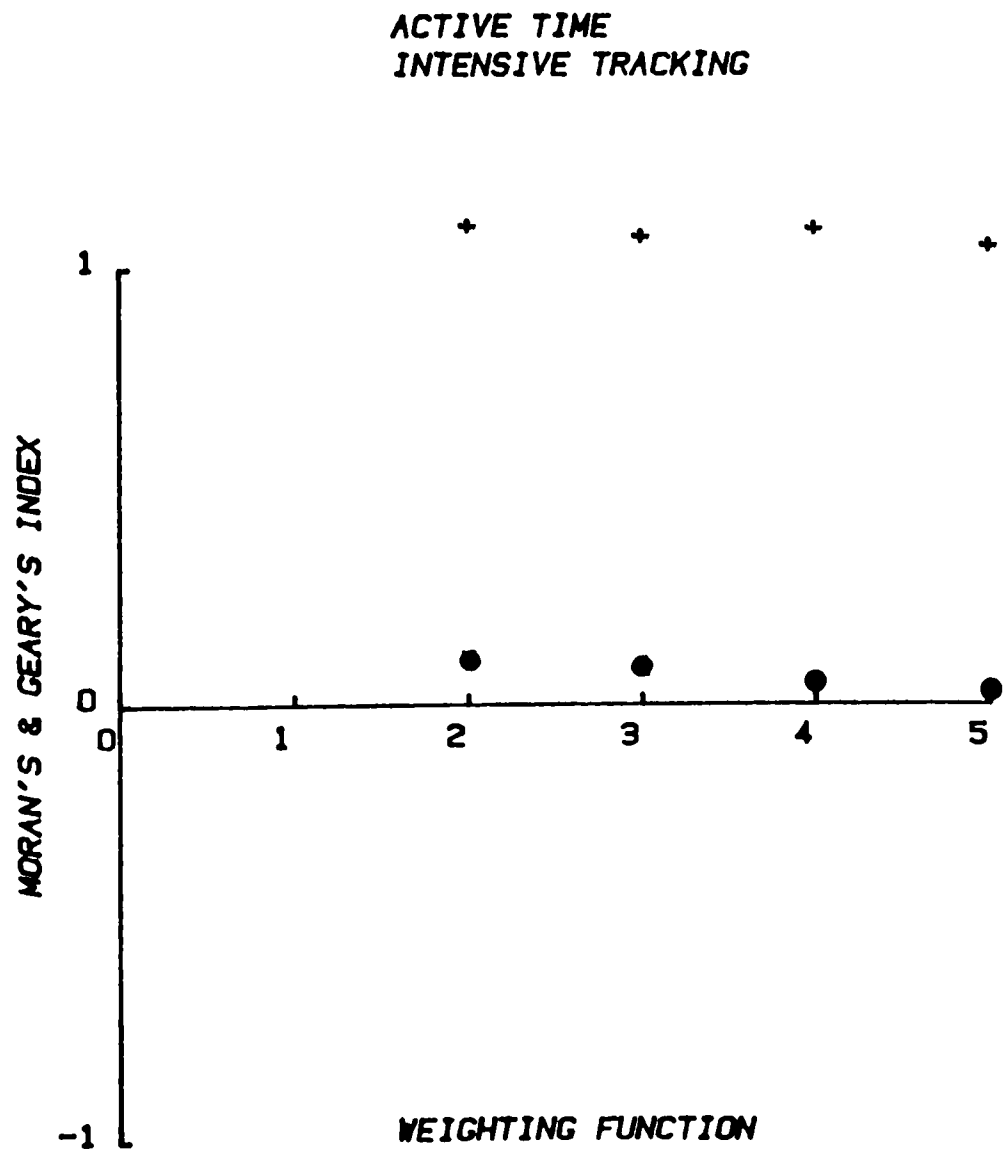
6-60a


PODGE 04-12/05/82
FREQUENCY OF CELL VISITS
INTENSIVE TRACKING
MORAN'S & GEARY'S INDEX
1
0
-1
0
1
2
3
4
5
WEIGHTING FUNCTION

6-60b


PODGE 04-12/05/82
ACTIVE TIME
INTENSIVE TRACKING
MORAN'S INDEX
1
-1
0
5
10
15
20
DISTANCE [UNIT LENGTHS]

6-61a


PODGE 04-12/05/82
ACTIVE TIME
INTENSIVE TRACKING
MORAN'S & GEARY'S INDEX
1
0
-1
0
1
2
3
4
5
WEIGHTING FUNCTION

6-61b

(DCA) of DCA run 19 (Chapter 2, program TCHANGE).

Programs DETSUM and DETPLOT compiled for each area unit times, frequencies and durations of visits. For patches, frequencies and durations of visits. For patches, durations of visits were classified by 5 minute intervals in 7 classes: less than 5 minutes, 5-10 min, 11-15 min, 16-20 min, 21-25 min, 26-30 min, more than 30 min. Program TRANSFORM compiled proportional and cumulative proportional frequencies. Program NEGEXP (adapted from a program written by A. Hart) used the original data of visit lengths to patches and compared them with expected visit lengths as derived from the function

$1 - e^{-x/t}$ t: parameters estimated as sample mean,

x: visit length (min).

This function describes the probability of occurrence of a certain visit length for a random process of movement, ie. equal probabilities to leave a patch independent of the visit length elapsed until a given moment. Differences between observed and expected distributions were tested with the Lilliefors test for the exponential distribution (Conover (1980: 362)), a test from the family of Kolmogorov-Smirnov goodness-of-fit tests.

The effect of the size of an area on its intensity of use and the relations between the two measures of intensity of use were investigated by linear regression analysis using the MINITAB statistical package available on both the departmental PDP-11 computer and the University's VAX 11/780.

6.2. Patterns of space use

The majority of studies considering the patterns of space use restrict their attention to the problem of reconciling a favourite model of home range usage with their data in order to calculate (home range size (section 5.1)). However, home range models make certain assumptions about the

utilization distribution (UD, Van Winkle 1975). These include an expected number of sites with a peak in activity (1 or several), the position of these sites within the range and the configuration of the range. Empirical justification of these assumptions is often lacking, for foxes at least (Macdonald, Ball & Hough 1980). Alternative non-parametric methods (Ford & Krumme 1979) can generate UD without a priori assumptions but, in their present formulation, still suffer from several drawbacks. They are based on an evaluation of activity summarized on a very coarse grid (7 x 7 points) and they do not indicate the location of activity relative to the real plane. Furthermore, they are most valuable for analysing data with little information per individual gathered for many individuals; consequently UDs are often generated by averaging over several individuals (the population UD or PUD). In view of these restrictions, application of either of these approaches seemed inappropriate.

In the following sections I shall concenrate on the following aspects of space use:

(1) Sites with peaks of activities:

- how many centres of activity are present?
- where are they located within a range?
- does the number of these sites and their distribution within a range vary between individuals?
- how useful is the concept of a centre of activity?
- do centres of activity coincide with peaks of resources?

(2) Scaling of space use:

- do regions of similar use exist?
- how large are they?
- in what fashion are they distributed?

(3) Predictability of space use:

- how well can use of a given area be predicted from the use of other

areas?

- how does predictability vary with distance between predicted and predictor areas?

(4) Variation within groups:

- how do space use patterns (point 1 to 3) vary between members of the same group?
- are there sex-specific differences?

Range use was investigated by evaluating measures of the intensity of use on a grid with cell size 50 by 50 metres, as described in section 6.1. Fig. 6.1-6.29 (foxes), 6.30-6.50 (badgers) and 6.51-6.61 (foxes) illustrate range use patterns and present the results of the computations of spatial autocorrelation functions. I shall start with an analysis of range use by foxes. A detailed description of one week of intensive tracking of a breeding vixen introduces the subject and conveys an idea of how to interpret the measures of intensity of use. A second detailed description of range use (by OLDMAHOG, section 6.2.2.) explains the interpretation of the Figures and precedes a condensed account of the remaining individuals.

6.2.1. One week with PODGE in the breeding season

Fig. 6.51-6.57 (at the end of section 6.2) describe the movements of the vixen PODGE in seven nights in early May 1982 (note that the last digit of the figure numbers corresponds to the appropriate number of each tracking night). The top picture of each figure shows the sequence of movements in relation to the structure and the habitats of the area while the bottom picture (viewed from the southwest) plots the duration of stay in each area on a grid of 50 by 50 m cells.

Signals were recorded automatically at the den every 15 min during the

daytime throughout this week, and confirmed that PODGE spent all day with her cubs in the den.

NIGHT 1: at 22.12 hours, PODGE leaves the area around the den with the cubs behind and proceeds rapidly zig-zagging over two large fields in the west of the range towards the back of Mrs. Gardiner's garden (22.25 hours), where food scraps are frequently provided for the foxes. PODGE then (22.30) moves towards HOME FARM where she spends 46 minutes around the barns, probably hunting rats, mice and collecting scavenge. She then visits the field south of Home Farm and moves quickly to the pasture field where she remains until 00.37, foraging for earthworms. She then moves back to the field south of the farm (root crops). Observations suggest that she is hunting for both mice and earthworms. She then passes the farm, moves onto the pasture fields southwest of Wytham Abbey at 1.13 (a good area for earthworms), before she moves back, passing the farm at 3.42 and returning to the den at 4.55 via the east side of the range.

Several interesting features emerge from PODGE's movements. Firstly, she spends hours at sites of special interest but moves quickly between them (Fig. 6.51b). Secondly, during her movements she visits, briefly, most of the range borders. As subsequent nights show (e.g. Fig 6.53b) these were not the most direct routes open to her. Finally, PODGE does not return to her cubs until early morning. This could put them at risk (Klenk 1971), unless the other group members are contributing to their well-being (e.g. Macdonald 1979b).

NIGHT 2: PODGE tracks again a portion of the western range border, at 00.30 and 2.12, spends 6 minutes at the farm (at 21.50) and ignores the northern range section. Instead, she concentrates on the field with root crops and the neighbouring pasture field in the south east. As in the previous night, she does not travel in direct route to her den, but visits the south east corner of the range, returning to the cubs at 5.40.

NIGHT 3: western border sections are visited again briefly. PODGE spends more than 3 hours around the farm and the farm house, visits briefly the site of intensive use of the previous night and visits for one and a half hours the area along the bracken-woodland-field border, where rabbits occur at high densities (Chapter 3). The eastern section of the border is visited again.

NIGHT 4: western and eastern sections of the range border receive a cursory visit. PODGE commutes between the area around the farm and the field with root crops, and an area of mixed marshland, bracken and deciduous woodland, where earthworms and rabbits are abundant. Again, cubs are not visited before 6.08 in the morning.

NIGHT 5: a Saturday, PODGE keeps away from the heightened human activity in the village, and spends 6 hours in the bracken and field area north west of the den. Brief excursions to the western and eastern border sections occur at 00.25 and 22.30, respectively. She probably revisited her cubs at 01.30 and, possibly at 4.00.

NIGHT 6: PODGE concentrates again on the southern areas of the range and stays within the woodland boundary except for an extensive excursion to the western range border.

NIGHT 7: PODGE starts another round-trip along the border of her range, this time commuting frequently between the area of her den and a spinney at the southeastern tip of Mrs. Gardiner's garden. Each time PODGE follows a different route and she finishes with a brief patrol along the western border of the range. During these trips PODGE moved her cubs to an earth in Mrs. Gardiner's spinney.

The similarity of movements on nights 1 and 7, round-trips along most sections of the range border, may indicate some long-term cyclicity in PODGE's ranging behaviour. Doncaster (1985) found cyclical regularities in the activity of Oxford's urban foxes.

A striking fact was the regularity with which PODGE visited the border of her range, sometimes via large detours. PODGE presumably faced the "travelling salesman" problem: how to visit a number of places with a minimum of effort in time or energy expenditure, so that a maximum of effort can be dedicated to the activities at a site. The solution of this problem is complicated by the fact that visiting a site may only be useful if she arrived at a particular time (e.g. before other foxes have eaten the scraps at Mrs. Gardiner's garden) or under certain climatic conditions (earthworms). Given these constraints there will be no general optimal solution, but a variety of alternatives equally applicable. In such a situation, rules of thumb are expected to be a simple and efficient device (Janetos & Cole 1981, Houston & McNamara 1984). One rule of thumb seems to be "visit stretches of the range border distant from foraging places either on the way to these places or on the way back" (all sections, Nights 1 and 7; eastern section Night 2 and 3; western section, Night 4). Several visits to range borders are, however, not covered by this rule (all sections Night 5; western section, Nights 2,3,6). These constitute true detours where PODGE 'goes out of her way' to visit the range border.

Fig. 6.58-6.59 summarize the entire week and show 3D and contour plots for the number of visits (NOV) and the duration of stay (DOS) per 50 by 50 m cell. In the contour plots, black areas are the result of contour lines sitting so close to each other that resolution of single lines becomes impossible, indicating steep slopes and dramatic changes in UI of neighbouring cells. The white areas surrounded by the black areas represent plateaux where the UI is higher than the top contour level chosen. The two plots complement each other in yielding a detailed visual impression of changes in UI. The contour plot presents a more detailed picture of the positions of areas of high and low UI, while the 3D plot gives a better indication of the magnitude of these changes.

There seem to be areas of high and low UI of similar activity. I will call these areas "activity patches" (to distinguish them from habitat patches of the habitat map). It is reassuring to find that PODGE seems to confirm the basic idea of the habitat map (a patch arrangement in contrast to a continuous gradient). However, the decline in the UI from these patches is uneven, different patches have different UIs and the determination of the size of these patches looks at best ambiguous. Is there a method that permits us to decide whether these patterns are 'real'? This is the problem of scaling space use. On a local level, how can we decide whether a given change in UI from one cell to another is sufficiently small to assign both cells to an area of 'similar' use (an activity patch), or sufficiently large to indicate that they are separate? On a general level, can we interpret changes in UIs on a large scale as 'patterns'; are there regularities (symmetries) in the distribution of UIs?

To answer these questions, and to reveal the patterns of spatial dependence between different sites, I computed the spatial autocorrelation function for classes of sites with increasing distance between each other (Appendices 5-7) and plotted them in Fig. 6.60a and 6.61a. Such a plot is called a spatial correlogram. Each point indicates how similar the UIs are of pairs of grid cells at a given distance, called the spatial lag. For instance, at spatial lag 1, where each cell is taken in turn and its UI compared with those of all cells that are immediate neighbours and have been visited at least once by the animal, the correlation has a value of 0. 26 for NOV and 0.17 for DOS (significant at $p<0.001$ and $p<0.01$). Positive autocorrelation indicates that cells exhibit similar UIs. In both Fig. 6.60a and 6.61a, significant positive spatial autocorrelation coefficients (SAC) are restricted to immediate neighbourhood (lag 1) for both measures of intensity of use. Pairs of cells at a distance of already two lags show independence of UI. What can we conclude from this?

The compilation of UIs as shown in Fig. 6.58 and 6.59 has indicated that there are preferred (activity patches) and neglected areas within the range. The computation of SACs provides us with a quantitative measure to indicate that (i) areas of similar use are small and restricted to a size of 50-100 m; (ii) UI of a site only depends on its immediate neighbours, the influence of the spatial location of a cell on its UI is a highly local affair.

The computation of SACs also helps us to investigate another visual impression from Fig. 6.58 and 6.59. The two measures of intensity of use, NOV and DOS, differ in one intriguing aspect: variation between cells in NOV is small as compared with the variation in DOS (Fig. 6.58a vs. Fig. 6.58b). DOS seems to be a better indicator of the status of a cell, ie. whether a certain area is merely used as a transition area between centres of activity or constitutes a centre of activity itself. There is a significant negative SAC for DOS for lag 6 (250 m), indicating a contrast of UI at this distance, but not for NOV!

The interpretation of the results of fitting spatial models to the tracking data (Fig. 6.60b and 6.61b) will be discussed in detail in the next three sections.

In summary, intensive tracking over a period of a week revealed the kind of activity that contributes to the formation of activity patches as well as the development of areas of low utilization intensity. These are areas which may be regularly visited but only for a short duration. Activity patches are not an artificial phenomenon; they are real as evidenced by the amount of time
the individual invests in them. PODGE is quite flexible in choosing different routes to reach the same site or connect different pairs of sites. Despite the heavy energetic demands on PODGE due to the cubs, she puts considerable effort into maintaining range borders. However, it may well be that such dedication to the range border is an essential prerequisite for

maintaining exclusive access to the resources within the range.

6.2.2. Range use by OLDMAHOG

OLDMAHOG represents Range 6, the Singing Way Range. Fig. 6.17a is a 3D plot of the UI of her range, based on fixes selected according to the 15 min independence interval criterion, on a grid of 100 by 100 metres, viewed from the southeast. Fig. 6.17b depicts a contour plot of these data (equal levels of UI are delineated by contour lines, separated by increments of 1 location per cell, the top contour line enclosing areas with more than 20 locations per cell).

It is obvious that not all cells are used in a similar manner. Several peaks can be identified, but there are also regions of medium height, and consequently medium UI, and little used areas. The major peaks occur in the south of the range while the arithmetic mean (centre) of the range seems rather devoid of intensive use. The most intensively used area is a site towards the southwest where a peak emerges from a plateau of high UI. This is favourite daytime lying-up site in mature deciduous woodland, but also intensively used at night, and close to the breeding territories of several cock pheasants and a number of rabbit warrens. (Note that there is no fox den). The extension of the range towards the northwest covers the pasture fields of the Wytham Park where earthworms are abundant. A trough of low UI, running from the southwest to the northeast, separates these areas from a second area of high UI in the southeast where abundant sweet chestnut trees attract many grey squirrels (Sciurus carolinensis), and several rabbit warrens and pheasant territories are present as well.

Spatial autocorrelation coefficients (SAC) were computed to analyse the scaling of space use in a quantitative manner (see previous section and Appendix 5). The results are plotted as a spatial correlogram in Fig.

6.18b.

For OLDMAHOG, positive correlations were identified for the first six lags. This means that up to a distance of 250 m there were more pairs of cells with similar UI than expected from a random arrangement of the observed in UIs in space.

At spatial lags of medium order (8 to 20, or 350 to 960 m) significant negative correlations were found. Thus, in a broad range of medium distances, too many pairs of cells of a given distance had dissimilar UIs as compared with a random arrangement of the same values in space. We therefore have to conclude that ups and downs in UIs are distributed in space in such a fashion that similar values stick together, but do so only over a limited range - with increasing distance, the proportion of dissimilar values increases, indicating a real change in UIs. At larger distances, correlations become positive again. As the contour plot (Fig. 6.17b) indicates, this is due to the similar level of comparatively low activity in the border zones of the range.

Fig. 6.18a shows the results of fitting several spatial models to the data. Two different SACs, Moran's I (circles if significant, stars if not significant) and Geary's c (zeros if not significant, filled zeros if significant) are plotted against the model number ("weighing function"). In contrast to the correlogram, where only pairs of cells of a given distance were considered per spatial lag, the spatial model includes all pairs of cells (except for Model 1 which is identical to spatial lag 1). Each model constitutes a proposal concerning how the UI of cells of a given distance exert an influence on the UI of a given cell. The influence of cells declines with distance according to a specific function:

Model 1: weight of influence = 1; 0 < distance < 0.99 lags

Model 2: weight of influence = exp -(distance)

Model 3: weight of influence = $1/(\text{distance})^2$

Model 4: weight of influence = exp -0.5 (distance)

Model 5: weight of influence = 1/distance

Models 2 to 5 are distinguished by an increased consideration of pairs of cells with large distances. Thus, with increasing model number, along the x axis in Fig. 6.18a, spatial effects over a large distance attain more importance. For our considerations, the exact function describing the influence of cells at varying distances from a given cell is not so important as a comparison between the results of the different models, ie. the question of how does an increasing consideration of cells at large distances change the degree of spatial dependence exhibited by the data? The value of the SAC indicates the degree of spatial dependence while the slope connecting the SACs from different models reveals the importance of cells at larger distances. Together, they point to the major structure of the range:

	High SAC values (Moran's I)	Moderate SAC values (Moran's I)
	(1)	(2)
Shallow slope (Moran's I)	range contains a fairly large proportion of land used in a uniform way; changes in UI to the periphery are gradual and moderate	range contains a mixture of areas of high and low UI; some are large and have similar UIs or are small and arranged in a regular fashion
	(3)	(4)
Medium slope (Moran's I)	range contains a fairly large proportion of land used in a uniform way; changes in UI towards the periphery are radical	range contains a mixture of areas of high and low UI of varying size

Several activity patches and larger areas with comparatively little use yield medium SAC values for OLDMAHOG and result in a medium slope (ie. the disturbance caused by considering cells at larger distances is moderate). I would therefore place her in category 4 of the above list.

What does the application of spatial models and correlograms tell us that we cannot deduce from visual inspection of 3D or contour plots? (1) Ups and downs in UIs from cell to cell can of course be identified from graphs but mere visual impression cannot indicate whether changes in UI are arranged in space in a random fashion. Why is this important. Because we do not want to be misguided in our inerpretation of the background of high or low UIs - we do not want to confound spatial inevitabilities with a

preference due to the intrinsic attractivity of a habitat. Specifically, if we want to test habitat preferences or other aspects of range use we have to make sure that the UI of area units are independent from each other. However, if we find spatial dependence - as described for OLDMAHOG - we have to adjust the test statistic (see Appendix 5).

(2) We can compare range use on a quantitative basis. A comparison of spatial models provides us with a mean[5] to compare range use patterns of different individuals. Of course, we can compare range use without computing SACs, but by using SACs we can attach a precise meaning to our comparison.

(3) The results of fitting spatial models gives us a compressed summary of the predictability of space use of an area unit by other area units. This is not only interesting per se, and important for statistical tests. Predictability of space use may be important for other individuals, whether they coinhabit the same range or are merely interested in the activities of their neighbours. Simply looking at 3D plots does not reveal predictability. Compare, for instance, the 3D plots of GRIZZLE (predictable) and OLDSABRE and TARU (unpredictable), or the two essentially linear ranges of SURPRISE (predictable) and LIO (unpredictable). The graphical presentation is here insufficient to provide the required information. Certainly the UI of a site is related to its intrinsic characteristics (e.g. section 6.2.1.). However, the presence of resources, for instance, is insufficient to 'guarantee' a certain level of UI. A good example is variation in range use within badger groups in section 6.2.5. or in the HOMEFARM fox group (section 6.2.4.). Take the range use by the two vixens, BRAMBLE and PODGE (Fig. 6.1-6.2, 6.23-6.24). Superficially they are similar. However, the analysis reveals that predictability of UI is high for BRAMBLE and moderate for PODGE. The extensive areas in the west of PODGE's range contribute to the disturbance caused by cells of dissimilar

values at larger distances and the greater heterogeneity of UIs near the peaks of activity depress the overall level of predictabilty. Consequently, both individuals are assigned to different categories of range use patterns (BRAMBLE: 3; PODGE: 2).

In summary, there are clear spatial dependencies in the way OLDMAHOG uses her range. Several preferred areas could be identified (activity patches) with an estimated diameter of between 50 and 250 metres. Activity patches were separated from each other by areas of low use. Changes in UI are rather pronounced as evidence by the broad range of spatial lags when pairs of cells show dissimilair values. These patterns of range use can be predicted from the UI of other cells to a significant and reasonable degree, if the influence exerted by cells at larger distances is reduced.

6.2.3. Range use by other foxes

The following summaries present for each individual results to the following aspects:

(1) Number of activity patches

(2) Habitat and resource presence in activity patches

(3) UI of the arithmetic mean (important for potential application of probabilistic home range models)

(4) Scaling of space use

(5) Predictability of UI as evidenced by the results of spatial methods

(6) Category of range use patterns

For three foxes, space used could not be distinguished from a random arrangement. It is then a difficult if not impossible to speak of 'patterns' of range use; then a categorization of range use pattern seemed

inappropriate.

BRAMBLE (vixen, Fig. 6.1-6.2; note the scale of the z-axis in Fig. 6.1a).

(1) There are three activity patches present.

(2) The northern activity patches centre around Home Farm and Mrs. Gardiner's garden and backyard (earthworms and scraps), the southern patch is a strip of pasture plus the border region of deciduous woodland-bracken-arable land (earthworms, rabbits).

(3) The arithmetic mean is not a centre of activity.

(4) Sizes of activity patches are small (lag 1-3), and there are definite troughs at several places (lags 7-8, 13-17). The overall range use is asymmetric and biased towards the northern part (no positive correlations at high lags).

(5) Increased consideration of cells at a larger distance result in a large reduction in the accuracy of prediction of the UI.

(6) All spatial models describe significant spatial dependence; but predictability decreases rapidly from a high level; therefore category 3.

ELKE (vixen, Fig. 6.3-6.4).

(1) Several small activity patches present.

(2) Activities centre around the Churchgrove Farm and the Binsey Farm and adjacent pastures (scraps, earthworms). The activity patch in the north is a preferred earthworm hunting ground (pasture).

(3) The arithmetic mean is not a centre of activity; the range is banana-shaped.

(4) Large proportions of the range are either intensively or comparatively little used. Activity patches are medium-sized (lags 1-4). They are clearly distinguished from other areas (negative SACs at lags 8-16). Overall range use is asymmetric.

(5) Spatial models do not reveal significant dependencies, except for Model 1.

(6) The separation in two areas with different base levels of UI results in a shallow slope; therefore category 2.

GASPER (dog-fox, Fig. 6.5-6.6).

(1) One large centre of activity present.

(2) This includes Home Farm and the pasture around Wytham Abbey (scraps, mice, earthworms) and Mrs. Gardiner's garden and backyard (scraps and earthworms).

(3) The arithmetic mean coincides with the peak in activity.

(4) Size of centre of activity is small (lag 1-3), decline of UI towards the periphery rapid (no positive SACs at medium lags). Occasionally visited sites outside the group range are responsible for some significant negative SACs at large lags.

(5) Models indicate a high degree of predictability, declining rapidly with increased influence of distant cells.

(6) The observed pattern is assigned category 3.

GRIZZLE (vixen Fig. 6.7-6.8).

(1) Two activity patches of small size (lags 1-2) and a complex of small peaks (a "plateau") in the southwest.

(2) Both peaks occur in areas of high earthworm abundance, one in pasture, the other in deciduous woodland.

(3) The arithmetic mean does not coincide with a peak in activity.

(4) UIs between the two activity patches are rather variable, one trough separating the northern patch from the "plateau" and the southern patch. The impression of a regular arrangement of the peaks is supported by a significant positive SAC at lag 10, but the decline towards the periphery is

asymmetric (lags 15-16).

(5) Overall predictability of space use is low, but the spatial dependence exhibited is significant.

(6) The regular arrangement of peaks produces a shallow slope in the decline of predictability (category 2).

KALI (vixen, Fig. 6.9-6.10).

(1) Several major areas are arranged in a roughly linear fashion from west to east.

(2) The westernmost patch covers a small woodland surrounded by fields and a small farm, Simpson's cottage; the next patch to the east lies in a field with long grass where I could frequently observe her catching mice; the complex in the east covers a residential areas with some allotments at the back and the easternmost area includes a small local school with a sports ground (scraps and earthworms).

(3) The range is banana-shaped, the arithmetic mean lies outside centres of activity.

(4) Patches are medium-sized (lags 1-4) and separated by several troughs; areas which are quickly crossed and that only serve as a connection from one major area to another (see section 6.2.6). The positive SACs at large lags indicate symmetrical UI, due to the position of activity patches at extreme positions, but an assymetric decline towards the west results in a last negative SAC.

(5) All spatial models describe significant spatial dependencies and have moderate success in predicting UIs.

(6) The regular linear arrangement produces a shallow slope in the decline of predictability if distant cells are progressively more considered; therefore category 2.

KBOOM (vixen, Fig. 6.11-6.12).

(1) Usage patterns are similar to OLDMAHOG. Two major areas separated by a trough.

(2) Peak areas include: Woodend Farm and Bean Wood, areas north of Bean Wood and particularly the backyards and parkland of the Buddhist centre and the long grass fields and gardens of the three houses east of the Buddhist centre where I frequently observed her hunting for rodents.

(3) The arithmetic mean is near a centre of activity.

(4) Patterns of use are very regular, e.g. the symmetrical decline of UI towards north, northwest and northeast, resulting in a perfect spatial correlogram.

(5) Spatial dependencies revealed by the models are pronounced and highly predictable, which is not surprising in view of the regularities exhibited in Fig. 6.11b.

(6) I place KBOOM in category 1 with a tendency towards category 3.

KOBUK (dog-fox, Fig. 6.13-6.14).

(1) One major activity patch and two smaller peaks are present.

(2) The major patch is identical with the area preferred by GASPER while the smaller peaks are close to the areas preferred by BRAMBLE.

(3) The arithmetic mean is close to the centre of activity.

(4) Patch size is medium, and UI decline asymmetrically towards the southeast (negative SACs at medium, and non-significant SACs at large lags).

(5) Spatial models reveal a high degree of predictability of UI from nearby cells.

(6) This leads to a similarly steep slope as in GASPER; therefore category 3.

LIO (dog-fox; Fig. 6.15-6.16).

(1) The major peak is situated in deciduous woodland close to a fox den and several rabbit warrens; a second smaller peak at a woodland/field border with a major pheasant roost.

(2) The arithmetic mean is close to the small peak of activity.

(3) The spatial arrangement of UIs corresponds to a random arrangement, except for lag 3.

(4) No spatial dependencies could be identified.

(5) Since no clear spatial pattern present, categorization seems inappropriate.

OLDSABRE (dog-fox, Fig. 6.19-6.20).

(1) One peak is evident.

(2) The peak lies in dense deciduous woodland; possibly rich in earthworms.

(3) The arithmetic mean is not at the centre of activity.

(4) No clear patterns are discernible; the spatial arrangement could be due to a random process, since there are no spatial dependencies.

(5) UI are not predictable and none of the models produce significant SACs.

(6) Therefore, no category provided.

OLDSABRE occupied the woodlands in the southern part of the Radbrook Common area. His range is exceptionally uniform in terms of habitat diversity. However, OLDSABRE was tracked for only a short time, and the number of fixes may be insufficient to reveal significant contrasts in UI.

PINTOOTH (vixen, Fig. 6.21-6.22).

(1) Several major peaks and a large plateau in the southeast are characteristic for this range.

(2) Peaks coincide with the sites of several farm houses and large rabbit warrens in the pasture/long grass area northeast and west of the Hill End

Camp Natural History school. The southeastern plateau covers a complex of pastures and hedges where PINTOOTH frequently foraged for earthworms and rabbits, and two school buildings (scraps).

(3) The arithmetic mean coincides with the centre of activity.

(4) The range is fairly symmetrically used, and peaks are separated by pronounced troughs, both contributing to a perfect spatial correlogram.

(5) High predictability of UI.

(6) Therefore category 1, with a tendency to 3.

PODGE (vixen, Fig. 6.23-6.24).

(1) Three major activity patches are present, in nearly identical location to those used by BRAMBLE.

(2) PODGE's range extends further south west and covers more ground towards the west (mainly agricultural land and, in the northwest, pastures).

(3) The arithmetic mean is not the centre of the range.

(4) Patch sizes are medium (lags 1-4). Extended areas of little UI between the major peaks contribute to the significant negative SACs at medium lags.

(5) The predictability of UI by the models is significantly lower than in BRAMBLE (section 6.2.4.). This is due to the extensive disturbance caused by cells of dissimilar value at large distances, and to the greater heterogeneity of UIs near the peaks of activity as compared with BRAMBLE.

(6) This usage pattern corresponds to category 2.

SURPISE (vixen, Fig. 6.25-6.26).

(1) Three major activity patches can be identified.

(2) Two patches are very close together in the east, and one, an area around a farm, in the west. This is an extremely one-dimensional range.

(3) The arithmetic mean is at the largest possible distance from any centre of activity.

(4) Patches are of medium size (lags 1-4). The symmetric appearance is reinforced by the positive SAC at large lags and the negative SACs at medium lags.

(5) Predictability is only moderate, but little affected by large weights of cells at larger distances.

(6) This corresponds to category 2.

TARU (vixen, Fig. 6.27-6.28).

(1) Several peaks are interspersed with areas of little UI.

(2) The western peaks correspond to an area completely covered by the Binsey allotments, whereas to the east TARU frequently foraged for rodents and earthworms on pasture and in a field of grassley.

(3) The arithmetic mean is close to a centre of activity.

(4) The spatial correlogram shows systematically changing, but insignificant SACs.

(5) The predictability of UIs from other cells is low, since range use cannot be distinguished from a random arrangement of UI.

(6) For this reason, a categorization seems inappropriate.

In summary, the patterns of range use were analysed for 14 foxes. They were associated with usage categories as follows:

category	1 :	2 individuals
	2 :	5
	3 :	3
	4 :	1
no pattern	:	3

This small list indicates that the most notable feature of space use in foxes is enormous variability, even within the same population, covering a

wide range from simple to complex patterns:

(i) two ranges were symmetrically used throughout the majority of the area (category 1).

(ii) three ranges had a large centre of activity but UI declined rapidly towards the periphery (category 3).

(iii) five ranges exhibit regularities that were of two kinds. Activity patches were regularly distributed, or ranges consisted of a well-used and a neglected section, within each of which UI may vary again (category 2).

(iv) one range showed a truly impressive array of activity patches interspersed with troughs of low activity (category 4).

(v) Three ranges were used in a way that could not be distinguished from a random arrangement of UIs in space (no pattern).

Most activity patches were clearly associated with specific resources. Most ranges were asymmetrically used or approached linearity (banana form). The arithmetic mean rarely coincided with a peak in activity. Both results underline the proposition that probabilistic home range models with a priori expectations of UD are inappropriate, at least for foxes.

6.2.4. Range use within the HOMEFARM fox group

In the HOMEFARM group range four foxes were tracked with sufficient intensity to facilitate exploration of intra-group variation in space use. Two adult males, GASPER and KOBUK and two females, BRAMBLE and PODGE, occupied the range. In section 6.2.3. it was shown that both males exhibited a fairly simple pattern of space use, highly predictable from the surrounding cells, and concentrated on one centre of activity. The two females exhibited a more complex pattern. They both used the same three activity patches; one of these patches coincided with the area most intensively used by the males. For the vixens, space use patterns were not

so predictable as for the males. The results of fitting the five different models, the SAC, were regressed against the number of the model, where models were arranged so that high model numbers indicated improved influence of cells that were at a large distance from a given cell. The steep slope of the regression lines of the two males (Table 6.2, Fig. 6.29) indicates a rapid decline of reliability of predicting UI if cells at larger distances attain more influence. For females, however, reliability of prediction, although generally lower, is less sensitive to changes in the weighting procedure. BRAMBLE has a considerably shallower slope than the two males, although the differences are not significant, whereas PODGE's slope is shallower than any of the others.

There are several possible explanations of the differences in patterns between males and females. First, if males dominate females, then females might be expected to move away from the centre of activity of the males whenever possible. Second, energetic considerations may encourage females to look for large, profitable prey, such as rabbits, during the breeding season. Such prey occurs only in the southeast and south of the HOMEFARM range. However, utilization patterns before, during and after the cub rearing season remained similar. Third, safety of cubs away from human disturbance is an important factor to consider. In 1981, BRAMBLE probably had cubs in Mrs Gardiner's garden close to prime food sources but then moved them after a week or so to the wood, where PODGE kept her cubs a year later. Obviously, females have to find a compromise between proximity to food and the protection of the cubs from danger.

Table 6.2 Analysis of the relationship between the spatial autocorrelation function, as computed with MORAN's I, and the influence of cells at a large distance on predicting the intensity of use of a given cell. Slopes were calculated for the 4 members of the HOMEFARM range.

a) regression equations:

BRAMBLE: sp.a. = 0.82 - 0.14 weight function
GASPER: sp.a. = 1.13 - 0.18 weight function
KOBUK: sp.a. = 1.06 - 0.18 weight function
PODGE: sp.a. = 0.42 - 0.07 weight function

b) non-parametric 95% confidence intervals for slopes (Conover (1980: 267))

BRAMBLE: $-0.18 < -0.14 < -0.1$
GASPER: $-0.30 < -0.18 < -0.13$
KOBUK: $-0.30 < -0.18 < -0.12$
PODGE: $-0.12 < -0.07 < -0.04$

c) significance of differences in slopes between individual (Spearman's rank correlation coefficient)

	Br.	G.	K.	P.
Br.	-	-0.625	-0.625	1.0
G.	n.s.	-	-0.1	1.0
K.	n.s.	n.s.	-	1.0
P.	$p < 0.001$	$p < 0.001$	$p < 0.001$	-

6.2.5. Range use by badgers.

The analysis of range use in badgers differs from that of foxes in that only results from intensive tracking nights were selected for the analysis. Since contour plots have already been presented in Chapter 5, the figures of this section are restricted to 3D plots and the results of the computations of SACs (correlograms and models) for both measures. To enable intra-group comparisons, individuals of a group are presented together. Otherwise the description follows in style the summaries for the foxes.

Range B1 (Botley Lodge). Fig. 6.30-6.31 depict the results for GEORGE, 6.32-6.33 for HELEN and 6.34-6.36 for SARA.

(1) All three individuals concentrate their efforts in the same area. In addition, GEORGE ranges extensively towards the southwest. Both GEORGE and HELEN have two, identical centres of activity at opposite ends of the range. SARA's only activity patch (according to duration of stay, DOS) coincides with the northern activity patch of GEORGE and HELEN.

(2) The activity patch in the north is a small area of deciduous woodland (sycamore/oak) with an understory of dog's mercury which is probably a good indicator of high earthworm abundance (Chapter 3). The activity patch in the south is partly woodland of the same type but also partly covered by dense thickets. Here tree stumps and fallen tree trunks provide a good medium for a rich invertebrate fauna. In this area I could frequently observe the gradual decay of fallen trees pulled apart by badgers over periods of several weeks, both in spring and autumn.

(3) The arithmetic mean falls into little used areas for all three group members.

(4) Cell visits by HELEN could not be distinguished from a random arrangement (Fig. 6.33). GEORGE produced significant negative SACs at

several medium lags, indicating a coarse partitioning of his range into two activity patches. This partitioning is especially pronounced for NOV; obviously the trough between the activity patches is wider for NOV than for DOS. GEORGE visits the area between the activity centres less regularly than the activity centres, but occasionally stays at the edge of the activity patches for quite a while.

At medium lags, SARA exhibits the same habits as GEORGE does for NOV. However, the symmetric distribution of UI over her range leads to high positive SACs at extreme distances. This is in contrast to the gradient shown by GEORGE due to his large extension towards the southwest, a little used area. Similar to PODGE, DOS is a clear indicator of the centre of activity in SARA's range. Although SARA visits many cells at relatively high frequencies, she spends only little time in them except for her preferred foraging area in the north.

For both SARA and GEORGE, variability of UI at a small scale is sufficient to reduce areas of similar use to a small size (only lag 1 significant).

(5) Predictability of UI is low for SARA but significant, while insignificant for both GEORGE and HELEN.

(6) All three grup members correspond to the situation typical for category 2: the simple structure of partioning the range in coarse sections makes predictability insensitive to changes in influence of cells at large distances. Small scale heterogeneity of UI is sufficient, however, to depress the reliability of prediction.

Range B2 (Upper Follies). Fig. 6.37-6.39 depict the results for ALI, 6.40-6.42 for NANI and 6.43-6.45 for WILF.

(1) Range use, as illustrated by the 3D plots is very similar for the two females. WILF includes an additional occasionally visited eastern section

in his range. No special sites of high activity could be identified, except the sett in the north of the range.

(2) Most of the utilized areas cover pasture, a prime earthworm habitat (Chapter 3). Small-scale variability of availability of earthworms in space and time seems to prohibit the formation of highly preferred, uniformly used areas.

(3) The arithmetic mean of the ranges is not characterized by activity peaks.

(4) ALI's pattern of range use is characterized by considerable heterogeneity in UI at such a small scale that the formation of uniformly used areas is prohibited; consequently the SACs are insignificant and fluctuate round zero. The small-scale heterogeneity is evident also in NANI's range use but overshadowed by medium-sized trends producing significant SACs at medium and high lags. The contrasting UI in the north (where the main sett is situated, an area heavily used by all three individuals) and the southwest create a gradient as evidenced by the strongly SAC at extreme distances. WILF's range use reveals heterogeneity of UI at a larger scale (lag 1 significantly positive) but otherwise similar to ALI.

(5) Reliability of prediction of UIs by the models is very low and dependencies are insignificant except for NOV of WILF and DOS of ALI, leaving the overall impression that the use of a given cell is basically independent from the use of other cells. UI may be find-tuned at a scale of the size or smaller than the selected cell size.

(6) Since it is difficult to speak of activity patches a categorization seems inappropriate.

Range B4 (Jew's Harp). Fig. 6.46-6.48 depict the results for PEACEFUL and Fig. 6.49-6.50 the results for VICIOUS.

(1) Three small peaks of activity are recognizable in VICIOUS' range. Four major activity patches occur in PEACEFUL's range.

(2) The westernmost activity patch in PEACEFUL's range is situated at the southeastern border of the pasture fields of Wytham Park (the area where microclimatic measurements were undertaken as described in Chapter 3). Another activity patch occurs around Wormstall Duck Pond, a small spinney at the bottom of the Park and surrounded by pastures. Two activity patches, one in the centre, and one in the east of the range. Both cover small areas of deciduous woodland, a mixture of sycamore and oak wood with an understory of dog's mercury, areas supposedly rich in earthworms. They border onto the mixed plantations further south which are also well used. These two activity patches are also frequently visited by VICIOUS, but he spends relatively more time in the plantations than PEACEFUL.

(3) The arithmetic mean falls close to highly used areas in both ranges.

(4) Peaceful's activity patches are relatively small (positive SACs for lag 1 and 2, NOV). These peaks are separated by a system of less visited troughs (lag 6-8). The activity patches are distributed in a regular fashion over the entire range and range use declines symmetrically towards the periphery. Both factors produce positive SACs at large lags again. Medium-scaled heterogeneity in UI is sufficiently large to create a less clear although, in trend, similar picture for DOS in PEACEFUL's range. The considerable small-scale heterogeneity of UI in VICIOUS' range prohibits the formation of larger patches. Little used areas, however, can be clearly recognized and lead to negative SACs at lag 3.

(5) Predictability of UI is only moderate for PEACEFUL and non-existent for VICIOUS.

(6) PEACEFUL corresponds to category 2.

In contrast to foxes, the badgers studied are very similar in their

basic pattern of range use. This pattern is characterized by a considerable small-scale heterogneity, preventing in many cases the formation of large, uniformly used areas. Then, the distribution of UI within a range can often not be distinguished from a random arrangement, at least not at the chosen scale of spatial resolution. In two groups, one high quality habitat type covers a large proportion of the actually utilized part of the group range, pasture for individuals of group 2 and deciduous woodland for individuals from group 1. Obviously, these badgers restricted their visits to areas of special interest to them and thus utilized only part of the group range. Where ranges span a variety of different habitats, UI proliferates and yields a more complicated picture. This is especially evident for PEACEFUL, but also applicable on ELIANE and NOEARS, two individuals not considered here before. Contour plots of their range use were presented in Chapter 5 (data selected according to the 15 min independence interval criterion). Both NOEARS and ELIANE displayed ranges with many areas of high UI interspersed with areas of low UI, qualifying for category 2. For both individuals, all spatial models were significant, but reliability of prediction of UI generally low (highest correlation coefficients for ELIANE: 0.22, and for NOEARS: 0.13).

6.2.6. Direction preferences in local movements

In this section I will investigate whether foxes and badgers show preferences for certain routes. One way of examining this question is to select a particular patch, hereafter called the 'origin patch', and investigate an individual's movements towards and away from it. The origin patch forms the base of a network of patches called the 'local window'. This window includes all patches immediately bordering onto the origin patch. If an individual visited during periods of intensive tracking, say

15 patches, then 15 local windows can be created, one for each patch. A 'link' was defined as the connection that an animal has travelled between two patches within one local window. For each link, the number of crossings is counted. Usually, the sum of Arrivals to a specific patch from all neighbouring patches equals the sum of Departures from that specific patch to all neighbouring patches (except for the first and the last patch of a given tracking sequence). However, the links leading to and from a given patch may be used to different extents. Three questions can be explored within this framework:

1. The frequency with which different links are crossed can give some indication of the existence of preferred paths. Do foxes and badgers have frequently used 'highways' and rarely used 'by-tracks'?

2. Do foxes and badgers have directional preferences in the way that they travel their home ranges?

3. If direction preferences occurred in several links associated with an origin patch, are the differences between the asymmetries significant? To investigate this, a procedure was devised that ranked all patches of a local window on a continuous scale according to the difference of Departures and Arrivals along each link (Appendix 8). The distances betwen the ranks of all patches were then simultaneously assessed to determine whether direction preferences varied significantly between links (evaluated per match).

In Fig. 6.62, transition frequencies of KBOOM are shown for all links between an origin patch and its neighbours. Frequent transitions occur between patches Y and X and between X and Z (patch preference), and in 77.8% of all transitions between X and Y KBOOM left Y and arrived in X (direction preference). The figure illustrates the difficulties of such an analysis that deals with natural and therefore unevenly shaped area units. For instance, the whole eastern surface of Y borders X (and the majority of crossings between Y and X start from Y to X), while only a fraction of the

Fig. 6.62.

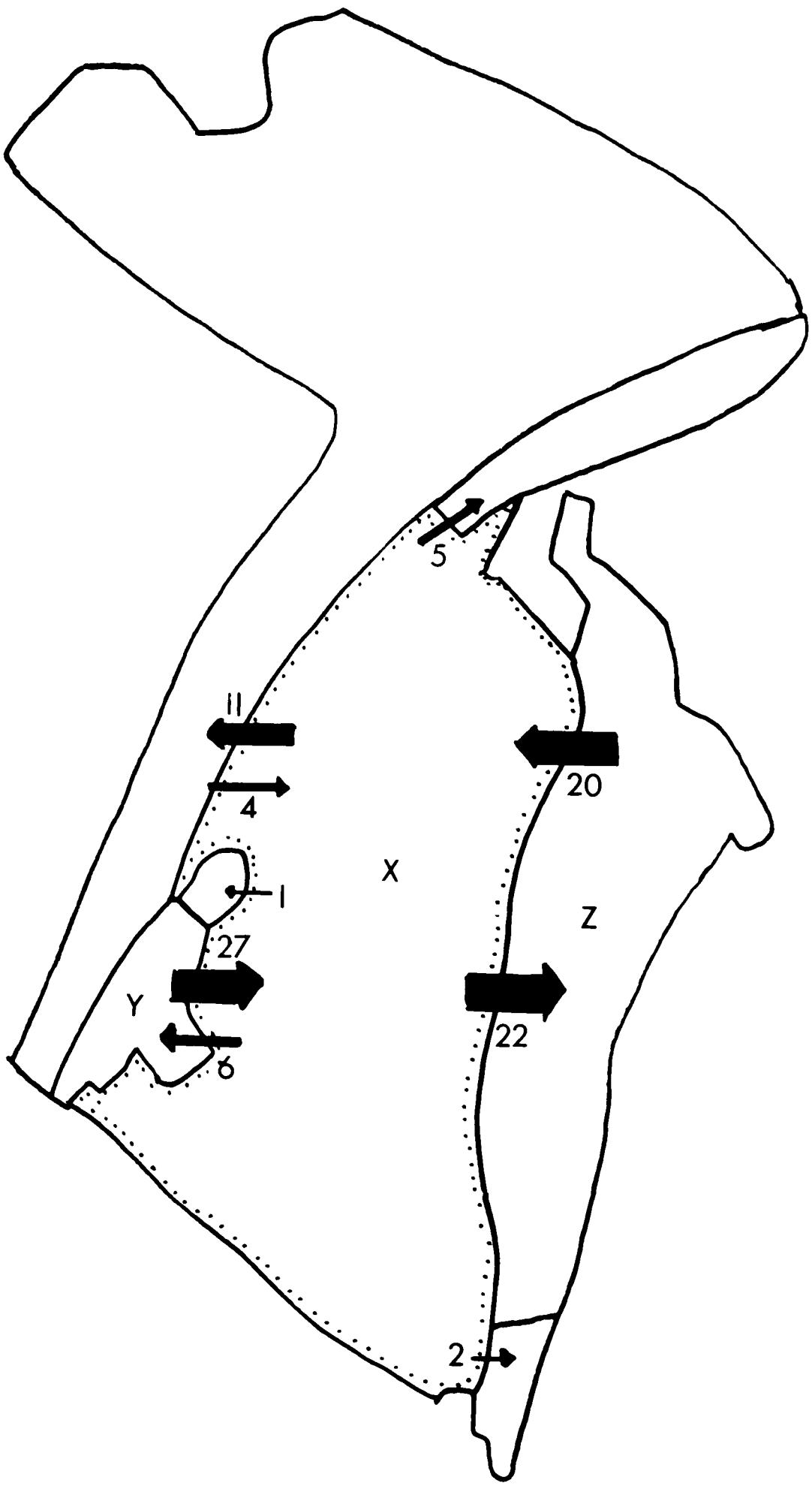
An example of a 'local window' as used in the analysis of local movements, for the vixen KBOOM.

x: the origin patch of the local window (borders indicated by the dotted line).

Arrows indicate transition frequencies, width of arrows gives an approximate impression of the intensity of exchange between two neighbouring patches.

Neighbouring patches only illustrated, if they had a link with the origin patch (for absence of links, note the northeast corner and the southern front of the origin patch).

Between patches X and Z there is a bridge, and between patches Y and X there is a strong asymmetry in transition frequencies.


5
11
4
1
27
Y
6
X
20
Z
22
2

western border section of X borders Y (the minority of crossings). It cannot be excluded that this asymmetry is due to the uneven distribution of surface borders. However, the total number of crossings between Y and X surpasses by far the number that would be expected if crossings were proportional to the amount of border line shared by two neighbouring patches. Here, a safe approach is to examine whether a link is heavily used, if there are large asymmetries (see below).

The bridge effect. Patch preference is indicated by asymmetries in the strengths of links between an origin patch and its neighbours. If for both patches their common link is the most frequently used link in both local windows, then this link is called a bridge. A bridge is therefore a place where an individual is most likely to walk across for both local windows (Fig. 6.63a).

Table 6.3 shows that the proportion of patches from which a bridge emerges varies considerably between individuals. The maximum incidence of bridges was 80% (SARA) indicating that this badger kept to fairly strict routes within a large proportion of her range (Fig. 6.64). SARA usually emerged from the main sett at the southwestern corner of her range and moved in a straightfoward fashion to the major feeding area in the north. In contrast to this pattern, another member of the same badger group, GEORGE moved around more freely (25% of patches had bridges emerging from them). This strictness of using particular routes may depend on the simplicity of the range structure. SARA had only one activity patch (section 6.2.5.). Can this be generalized, e.g. the more complex a range is utilized, the fewer clear preferred areas of visiting through can be expected? This is not necessarily true. KALI, the fox with the largest proportion (59%) of patches with bridges, had several centres of activity which were generally visited following the same route (Fig. 6.9b). SARA's and KALI's intensively used areas assume the shape of a banana, ie. a quasi-linear range. But even

Table 6.3 Patterns of local movements of badgers and foxes as analysed by transition matrices. Bridge patches: patches from which a bridge emerged (see text for definition); cases of suction: number of local windows with a suction effect (see text for definition); windows with significant asymmetries: number of local windows where asymmetries in transition frequencies varied significantly amongst neighbouring patches (see Appendix 8)

1 Animal	2 Season of tracking	3 No. of local windows	4 No. of bridge patches	5 ratio x 4/3	6 average no. of neighb. patches	7 windows with signif. asymmetries	8 ratio 7/3	9 no. of cases of suction	10 ratio 9/7
Ali	Oct	12	4	0.33	4.42	0	0	-	-
George	May-June	8	2	0.25	3.00	0	0	-	-
Nani	Oct	12	6	0.50	4.83	3	0.25	0	0
Peaceful	Jun-Sept	12	6	0.50	4.00	0	0	-	-
Sara	Oct	10	8	0.80	4.10	4	0.40	1	0.25
Vicious	May	5	2	0.40	3.60	4	0.80	0	0
Wilf	Oct	17	6	0.35	4.88	11	0.65	1	0.09
Elke	Feb-Apr	13	4	0.31	3.08	0	0	-	-
Kali	Jun-Jul	32	19*	0.59	5.25	2	0.11	0	0
Kboom	Feb-Apr	26	9*	0.35	4.08	12	0.46	4	0.33
Podge	Feb-Jun	27	4	0.15	5.37	0	0	-	-

* 3 patches had equal transition frequencies

Fig. 6.63

Explanation of the bridge and the suction effect.

Circles: two neighbouring origin patches of their respective local windows.

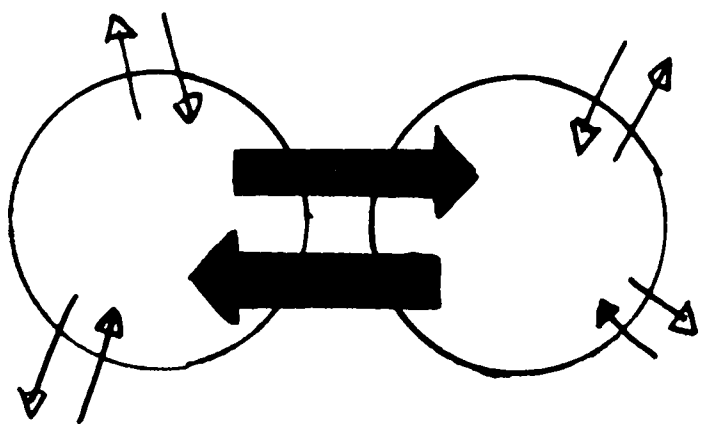
Filled arrows: links indicating where the bridge or the suction effect is placed.

Dotted arrows: links with neighbouring patches.

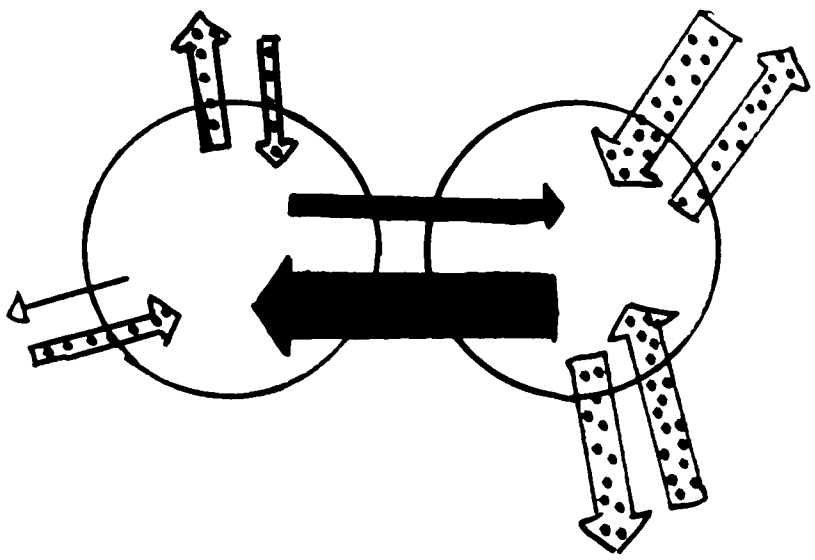
Width of arrows indicates approximate strength of link.

a: Bridge effect: the common link of both origin patches is the most frequenty used link within their respective local windows. This link may, or may not be asymmetric.

b: Suction effect: asymmetries in transition frequencies vary amongst the three links of the left origin patch. The strongest link, the link to the right origin patch, displays also the highest asymmetry. This link may also be a bridge (as shown in the figure).



6-63a.

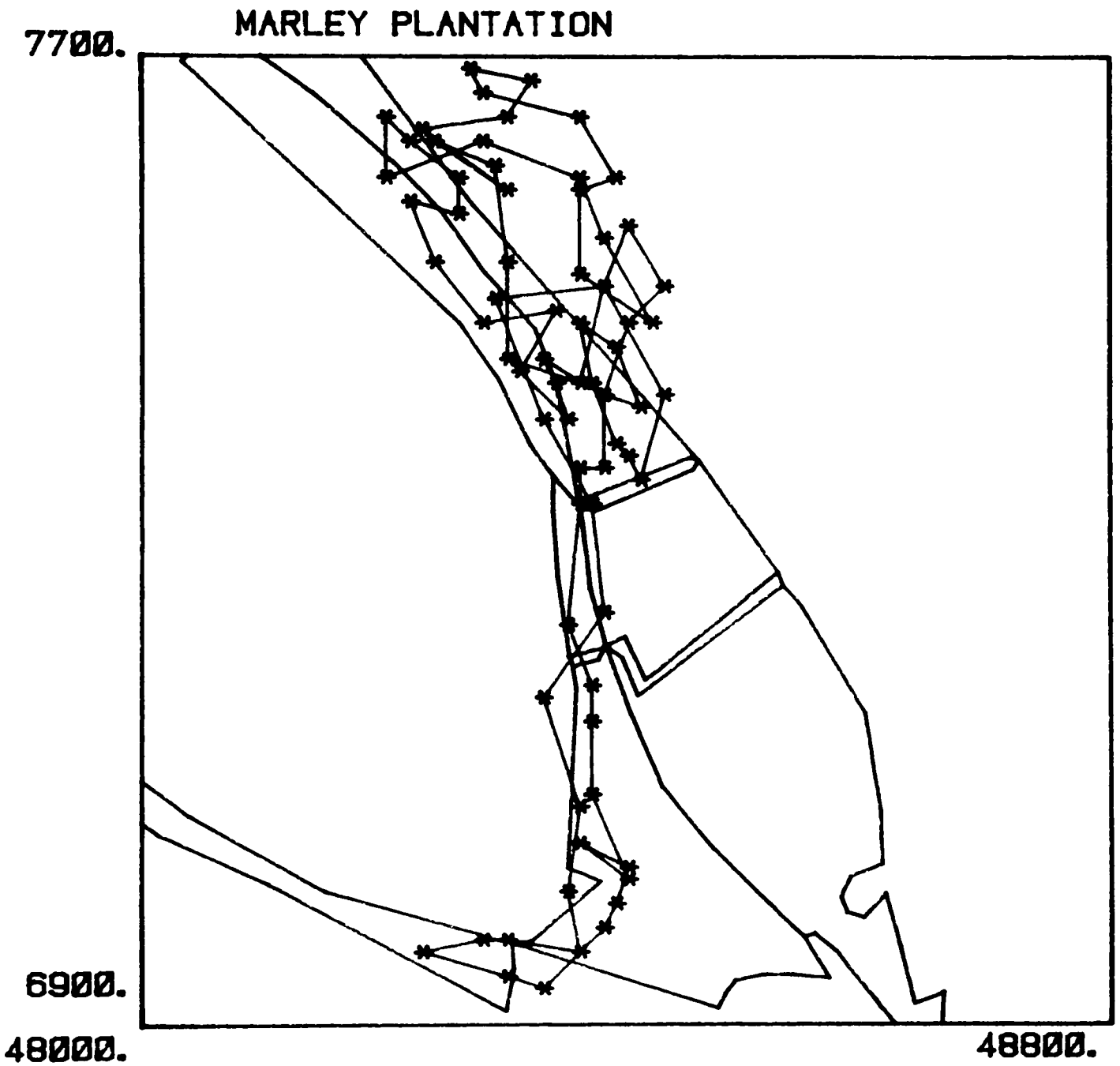


6-63b.

Fig. 6.64

Movements of the badger SARA in one night, illustrating the directionality of local movements.

Radio locations were plotted with program PLOT, and the section of the habitat map by program MAPITH (see Fig. 6.51 for details). Scale: 800 by 800 metres. Sara moves from the southeasternmost fix, the sett, to the major feeding areas in the north along a very strict route, at the edge of the woodland to the neighbouring wheat fields.



** SARA ** (BADGER)

DATE: 16 - 17 OCT 83
TIME: 19:45 TO 06:45

80 RADIO LOCATIONS

for animals with several centres of activity spread evenly (PEACEFUL, KBOOM), some links are clearly more attractive than others.

A detailed list of habitats associated with bridges is presented in Table 6.4a. In 73% of the cases for badgers, bridges involved transitions between habitats of low and high quality as defined for the log-linear models of latrine use (section 5.4). For PODGE, one bridge occurred along the route where she patrolled the eastern sections of her range border, while the second bridge lied in the area where she was likely to hunt for rabbits (section 6.2.1.; cf. also Chapter 3).

The suction effect. Although many links differed in the frequency distribution of transition frequencies, few of these asymmetries were significant within each local window (column 7, Table 6.3). Asymmetries were most pronounced when the neighbouring patch with the strongest link to an origin patch was also the most 'dominant' patch (see Appendix 8). In this case, the Ratio

Number of Departures from Origin Patch divided by the

Number of Arrivals at Origin Patch

usually drops below 0.5 (Table 6.4b). I call this the 'suction effect': if the animal enters the origin patch, it is most likely to do so from the 'dominant' neighbouring patch (fig. 6.63b). In 4 of the 6 cases of suction (column 9, Table 6.3), the link to the neighbouring patch also constituted a bridge. Then, an animal that has arrived in a neighbouring patch with a link to a "sucking" origin patch is also most likely to depart to the origin patch. However, such a direction preference seems rare as compared with the frequency of occurrence of bridges.

In summary, both foxes and badgers do not move indiscriminately within a local network of habitat patches but often restrict their "degrees of

Table 6.4 Habitat associations of patches with bridges and suction effects (for explanation see text)

a) bridge effect

Animal	habitat of patch 1	habitat of patch 2
Ali (B)	summer cereals	pasture
	summer cereals	pasture
George (B)	deciduous woodland	deciduous woodland
Nani (B)	summer cereals	pasture
	farm buildings	pasture
	summer cereals	pasture
Peaceful (B)	mixed plantations	deciduous woodland
	summer cereals	pasture
	summer cereals	pasture
Sara (B)	summer cereals	deciduous woodland
	deciduous woodland	deciduous woodland
Vicious (B)	mixed plantations	deciduous woodland
Vilf (B)	pasture	pasture
	summer cereals	pasture
	road	grassland
Elke (F)	deciduous woodland	pasture
	pasture	pasture
Kali (F)	summer cereals	deciduous woodland
	summer cereals	deciduous woodland
	summer cereals	deciduous woodland
	summer cereals	deciduous woodland
	road	grassland
	terraced houses	deciduous woodland
	detached houses	allotments
	grassley	grassley
	summer cereals	terraced houses
	sports ground	school buildings
Kboom (F)	deciduous woodland	deciduous woodland
	pasture	pasture
	summer cereals	deciduous woodland
	pasture	deciduous w./grassland
Podge (F)	summer cereals	bracken
	pasture	root crops

b) sucking effect

Animal	habitat of origin p.	hab. of. neighb. patch	Ratio Dep/Arr for origin p.
Sara	deciduous woodland	deciduous woodland	0.105
Vilf	summer cereals	deciduous woodland	0.462
Kboom	deciduous woodland	deciduous woodland	0.222
	parkland	grassley	0.563
	pasture	pasture	0.563
	summer cereals	deciduous woodland	0.313

freedom" of movements. Some links are strongly used, mostly in both directions (bridges). Even though transition frequencies often vary between directions of movement per link, they rarely vary significantly within a local network. In a few cases, movement patterns exhibit strong biasses in favour of one direction (suction effect).

6.2.7. Conclusions

I have already discussed at length the advantages of using spatial autocorrelation functions in addition to a visual inspection of 3D and contour plots. In section 6.4 I shall use some of the results to correct test statistics used to evaluate habitat utilization. Application of SACs has quantified the scale of changes in range use. Here a remarkable difference between the two species appeared. Range use by foxes was very variable between individuals but relatively coarse-grained. Range use by badgers was quite similar between individuals and fine-grained.

I hope to have shown that this is the result of differences in prey preferences and perhaps techniques of range maintenance. Several badgers used the group range only partly, most of which corresponded to preferred habitats. Heterogeneity of range use is compatible with observed spatial and temporal variation in availability of earthworms (Chapter 3). Differences between NOV and DOS in badgers are slight, except for SARA. In foxes, however, maintenance of range not only requires considerable detours but also frequent visits by the range inhabitant to the range borders. In contrast, range edges of badgers are very little visited. In foxes, activity patches coincide with areas of abundance of a large variety of different prey types, ranging from human scraps over earthworms to rabbits. Foxes adapt their movements to the different kinds of locally available prey - consequently scale and pattern of space use vary considerably from range

to range.

6.3. Simultaneous movements within the UPPER FOLLIES badger group

Simultaneous radio-tracking of all members of a badger group is essential for an estimate of the likelihood of interference and the level of competition within a group. This bears on a variety of problems related to the development of groups, group sizes, structure and maintenance (Chapter 7). In my analysis I will consider two aspects:

1. Do group members somehow 'adjust' their movements in order to minimize interference, ie. do individuals coordinate their movements?
2. Given the patterns of movements, what levels of interference pressure (signs of possible competition) do occur?

6.3.1. Coordination of movements

The analysis of spatial dependencies of the movements of an individual per se (section 6.2) has shown that there are basically no spatial effects. We can therefore investigate patterns of visits without having to fear influences due to the absolute location of a cell. The question of coordination of movements between individuals is particularly difficult to tackle. It is a problem that I shall treat in several steps.

1. Individuals do not move <u>randomly</u> in space as expected from a truely random process (e.g. section 6.4). What is the appropriate null hypothesis for independence of movements of two individuals in relation to each other?
2. Coordination of movements between two individuals is ambiguous to interpret, since such coordination may be intentional (as exemplified by a situation of social attraction) or unintentional (if the movements of both

individuals are independently governed by an external factor, e.g. climate). Can we resolve this problem with reference to the distances between individuals involved?

3. If coordination of movements was intentional, what evidence do we have to identify simple rules that could govern coordinate movements?

Fig 6.65-6.67 show how the distance between all three pairs of individuals (ALI-NANI, NANI-WILF, ALI-WILF) varies during seven nights. Distances between ALI and NANI are on average slightly less than those between NANI and WILF and ALI and WILF. If the frequency distributions of all pairs are compared with each other, significant differences emerge (Table 6.5a). ALI and NANI are closest, but similar to NANI and WILF, while ALI and WILF are farthest away. However, differences in the frequency distribution of absolute distances could result from different sized ranges and ranges with different degrees of overlap. Although all three ranges overlap to a large extent (cf. contour plots in Chapter 5 and 3D figures in section 6.2.), overlaps are not perfect and range sizes are different. Therefore a comparison of distances per se is insufficient. Furthermore, we require an expected frequency distribution under the null hypothesis of independence of movements of two individuals in relation to each other.

Doncaster (1985) has developed a method by which the effects of partial range overlap and synchrony of movements can be teased apart. He refers to range overlap of two animals as "static interaction" (see also Macdonald, Ball and Hough 1980). This overlap yields an estimate of the expected frequency distribution of distances between two individuals under the assumption of no coordination of movement of each other ("dynamic interaction"). All possible permutations of distances of each fix of badger A from all fixes of badger B are computed, without reference to the actual time of the fixes. Thus, the static interaction measures the displacement

Fig. 6.65–6.67

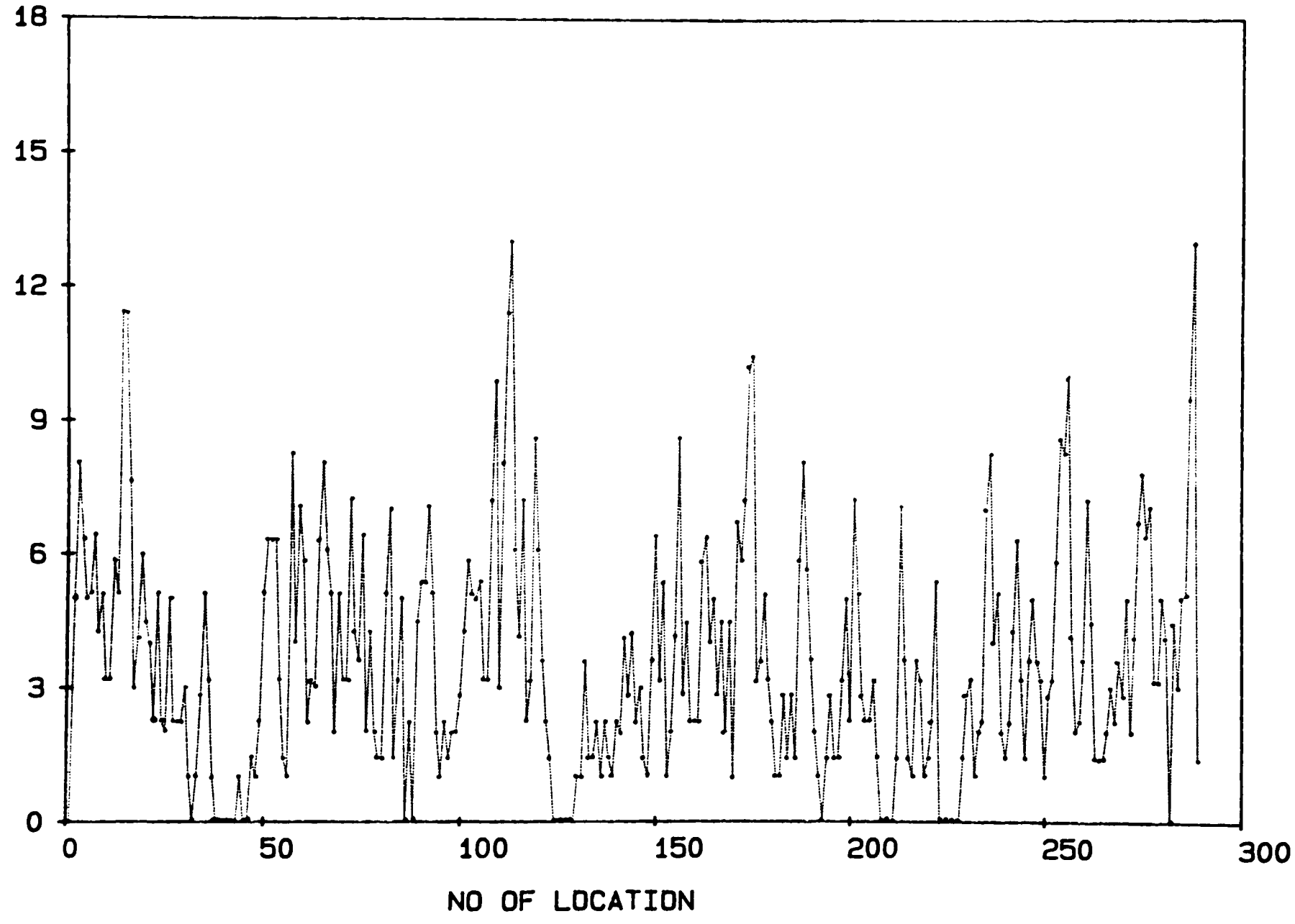
Distances between pairs of badgers from group B2, the UPPER FOLLIES group.

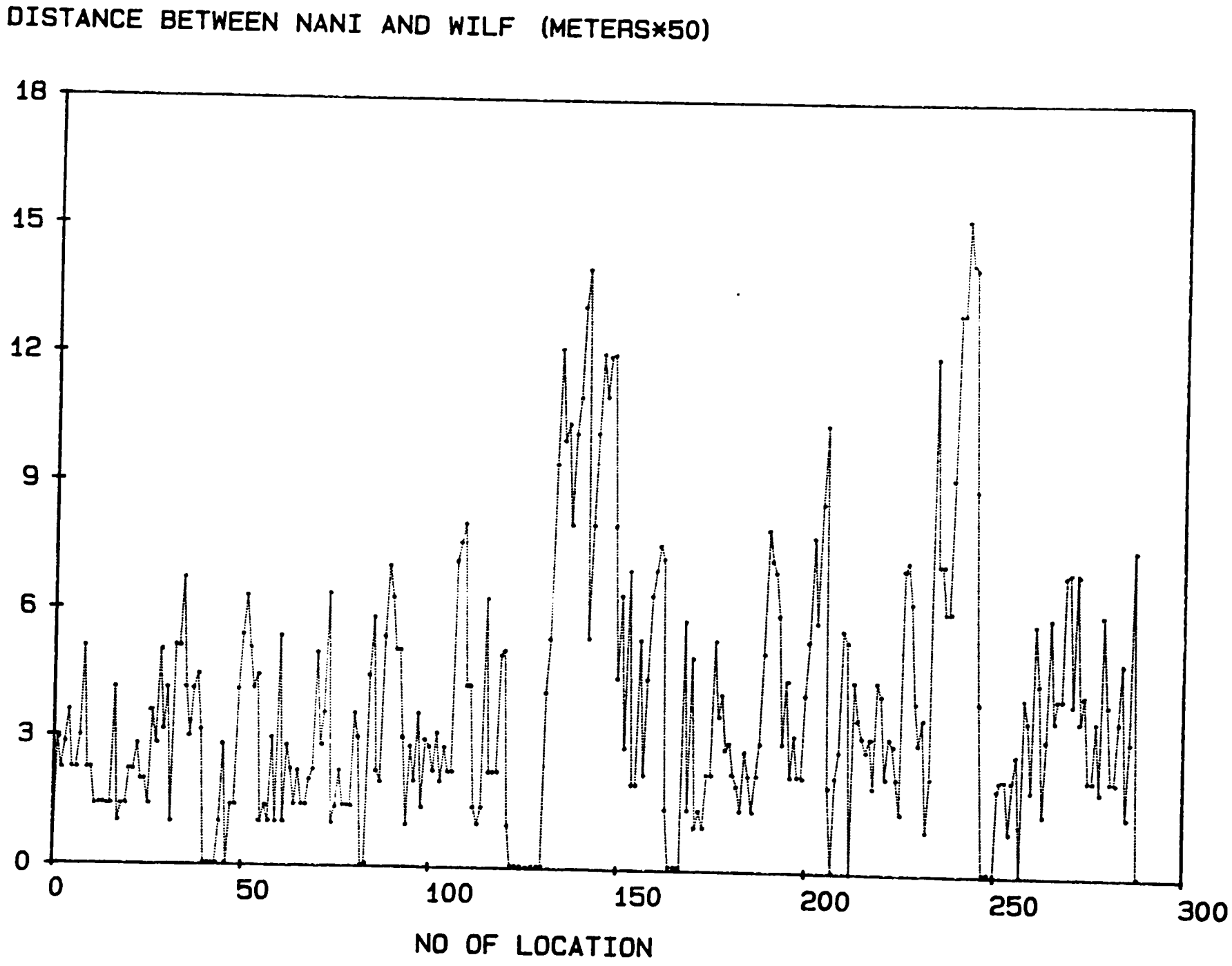
6.65: ALI and NANI

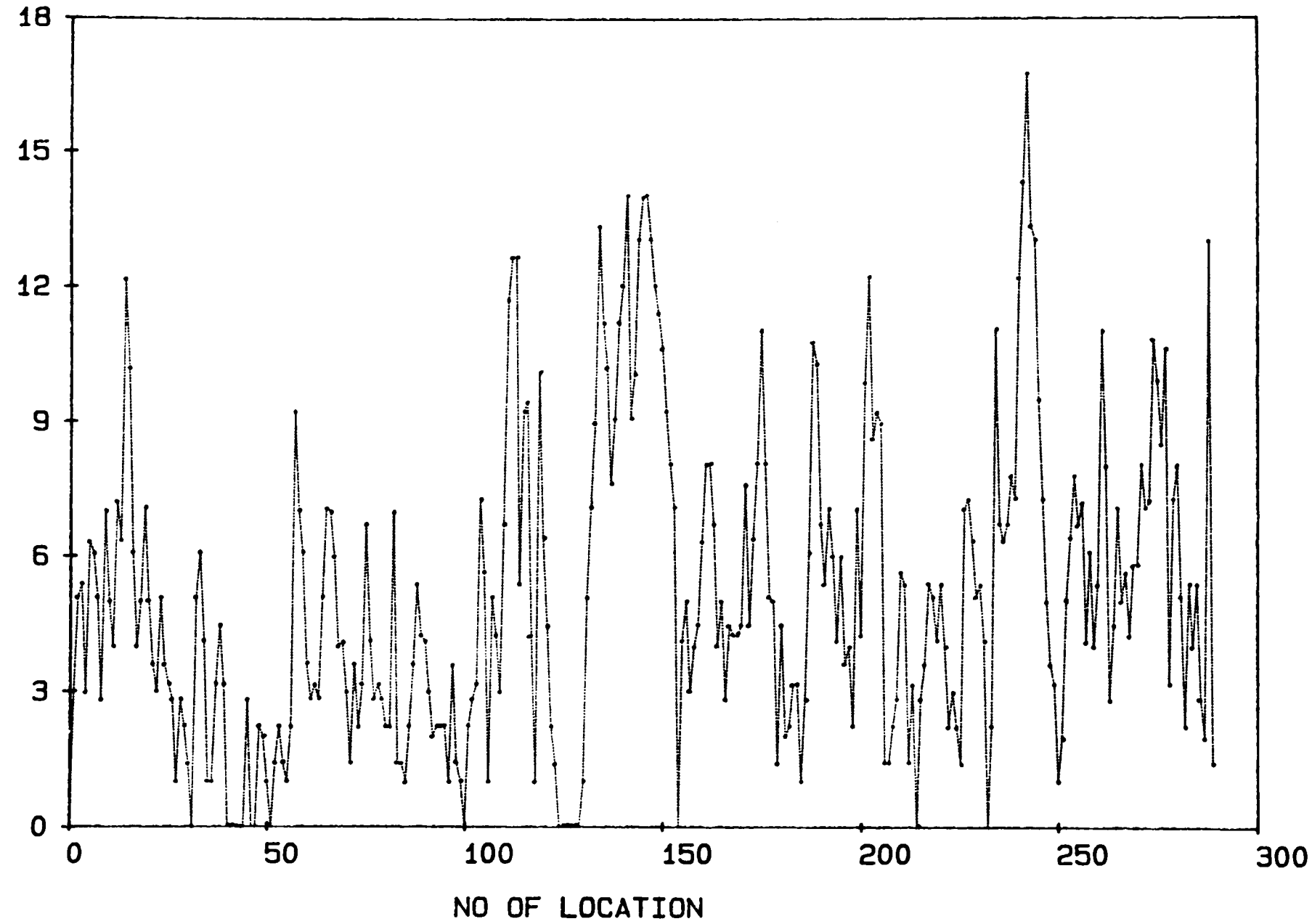
6.66: NANI and WILF

6.67: ALI and WILF

Distances are plotted in metres, the y-axis is scaled in 50 m units. x-axis shows the number of location. The plotted period spans an entire week, daytime locations are excluded. Subsequent distances (bigger dots) are connected by a small dotted line to improve the visualisation of distance changes.


DISTANCE BETWEEN ALI AND NANI (METERS*50)
18
15
12
9
6
3
0
0
50
100
150
200
250
300
NO OF LOCATION


DISTANCE BETWEEN NANI AND WILF (METERS*50)
18
15
12
9
6
3
0
0
50
100
150
200
250
300
NO OF LOCATION


DISTANCE BETWEEN ALI AND WILF (METERS*50)
18
15
12
9
6
3
0
0
50
100
150
200
250
300
NO OF LOCATION

between the two distributions of fixes of a pair of badgers in terms of the range of all possible separations of one badger from another. One way of presenting the result is indicated by the continuous "null hypothesis line" in Fig. 6.68. Here, the cumulative probability is plotted for two individuals being closer than, or equal to, a certain separation. This is compared with the observed frequency distribution (plotted as cumulative probability) of separation distances for simultaneously recorded fixes. As Doncaster (1985) shows, the slightly concave null hypothesis lines illustrated for all three pairs of individuals in Fig. 6.68–6.70 indicate a large range overlap of all individuals. Steep gradients in the observed cumulative probabilities (e.g. Fig. 6.68 for the first 100 m of separation) imply a large proportion of fix pairs at which the animals were close together. Then, the movement vectors of both animals tend to be parallel and point in the same direction at that separation. Shallow slopes indicate a small proportion of fix pairs accounted for by a larger spectrum of separations, as would result from badgers moving in opposite directions (e.g. Fig. 6.68 separation between ca. 300 m and 500 m).

How can interdependence of movements ("dynamic interaction") be inferred from these two graphs? No dynamic interaction is present, ie. individuals move independently with respect to each other, if the slope of the null hypothesis line parallels the slope of the observed line. Positive dynamic interaction, or attraction is shown over that range of separations where the observed line has a steeper gradient than the null hypothesis line. Then, this range of separation is more frequently observed than would be expected if there was no interdependence of the movements of the two animals. Negative dynamic interaction, or repulsion, is present if the observed line has a shallower gradient than the null hypothesis line; these ranges of separation are less frequently observed than would be expected from independent movements with respect to each other.

Fig. 6.68-6.70

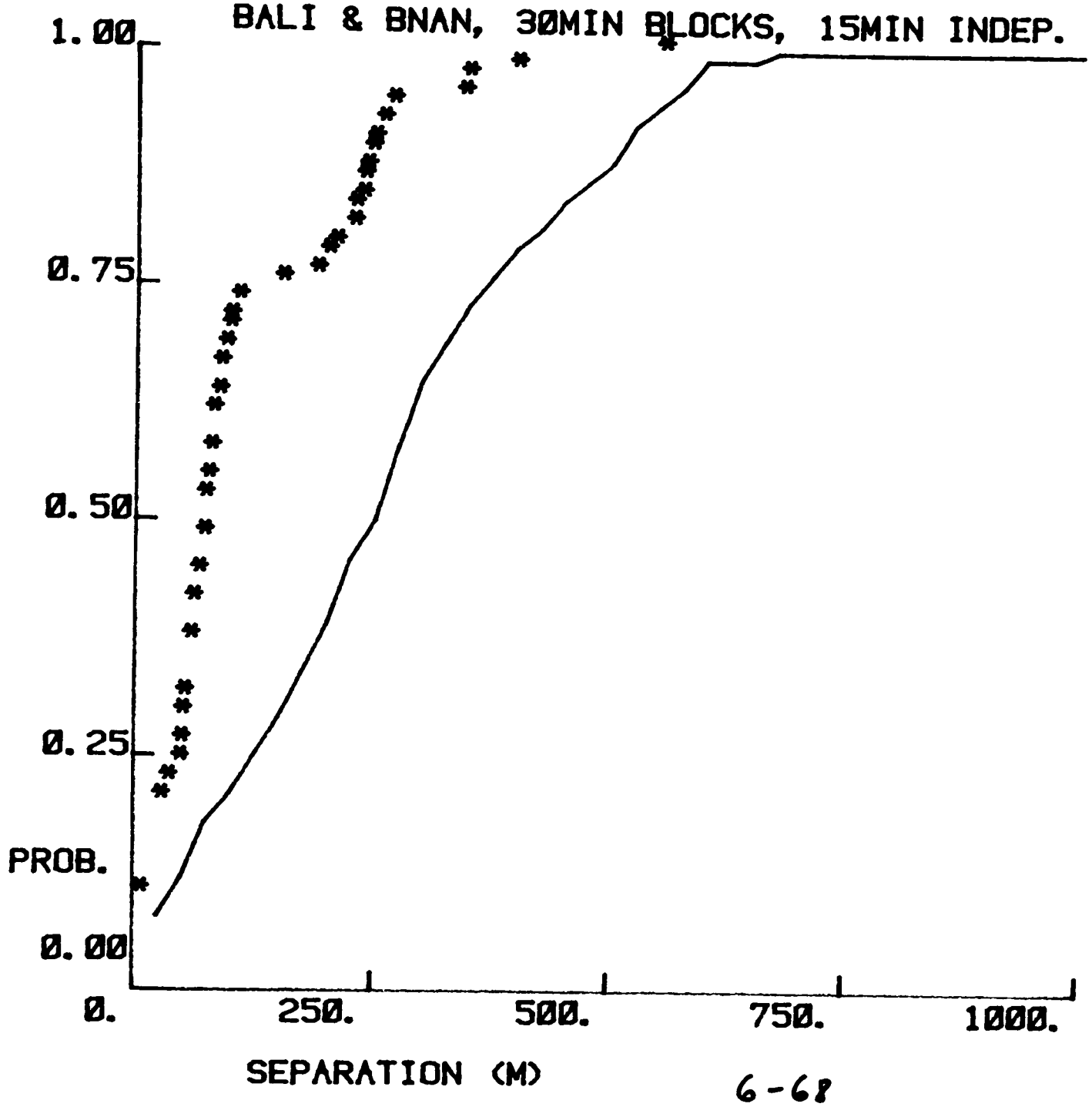
The non-parametric estimation of dynamic interaction between pairs of badgers from the UPPER FOLLIES group.

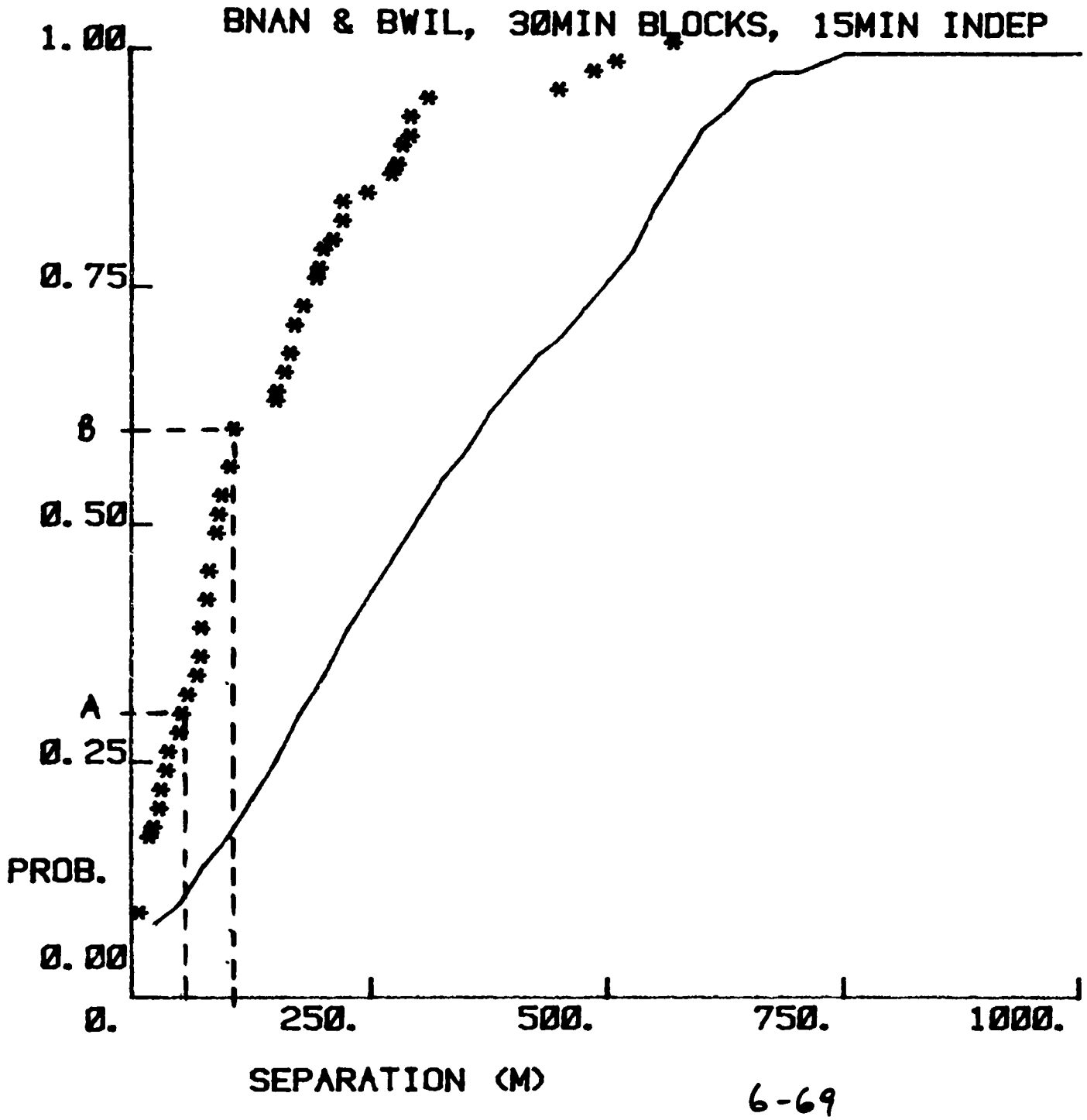
6.68: inteeraction between ALI and NANI

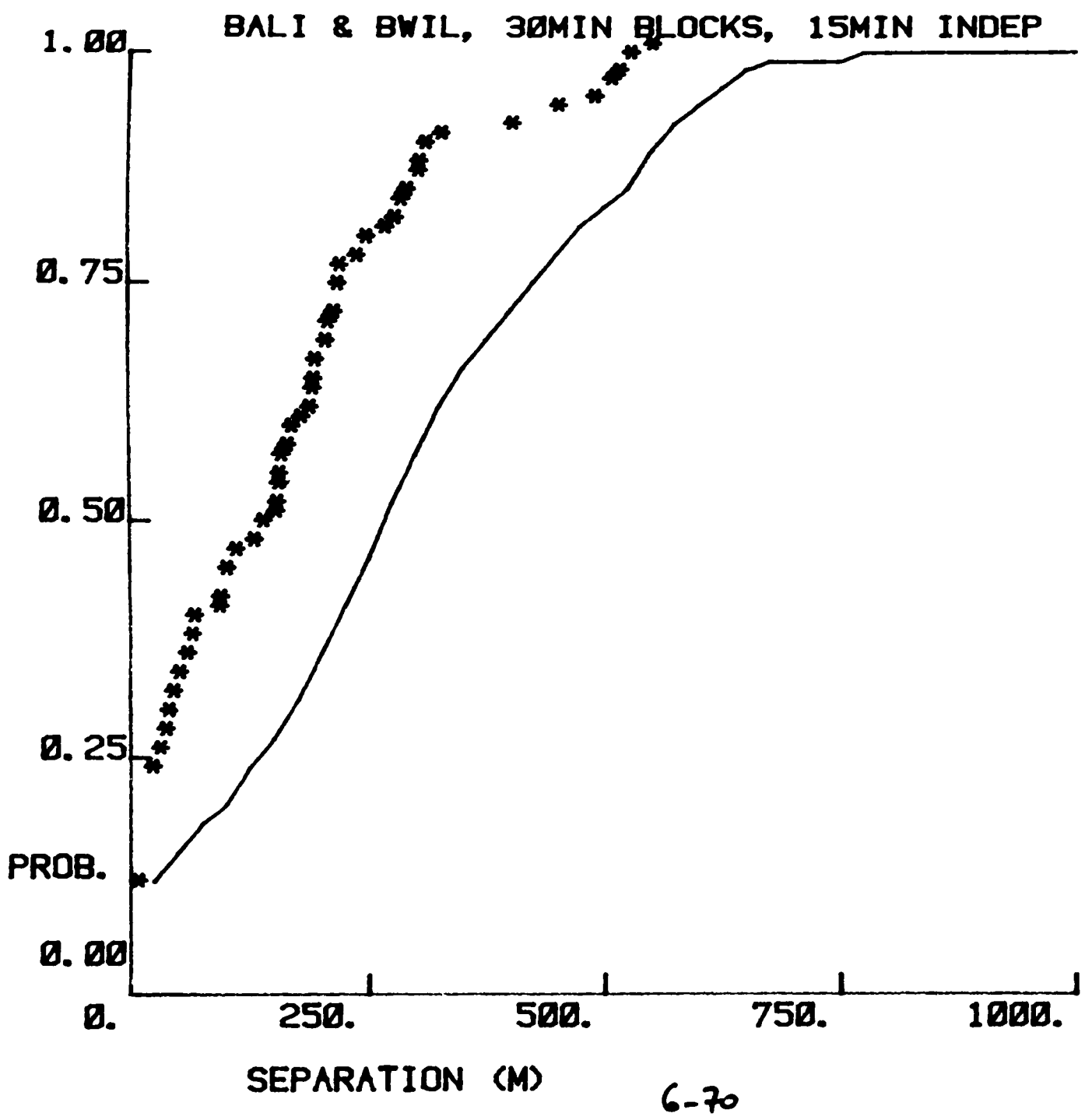
6.69: interaction between NANI and WILF

6.70: interaction between ALI and WILF

Original data files of a pair of foxes are merged by program FRADAT (Doncaster (1985)), to yield a list of coordinate pairs. Each pair of coordinates identifies the closest separation of the two animals during a short time interval. Day locations are ignored and an independence interval is applied (15 min), to ensure approximate independence of data. The time interval was chosen as 30 minutes. Output of program FRADAT is then utilized by programs TWOFOX and PROESP (both from Doncaster (1985)) which compute the probability of two animals being separated by up to and equal to the distance given. The actual separations computed by program PRADAT are plotted as discrete points, while the "null hypothesis line" plots the cumulative probability of all possible separations and therefore represents static interaction in the absence of dynamic interaction. Dynamic interaction is present for the range of separations over which the cumulative observed separations have a steeper gradient than the null hypothesis line (positive dynamic interaction) or a shallower gradient (negative dynamic interaction).


BALI & BNAN, 30MIN BLOCKS, 15MIN INDEP.
1.00
0.75
0.50
0.25
PROB.
0.00
0.
250.
500.
750.
1000.
SEPARATION (M)


BNAN & BWIL, 30MIN BLOCKS, 15MIN INDEP
1.00
0.75
B
0.50
A
0.25
PROB.
0.00
0.
250.
500.
750.
1000.
SEPARATION (M)


BALI & BWIL, 30MIN BLOCKS, 15MIN INDEP
1.00
0.75
0.50
0.25
PROB.
0.00
0.
250.
500.
750.
1000.
SEPARATION (M)

In Fig. 6.68–6.70, all three pairs show dynamic positive interaction at low separation distances. The positive dynamic interaction is particularly strong for the two females, ALI and NANI, ie. those two individuals that are expected to suffer most from intragroup competition (Chapter 7). At larger distances all pairs exhibit negative dynamic interactions.

Doncaster (1985) has simulated a large number of possible cases and suggests the following interpretation: positive dynamic interactions at small separation distances are typical of stable social coordination, e.g. in order to realize some mutually shared goal, with parallel movement vectors in the same direction. Both animals appear to be "bound together" and move in synchrony, apparently under the influence of a shared stimulus. He calls this type of interaction "intentionally synchronous time-tabling". A typical case is the common pressure of a similar resource need.

To what extent may the observed synchrony of movements be simply a by-product of two individuals following the same schedule, but independent (or unaware) of each other ? This interpretation cannot be excluded on statistical grounds; intentionality cannot be derived from or rejected by the computations illustrated in Fig. 6.68–70. One likely possibility is the effect of an external factor – e.g. the weather induces all group members to proceed to the same area where worms are available in a given night. Coordination at medium separation distances may be to some extent due to such unintentional coordination – individuals moving towards roughly the same area – but at closer distances, less than 50 or 100 m, the probability of noticing each other and thus the scope for intentional coordination increases rapidly. The graphs in Fig. 6.68–6.70 do <u>not</u> support the suggestion that interference between individuals and consequent agonistic encounters occurred at small separations. If two badgers were close together, they were peacefully close.

I suggest that, for badgers at least, synchronous time-tabling helps individuals to organize their foraging activities so that each individuals

achieves maximum foraging success. In the case of badgers, foraging success is probably measured in terms of maximizing energy intake per time unit (see Kruuk 1978b, Chapter 7). If individuals moved indiscriminately with respect to each other, they may on average encounter more often a depeleted patch or a patch that has not fully recovered yet (details see Chapter 7) than if they organized the exploitation of resources in order to maximize the renewal period for each food patch (see below). On the other hand, if individuals stayed very close to each other (within 10 m or so) they may have to spend additional time on the careful arrangement of their foraging track in relation to each other, otherwise they run the risk of crossing just depleted areas. Conditions permitting two individuals to forage in very close proximity without any detrimental effects should be rare. Hence, if the common resource need drives individuals towards the same area, then within that area they should keep at distances sufficiently close to facilitate intentional coordination, but far away not to tread upon each others toes (porcupine principle, Schopenhauer). The result is a large proportion of separations between 20 and 70 metres.

Two questions arise. (i) are there any rules in movement that could help individuals to maintain coordination at distances between 20 and 100 metres, and (ii) which renewal periods can be observed? (To show that synchrony of movements actually <u>improves</u> foraging rates in comparison to indiscriminate movements one would need to compare this range with a situation where no such synchrony occurred, but these data are not available.)

The first question can be rephrased by asking whether simple rules exist whereby an individual can deduce its movements relative to other group members, if it can monitor only the location of one of them? Even coordinating with one individual, and forgetting about the third one, would be better than nothing. To investigate this, I compiled the number of occurrences that ALI approached or withdrew from WILF, given a certain

constellation of changes in distance from one recording time to the next between the two other pairs (Table 6.6b). Suppose that ALI can monitor its location to NANI (that this is plausible is discussed below). There are then two possibilities: she approaches NANI or withdraws from her. The a priori expectation of her movement direction towards the third individual, WILF, is independence of the situation between the two other pairs. Given the expected probability of 0.5 for each possibility and independent data points, the binomial test can decide whether the observed frequencies (Table 6.7) match expected ones. Successive differences in distances are broadly independent (Table 6.6a), hence the binomial test was used. In both cases of approach to and withdrawal from NANI, ALI can be quite certain to also approach WILF or withdraw from him. The possibilities of movements discussed here are illustrated in Fig. 6.71.

How could ALI monitor NANI's position? All three individuals spent most of their time on several pastures - a large homogenous area that constitutes a small valley within the group range. This is an open area and individuals certainly had means to stay in contact by acoustic signals or, more likely, by scent transferred through the air, if they stayed fairly close together. ALI and NANI, for instance, were within 50 m of each other on 31% of occasions and within 105 m in 60% of occasions (Fig. 6.68, probabilities A and B, respectively). Furthermore, there are some hints that badgers frequently paste mark areas where they forage (Macdonald 1977a). Other individuals that come across such a mark would know that this area had been "harvested" previously and, provided they can evaluate the time since deposition, estimate the recovery time of the patch.

Can these results be generalized for other groups that live in different environments? I believe that these three badgers were in circumstances which facilitated coordination, and where the pressure on the area by all group members was exceptionally high (the valley constitutes just one large patch). In this context I propose a new function for

Table 6.5 Evaluation of data from simultaneous radio-tracking in Range B2.

a) frequency of occurrence of distances (in units of 50 m) between pairs of animals; data from the entire period of simultaneous tracking.

Distance class	ALI-NANI	NANI-WILF	ALI-WILF
0.00 - 1.67	78	73	46
1.68 - 3.35	85	88	60
3.36 - 5.03	47	47	51
5.04 - 6.70	43	34	44
6.71 - 8.38	23	24	40
8.39 - 10.06	6	5	16
10.07 - 11.73	5	6	14
> 11.73	2	12	18

differences in frequency distribution of pairs:

ALI-NANI and NANI-WILF : G = 15.87, df=7, p < 0.05
ALI-NANI and ALI-WILF : G = 75.63, df=7, p < 0.001
ALI-WILF and NANI-WILF : G = 53.57, df=7, p < 0.001

b) differences in the frequency distribution of number of cell visits :

cell size	df	Ali & Nani G/signif.	Nani & Wilf G/signif.	Ali & Wilf G/signif.
25	3	5.611 ns	7.897 < 0.05	4.581 ns
50	3	9.779 < 0.025	40.497 < 0.001	25.153 < 0.001
100	4	30.412 < 0.001	71.215 < 0.001	34.825 < 0.001

c) frequency of occurrence of mean length of stay per cell

	Length of stay (min)											
	1-15 cell size			16-20 cell size			21-30 cell size			30 cell size		
	25	50	100	25	50	100	25	50	100	25	50	100
Ali	43	36	5	4	9	8	4	2	4	2	2	2
Nani	50	44	8	2	2	7	3	4	6	4	2	1
Wilf	39	47	14	0	6	7	8	9	11	1	1	1

tests on independence between length of stay and individual identity:

25 m cells: (Ali, Nani, Wilf) vs. (1-15, 16-30, 30 min)
G = 2.978, df = 4 ns.

50 m cells: (Ali, Nani, Wilf) vs. (1-15, 16-20, 20 min)
G = 6.955, df = 4 ns.

100 m cells: (Ali, Nani, Wilf) vs. (1-15, 16-20, 20 min)
G = 2.706, df = ns.

Table 6.6 Patterns of changes of distances between pairs of individuals at successive locations

a) runs test to check whether successive differences in distances between pairs of animals are randomly arranged (independent from each other); test procedures follow Sokal & Rohlf (1981).

Night	Ali–Nani				Nani–Wilf				Ali–Wilf			
	No. runs	N	t_s	sig.	No. runs	N	t_s	sig.	No. runs	N	t_s	sig.
1	20	33	-0.71	ns	19	30	-0.3	ns	21	39	-1.82	ns
2	24	35	0.41	ns	24	35	0.41	ns	22	37	-0.93	ns
3	20	37	-1.73	ns	20	33	-0.71	ns	17	37	-2.93	<0.005
4	27	34	1.95	ns	18	33	1.56	ns	13	37	-4.53	<0.001
5	22	36	-0.68	ns	24	37	-0.13	ns	22	36	-0.68	ns
6	15	33	-2.83	<0.005	18	36	-2.30	<0.005	20	41	-2.65	<0.01
7	22	36	-0.68	ns	24	34	0.7	ns	26	38	0.39	ns

In 16 out of 21 cases (76%) are distance changes randomly arranged in 5 out of 21 cases (24%) distance changes are not independent from each other.

b) frequency of change of distance between Ali and Wilf at two successive locations, given a certain change of distance between Ali and Nani and Nani and Wilf (data pooled from all nights)

group	change of distance between Ali/Nani	Nani/Wilf	change of distance between Ali and Wilf a) Ali approaches Wilf	b) Ali withdraws from Wilf
1	approach stay equal approach	stay equal approach approach	58	17
2	stay equal withdraw withdraw	withdraw stay equal withdraw	23	61
3	approach	withdraw	29	22
4	withdraw	approach	31	23

Table 6.7 Rules of movement as derived from patterns of changes of distance between pairs of individual animals. Data pooled from all nights (as in Table 6.).

a) consider a movement of Ali <u>towards</u> Nani

total number of occurrences: 126
(1A+1B+3A+3B of Table 6.6)

number of occurrences that Ali then also approaches Wilf: 87
number of occurrences that Ali then withdraws from Wilf: 39

expected probability for Ali approaching Wilf = 0.5
withdrawing from Wilf = 0.5

binomial test (observed probability vs. expected probability): exact probability 6.49×10^{-6} summed, one-tailed probability 1.14×10^{-5}

b) consider a movement of Ali away from Nani:

total number of occurrences: 138

no. of occurrences that Ali also withdraws from Wilf: 84
no. of occurrences that Ali approaches Wilf: 54

expected probabilities: as above

binomial test (observed vs. expected): exact probability 0.0026 summed, one-tailed probability 0.0066

c) conclusions: the changes in distance between Ali and Wilf are highly non-random with respect to a given movement of Ali towards or away from Nani. Thus, for Ali it suffices to keep approximate track of its distance towards <u>one</u> group member in order to evaluate its position towards the third.

Fig. 6.71

Changes in distance between three individuals at two subsequent locations. The left dot of each diagram represents ALI, the middle one NANI, and the right dot WILF. Black bars represent distances between individuals at the same point in time, dotted arrows indicate the direction of movement of each individual from one location to the next. Stars label those sections that add together to the distance between ALI and WILF.

1: ALI approaches NANI and NANI approaches WILF

A: ALI also approaches WILF

B: ALI withdraws from WILF

2: ALI withdraws from NANI and NANI withdraws from WILF

A: ALI approaches WILF

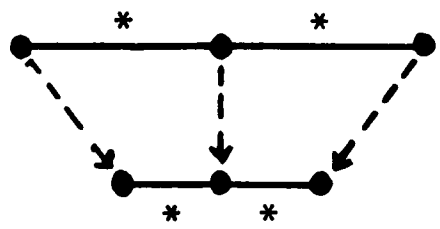
B: ALI withdraws from WILF

3: ALI approaches NANI and NANI withdraws from WILF

A: ALI approaches WILF

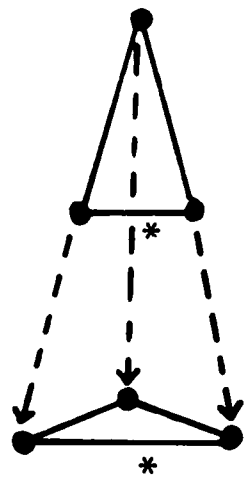
B: ALI withdraws from WILF

1A



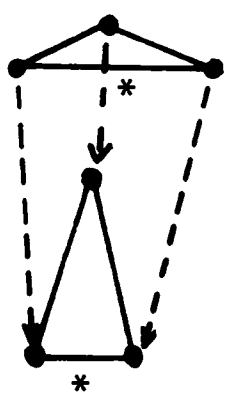
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1B



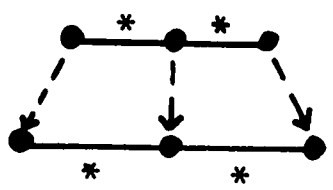
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2A



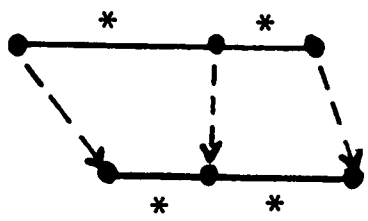
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2B



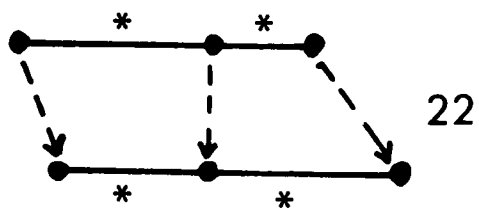
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3A



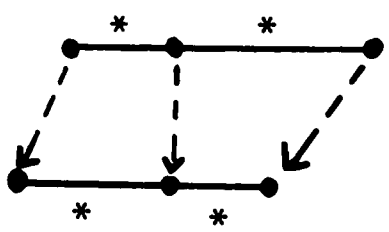
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3B



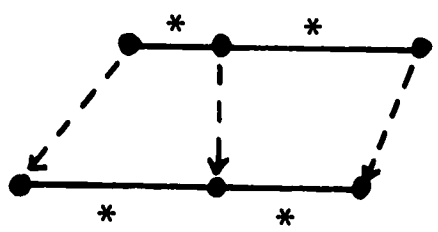
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4A



31

4B



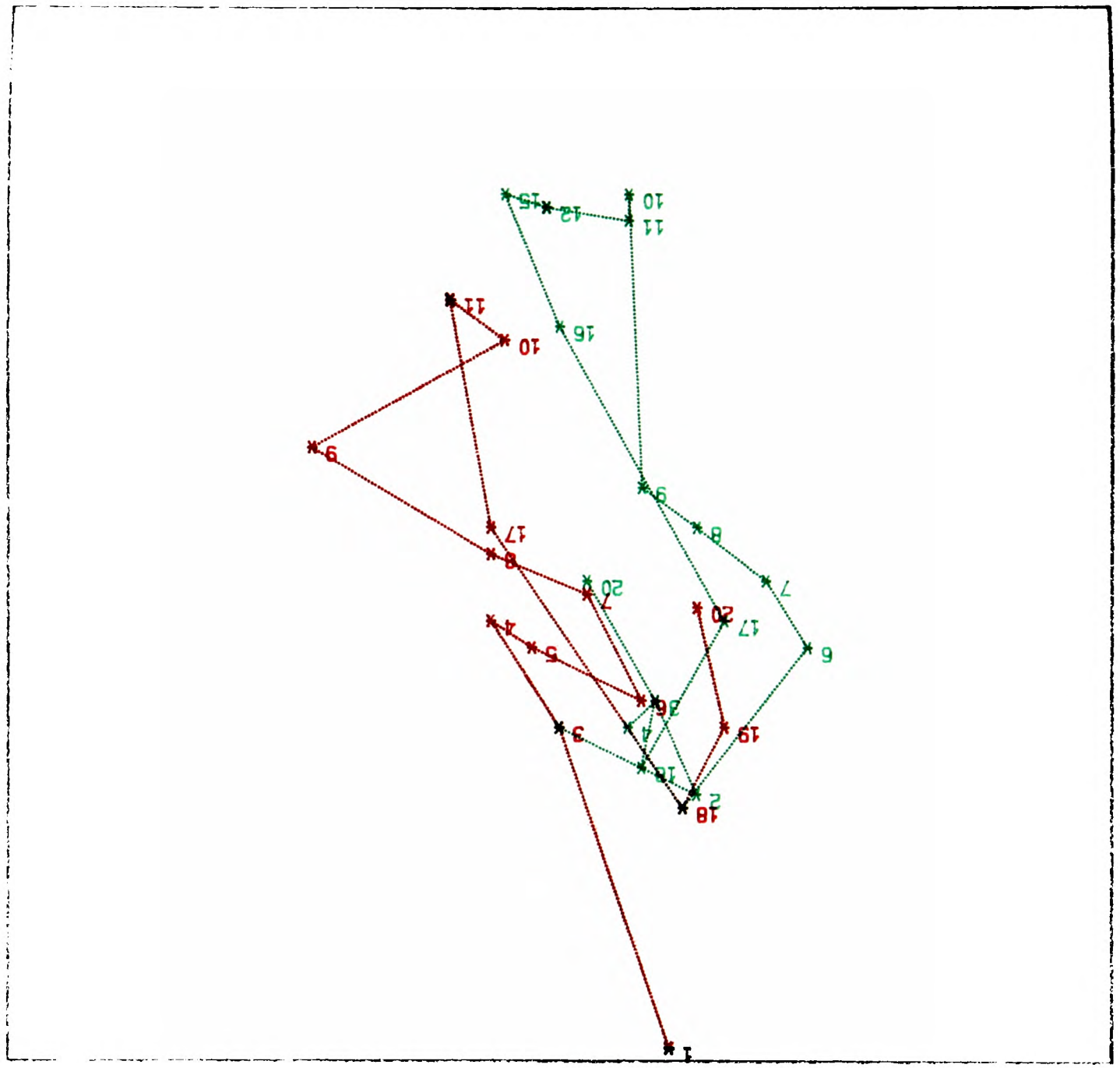
23

6-71

Fig. 6.72

Movements of NANI (red) and WILF (green) in night 1 from 20.00 hours to 00.50 hours.

Scale: 800 by 800 metres. Each location is separated from the next one by 15 min. If labels of subsequent locations differ by more than 1, then the animal stayed at the previous location for several locations.


1
2
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19
20

latrines that occur within the boundaries of the group range: they could serve as convenient markers to indicate whether or not, and how long ago, a certain area has been visited by other badgers (section 5.4.). The widely quoted observation that members of the same clan emerge and move away from the sett in apparent ignorance of each other (Neal 1977, Long & Killingley 1983), is not an objection to this suggestion. For these individuals it suffices to know at a foraging site whether another individual had been there already.

6.4.2. Renewal periods and interference pressure

In this section I shall investigate possible effects of group members on each other's foraging success. An area unit is selected (cells of sizes 25 by 25, 50 by 50 and 100 by 100 m) and the pattern of visits to this cell (and all other cells) are recorded. The interval between two successive visits is called the revisit interval. If visits by all group members are considered, the revisit interval also constitutes the renewal period of the resource in the cell (ie. the time available for worms to recover and surface again since the last visit).

1. How often are cells visited?

Fig. 6.74 depicts the frequency distribution for each individual for cells with one more visits over all 7 nights. The effect of cell size can be seen in two different ways. Within the same individual, the proportion of cells visited only once decreases rapidly with increasing cell size. If the frequency distribution of all three individuals are compared, no differences are found for the 25 m cells (except NANI and WILF) while for both other size categories all distributions are different from each other (Table 6.5b). For 25 and 50 m cells, the highest proportion of cells are those visited only once.

2. How long do badgers stay on average in a cell?

Fig. 6.74

Proportion of cells that are visited for a certain number of times by the UPPER FOLLIES badgers.

G.D.A: cells of size 25 m

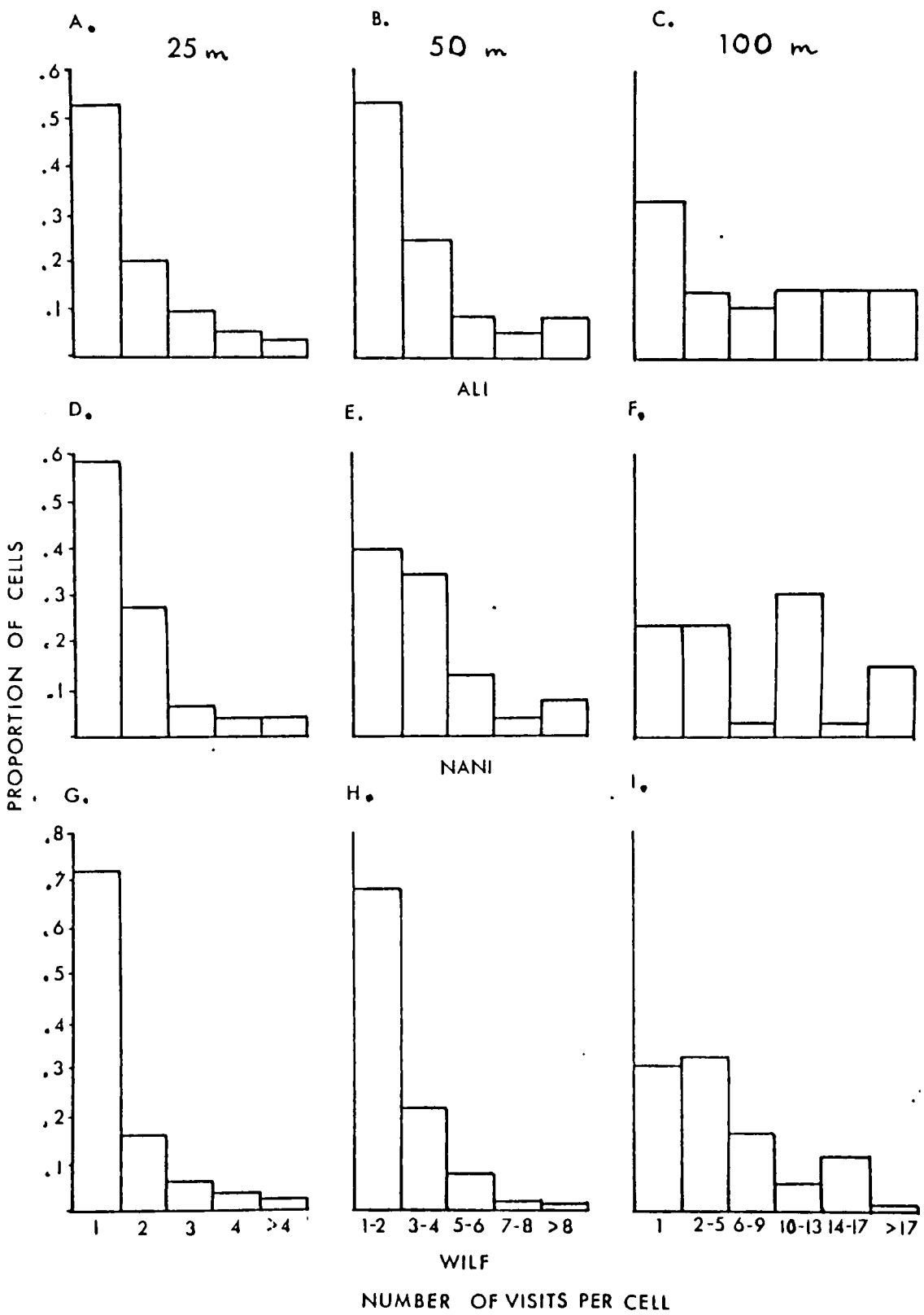
H,E,B: cells of size 50 m

I,F,C: cells of size 100 m

ALI: diagrams A,B,C

NANI: diagrams D,E,F

WILF: diagrams G,H,I


A.
25 m
B.
50 m
C.
100 m
.6
.5
.4
.3
.2
.1
D.
E.
ALI
F.
PROPORTION OF CELLS
NANI
G.
H.
I.
.8
.7
1
2
3
4
>4
1-2
3-4
5-6
7-8
>8
1
2-5
6-9
10-13
14-17
>17
WILF
NUMBER OF VISITS PER CELL

Badgers rarely stay longer than 30 minutes, no matter how large the cell (Table 6.5c). All individuals show similar behaviour.

3. How much time elapses between successive visits? Variation of mean revisit intervals is considerable, as evidenced by Fig. 6.75 and 6.77-6.79, but largely independent of the mean duration of stay per cell.

4. Do the movements and visits by other individuals exert any influence on the behaviour of a given individual? To test this, I compared two indicators of visit patterns with the total number of visits per cell, the "total group pressure".

(i) Duration of stay is positively correlated with total group pressure for NANI and WILF (Fig. 6.76, Table 6.8b). Apparently, frequently visited areas are of high intrinsic value; it pays individuals to go there and stay longer than elsewhere.

(ii) At small cell sizes, mean revisit interval for a given individual per cell and total group pressure are independent from each other (Fig. 6.77-6.79). At the large cell size, when the likelihood of revisiting the same cell increases, there is a significant negative correlation for ALI and NANI: the more often an area is visited by all group members, the less time elapses between successive visits of the same individual. This correlation could be the result of a statistical artefact, since an individual's contribution to group pressure enters the predictor variable. However, as Table 6.8a and Fig. 6.80-6.82 show, number of visits of an individual does not necessarily correlate positively with the total group pressure, as might be expected, at least not for ALI for 100 m cells.

The relationships identified above are consistent with the suggestion that these badgers behaved similarly because of the high intrinsic value of certain areas. Valuable cells are visited often, the animals stay longer and therefore, on average, return sooner to favourite cells. A close inspection of Fig. 6.77-6.79 reveals that only a small proportion of revisit intervals per individual is below 10 hours. The revisit interval critical

Table 6.8 Relationships between various measures of visit intensity (pressure) per cell. Data from simultaneous radio-tracking of Ali, Nani and Wild in group B2.

a) correlation (Spearman's rho) between number of visits per 100 m cell of an individual and the number of visits by the rest of the group to the same cell:

Individual	rank correlation	df	significance
Ali	0.33	18	ns
Nani	0.662	21	<0.002
Wilf	0.588	30	<0.002

b) correlation (Spearman's rho) between average duration of stay per 100 m cell of an individual and the total number of visits by all members of the group to the same cell:

Individual	rank correlation	df	significance
Ali	0.431	18	ns
Nani	0.662	21	<0.002
Wilf	0.544	30	<0.01

c) correlation (Spearman's rho) between average revisit interval of an individual per 100 m cell and the total number of visits by all members of the group to the same cell:

Individual	rank correlation	df	significance
Ali	-0.716	18	<0.002
Nani	-0.590	21	<0.01
Wilf	-0.291	30	ns

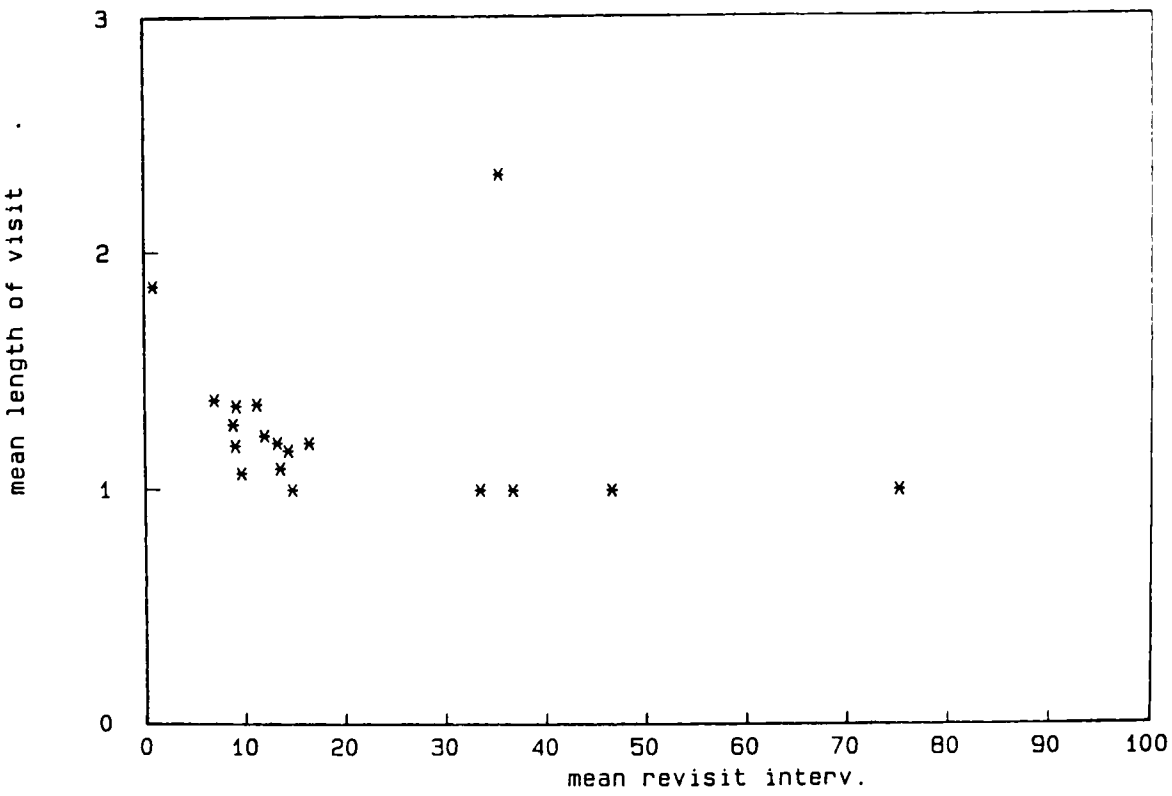


Fig. Relationship between mean length of visit (15 min units)
6-75a and mean revisit interval (hours) per 100 m cell (ALI)

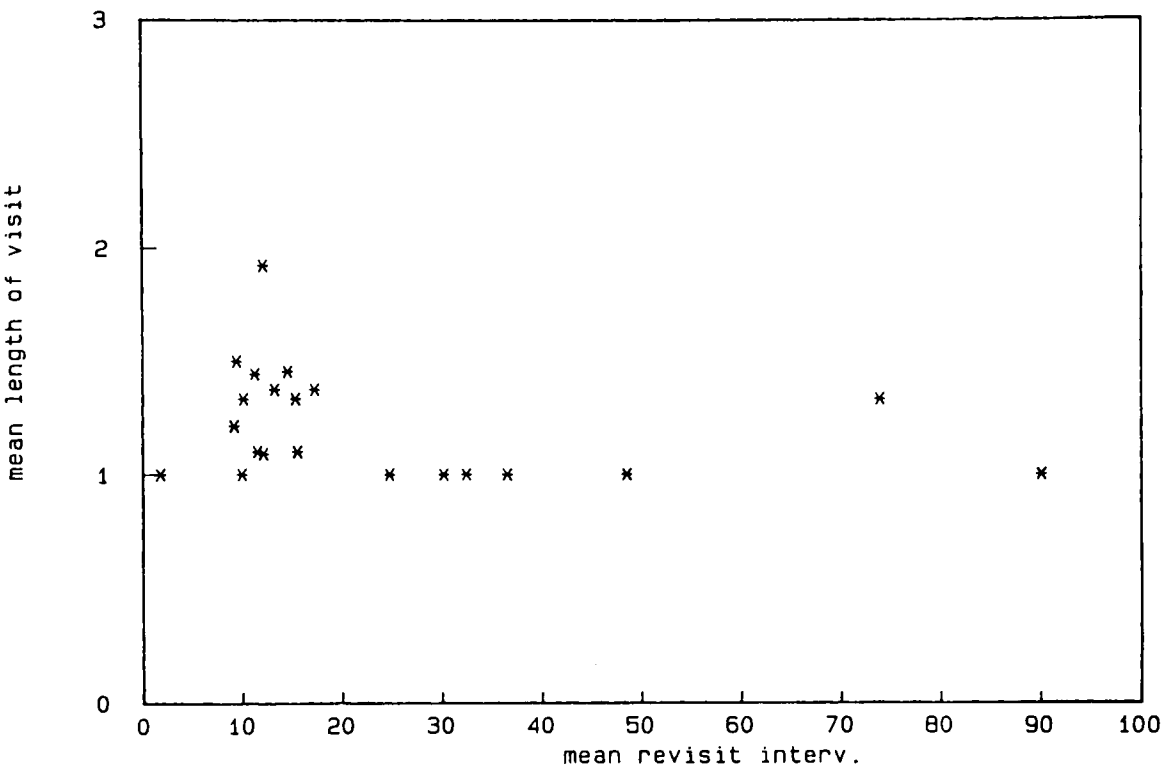


Fig. Relationship between mean length of visit (15 min units)
6-75b. and mean revisit interval (hours) per 100 m cell (NANI)

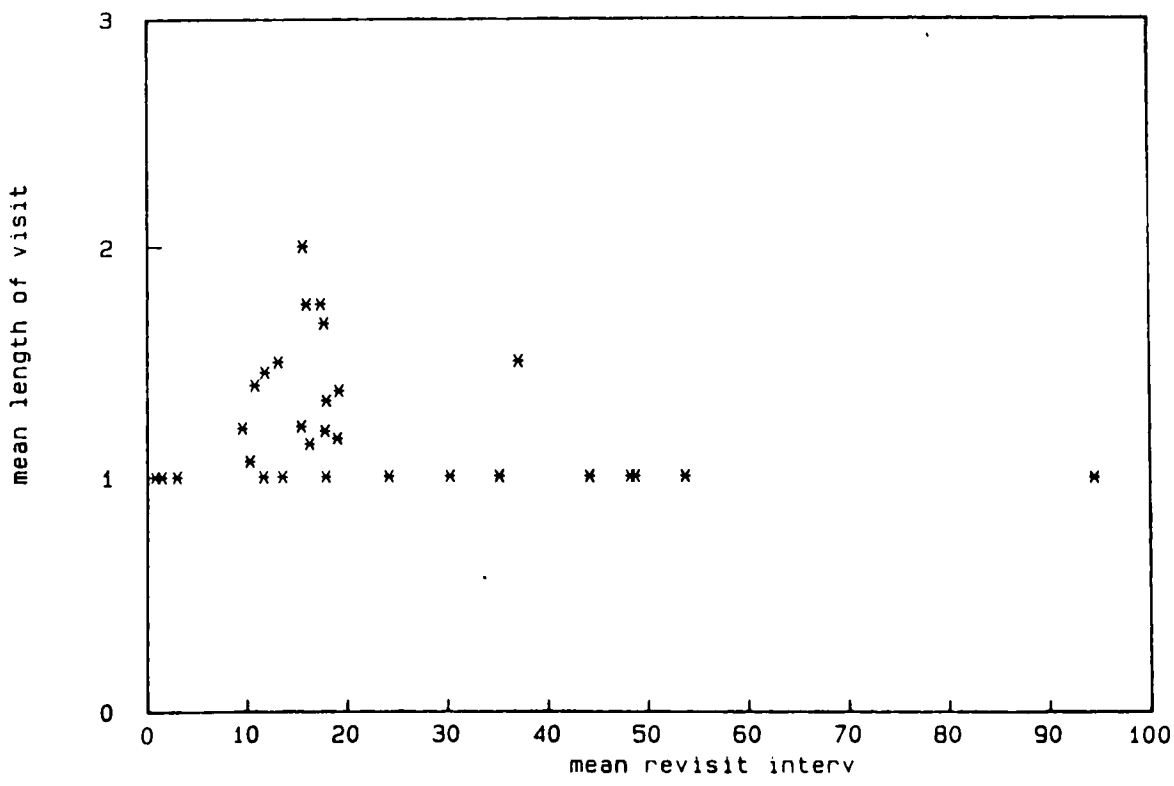


Fig. Relationship between mean length of visit (15 min units)

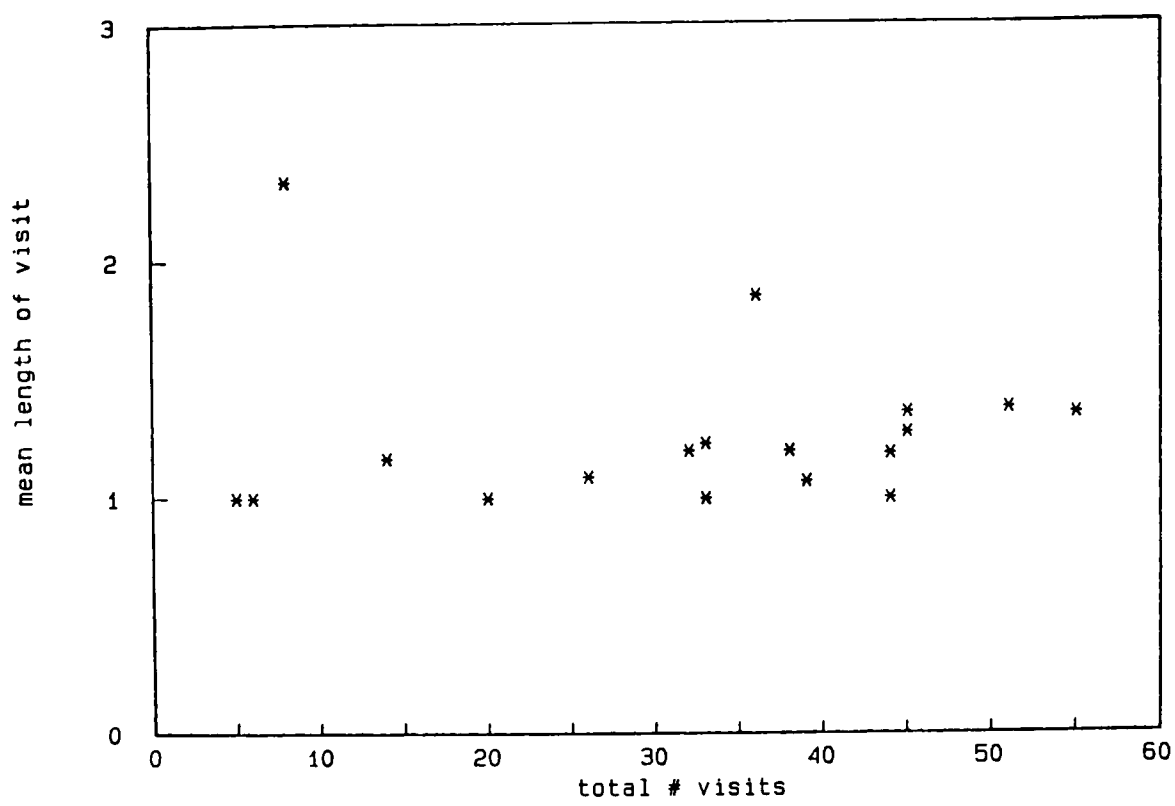


Fig. 6-76a. Relationship between mean length of visit (15 min units) by ALI per 100 m cell and total number of visits

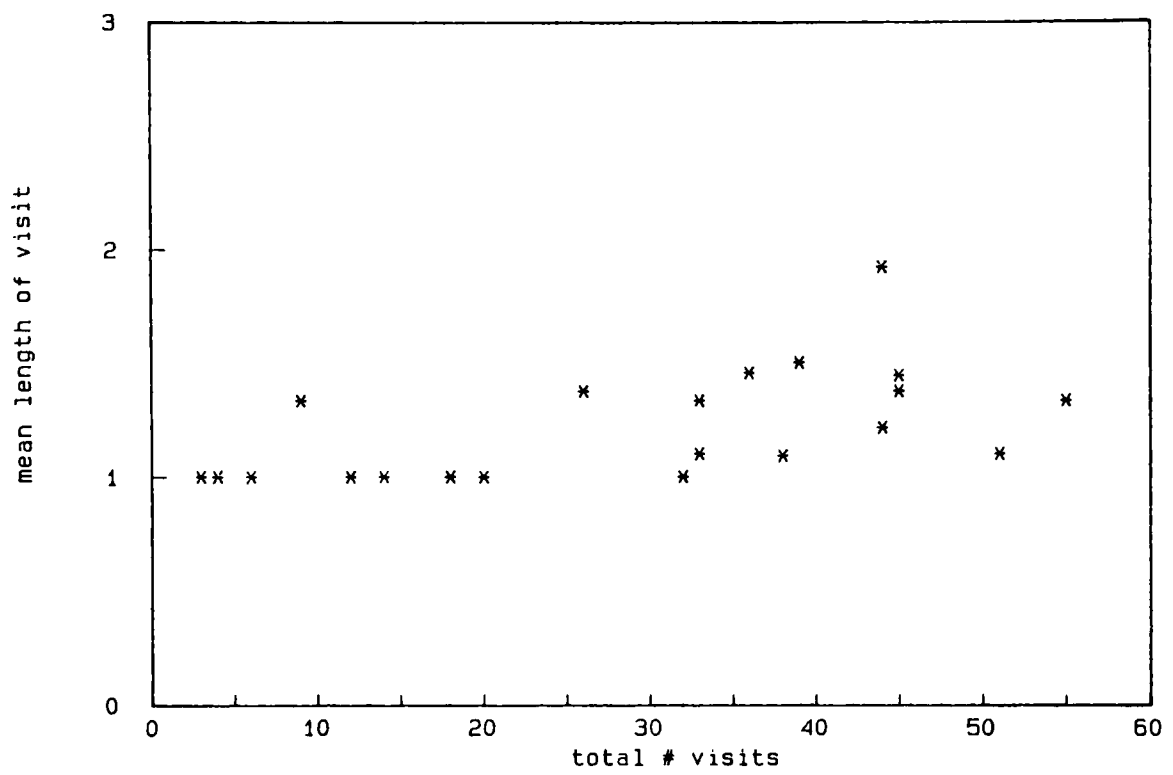


Fig. 6-76b. Relationship between mean length of visit (15 min units) by NANI per 100 m cell and total number of visits

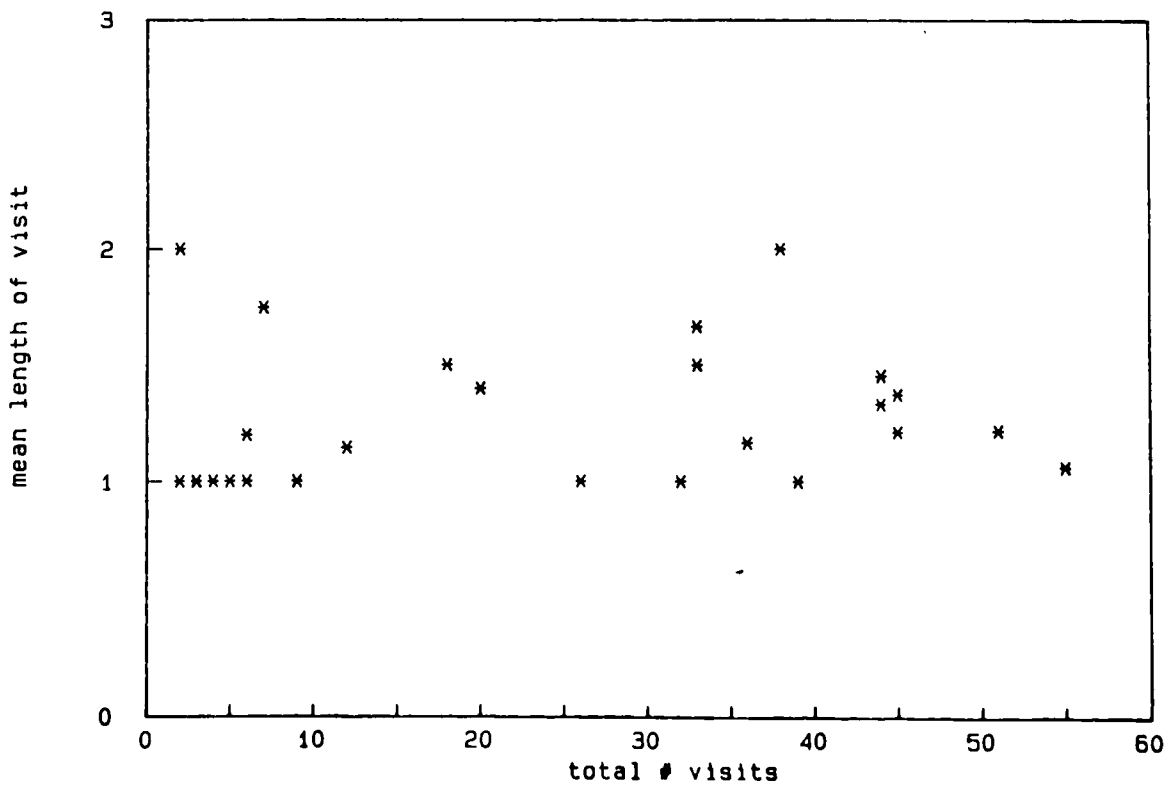


Fig. 6-76c. Relationship between mean length of visit (15 min units) by WILF per 100 m cell and total number of visits

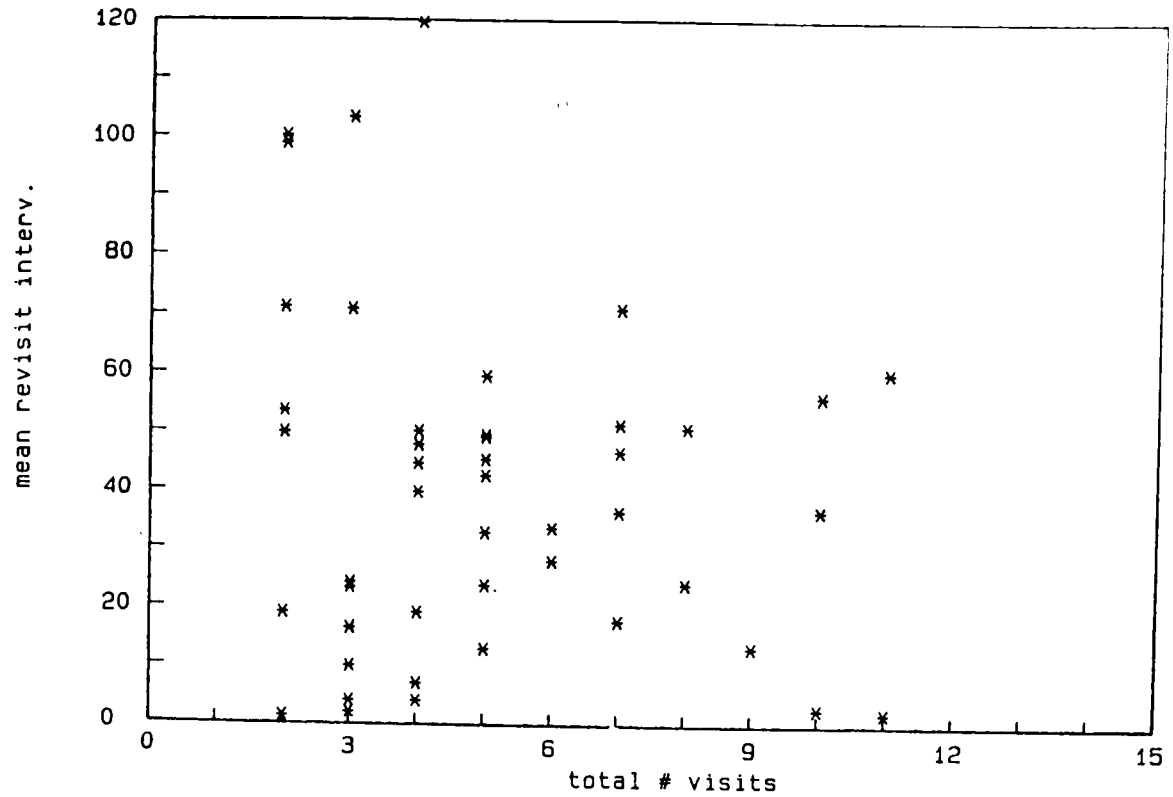


Fig. Relationship between mean revisit interval (hours) of ALI 6-77a. per 25 m cell and total number of visits to the same cell

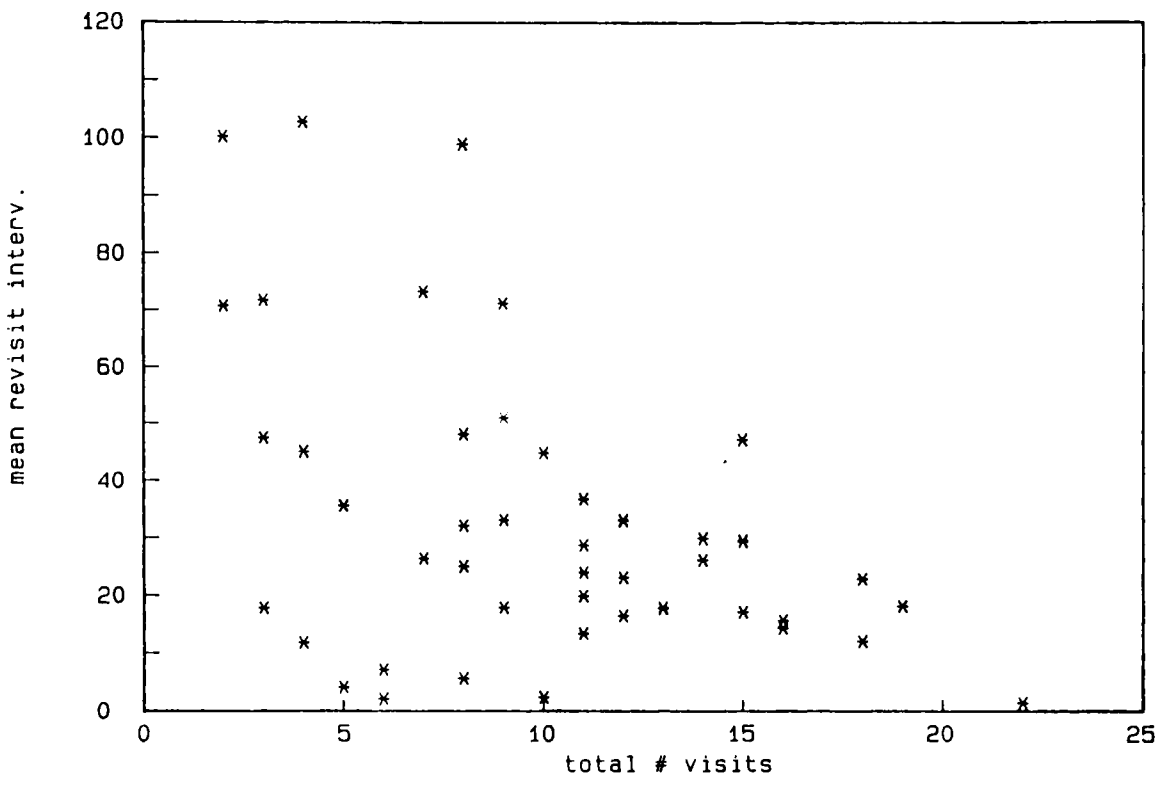


Fig. Relationship between mean revisit interval (hours) of ALI 6-77b. per 50 m cell and total number of visits to the same cell

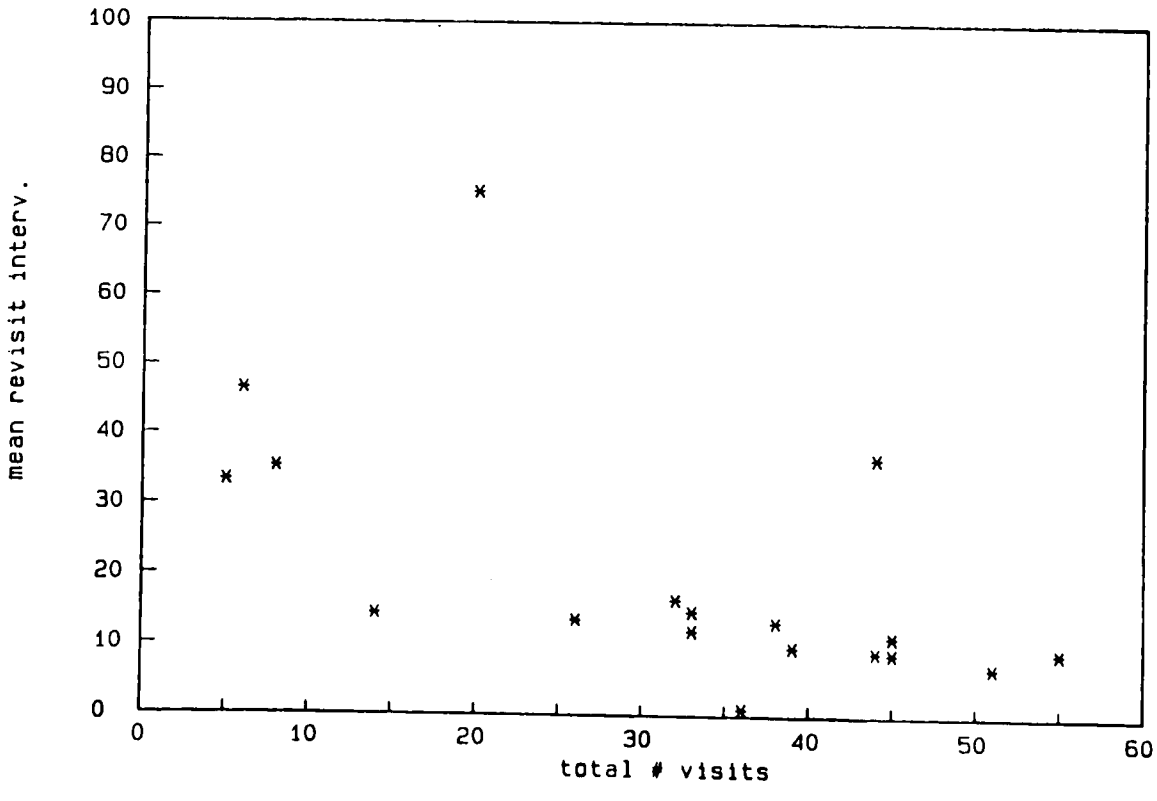


Fig. Relationship between mean revisit interval (hours) of ALI 6-77c. per 100 m cell and total number of visits to the same cell

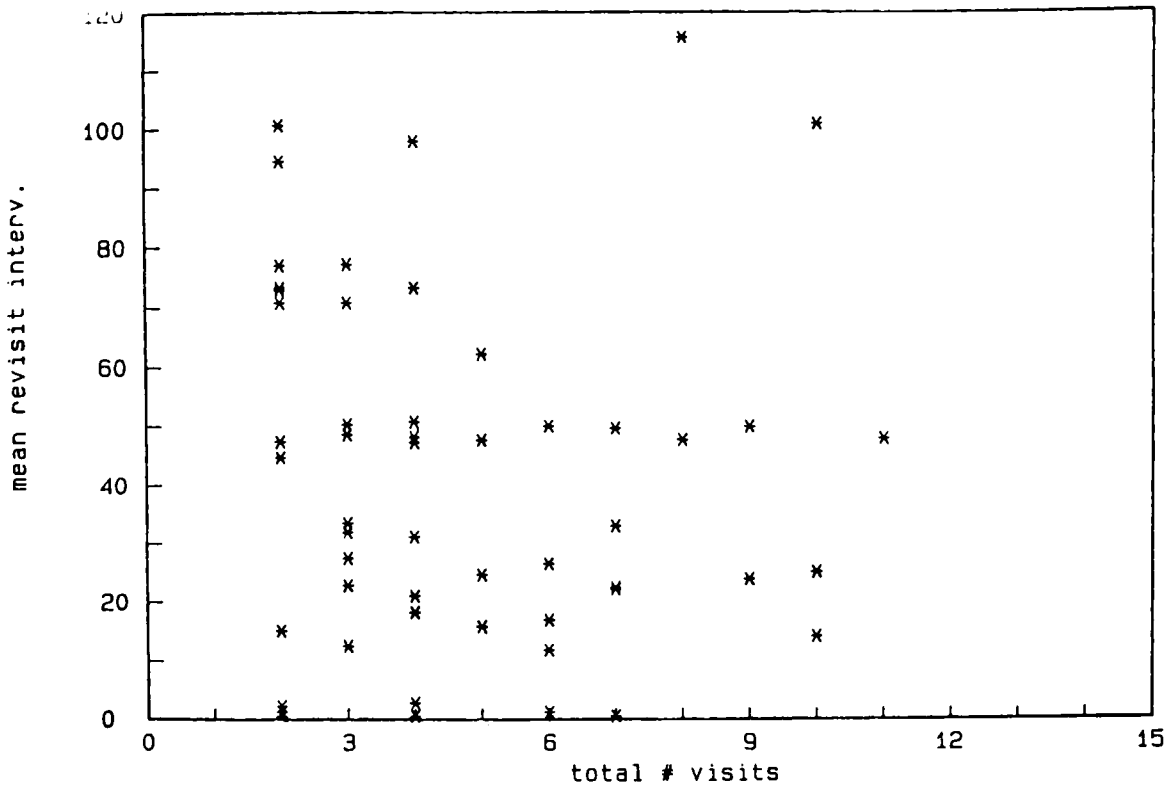


Fig. Relationship between mean revisit interval (hours) of NANI 6-78a per 25 m cell and total number of visits to the same cell

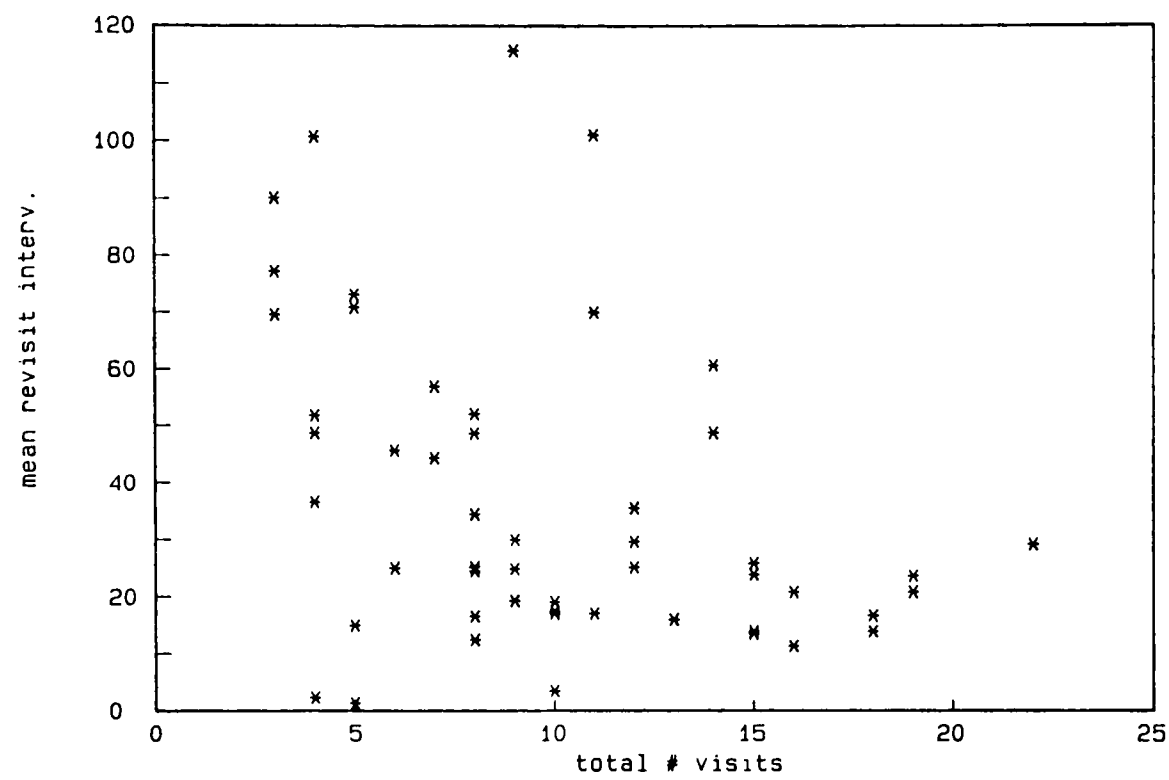


Fig. Relationship between mean revisit interval (hours) of NANI 6-78b. per 50 m cell and total number of visits to the same cell

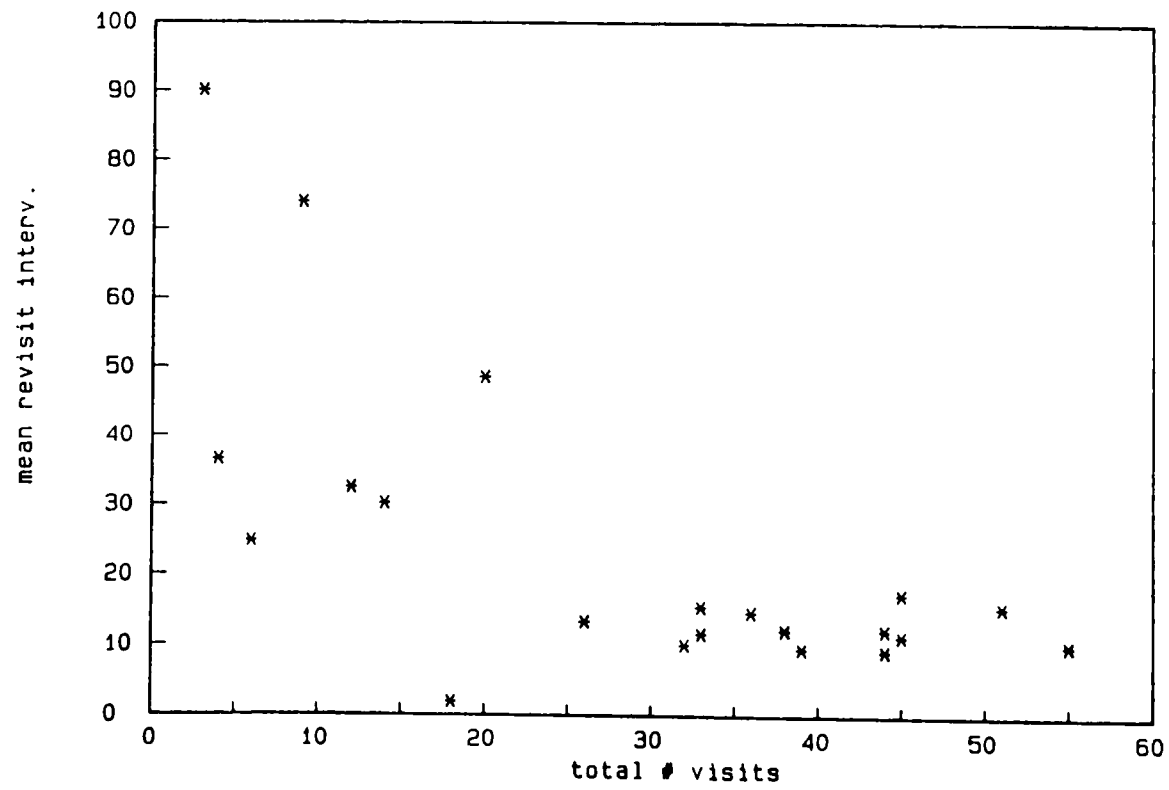


Fig. Relationship between mean revisit interval (hours) of NANI 6-78c per 100 m cell and total number of visits to the same cell

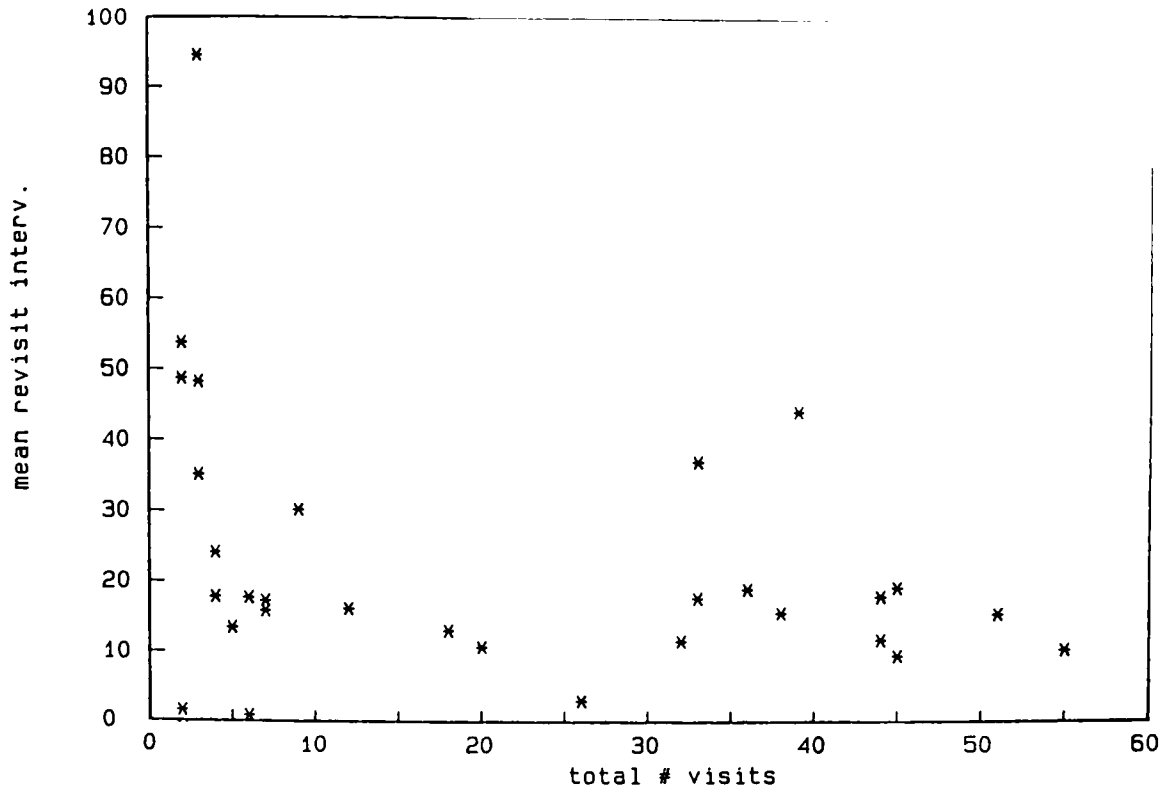


Fig. Relationship between mean revisit interval (hours) of WILF 6-79c, per 100 m cell and total number of visits to the same cell

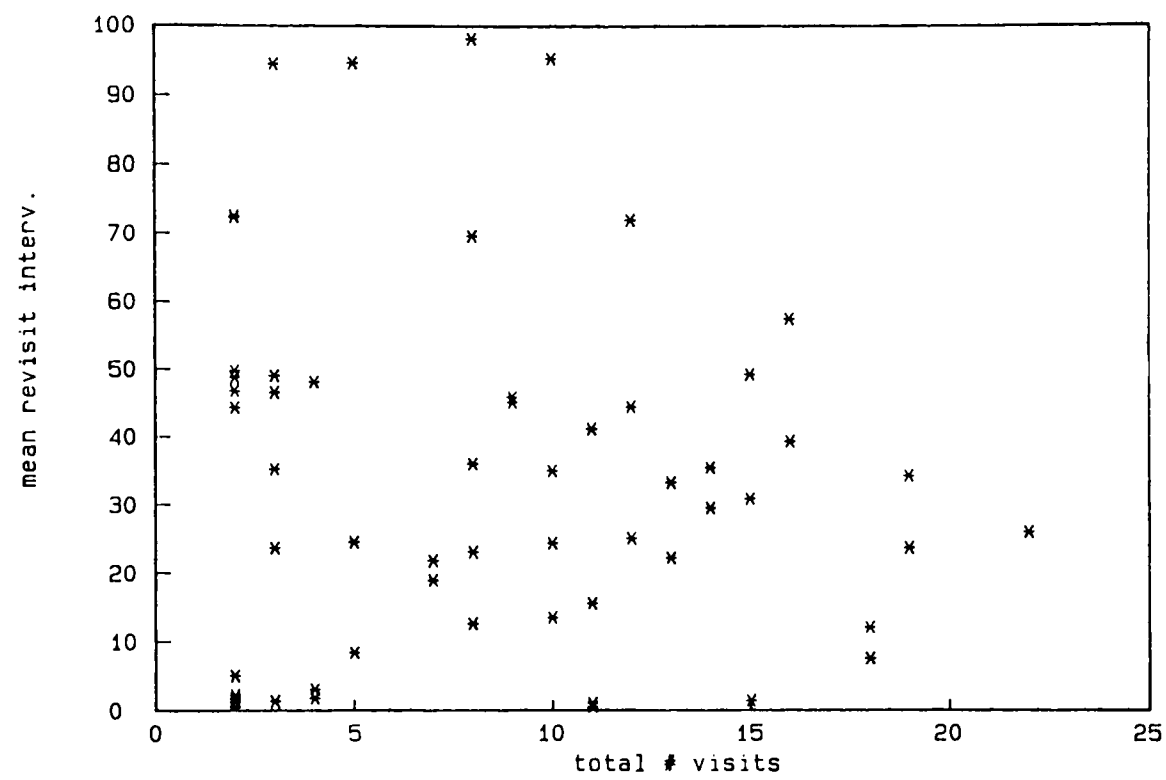


Fig. Relationship between mean revisit interval (hours) of WILF 6-79b, per 50 m cell and total number of visits to the same cell

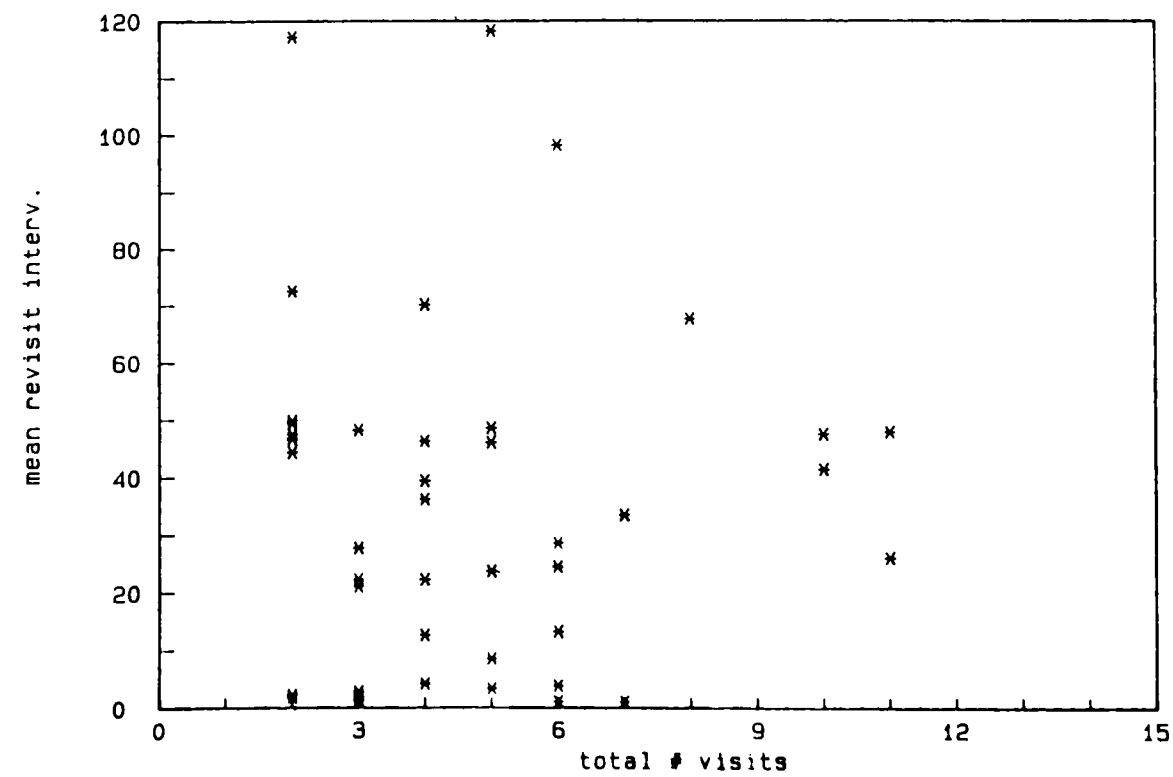


Fig. Relationship between mean revisit interval (hours) of WILF 6-79a, per 25 m cell and total number of visits to the same cell

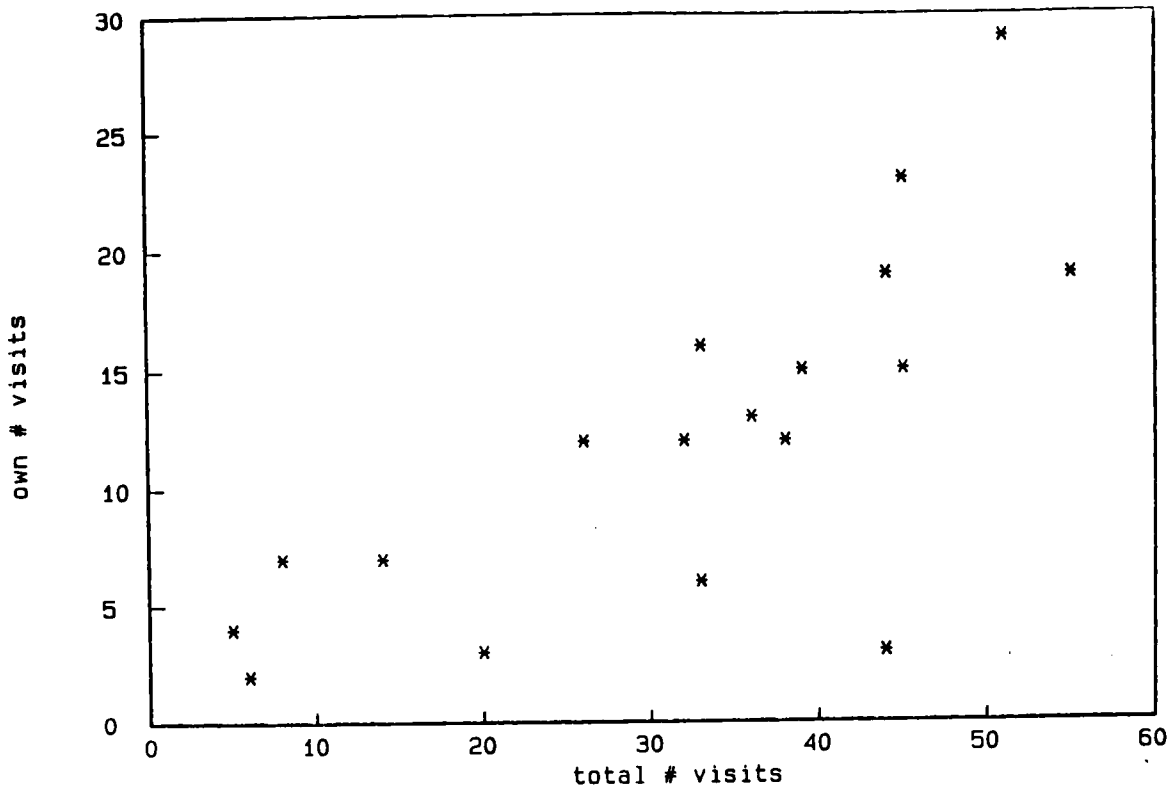


Fig. Relationship between own number of visits per 100 m cell 6-80c. and total number of visits to the same cell, for ALI

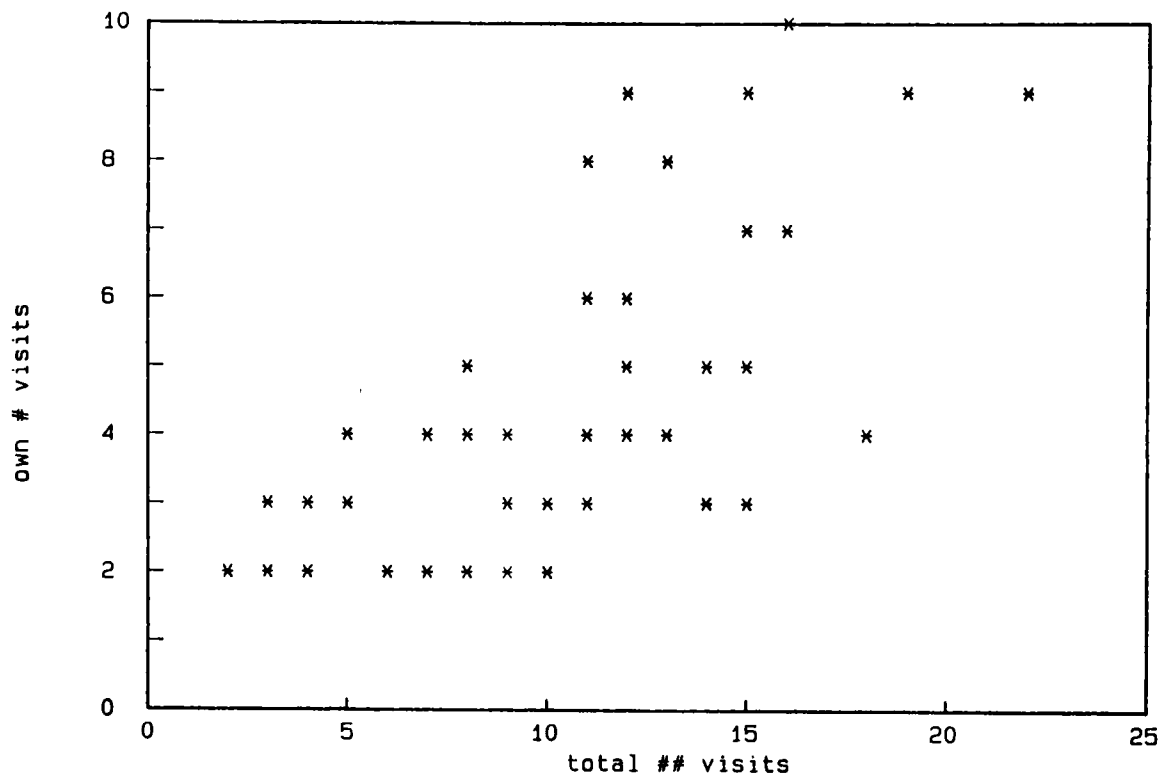


Fig. Relationship between own number of visits per 50 m cell 6-80b. and total number of visits to the same cell, for ALI

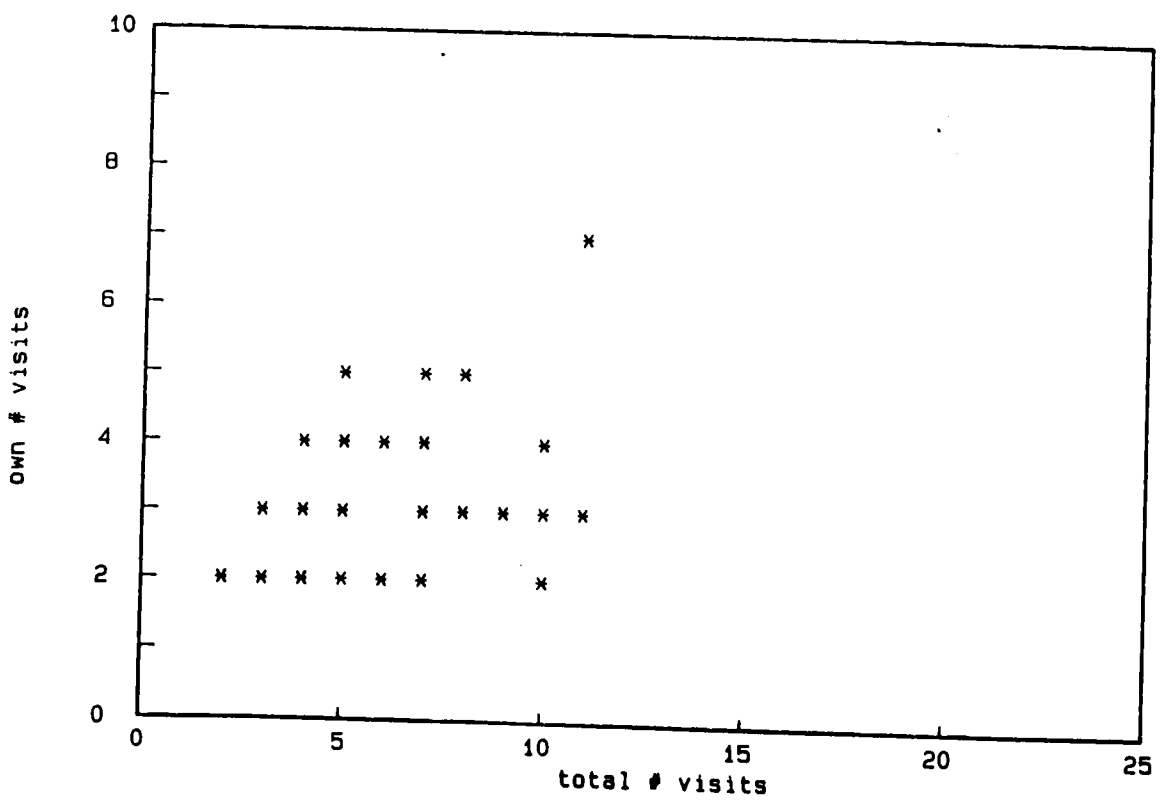


Fig. Relationship between own number of visits per 25 m cell 6-80a. and total number of visits to the same cell, for ALI

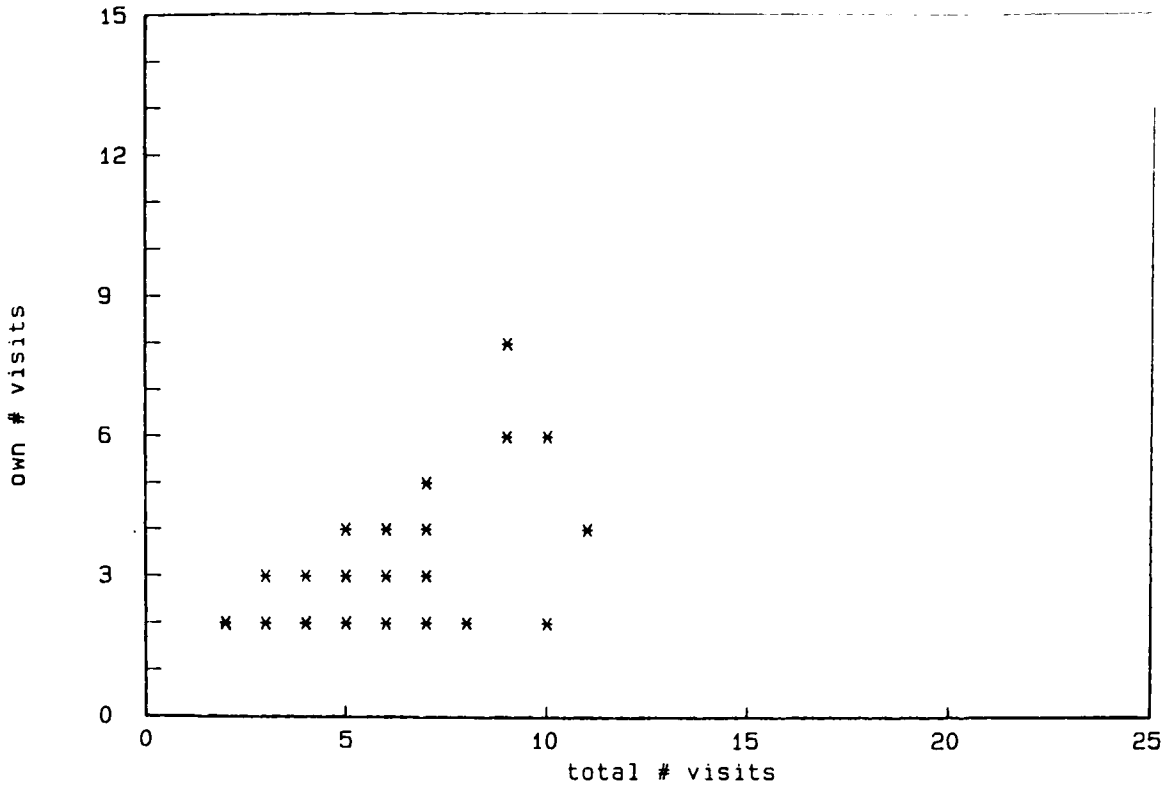


Fig. 6-81a. Relationship between own number of visits per 25 m cell and total number of visits to the same cell, for NANI

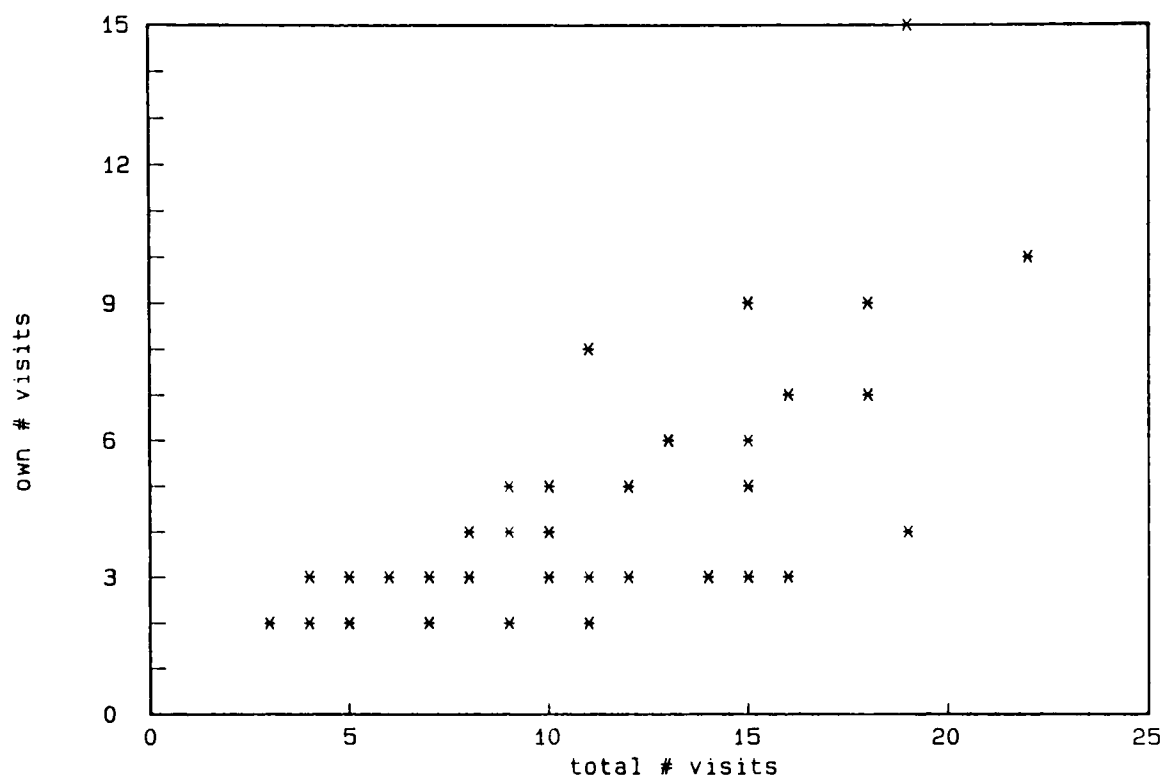


Fig. 6-81b. Relationship between own number of visits per 50 m cell and total number of visits to the same cell, for NANI

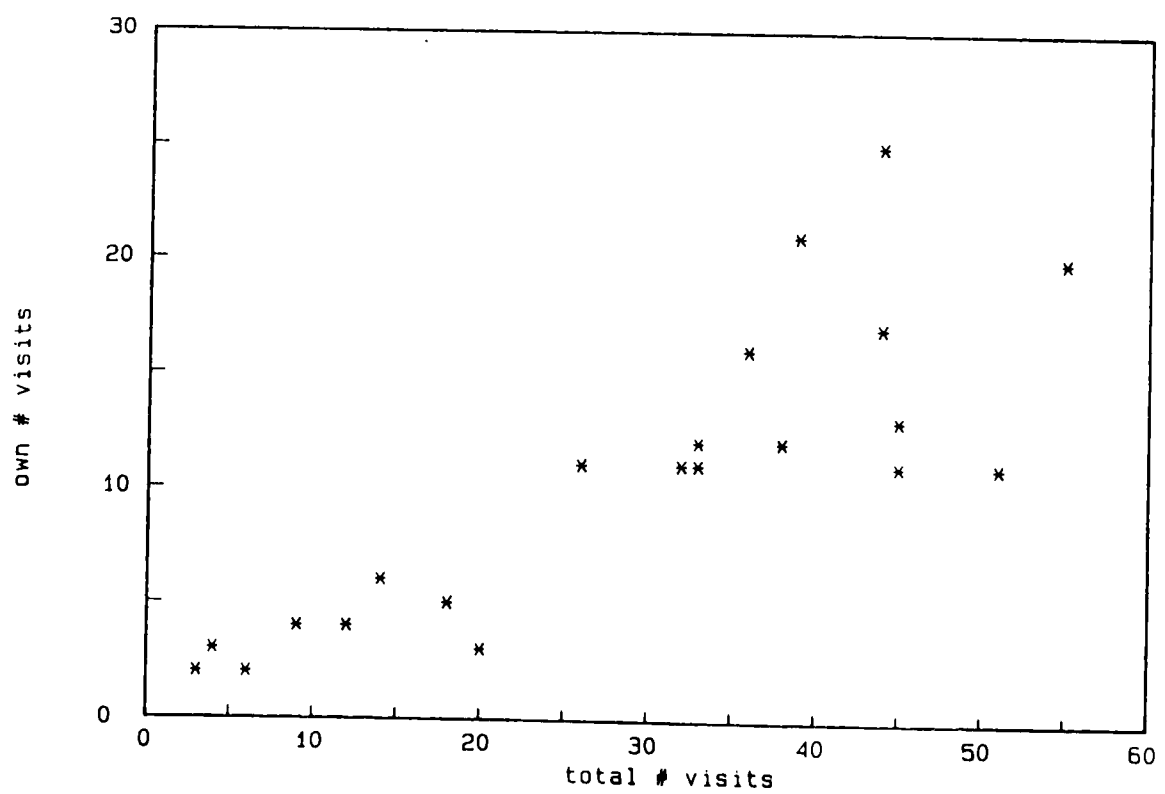


Fig. 6-81c. Relationship between own number of visits per 100 m cell and total number of visits to the same cell, for NANI

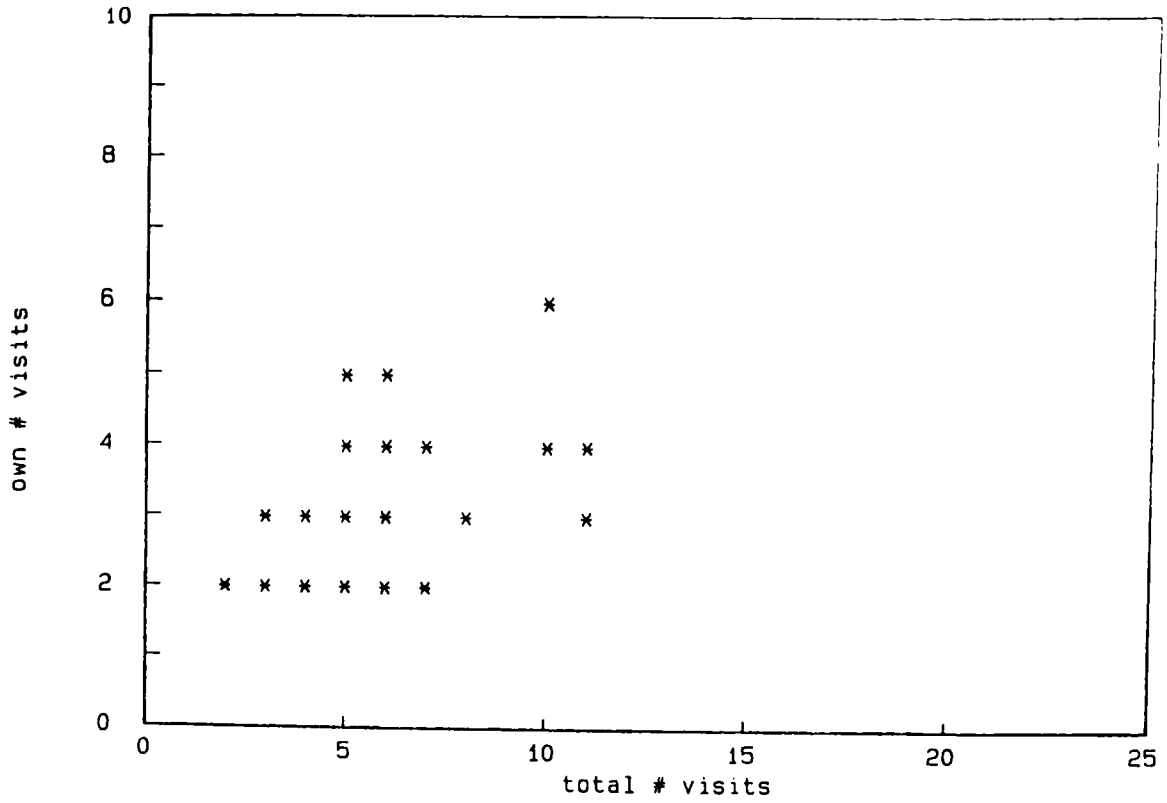


Fig. Relationship between own number of visits per 25 m cell 6-82a. and total number of visits to the same cell, for WILF

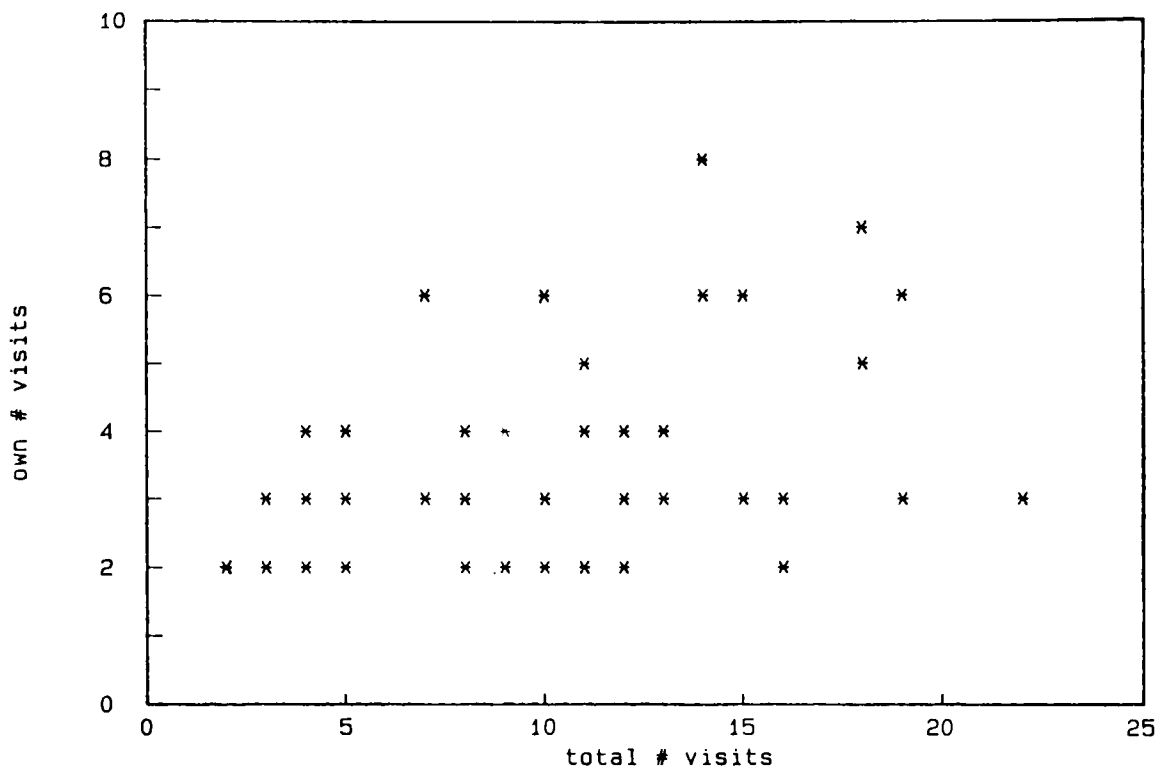


Fig. Relationship between own number of visits per 50 m cell 6-82b. and total number of visits to the same cell, for WILF

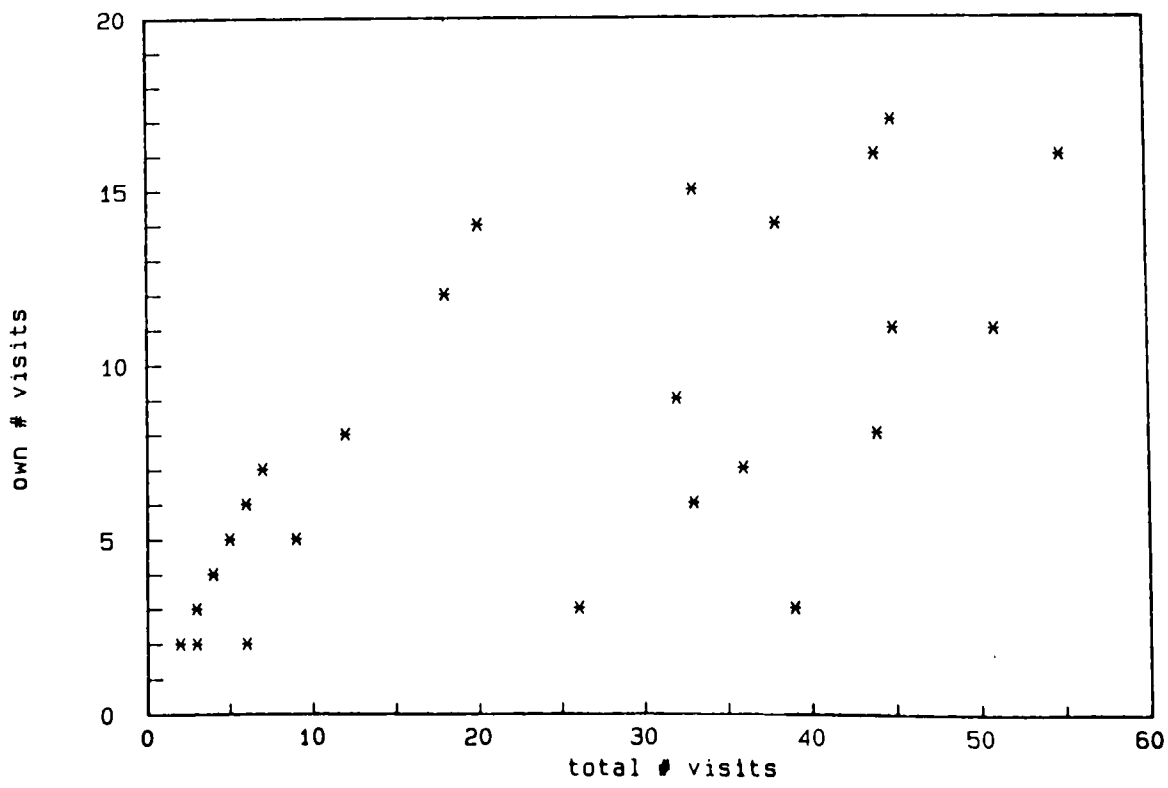


Fig. Relationship between own number of visits per 100 m cell 6-82c. and total number of visits to the same cell, for WILF

for a depression in foraging rate, ie. the interval that a patch takes to recover to an equilibrium density of surfacing worms, is much below that (Chapter 7). The significance of the relationships reported above cannot be taken at face value, since independence of data points cannot be assumed. However, all that is required is to yield a general impression that prepares us for the following discussion.

In Table 6.9 results are presented of the computation of frequencies of renewal periods. Here, in contrast to the previous analyses, all visits to a cell, regardless of the individual responsible for it, have been pooled. Frequencies are listed as mean renewal periods per cell. In BLOCK A, frequencies are listed for six-hour-blocks while in BLOCK B the first Block is listed in detail. Renewal periods were calculated for two cases: (i) the previous visitor is identical with the present visitor; (ii) the two are two different individuals.

If individuals coordinated their movement, I would expect them to be cautious about entering an area that has recently been visited by another individual. No such precaution applies if the animal visits an area again where it was the previous visitor, provided it has the sensory capacties to remember the state of the art at its last visit. Therefore, in case 1 I expect individuals to return to cells earlier than case 2 individuals. This expectation hinges crucially on the proposed size of a foraging patch as perceived by the badgers. The spatial analysis of section 6.2 indicates independence of utilization intensities for cells of size 50 by 50 m, proposing a small patch size as perceived by badgers. Furthermore, the mean length of visits did not increase when cell sizes were enlarged from 50 to 100 m (Table 6.5). One interpretation of this result is that an individual foraged in an area of 50 by 50 metres (or less), and, once finished, vanished to another site at a medium distance. If the true patch size was 100 m, or even larger, slowly meandering "worming" badgers should have spent more time per 100 m cell. Therefore I conclude that the cell size most

Table 6.9 Frequencies of renewal periods (= revisit intervals) of visits to 50 m cells in Range B2. Only simultaneous radio-tracking of ALI, NANI and WILF considered.

a) mean renewal periods per cell, all cells, classified in 6-hour blocks; visits to the sett excluded

	MEAN RENEWAL PERIOD/50 m CELL					
	PREVIOUS = CURRENT VISITOR			PREVIOUS ≠ CURRENT VISITOR		
	25m	50m	100m	25m	50m	100m
0–5.9 hours	35	24	14	14	21	16
6.0–11.9 hours	10	15	4	7	23	7
12.0–17.9 hours	23	18	4	12	11	2
18.0–23.9 hours	19	14	1	17	11	1
24.0 + hours	67	21	13	110	27	14

25 m: G = 32.58 df = 3 p<0.01
50 m: G = 10.59 df = <0.05
100 m G = 8.30 df = 3 ns

all calculated for relative frequencies

b) mean renewal periods per cell, all cells, only renewal periods less than 6 hours considered (class 1 from a)), visits to the sett excluded

	PREVIOUS = CURRENT VISITOR			PREVIOUS ≠ CURRENT VISITOR		
	25m	50m	100m	25m	50m	100m
simultaneous occupation of cell or 0 min interval	0	0	0	1	0	1
1–15 min	5	2	0	1	0	0
16–30 min	0	0	0	0	0	1
31–45 min	0	2	3	3	0	2
46–60 min	4	4	0	0	1	0
61–90 min	1	4	2	1	2	2
91–120 min	8	7	1	2	13	2
2.01–2.99 hours	6	1	1	2	0	3
3.00–3.99 hours	9	1	2	1	2	2
4.00–4.99 hours	1	1	1	1	0	1
5.00–5.99 hours	1	2	4	2	3	2

25 m (0.60 min, 61 min–2.99 h, 3.0–5.99 h): G = 5.20 df = 2 ns
50 m (0–90 min, 91 min–2.99 h, 3.0–5.99 h): G = 72.05 df = 2 p<0.001
100 m (0.90 min, 91 min–3.99 h, 4.0–5.99 h): G = 17.90 df = 2 p<0.001

suitable for this kind of investigation is 50 by 50 m (cf. Chapter 5). However, for completeness I have also included the results for the two other cell sizes (Table 6.9).

No differences between the two cases (previous visitor = current visitor and previous visitor ≠ current visitor) were found for 100 m cells for BLOCK A data (coarse 6 hour blocks), and the 25 m cells for the detailed analysis of renewal periods of less than 6 hours (BLOCK B data). In 3 out of 4 situations with significant differences, case 1 visitors returned sooner to the same cell than case 2 visitors; only 100 m cells in BLOCK B showed the reverse. Noteworthy is the sudden increase of frequency of renewal periods after ca 1.5 hours, in all cases. In general, short renewal periods constitute only a small fraction of all renewal periods (Table 6.9a). Even from the point of view of worst possible case, the 100 m cell records, interference is limited, since in those 4 cells where the current visitor may experience a reduced foraging rate (cells with renewal periods of 0 - 45 min), the probability of hitting the spot depreciated by the previous visitor is on average only one fourth of the probability of hitting the same spot in a 50 by 50 m cell.

In summary, badgers within the same group seem to coordinate their movements relative to each other. Simple rules were identified that aid in maintaining the coordination. It could not conclusively show to what extent the coordination is solely due to intentionality or a by-product of similar pressures by an external factor. Interference between individuals as evidenced by agonistic encounters could not be found. Actual levels of interference as evidenced by the pattern of distribution of renewal periods are small.

6.4. Habitat utilization

In sections 6.2. I have already indicated that areas of intensive use often coincide with the presence of specific resources. In this section I will investigate in more detail how the intensity of use of a specific area within an animal's range relates to the presence (or absence) of resources therein. As already discussed in Chapter 2, I will use habitats as defined by the habitat map as an indicator of resource presence, although the relationship between resource abundance and habitat type may not necessarily be straightforward. The analysis is centred around the following questions:

1. Which habitats are visited?
2. Does intensity of use, as measured by the number of visits (NOV) and duration of stay (DOS), vary between habitats? Which habitats are preferred?
3. What are the habitat and resource characteristics of those area units within a group range actually utilized by individuals?
4. How does intensity of use relate to resource presence?
5. What are the effects of the size of a patch or a habitat on its use by resident animals?
6. How do patterns of visits to uniform areas compare with simple random movements?

Before I present the results, two notes of caution are appropriate. The first relates to the problem of spatial dependence, as discussed in Appendices 5-7. This concerned the influence of the location of a given unit area could exert on the probability of being visited. In section 6.2 spatial correlograms indicated the scale at which this effect operates. Spatial dependence influences the error probability (type 1 error) of a test statistic. Positive spatial dependence leads to an undesirable increase of the actual alpha level, while negative spatial dependence <u>decreases</u> the alpha-level and produces a conservative estimate (Appendix 5, Cliff & Ord

1981). Therefore, the average overall individuals of a species of

> the number of the highest lag with a significant positive spatial autocorrelation before the first insignificant or negative autocorrelation value

of the correlograms of section 6.2 was computed as an index of the scale of spatial dependence. This index is 3.2 for foxes (n=14, Fig. 6.1-6.28) and 0.5 for badgers (n=8, Fig. 6.30-6.50), indicating a significant spatial interdependence for foxes but none for badgers at the chosen level of spatial resolution. Thus, the test statistics computed in sections 6.5.1. - 6.5.3. were modified according to the following rules:

- for foxes: (i) a test statistic is distributed according to the chi square distribution: divide the test statistic by 3, but leave the degrees of freedom unchanged.
  (ii) all other test statistics: divide the degrees of freedom by three.
- for badgers: no corrections required.

The second note of caution relates to the degree by which a measure of the intensity of use of an area does actually reflect this area's "importance" to an individual. For instance, PODGE stayed in the western and eastern peripheral areas of her range only for brief periods, but the regularity of visits and the fact that they must have caused some inconvenience to her can be interpreted in the sense that these were important visits necessary to maintain and defend the range. Here, the intensity of use in relation to habitat type does not capture the essence of these visits. Another example is the backyard (garden) of houses in suburbs (e.g. in KALI's range), where, say, watchdogs are present during most of the

night. These gardens may represent valuable resources to the fox, yet it may have to wait in the neighbouring fields for a long time until a suitable moment when it can nip in for 10 minutes and take everything previous from the compost heap before vanishing into the neighbouring fields again. Yet in my compilation of events, the short period of visiting the garden may be underrated in comparison with the waiting time in the neighbouring field. This is not meant to imply that a consideration of intensity of use is totally useless; it just serves to remind us of the limits of this approach. In section 6.5.4 I will describe an alternative approach that goes beyond a simple compilation of NOV and DOS.

6.4.1. Habitat preferences

Habitat utilization was analysed for seven foxes (ELKE, KALI, KBOOM, OLDMAHOG, PODGE, TARU, LIO) and seven badgers (ALI, GEORGE, NANI, PEACEFUL, SARA, VICIOUS, WILF) with sufficient intensive tracking data. NOV and DOS were analysed for 50 by 50 m cells. Variation in utilization intensity (UI) was significant between habitats for which sufficient cells were present that were completely covered by that habitat (n=478 for foxes and n=256 for badgers) (Table 6.10)). If the correction for spatial dependence is considered in foxes, the variation is still significant for NOV but not for DOS. However, for this particular sample, spatial dependence may be relatively weak, since cells covered with only one habitat must be separated from cells covered by another habitat by at least one cell where the transition occurs.

Table 6.11 and 6.12 present the results of multiple comparison tests between habitats of high and low UI for badgers and foxes, respectively. Not surprisingly, high quality habitats with respect to earthworms experience on average a higher UI than low quality habitats in badgers (for definitions see section 5.4.). There may be a bias due to the fact that

Table 6.10 Habitat utilization as measured by the intensity of use of 50 m grid cells covered by a uniform habitat (ie. a diversity of 1). Primary habitats: habitat that covers more than 50% of a cell area; secondary habitat: a second most common habitat

a) differences in utilization of cells of different habitats

Species	measure of intensity of use	N	df	H (Kruskal-Wallis)	signific.
Fox	no. of visits	478	9	55.56	p<0.001
	duration of stay	478	9	32.68	p<0.001
Badgers	no. of visits	256	4	27.34	p<0.001
	duration of stay	256	4	26.26	p<0.001

b) differences in intensity of use between cells with different secondary habitats, given a certain primary habitat

x) secondary habitats with high intensity of use

Species	primary habitat	secondary habitat	measure of intensity of use	df	H	significance
Fox	deciduous woodland	pasture marsh land[x] summer cereals bracken[x] mixed plant.	no. of visits	4	8.768	p = 0.07
Badger	deciduous woodland	summer cereals mixed plantat. river with hedges	no. of visits	2	7.929	<0.025
	deciduous	summer cereals	duration of stay		6.529	<0.05

d) do fox and badger ranges differ in the average diversity of grid cells visited by range inhabitants?
t = 2.37, df = 1337.1, p = 0.018

Species	Mean diversity	S.E. of mean
Fox	1.720	0.025
Badger	1.630	0.028

Table 6.11 Habitat utilization as measured by the intensity of use of 50 m grid cells covered by a uniform habitat, by badgers. Multiple comparison tests. Only significant differences listed

Habitat with high intensity of use	Habitat with low intensity of use	actual value	critical value	significance
a) number of visits				
pasture	summer cer.	44.6	34.7	0.001
winter cereals	summer cer.	66.7	56.8	0.55
deciduous w.	summer cer.	59.4	40.6	0.001
deciduous w.	mixed plant.	36.3	31.4	0.05
b) duration of stay (hours)				
pasture	summer cer.	53.6	35.4	0.001
pasture	deciduous w.	35.5	33.7	0.005
pasture	mixed plant.	50.8	49.2	0.001

Table 6.12 Habitat utilization as measured by the intensity of use of 50 m grid cells covered by a uniform habitat, by foxes. Multiple comparison tests. Only significant differences listed.

Habitat with high intensity of use	Habitat with low intensity of use	actual value	critical value	significance
1. Number of visits				
grassley	terraced house	130.5	127.5	0.01
root crops	terraced house	186.9	180.6	0.002
grassley	pasture	135.5	77.1	0.001
grassley	summer cereals	104.0	75.1	0.001
grassley	deciduous w.	95.7	80.4	0.001
grassley	mixed plant.	192.7	136.4	0.001
grassley	sport grounds	146.5	144.9	0.002
allotments	pasture	75.0	73.0	0.05
summer cereals	pasture	31.5	27.1	0.05
root crops	pasture	191.9	128.1	0.001
deciduous w.	pasture	39.8	38.1	0.02
root crops	allotments	116.9	101.6	0.05
allotments	mixed plant.	132.2	130.3	0.01
root crops	summer cereals	160.4	126.9	0.001
summer cereals	mixed plant.	88.7	85.8	0.02
root crops	bracken	124.9	110.3	0.05
root crops	deciduous w.	152.1	130.2	0.001
root crops	mixed plant.	249.1	170.5	0.001
root crops	sport grounds	202.9	185.1	0.001
bracken	mixed plant.	124.2	108.0	0.05
deciduous w.	mixed plant.	97.0	88.2	0.02
2. duration of stay				
root crops	terraced house	184.8	180.9	0.005
grassley	pasture	53.5	50.7	0.05
grassley	summer cereals	95.1	77.7	0.002
root crops	grassley	100.6	92.9	0.05
grassley	deciduous w.	73.2	69.4	0.01
grassley	mixed plant.	152.7	150.4	0.001
root crops	pasture	154.1	141.3	0.001
pasture	mixed plant.	99.2	95.6	0.02
root crops	allotments	134.7	132.9	0.02
allotments	mixed plant.	118.6	109.3	0.05
root crops	summer cereals	182.4	140.0	0.001
root crops	bracken	132.2	121.6	0.05
root crops	deciduous w.	173.8	143.5	0.001
root crops	mixed plant	253.3	188.1	0.001
root crops	sport grounds	137.7	121.6	0.05
bracken	mixed plant.	121.1	119.1	0.05

most intensive tracking data were obtained during periods of good earthworm availability (April-May and September-November); it can be expected that utilization of arable fields increases during the summer months (Chapter 4).

For foxes, the picture is more complicated. Highly valued areas are grassley and root crops (rabbits/earthworms) and deciduous woodland, but also summer cereals. However, if the correction for spatial dependence is considered, the significant pairs of Table 6.12:I with a probability level of more than 0.001 would turn insignificant while the comparisons under II: would be inadmissible. Even then, pasture, sports grounds and terraced houses remain little visited in comparison with other habitats.

If cells are considered where several habitats occur (Table 6.10b), the effect of neighbouring habitats can be considered. For this purpose the habitat with the highest proportion of area per cell was designated as "primary habitat", and the habitat with the second highest proportion as "secondary habitat". Cells were excluded, if primary habitats occupied less than 50% of the cell area (to ensure "dominance" of primary habitat). In foxes, no significant effects on UI due to secondary habitats could be identified, while in badgers UI of deciduous woodland in zones of transition depended on the secondary habitat, both for NOV and DOS. UI of the primary habitat (deciduous woodland) was high if the secondary habitat is mixed plantations, but low if consisting of cereals, rivers or even pasture. This is consistent with Kruuk's (1978a) observations of frequent use of mixed plantations by his badgers in the Jews Harp group.

6.4.2. Habitat characteristics and resource levels in visited cells

Here, the following parameters were considered: habitat diversity, ie. the number of different habitats that occur per cell, the DCA-scores (badgers only, since only here did an appreciable proportion of range occur in the area of habitat recording) and the worm biomass index (for

computation procedures see section 6.1).

Fox ranges had a higher habitat diversity than badger ranges (Table 6.10c). Diversity was also significantly variable between fox ranges (table 6.13c), but not significant, if the modified test statistic is used. Similarly, badger ranges had equivalent levels of habitat diversity (Table 6.14c). Habitat diversity was closely, and inversely, related to the worm biomass index per cell, both for foxes and badgers (Table 6.13b, 6.14b). This dependence is linear, for foxes at least (Table 6.13b).

Mean worm biomass per cell varies significantly between ranges, both for foxes and badgers. In foxes, this variation does not contribute to an overall difference in earthworm consumption between ranges (Chapter 4). Similarly, in badgers, the differences listed here do not produce significant differences in earthworm consumption for the ranges concerned (Table 4.12b, September to November). However, the reasons are different for the two species (see below).

DCA scores in range B4 correlate significantly with worm biomass on the first three axis (Table 6.14d). This supports Shute and West's (1982) proposal that general habitat inventories are also very useful for special applications. During habitat recording, no specific variable was selected as earthworm indicator, yet the resulting ordination yields a structure that is correlated with earthworm abundance.

6.4.3. Intensity of use in relation to resource density.

Here I considered the relationship between UI and the worm biomass index per cell as an example. Table 6.15 presents the results of correlating UI with worm biomass for individual badgers and for foxes. In foxes, despite wide variation in mean worm content per cell between ranges (see previous section), no significant differences could be found in earthworm consumption between ranges (Chapter 4). Consequently, UI should be independent of the

Table 6.13 Resource characteristics and habitat structure of 50 m grid cells visited by individual foxes during periods of intensive tracking.
Worm biomasses in kg cell^{-1}, diversity = the number of different habitats occurring in one 50 m grid cell

a) do fox ranges differ in the average worm biomass of grid cells visited by range inhabitants?

Individual	Range		mean biomass per cell
Podge	Homefarm	F1	133.39
Elke	Churchgrove	F2	169.19
Kali	Tilbury	F4	84.31
Kboom	Woodend	F5	127.75
Oldmahog	Singing Way	F6	145.30
Taru	Binsey	F9	48.06
Lio	Marley	F11	144.10

Kruskal-Wallis one-way analysis of variance, H = 155.4, df = 6, $p<0.001$

b) do grid cells with varying diversity differ in the average worm biomass? (all fox ranges)

H = 96.73, df = 3, $p<0.001$

Worm biomass = 184 - 33.8 diversity; r^2 = 95.2, $p<0.001$

c) do fox ranges differ in the average diversity of grid cells visited by range inhabitants?

H = 23.40, df = 6, $p<0.001$

Table 6.14 Habitat structure and resource characteristics of 50 m grid cells visited by individual badgers during periods of intensive tracking. Worm biomass in kg $cell^{-1}$; diversity = the number of different habitats occurring in one 50 m grid cell. DCA-scores: results of DCA-run 19 (Chapter 2).

a) do badger ranges differ in the average worm biomass of grid cells visited by range inhabitants?

Range	mean biomass per cell
B1	165.71
B2	166.09
B3	142.84

Kruskal-Wallis one-way analysis of variance, H = 16.88, df = 2, p<0.001

b) do grid cells with varying diversity differ in the average worm biomass per badger group range?

Range	Kruskal-Wallis one-way analysis of variance (H)	df	significance
B1	30.46	2	<0.001
B2	37.9	2	<0.001
B2	3.497	2	ns

c) do badger ranges differ in the average diversity of grid cells visited by range inhabitants?

H = 4.857, df = 6, n.s.

d) is there a systematic relationship between habitat structure, as expressed by the DCA scores of grid cells on the first four DCA axes, and worm biomass per grid cell?

Data from Range B4 only, rank correlation of cell scores on different DCA axes and worm biomass

DCA axis	df	correlation coefficient	significance
one	81	0.557	<0.001
two	81	0.232	<0.05
three	81	0.458	<0.001
four	81	-0.042	ns

worm biomass per cell. This is the case if the modified test statistic is considered for DOS, while there are in fact slightly negative, although significant correlations between UI and worm biomass for NOV (Table 6.15c). In Chapter 5, however, earthworm consumption per group range was positively correlated with the proportion of pasture and deciduous woodland per group range. How can these differences be resolved?

In one sense, the two results cannot be compared directly. The correlation between pasture and deciduous woodland and earthworm consumption was restricted to the proportion of high quality earthworm habitat per group range. The above, negative correlation is a result of indexing all cells, ie. also cells with low quality habitat. (We shall see below that this is a difference that matters also for badgers). Such cells, however, may be visited by foxes in order to hunt rabbits or mice, which are time consuming activities. For a wide range of worm biomasses, the worm biomass may simply be irrelevant to a fox - only areas with high worm abundance may be of interest and guarantee an energy intake comparable with that achieved by hunting for rabbits (Chapter 3). An additional complication is the fact that earthworm availability may be quite different from earthworm abundance, and certainly more so in open areas such as pastures or grass ley (if cut) than in deciduous woodland (Chapter 3).

In badgers, UI is either positively correlated or independent from the worm biomass index per cell (Table 6.15a and b). For the two individuals from Range B4, PEACEFUL and VICIOUS, a relatively low average worm biomass per cell was previously computed (Table 6.14); consequently the UI is independent of worm biomass, due to a high level of UI in mixed plantations. Some reasons for this were discussed in Chapter 3. UI of cells by PEACEFUL is, however, correlated with the DCA cell scores on DCA axis 1 (Spearman's $rho=0.293$, $n=45$, $p<0.05$). Mean DCA scores on axes 1 to 4 of cells visited by PEACEFUL are 97.33, 112.20, 112.76, and 143.37. No differences were found on the DCA scores of cells between PEACEFUL and VICIOUS on any of the DCA axes.

Table 6.15 Intensity of use of 50 m grid cells by foxes and badgers in relation to the worm biomass per cell. All correlation coefficients are Spearman rank correlation coefficients

a) Number of visits versus worm biomass (badgers)

Animal	Range	Number of cells	Correlation coefficient	Significance
George	B1	74	0.421	<0.001
Sara	B1	81	0.262	<0.02
Ali	B2	70	0.470	<0.001
Nani	B2	67	0.150	ns
Wilf	B2	112	0.283	<0.005
Peaceful	B4	107	0.073	ns
Vicious	B4	38	-0.130	ns

b) Duration of stay (in hours) versus worm biomass (badgers)

Animal	Range	Number of cells	Correlation coefficient	Significance
George	B1	74	0.396	<0.001
Sara	B1	81	0.194	ns
Ali	B2	70	0.521	<0.001
Nani	B2	67	0.175	ns
Wilf	B2	112	0.275	<0.005
Peaceful	B4	107	0.135	ns
Vicious	B4	38	-0.04	ns

c) Intensity of use versus worm biomass (foxes)

Number of visits Spearman's rho = 0.192, df = 1050, p<0.001
Duration of stay " " = 0.087, df = 1050, p<0.005

For other individuals, the majority of correlations of UI with the worm biomass index per cell is significantly positive. These are individuals with, on average, high worm biomass indices per cell.

In summary, the index of worm biomass chosen here is not a wholly satisfying predictor of small-scale range use. For foxes, this may be due to the fact that worm biomass may be irrelevant for many cells that they visit. In badgers, it is a reliable predictor, if the overall biomass level is high. Obviously, an indicator of earthworm availability would be a much more satisfying parameter - but this was impossible to measure in this study.

6.4.4. Patterns of visits to different habitats

In this section, patches from the habitat map are the basic units of investigation. The effects of the size of a patch and a habitat (ie. the sum of all patches per range that belong to the same habitat) are illustrated in Fig. 6.83 (badgers) and 6.84 (foxes). Corresponding correlation and regression analyses can be found in Table 6.16. The results are similar for both species. The larger the area of a particular habitat per range, the more often and the longer it is visited. However, there is no linear dependency between area of single patches and UI (cf. Fig. 6.83c, d, 6.84c, d, Table 6.16). A small patch may often be visited despite its size; similarly, large patches may rarely be visited, if they are of no interest.

Both measures of UI are highly correlated (Fig. 6.85–6.86, badgers; Fig. 6.87–6.88, foxes; Table 6.16). For both single patches and habitats, often visited areas are visited for a long time and rarely visisted areas are inspected only briefly . In Fig. 6.86 and 6.88, the relationship between NOV and DOS is investigated in more detail. Two classes of durations of visits were compared with NOV: very short visits (less than 5

Table 6.16 Relationships between different measures of intensity of use and size of patches and habitats. I: Foxes, II: Badgers. H: Habitats, P: Patches. Significance of all Spearman's rank correlation coefficients, and the slopes of listed regression. Equations: $p<0.001$, except for x), where $p<0.003$. Regression equations not listed, if not significant or R^2 less than 10%

Predicted variable		predictor variable		Rank corr.	df	regression equation	R^2 (%)
I: Duration of stay	(H)	number of visits	(H)	0.885	24	y = -0.86 + 0.285 x	95.1
" " "	(P)	" " "	(P)	0.828	259	y = -0. 696 + 0.398 x	72.7
No. of visits < 5 min	(H)	No. of visits	(H)	0.918	24	y = 0.86 + 0.279 x	92.8
" " "	(P)	" " "	(P)	0.729	259	y = 0.211 + 0.255 x	69.8
No. of visits >30 min	(H)	No. of visits	(H)	0.793	24	y = -0.134 + 0.124 x	87.7
" " "	(P)	" " "	(P)	0.506	259	y = -0.39 + 0.283 x	60.3
Duration of stay (H)	(H)	area of habitat in range		0.692	24	y = 6.48 + 0.349 x	80.7
" " "	(P)	area of patches		0.439	259		
No. of visits	(H)	area of habitat in range		0.643	24	y = 28.0 + 1.13 x	72.1
" " "	(P)	area of patches		0.327	259		
II. Duration of stay	(H)	Number of visits	(H)	0.989	15	y = -1.51 + 0.41 x	96.4
" " "	(P)	" " "	(P)	0.954	63	y = -1.01 + 0.456 x	87.2
No. of visits < 5 min	(H)	" " "	(H)	0.850	15		
" " "	(P)	" " "	(P)	0.447	63		
No. of visits <30 min	(H)	Number of visits	(H)	0.869	15	y = -0.85 + 0.187 x	91.7
" " "	(P)	" " "	(P)	0.838	63	y = -0.805 + 0.299 x	67.7
Duration of stay	(H)	area of habitat in range		0.724	15	y = 6.69 + 1.13 x	74.4
" " "	(P)	area of patches		0.464	63		
No. of visits	(H)	area of habitat in range		0.729	15	y = 19.9 + 2.75 x	77.7
" " "	(P)	area of patches		0.351x)	63		

Fig. 6.83-6.84

Utilization intensity of habitats (ie. all habitat map patches belonging to the same habitat type summarized) and patches (as delineated by the habitat map) in relation to the size of the area of the respective area unit. Measures of utilization intensity are duration of stay (TIME) and number of visits (NO. OF VISITS). In Fig. 6.83, results are presented for all badgers, in fig. 6.84, for all foxes. Intensively tracked nights only.

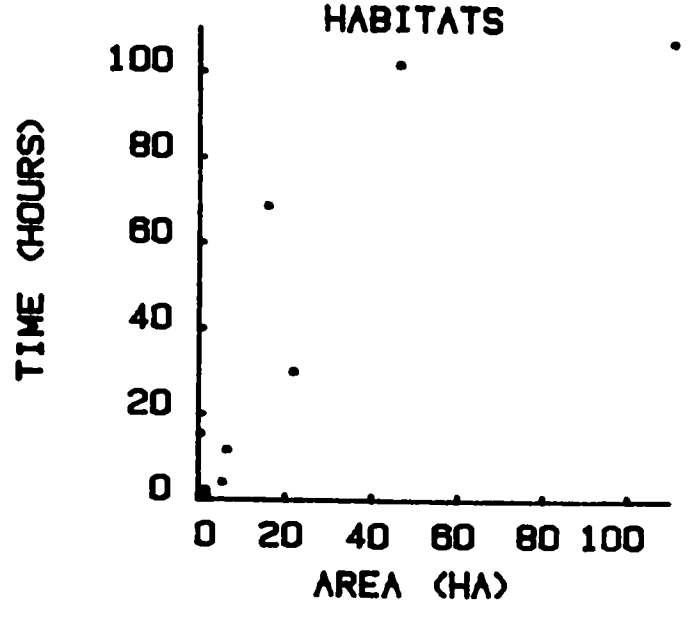
Fig. 6.85-6.87

Relationship between the two measures of intensity of use. 6.85: badgers, 6.87: foxes.

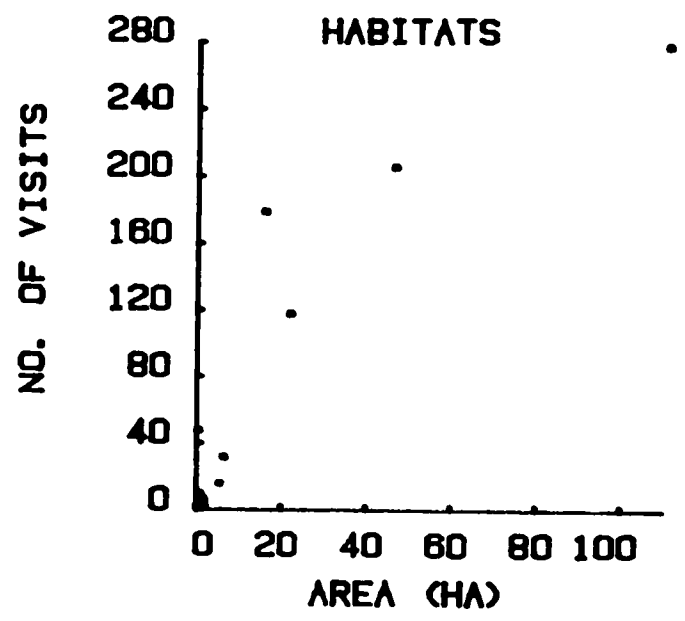
Fig. 6.86-6.88

Utilization intensity of habitats and patches (as defined for Fig. 6.83-6.84) as expressed by the number of short (5 min) and long (30 min) visits in relation to the total number of visits to the same area. 6.86: badgers, 6.88: foxes.

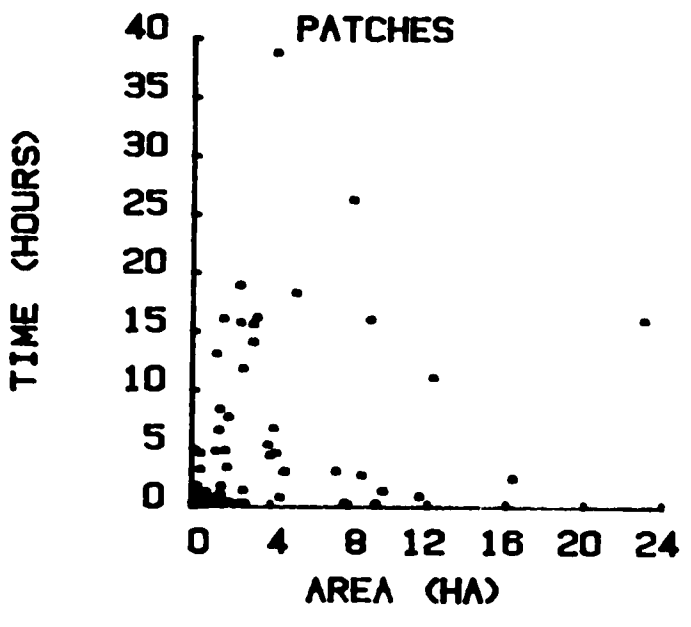
a.


HABITATS
TIME (HOURS)
100
80
60
40
20
0
0 20 40 60 80 100
AREA (HA)

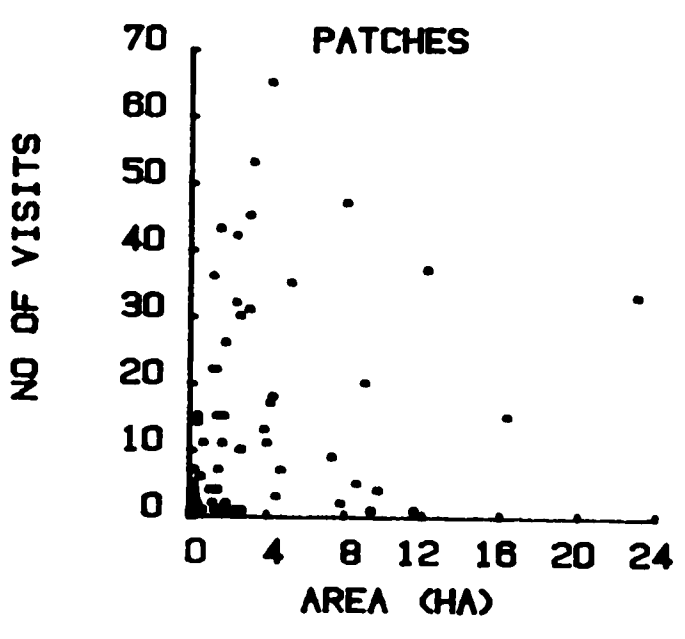
b.


HABITATS
NO. OF VISITS
280
240
200
160
120
80
40
0
0 20 40 60 80 100
AREA (HA)

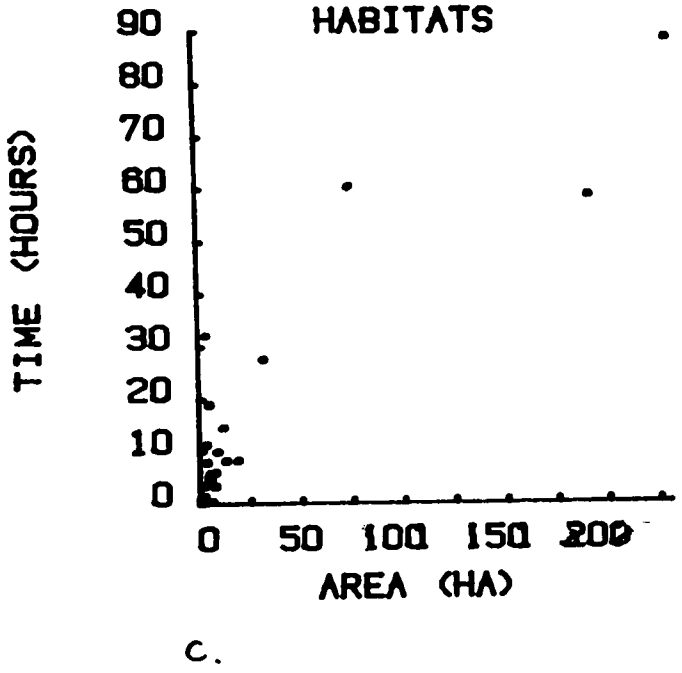
c.


PATCHES
TIME (HOURS)
40
35
30
25
20
15
10
5
0
0 4 8 12 16 20 24
AREA (HA)

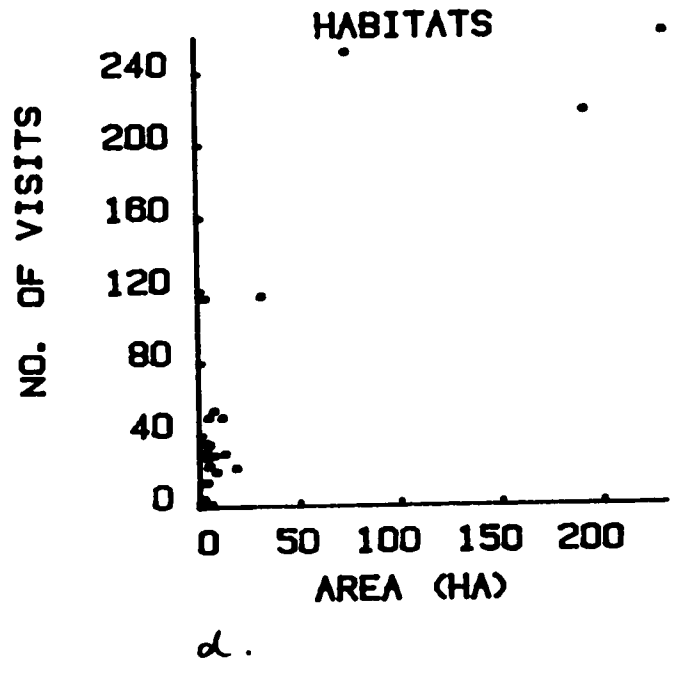
d.


PATCHES
NO OF VISITS
70
60
50
40
30
20
10
0
0 4 8 12 16 20 24
AREA (HA)

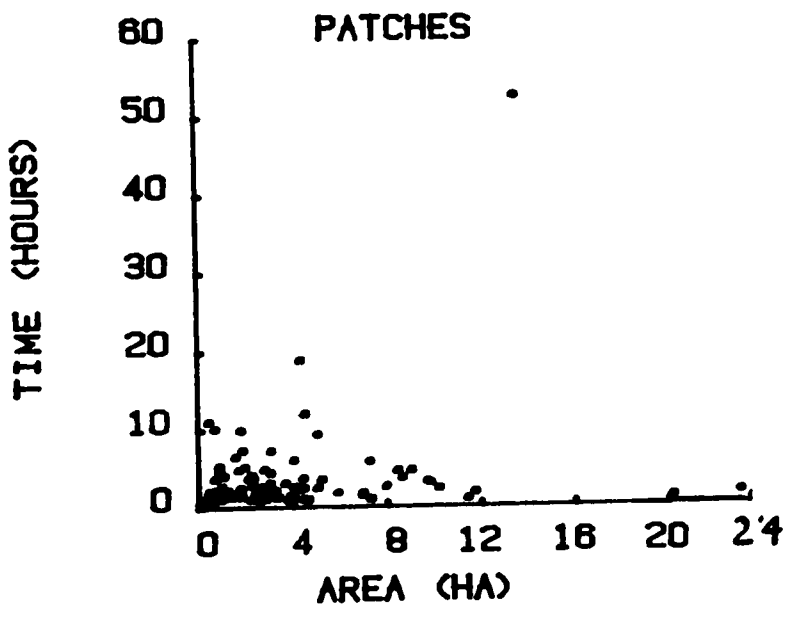
a.


HABITATS
TIME (HOURS)
90
80
70
60
50
40
30
20
10
0
0
50
100
150
200
AREA (HA)

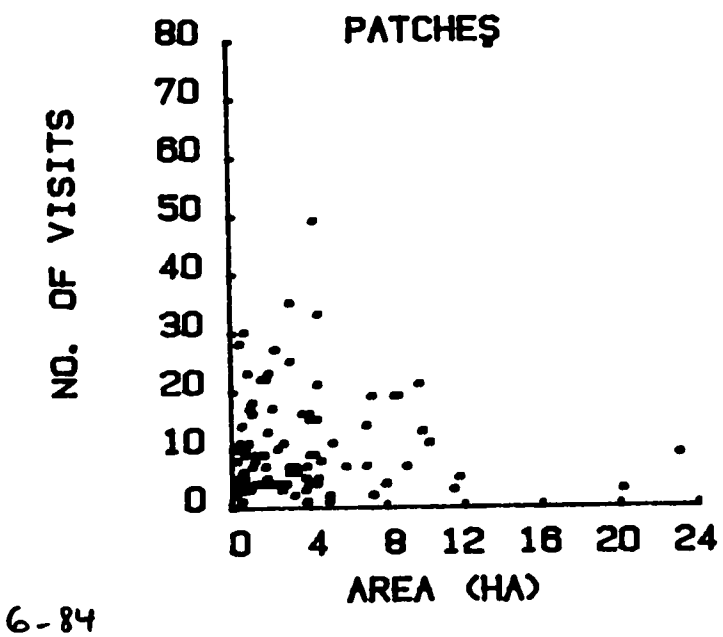
b.


HABITATS
NO. OF VISITS
240
200
160
120
80
40
0
0
50
100
150
200
AREA (HA)

c.

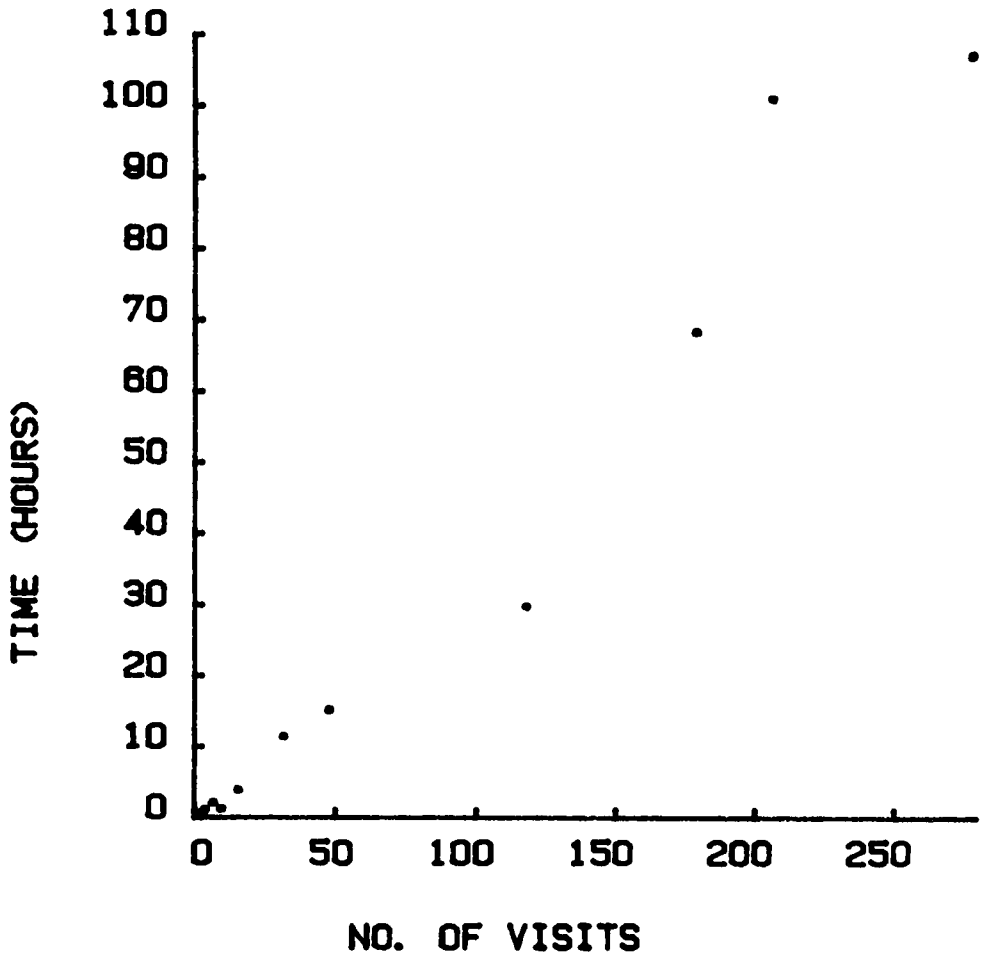

PATCHES
TIME (HOURS)
60
50
40
30
20
10
0
0
4
8
12
16
20
24
AREA (HA)

d.


PATCHES
NO. OF VISITS
80
70
60
50
40
30
20
10
0
0
4
8
12
16
20
24
AREA (HA)

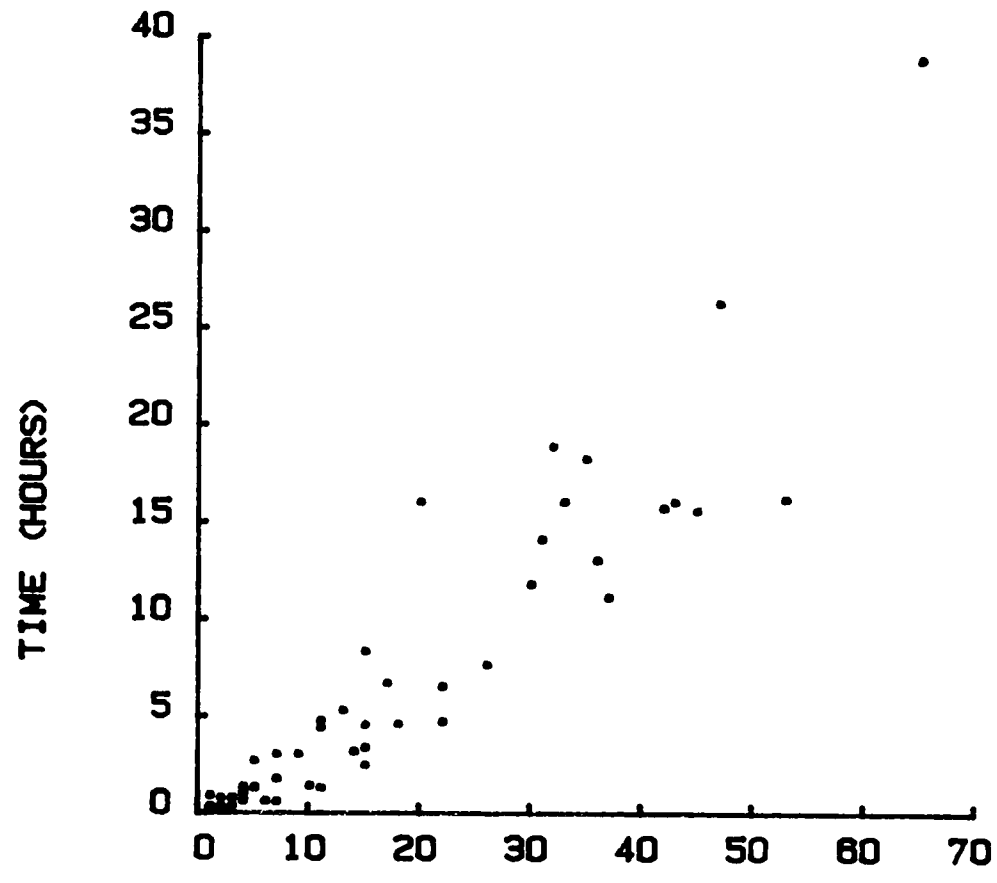
a.

ALL BADGERS - HABITATS

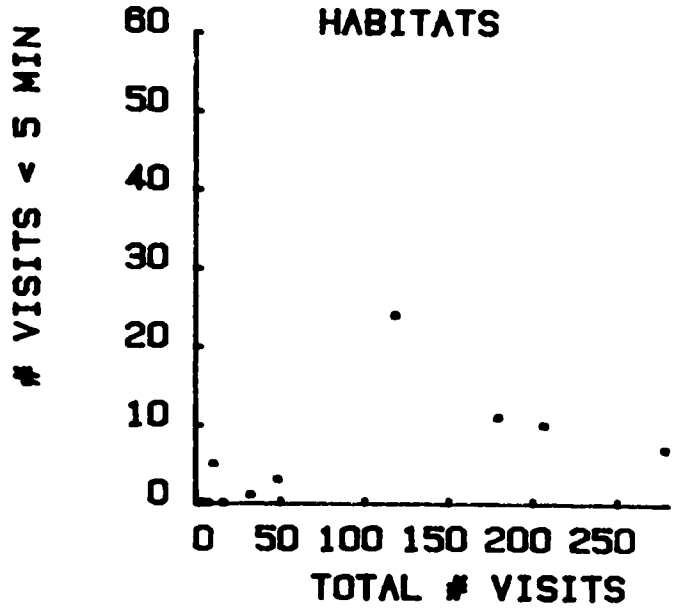


b.

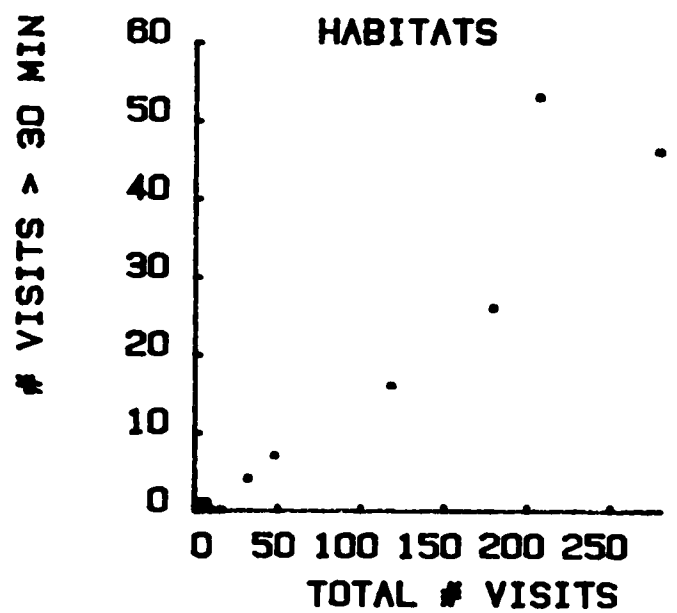
ALL BADGERS - PATCHES



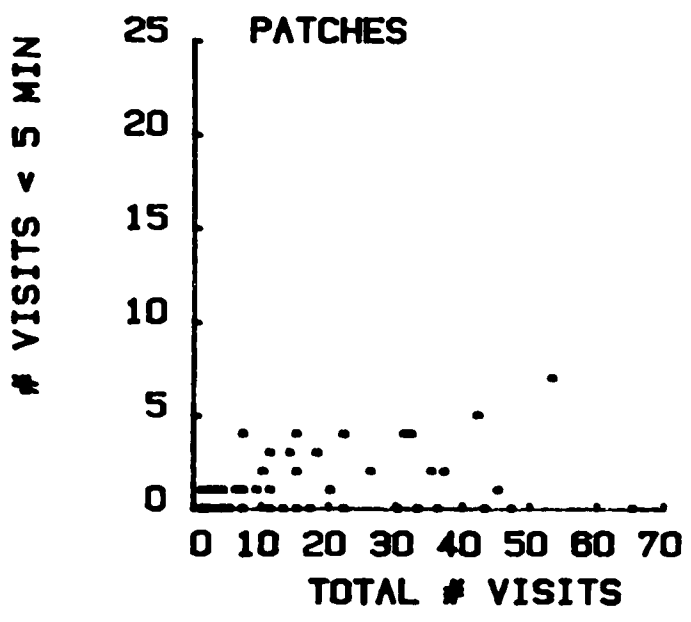
a.


HABITATS
VISITS < 5 MIN
60
50
40
30
20
10
0
0 50 100 150 200 250
TOTAL # VISITS

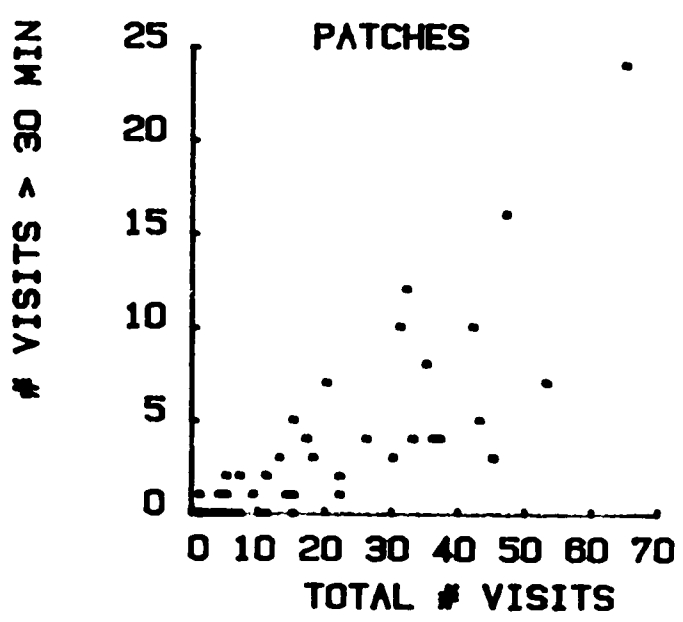
b.


HABITATS
VISITS > 30 MIN
60
50
40
30
20
10
0
0 50 100 150 200 250
TOTAL # VISITS

c.

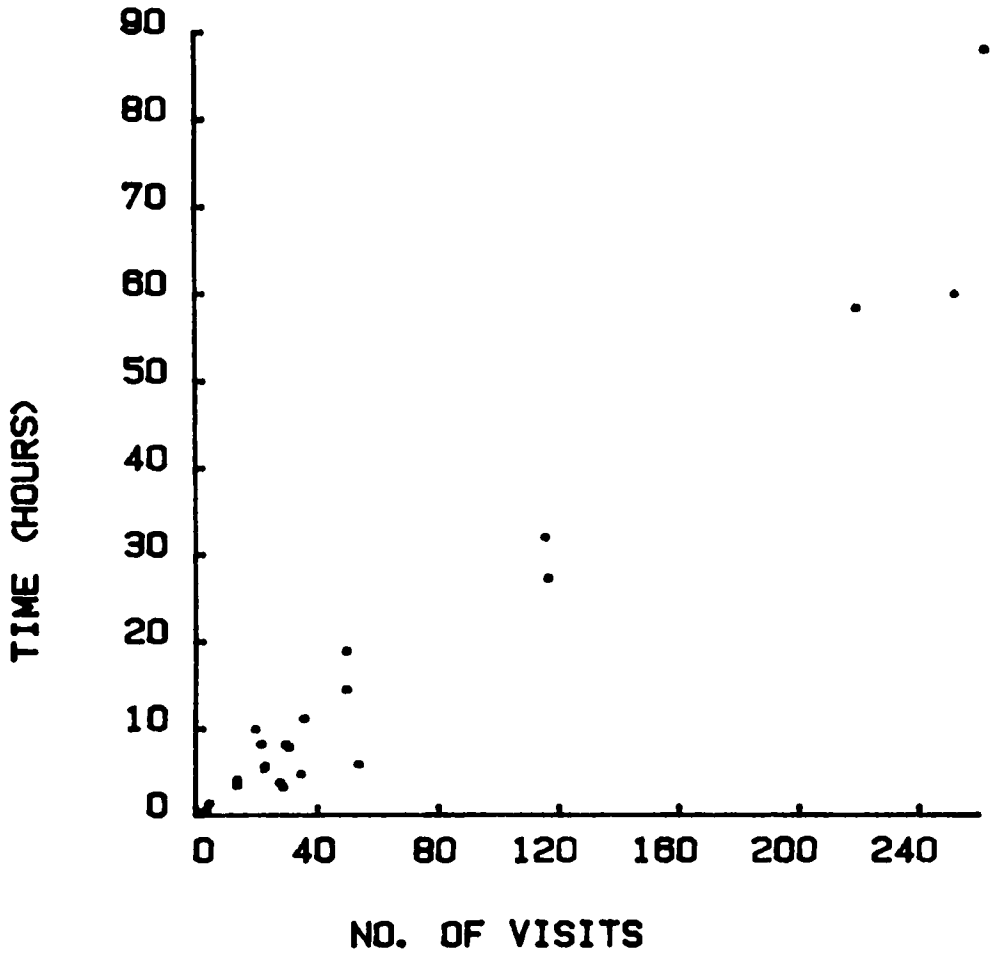

PATCHES
VISITS < 5 MIN
25
20
15
10
5
0
0 10 20 30 40 50 60 70
TOTAL # VISITS

d.


PATCHES
VISITS > 30 MIN
25
20
15
10
5
0
0 10 20 30 40 50 60 70
TOTAL # VISITS

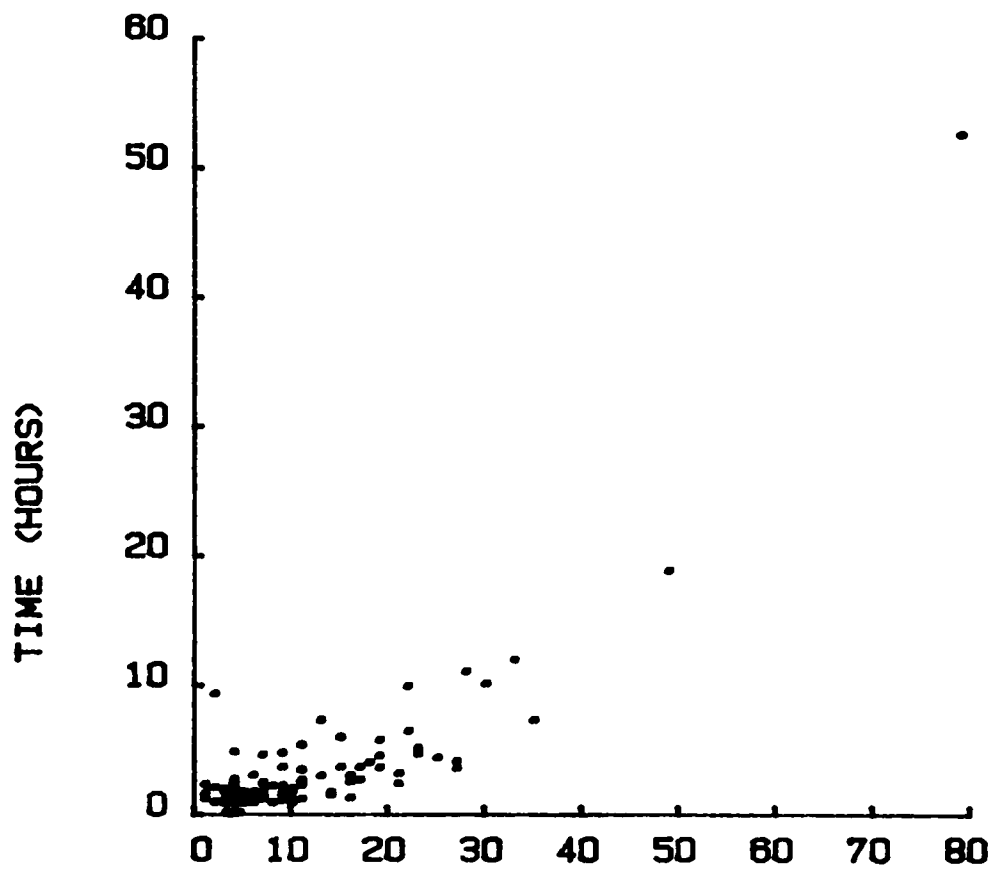
a.

ALL FOXES - HABITATS

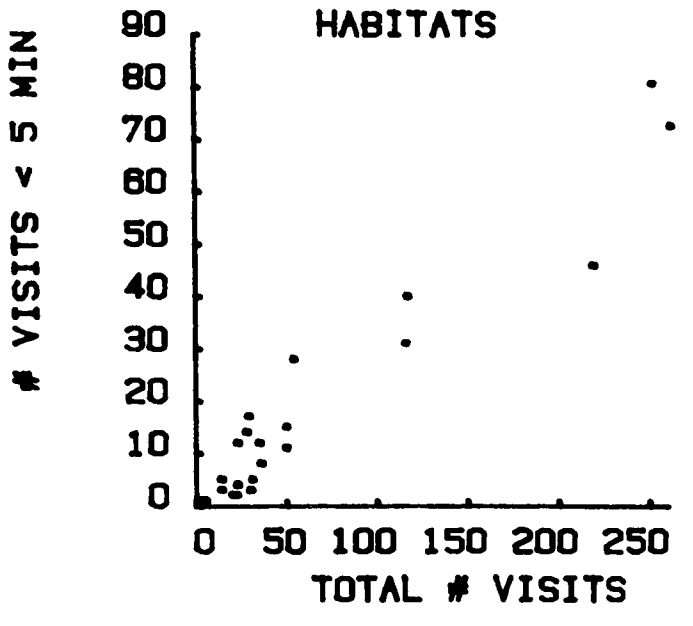


b.

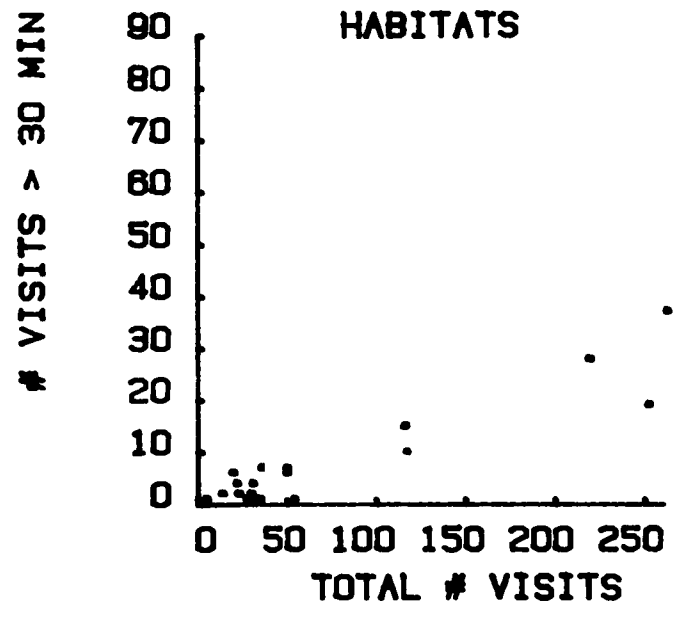
ALL FOXES - PATCHES



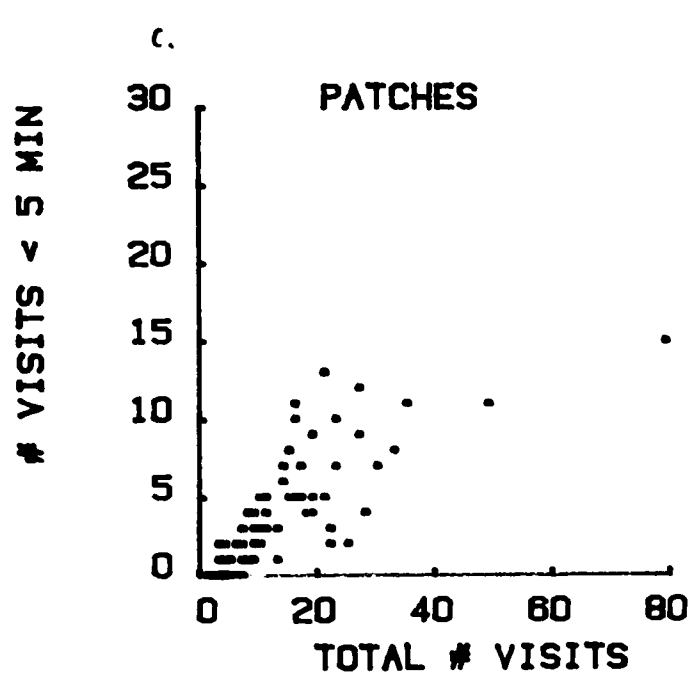
a.


HABITATS
VISITS < 5 MIN
TOTAL # VISITS
0
10
20
30
40
50
60
70
80
90
0
50
100
150
200
250

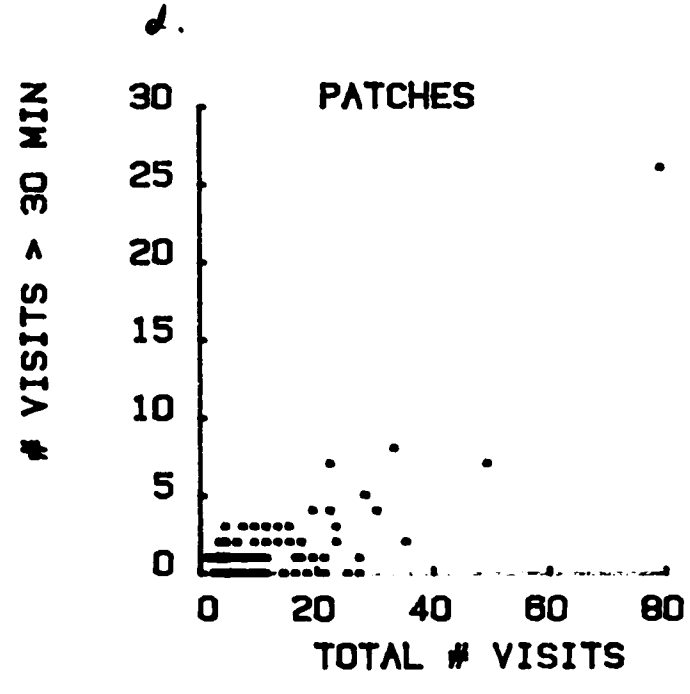
b.


HABITATS
VISITS > 30 MIN
TOTAL # VISITS
0
10
20
30
40
50
60
70
80
90
0
50
100
150
200
250

c.


PATCHES
VISITS < 5 MIN
TOTAL # VISITS
0
5
10
15
20
25
30
0
20
40
60
80

d.


PATCHES
VISITS > 30 MIN
TOTAL # VISITS
0
5
10
15
20
25
30
0
20
40
60
80

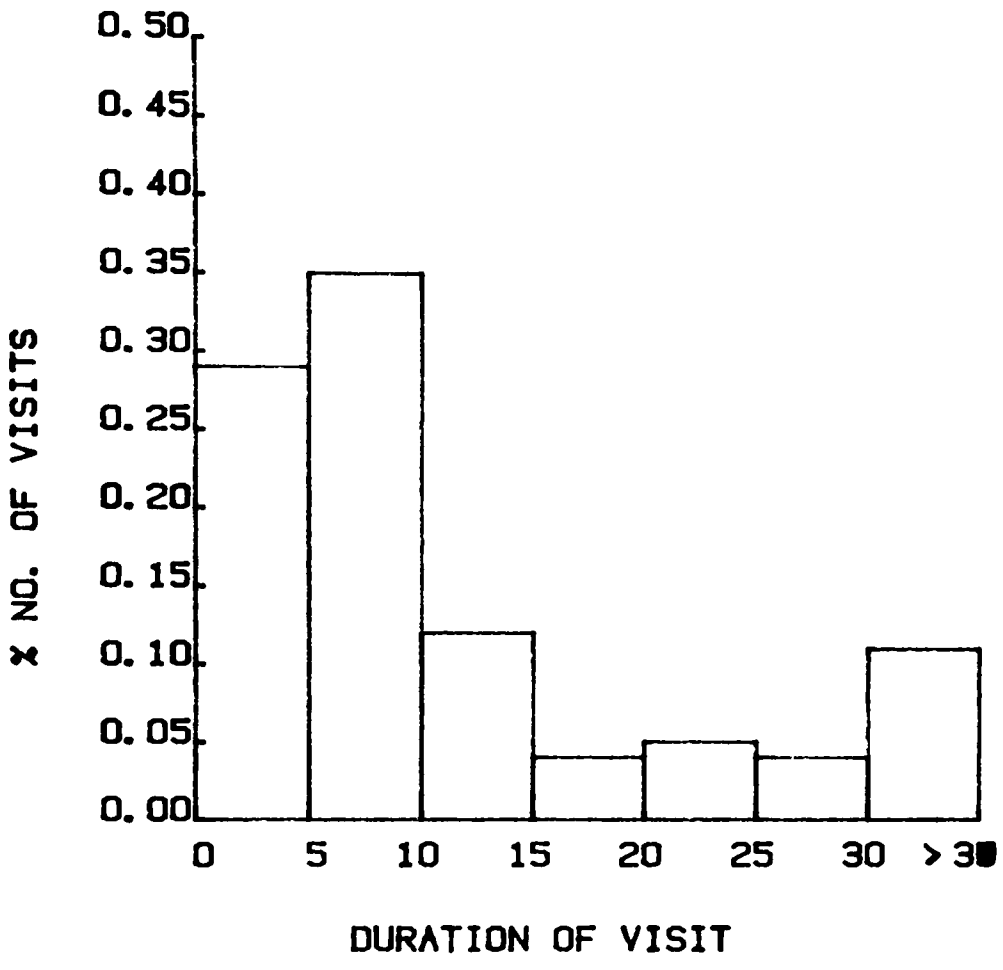
minutes) and very long visits (more than 30 minutes). In foxes, there is again a clear linear relationship (Table 6.16): often visited habitats and patches are frequently visited for only brief periods (here is a steep increase) and for long periods (here with a shallow slope). In badgers, however, dispersion of data points is considerable and for short periods, the relationship between DOS and NOV is not as clearcut as for foxes (significant positive rank correlations, but invalid regressions).

There are at least two ways to interpret the differences between species. High frequency of short-time visits by foxes may be a consequence of frequent border patrolling (see section 6.2.1.). In badgers, such frequent patrolling is not necessary due to the latrine marking system (section 5.4); and if badgers mark at a latrine, their DOS in the patch with the latrine may well exceed 4 minutes. The second explanation suggests frequent updating of resource availability as cause for many short-time visits in foxes. Foxes consume many different kinds of prey and are not as fixed on one prey type as are badgers with earthworms (Chapter 4). Although the foxes may have an approximate knowledge of where to find specific prey, availability may change rapidly (Chapter 3). Furthermore, foxes occupy larger ranges and therefore updating may be more frequently required. Increased flexibility in prey selection of foxes (relative to badgers) may induce them to reconnoit several possibilities briefly before they decide what to concentrate on. Badgers, however, do concentrate on earthworms and may restrict their movements ("degrees of freedom") in extreme ways (section 6.2.6.). This interpretation is supported if the frequencies of classes of DOS are compared (Fig. 6.89; $G=43.43$, $df=6$, $p<0.001$); badgers spend a long time more often in a patch than foxes.

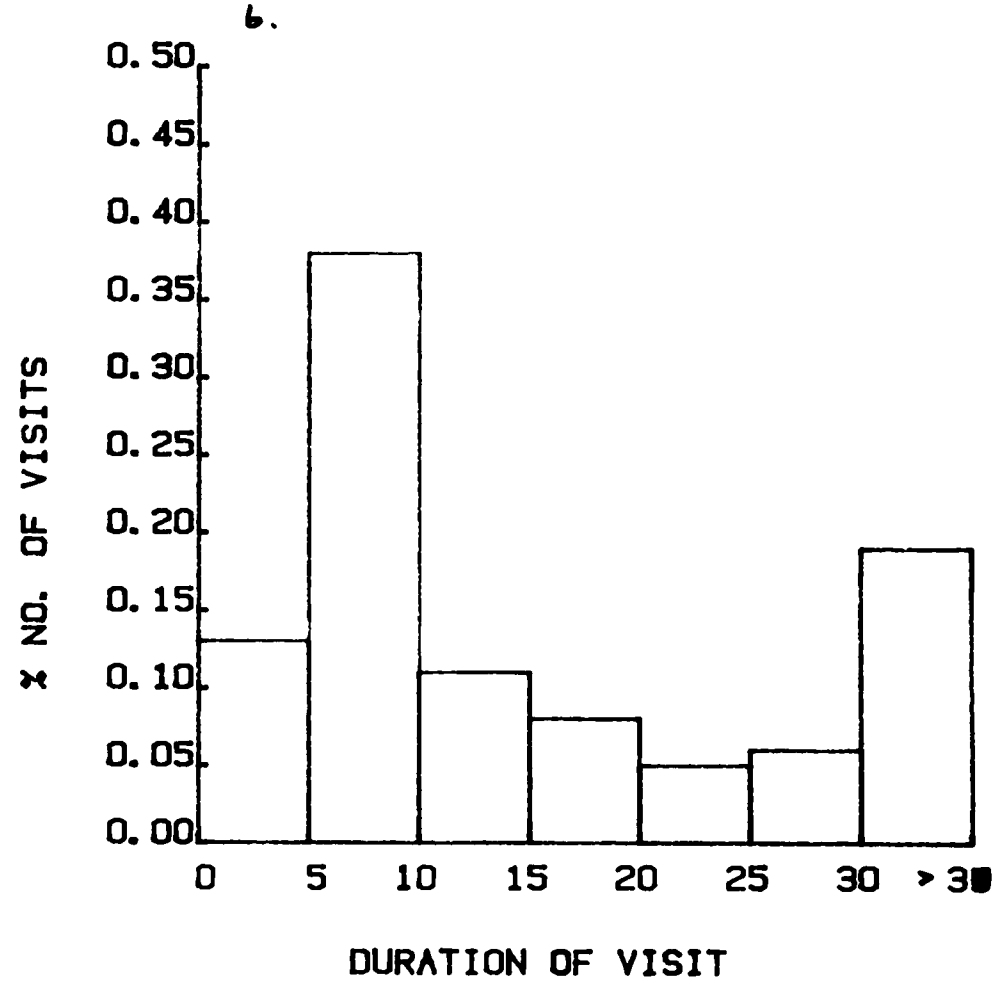
To substantiate these suggestions, the UI of patches from different habitats were compared using the duration classes of Fig. 6.89. In Table 6.17 and 6.18, two duration classes with significant differences in the UI between habitats are contrasted, one short duration (< 5 min) and one long

PROPORTION OF VISITS OF CERTAIN DURATION CLASSES TO PATCHES SUMMARIZED OVER ALL HABITATS. LEFT: FOXES, RIGHT: BADGERS.

a.



b.



duration class (foxes: 21-25 min, badgers: 26-30 min). Of particular interest are habitats with a shift in emphasis from frequent visits of short duration (Table 6.17b) to few visits of long duration (Table 6.17d). To these habitats belong, for foxes, long grassland, deciduous woodland, and parkland. Long grassland is the same habitat that was a good predictor of rabbit consumption in Chapter 5. Increased success of foxes hunting for rabbits in long grassland or its vicinity may derive from two conditions. Firstly, rabbits that are caught by surprise by a fox in this habitat may have reduced chances of escaping. However, this is not a preferred habitat of rabbits, so that it does not pay foxes to devote prolonged effort to searching systematically for them there (also bearing in mind the increased probability that they will be detected by other rabbits). It is more likely that foxes use long grassland as a protective shield to approach unsuspecting rabbits in neighbouring habitats.

In badgers, pasture and deciduous woodland complement each other in usage characteristics (Table 6.18). Deciduous woodland is visited more often than pasture for short periods while the reverse is true for long visits.

Systematic comparisons of habitats on UI within certain duration classes are illustrated in Fig. 6.90 to 6.97. Fig. 6.90-6.97 present absolute, proportionate and cumulative proportionate frequency distributions of seven classes of DOS for selected habitats for badgers and foxes. These can be compared with frequency distributions for DOS that would be expected from simple random movements (see section 6.1). Habitat 44 in Fig. 6.90 is an example of a pattern of visits that is indistinguishable from such a process (Table 6.19): short visits occur more often than medium-term visits; long-term visits are highly unlikely. As Fig. 6.91 shows, the proportionate frequency distribution for this null-model would show a similar shape as for absolute frequencies while the coumulative curve (Fig. 6.91b) is ideally convex and rapidly approaches 100%. Deviations from the null model can

Table 6.17 Frequency of visits of foxes to habitats (summarized over habitat map patches) of a limited duration. Only significant comparisons listed

(a) Kruskal-Wallis one-way analysis of variance: on number of visits (5 min) versus habitats: H = 23.1, df = 12, p < 0.05.

(b) multiple comparison tests

Habitat with high frequency	Habitat with low frequency	Actual value	Critical value	Signifi-cance
grassley	detached hous.	59.60	56.63	<.05
long grassl.	pasture	52.80	51.06	<.02
long grassl.	hedge	58.90	50.25	<.05
long grassl.	mixed plant	83.70	80.46	<.005
grassley	pasture	60.60	58.94	<.005
grassley	hedge	91.50	86.33	<.002
summer cer.	pasture	27.80	27.62	<.05
deciduous w.	pasture	25.20	23.61	<.05
farm	mixed plant.	66.70	57.91	<.05
summer cer.	mixed plant.	58.10	53.97	<.02
deciduous w.	mixed plant.	56.10	51.21	<.02
parkland	mixed plant.	66.10	56.18	<.05

(c) Kruskal-Wallis analysis of variance: on number of visits between 20-25 min vs. habitats: H = 24.94, df = 12, p<0.025

(d) multiple comparison tests

grassley	detached hous.	47.90	41.40	<.05
summer cer.	detached hous.	41.30	34.86	<.05
bracken	detached hous.	60.80	58.09	<.005
grassley	long grassl.	47.90	47.60	<.02
summer cer.	long grassl.	41.30	39.53	<.02
bracken	long grassl.	60.80	56.19	<.005
grassley	hedge	40.70	35.64	<.05
grassley	deciduous w.	32.40	30.24	<.05
grassley	parkland	47.90	47.60	<.02
bracken	pasture	37.10	34.38	<.02
summer cer.	hedge	34.10	32.95	<.02
summer cer.	deciduous w.	25.80	24.18	<.02
summer cer.	parkland	41.30	39.53	<.02
bracken	hedge	53.60	49.62	<.005
bracken	deciduous w.	45.30	41.63	<.005
bracken	parkland	60.80	56.19	<.005
bracken	river & hedges	41.20	37.22	<.05
bracken	river, no hedg.	45.40	42.20	<.05

Table 6.18 Frequency of visits of limited duration of badgers to habitats (summarized over habitat map patches). Only significant comparisons listed.

(a) Kruskal-Wallis one-way analysis of variance on number of visits < 5 min vs. habitats:

H = 8.815, df = 3, p<0.05

Habitat with high value	Habitat with low value	Actual value	Critical value	Signifi-cance
deciduous w.	pasture	13.1	12.30	<.005

(b) multiple comparison tests

(c) Kruskal-Wallis one-way analysis of variance on number of visits between 25 and 30 min vs. habitats:

H = 11.25, df = 3, p<0.025

(d) multiple comparison tests

pasture	deciduous w.	13.20	13.12	<.002
pasture	mixed plant.	16.10	15.74	<.002
summer cereals	mixed plant.	10.30	9.98	<.05

Table 6.19 Comparison of patterns of stay in habitat map patches with simple random movements (negative exponential distribution of probability of leaving a site after a given time of stay).

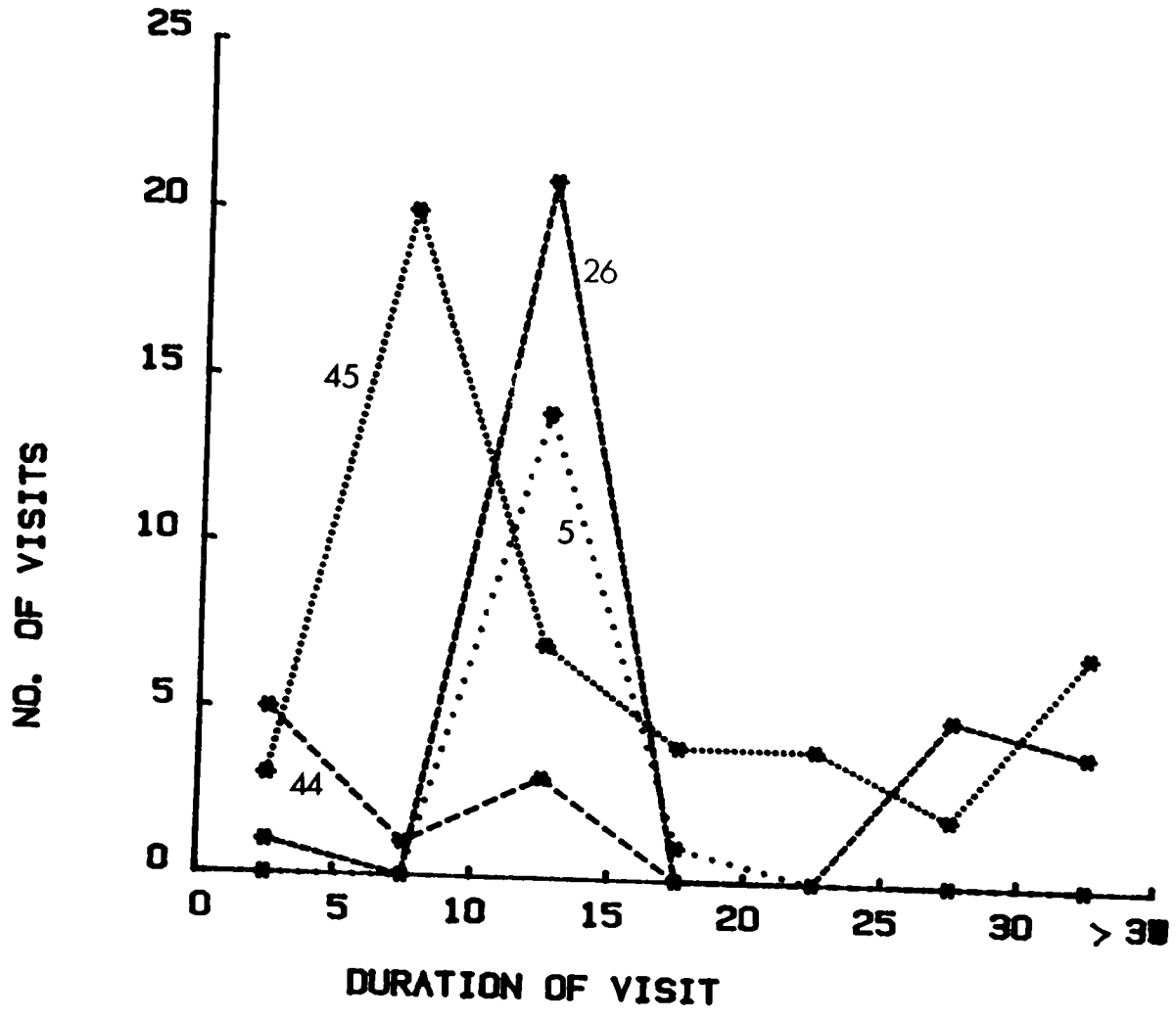
t: sample mean
L: Lilliefors statistic
N: sample size

Species	habitat	t	L	N	sig.
Foxes	long grassland	.107	1.796	53	<.01
	grassley	.236	1.686	116	<.01
	pasture	.280	2.871	218	<.01
	farm	.248	1.600	115	<.01
	summer cereals	.329	3.539	261	<.01
	bracken	.277	1.297	49	<.01
	deciduous woodland	.288	2.990	251	<.01
Badger	long grassland	.279	3.346	15	<.01
	pasture	.460	5.776	205	<.01
	road	.217	1.840	31	<.01
	summer cereals	.428	2.465	277	<.01
	deciduous woodland	.363	2.356	117	<.01
	mixed plantations	.292	1.691	178	<.01
	river & hedge	.152	0.791	9	ns
	river, no hedge	.296	2.956	47	<.01

easily be picked out by looking at the cumulative frequencies: concave or sigmoid curves indicate a larger proportion of visits of long duration classes than expected. Pasture (habitat 7) in Fig. 6.93b is a conspicuous example. Habitats with reduced resource presence, such as long grass and riverrine environments (Fig. 6.90–6.91) show patterns that resemble the results of random movements. An interesting exception is habitat 26, road. I have frequently observed badgers strolling slowly along the periphery of a track or an asphalt road where they search for beetles and particularly for snails in the long grass. All habitats of Fig. 6.93 deviate significantly from the suggested null model. (Note that the comparison with the expected distsibution is independent from the class sizes chosen for illustration, as described in section 6.1). Furthermore, the three individuals ALI, MANI and WILF were excluded from these analyses, since the way they were tracked (cf. section 6.4) would have biased the frequency distribution towards the 11–15 min class).

Fig. 6.94–6.97 illustrate frequency distributions of visit durations for selected habitats in foxes. Again, visit patterns of the habitats illustrated deviate from the null model. An interesting exception provides long grassland (habitat 5), which, unlike all other habitats, experiences too few long duration visits to comply with the simple random process. Reasons for this have been discussed above.

In summary, patterns of visits to habitats as expressed by the frequency of visits of certain duration classes reflect prey preferences (as indicated before) and indicate movement and foraging 'styles' of the two species. Despite these differences, movements of individuals of both species are not compatible with simple random movements.

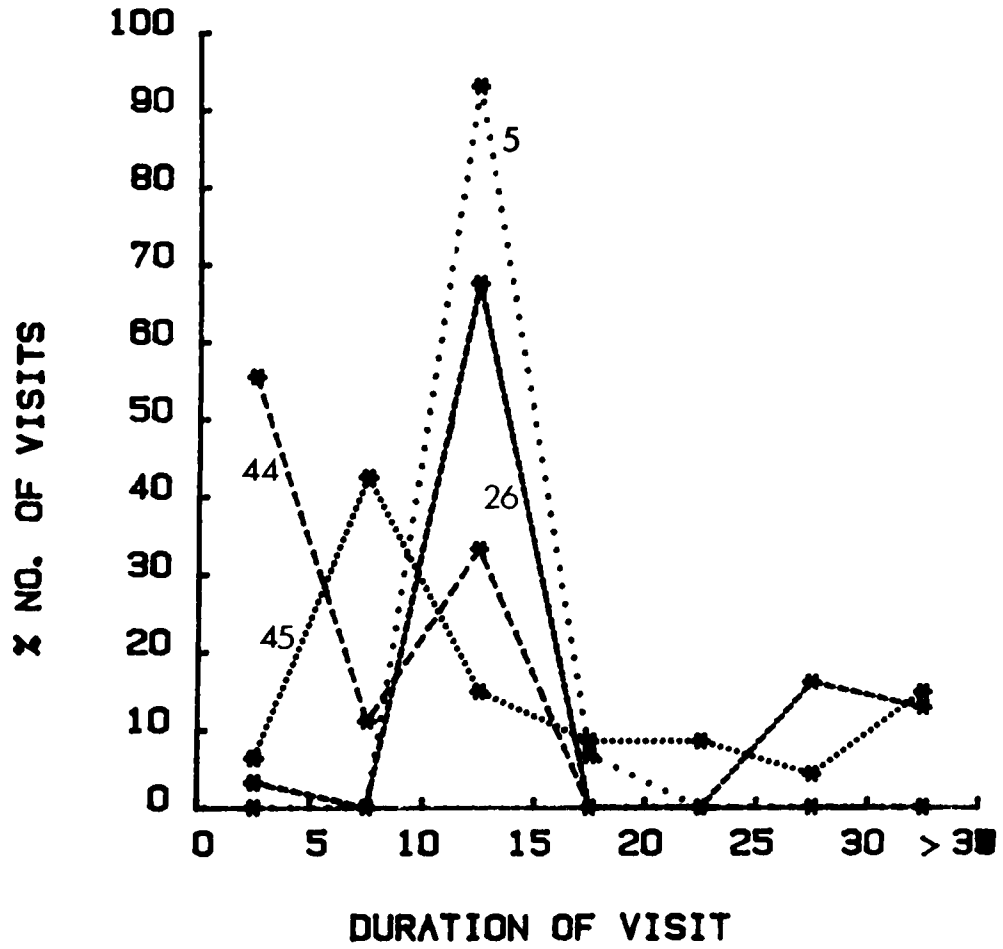


VISITS BY BADGERS TO PATCHES
SUMMARIZED OVER HABITATS
ONLY INTENSIVELY TRACKED
INDIVIDUALS

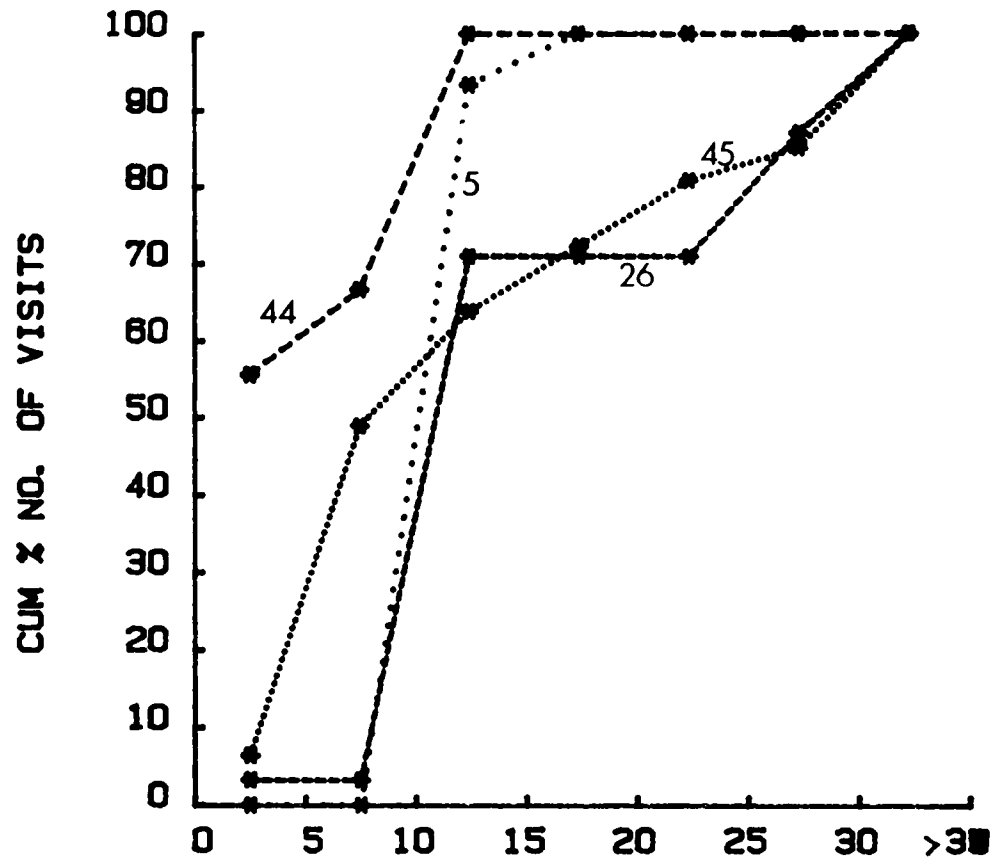
5 - LONG GRASS
26 - ROAD
44 - RIVERRINE WITH HEDGES
45 - RIVERRINE WITHOUT HEDGES

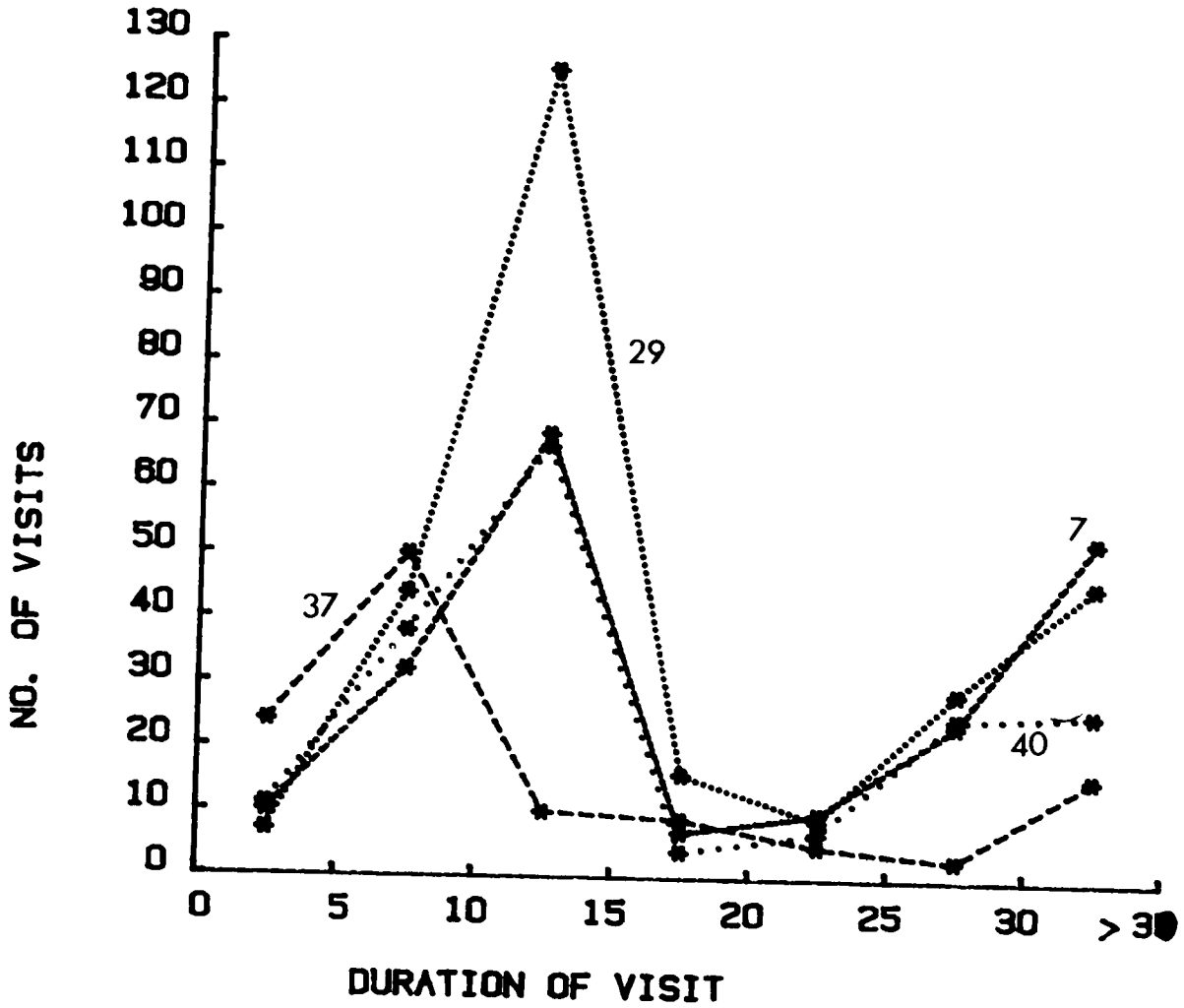
BADGER VISITS SUMMARIZED OVER HABITATS
5 - LONG GRASS; 26 - ROAD; 44 - RIVERRINE WITH HEDGES; 45 - 45 - RIVERRINE WITHOUT HEDGES

a.



6.





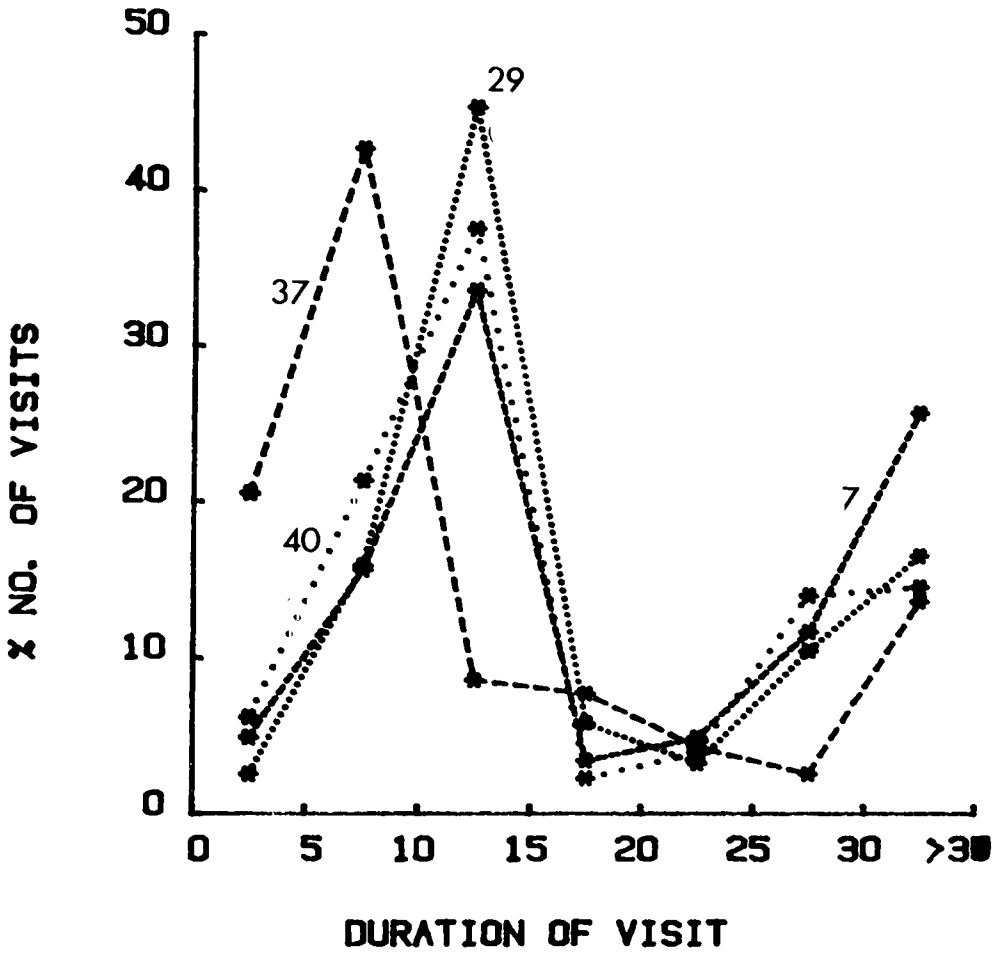
VISITS BY BADGERS TO PATCHES
SUMMARIZED OVER HABITATS
ONLY INTENSIVELY TRACKED
INDIVIDUALS

29 - SUMMER CEREALS
7 - PASTURE
37 - DECIDUOUS WOODLAND
40 - MIXED PLANTATIONS

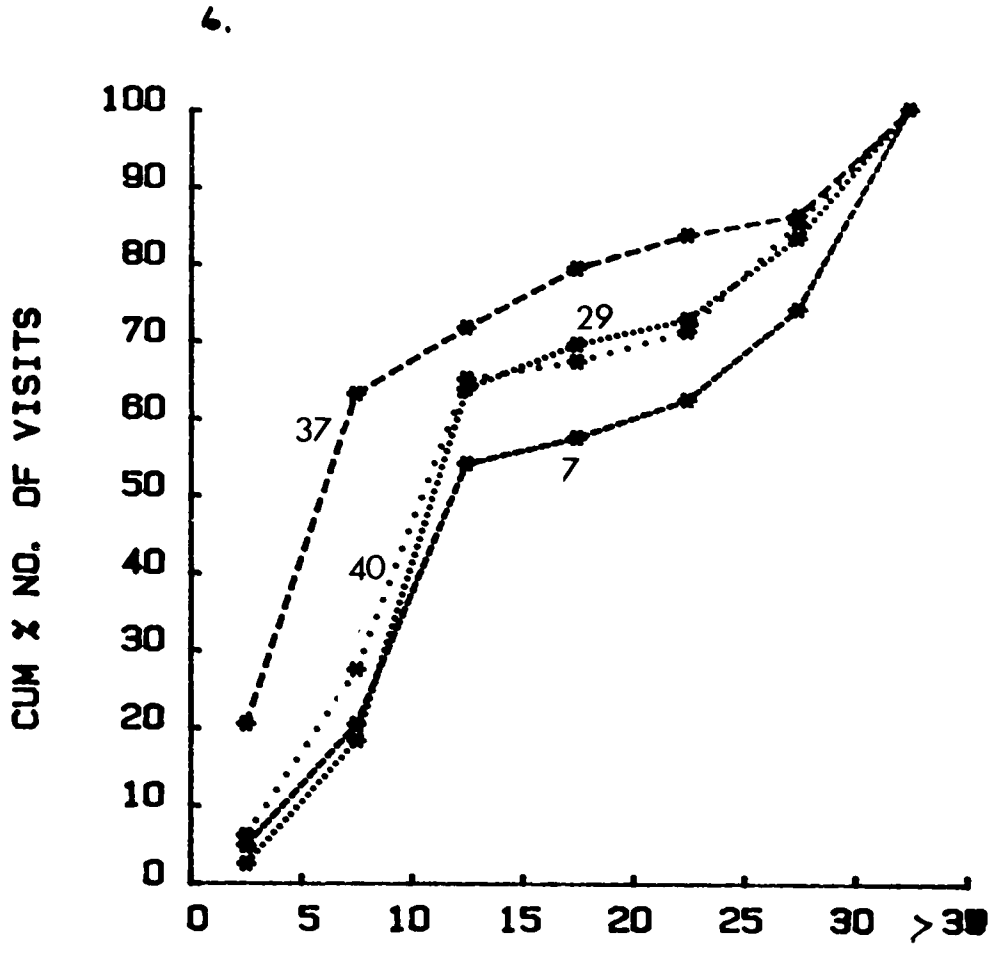
6-92

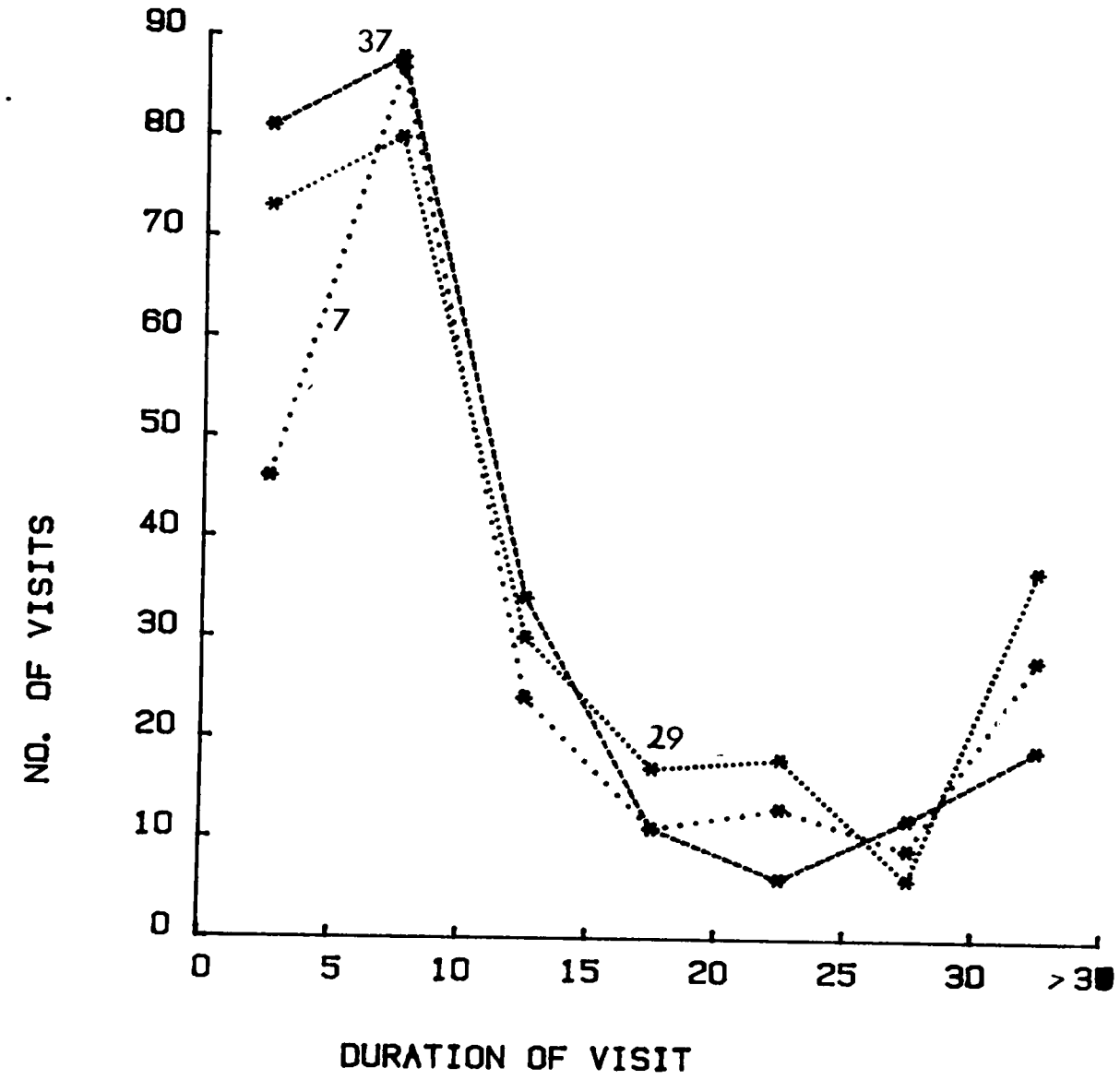
BADGER VISITS SUMMARIZED OVER HABITATS
7 - PASTURE; 29 - SUMMER CEREALS; 37 - DECIDUOUS WOODL.; 40
40 - MIXED PLANTATIONS

a.



b.





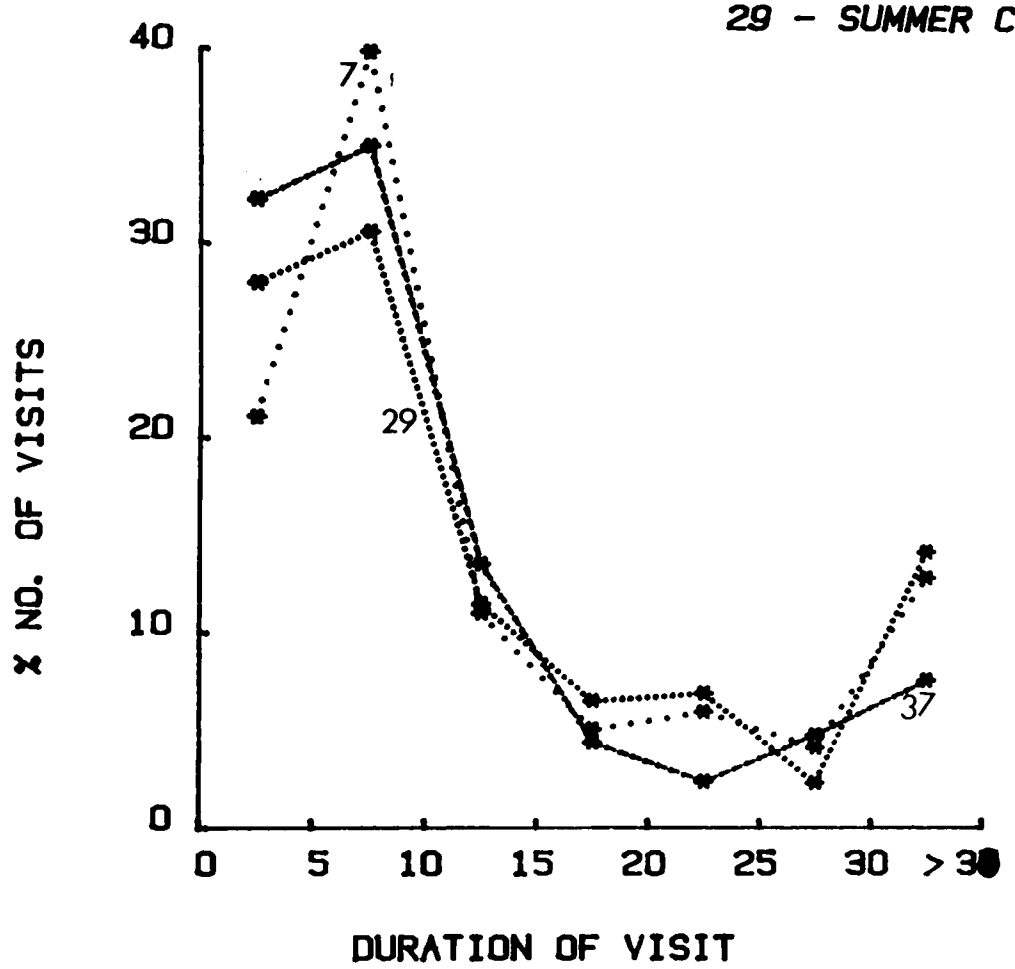
VISITS BY FOXES TO PATCHES SUMMARIZED OVER HABITATS ONLY INTENSIVELY TRACKED INDIVIDUALS.

29 - SUMMER CEREALS
37 - DECIDUOUS WOODLAND
7 - PASTURE

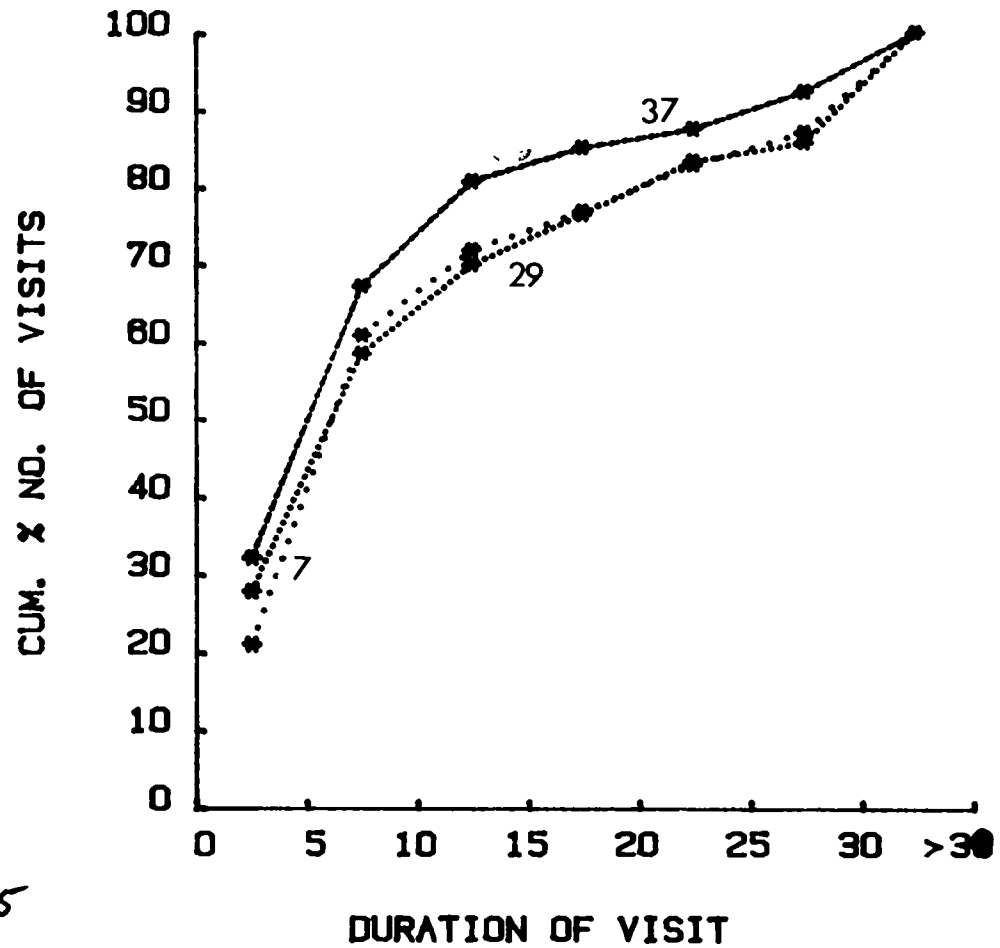
6-94

FOX VISITS SUMMARIZED OVER HABITATS
29 - SUMMER CEREALS, 37 - DECIDUOUS WOODLAND, 7 - PASTURE

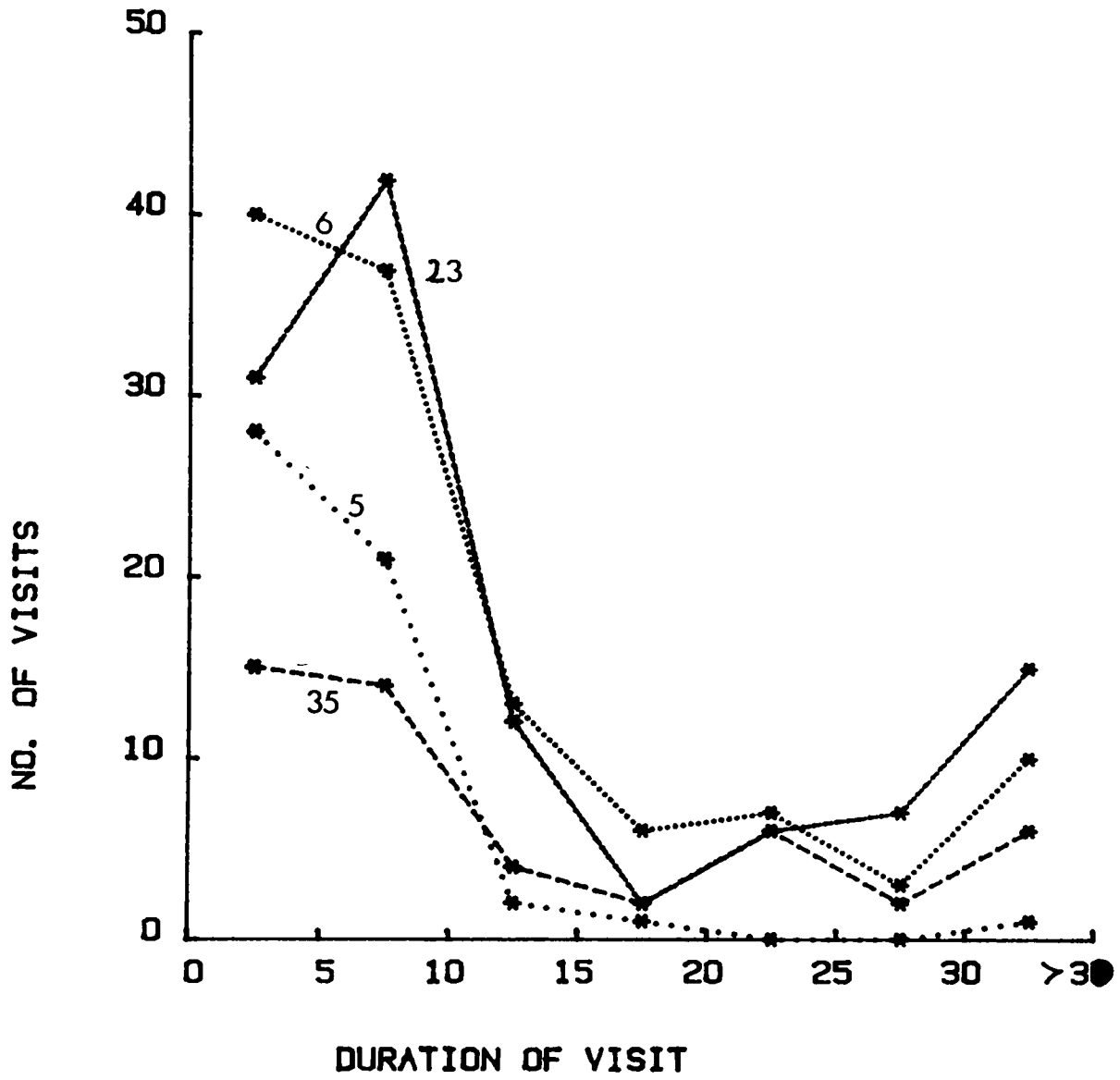
a.



b.



6-95

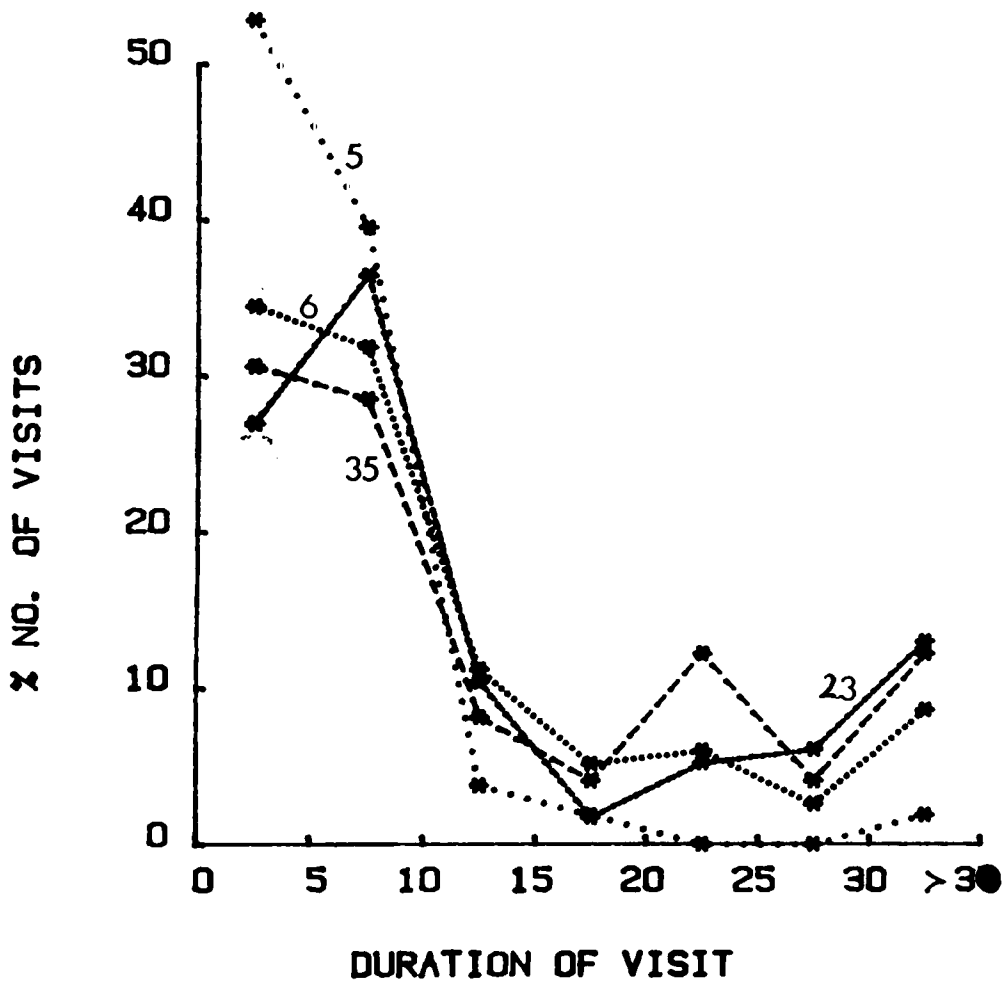


VISITS BY FOXES TO PATCHES
SUMMARIZED OVER HABITATS
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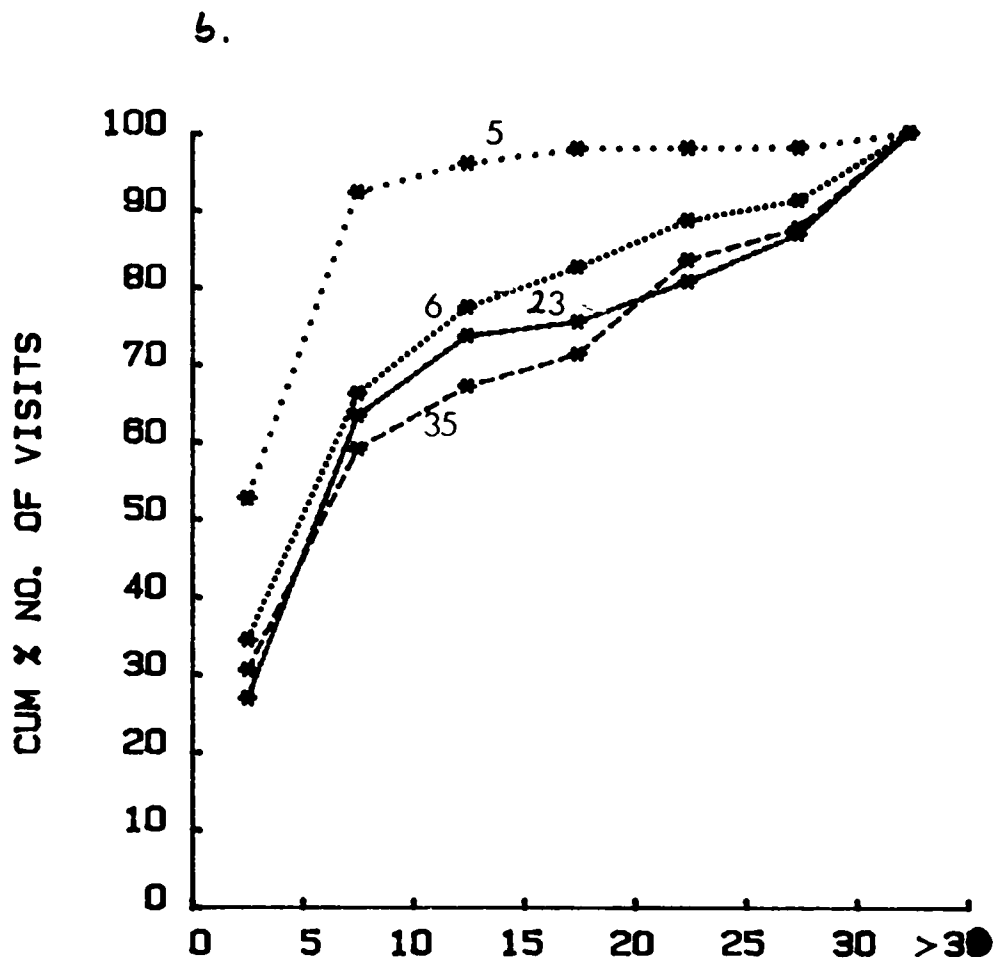
6 - GRASSLEY
23 - FARMLAND
5 - LONG GRASS
35 - BRACKEN

FOX VISITS SUMMARIZED OVER HABITATS
5 - LONG GRASS; 6 - GRASSLEY; 23 - FARM; 35 - BRACKEN

a.



b.



7. Spatial organisation and reproductive strategies in badgers.

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7. Spatial organisation and reproductive strategies of badgers.

7.1. Introduction.

The previous chapters have illustrated how the intricate relationship between the movements of individuals, the resulting spatial utilization patterns and the characteristics of habitats and resources shape the badger's social system in Wytham. A variety of recent field studies (Kruuk 1978a, Kruuk & Parish 1979, 1982a; Harris 1982, 1984; Cheeseman et al 1985; Martin-Franquelo & Delibes 1985) suggest that there is considerable variation in the spatial and social organisation in badgers. I hope to reconcile these diverging descriptions of badger social organisation by considering the relationship between resources and social and spatial organisation in the wider context of life history and reproductive patterns.

I shall start with an examination of the reproductive biology of the female badger. Energetic costs of pregnancy and lactation are considerable (section 7.2), since females provide most of the parental investment. This, together with additional factors concerning post-weaning development, survival prospects for the first harsh period, and the potential future reproductive success of the young, places considerable selection pressures on the timing of birth, favouring a date early in spring (section 7.2). If the main food resource is economically defendable, females can improve their breeding success by striving for exclusive access to areas containing these resources for themselves and their offspring. If intrusion pressure from other females and resource density on the defended areas is high, then females could form coalitions with other females to share defense costs. Since females carry the main burden of parental investment, standard sociobiological theory predicts that they should exhibit mate choice (Trivers 1972, 1985). The sexual dimorphism shown by badgers (Anderson &

Trewhella 1985) is an indication that sexual selection may have been operating on males competing with each other for females. If females can improve their fitness by choosing their mates carefully, then they should come into oestrus when the prospects for mate choice are good. For badgers, this is the time shortly after parturition, since the males reach their peak in body size in February. Since there is powerful selection pressure for birth early in the year, the evolution of delayed implantation is a possible solution to the problem of timing mate choice, since it allows the mating season to vary independently from the time of parturition (Sandell 1985). The evolution of seasonal delay has far-reaching implications for the reproductive behaviour and the spatial distribution of males. Uncertainty of paternity caused by repeated ovulations of females and their abilities to select between different blastocysts (Ahnlund 1980) requires males to maximise mating attempts and defend exclusive access to females. Territoriality and the formation of male coalitions are two strategies by which males can attempt to limit other males' access to females.

The formation of intrasexual coalitions are submitted to a cost-benefit analysis (sections 7.3. and 7.4). The costs and benefits of defending exclusive access to a resource (for males: females, for females: protein-rich food) are analysed as a function of the qualities of the resource (density, availability, renewal and dispersion) and the population density (intrusion pressure). A model of the social organisation of the badgers based on the results of this analysis (section 7.5) can be shown to accommodate the diverging results of previous studies.

7.2. Energetics of female reproductive effort

In the seasonal environment that occurs throughout the range of the European badger, resource availability changes considerably over time (Chapter 3). Thus, the timing and intensity of reproductive activities are

important, if costly activities such as lactation are to coincide with a peak in food availability. The two most important reproductive events for the female are the time of mating and the time of parturition. In the following sections, three factors are discussed that exert selection pressure on the time of parturition (Sandell 1985): the energetic costs of pregnancy and lactation, the time needed by the young to gain sufficient foraging efficiency and the time available for the post-weaning development of the young until the next harsh period.

7.2.1. Energetics of maternal investment.

Few studies have hitherto attempted to describe in detail how much energy carnivore parents have to devote to rear young successfully. Within the mustelids, the studies by Moors (1974, 1980) on weasels (Mustela nivalis) and Powell & Leonard (1983) on fisher (Martes pennanti) form an exception. Based on these studies I have developed a model of the energetic requirements of females during the lactation period. Appendix 9 describes the development of the equations and details of computation for an estimate of the total daily energy expenditure (TDEE) of a lactating female badger. Two growth rates for young were selected (Appendix 9) to represent different levels of maternal investment (30 g/day and 40 g/day). The resulting equations are:

$$\text{TDEE (kcal/day)} = ((\text{hours resting}/24) \times 298.19 + (\text{hours active}/24) \times 522.087 + (120.066 + 187.11 \times (0.091 \text{ (growth rate 30 g/day)} + 0.03 \times \text{kit age})^{.738})) / 0.855$$

TDEE (kcal/day) =((hours resting/24) x 298.19 + (hours active (growth rate /24) x 522.087 + (160.088 + 187.11 x (0.091 40 g/day) + 0.04 x kit age)$^{.738}$)) / 0.855

Fig. 7.1 shows a plot of TDEE from the time of birth of the young (day 1) to the approximate time of weaning (day 90) for high (graph A) and low growth rates (graph B). Also shown is lactation energy expenditure for both growth rates (graph C and D). Final energy expenditure is almost twice as high as at the beginning. A comparison of energy expenditure with and without lactation is provided in Fig. 7.2. Here the quotient

$$R = \frac{\text{Maintenance Energy + Activity Energy + Lactation}}{\text{Maintenance Energy + Activity Energy}}$$

is plotted against time. Towards the end of the lactation period, energy expenditure is 2.5 (low) to 3.2 times (high growth rate) higher than energy expenditure without lactation, or lactation comprises up to 67 % of TDEE ! This result corresponds closely to estimates for small mustelids (Moors 1980) where energy needs during lactation are estimated to be 2 to 3 times above average values.

How does this additional energy expenditure translate into additional foraging effort ? Since badgers in Wytham eat mainly earthworms during spring (Chapter 4), I considered the time females need to devote to hunting for additional earthworms in order to obtain a balanced energy budget. Since it can be safely assumed that badgers catch worms as efficiently as foxes, I computed the additional foraging time using (for comparative purposes) the two capture rates determined by Macdonald (1980; see section 3.7) for foxes worming on average nights (2.06 worms/min) and good nights (4.04 worms/min). If energy intake is set equal to energy expenditure, ie digestive efficiency set to 100 %, then total foraging time for a non-lactating female comprises

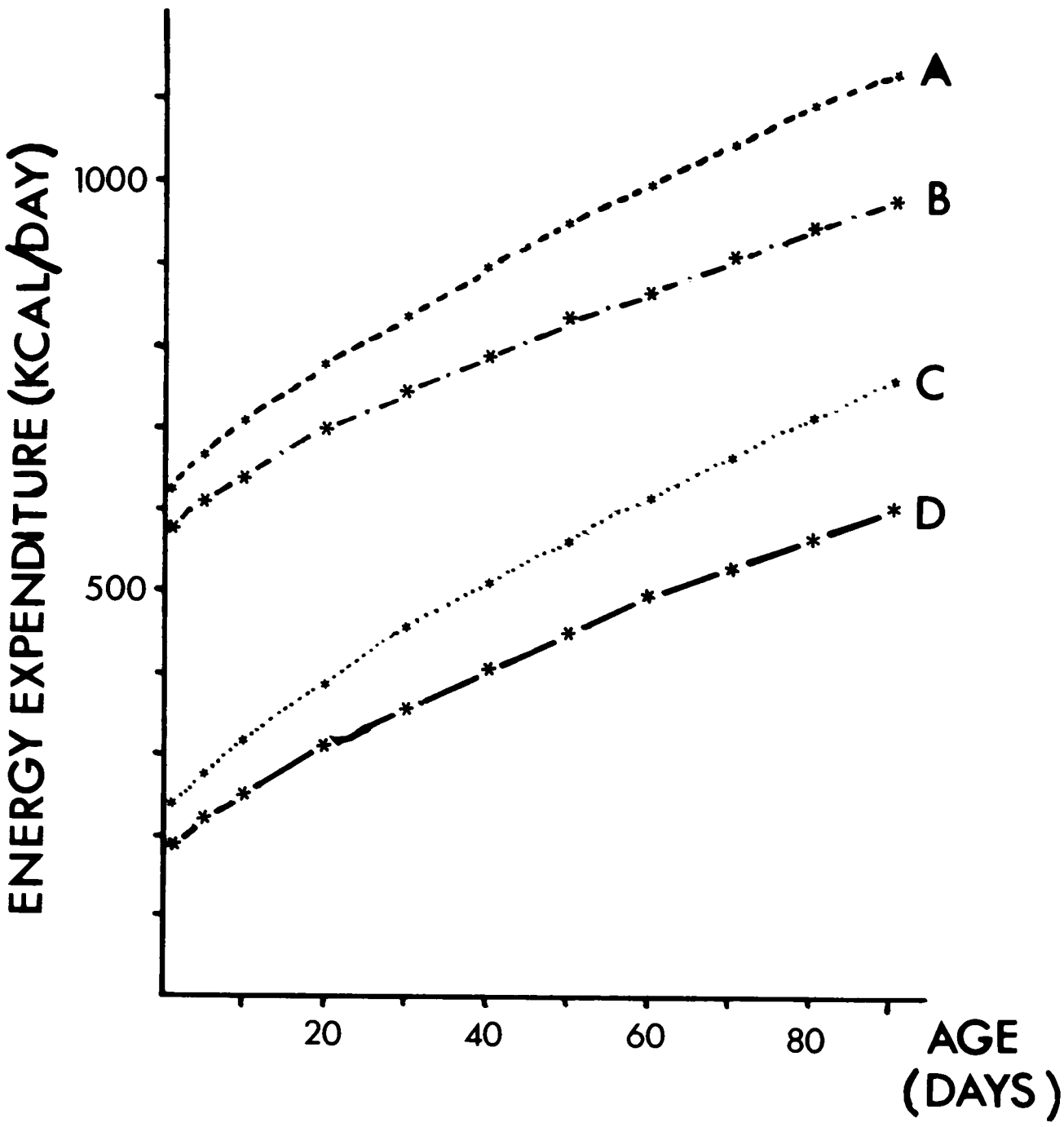
Fig. 7.1. Daily energy expenditure (kcal day^{-1}) by lactating female badgers in relation to age of young (= days of lactation).

A, B: total daily energy expenditure;
C, D: lactation energy expenditure per day.

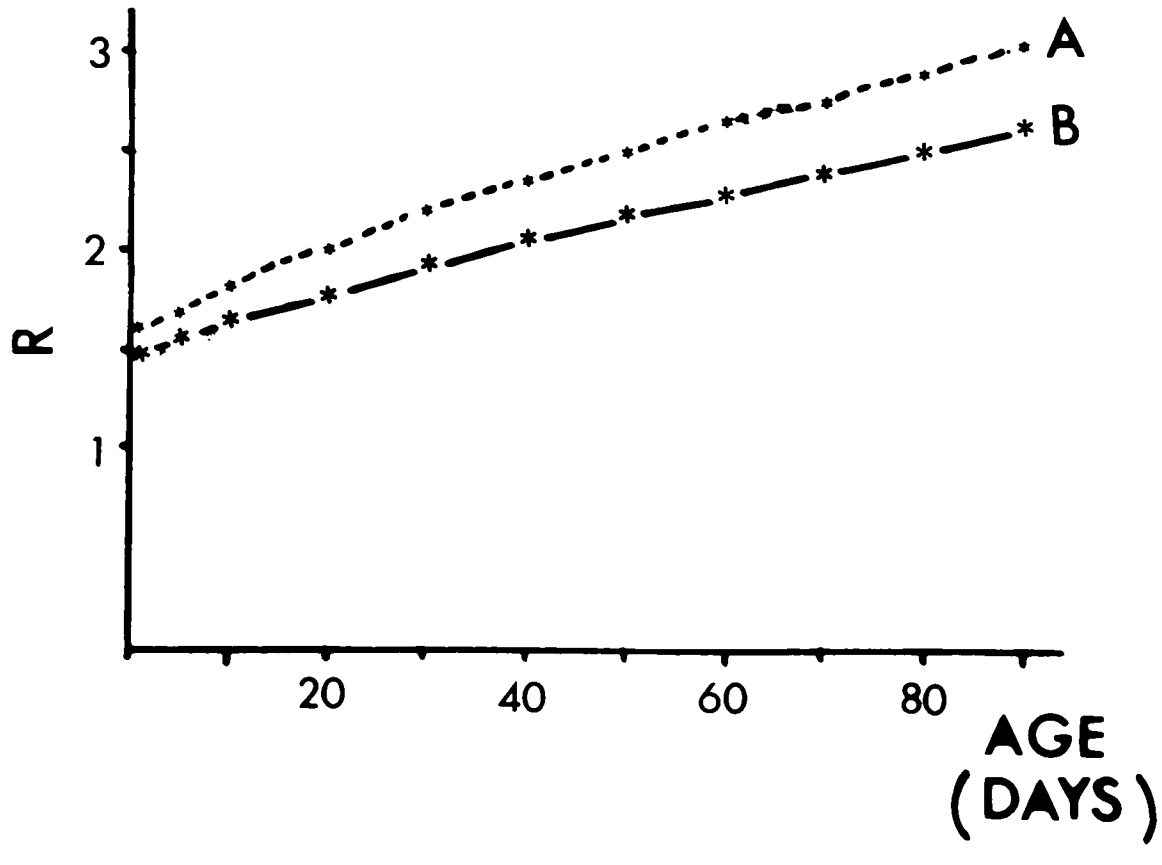
A, C: high maternal investment (growth rate 40 g day^{-1});
B, D: low maternal investment (growth rate 30 g day^{-1}).

Fig. 7.2. Factor R vs. age of young. R indicates the degree to which a lactating female badger's daily energy expenditure surpasses that of a non-lactating female (R=1).

7-1


ENERGY EXPENDITURE (KCAL/DAY)
1000
500
20
40
60
80
AGE
(DAYS)
A
B
C
D

7-2


R
3
2
1
20
40
60
80
AGE
(DAYS)
A
B

86.2 min/day (average capture rate) or 43.95 min/day (good capture rate). Kruuk (1978b) has derived similar estimates.

Foraging time for a lactating female was computed for the two levels of maternal investment considering both average and good foraging success. The results are plotted in Fig. 7.3. Foraging time increases in a similar fashion as daily energy expenditure from parturition to weaning. However, differences in maternal investment are less important than differences in foraging success (cf. graphs A and B with C and D in Fig. 7.3a). The difference is less clear-cut but still prevalent, if foraging time spent on replacing lactation energy expenditure alone is considered (Fig. 7.3b). If foraging time is limited, females should aim to increase foraging success rather than reduce maternal investment in milk production which would inhibit cub growth rates. Thus areas with high earthworm densities are extremely important to lactating females during the breeding season.

If foraging success is average and maternal investment high, then foraging time reaches a maximum of 255 min/day towards the end of lactation (Fig. 7.3a, graph A). How realistic is this figure ? Even, if energy loss through excretion (urine, faeces, and scent) is neglected, there are two factors that could lead to an underestimation of energy expenditure: the estimate of Activity Energy may underestimate actual energy expenditure and digestive efficiency may not reach 100 %.

Calculations of Activity Energy were based on an average speed of 10.74 m/min, a slow trot. Obviously badgers sometimes move faster, and my estimates of movement speeds are only minimum estimates (see Chapter 6). However, really fast movements are rare (Chapter 6) and I had ample opportunity to actually observe badgers moving in a characteristic slow trot. In contrast to foxes catching rabbits or fishers catching porcupines (Erethizon dorsatum) (Powell 1982), prey capture does not involve high speeds resulting in sudden increases in energy expenditure, nor does the act of copulation for female badgers (Neal 1977, Paget & Middleton 1974).

Fig. 7.3. Foraging time of lactating females foraging for earthworms necessary to balance

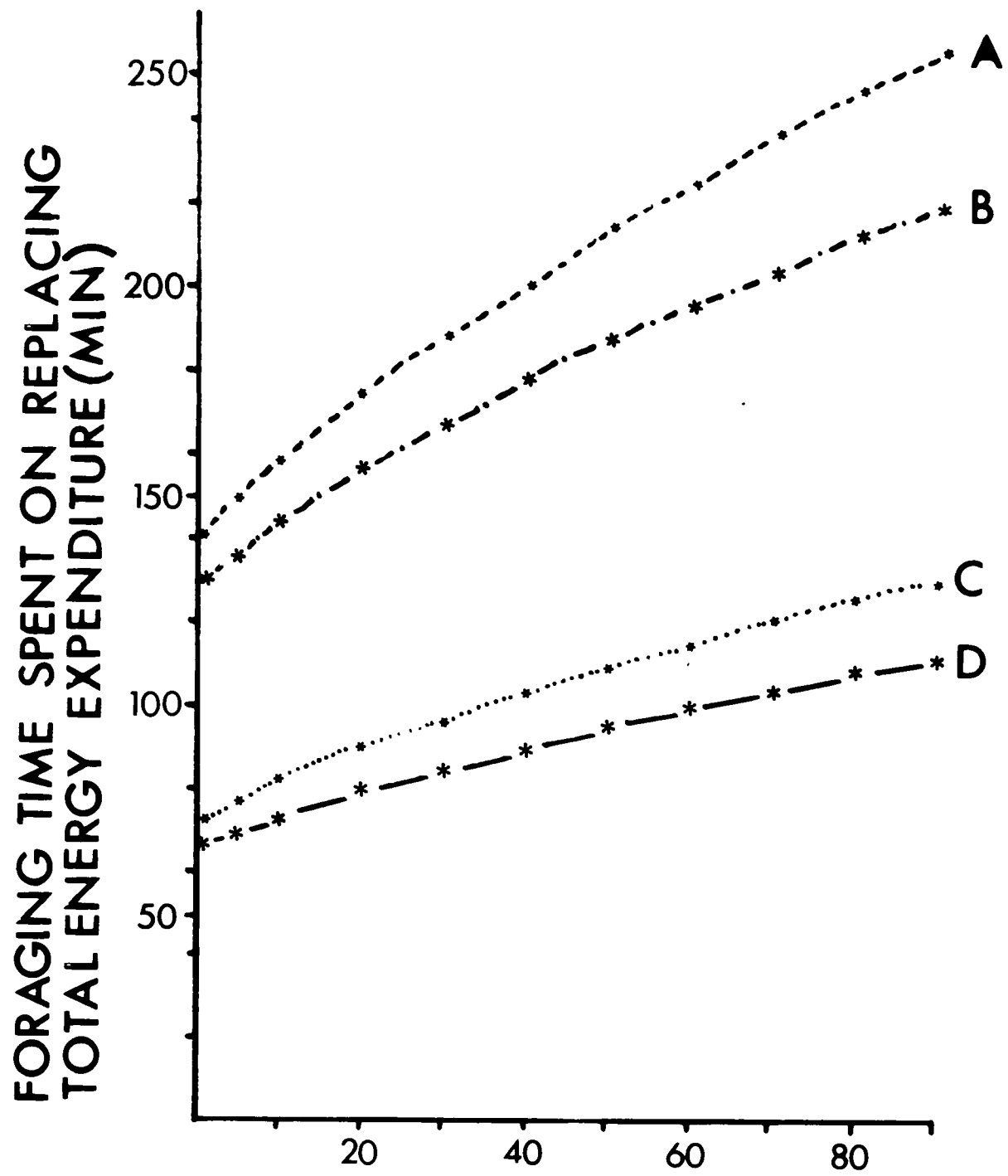
a. total daily energy expenditure
b. lactation energy expenditure per day

vs. age of young.

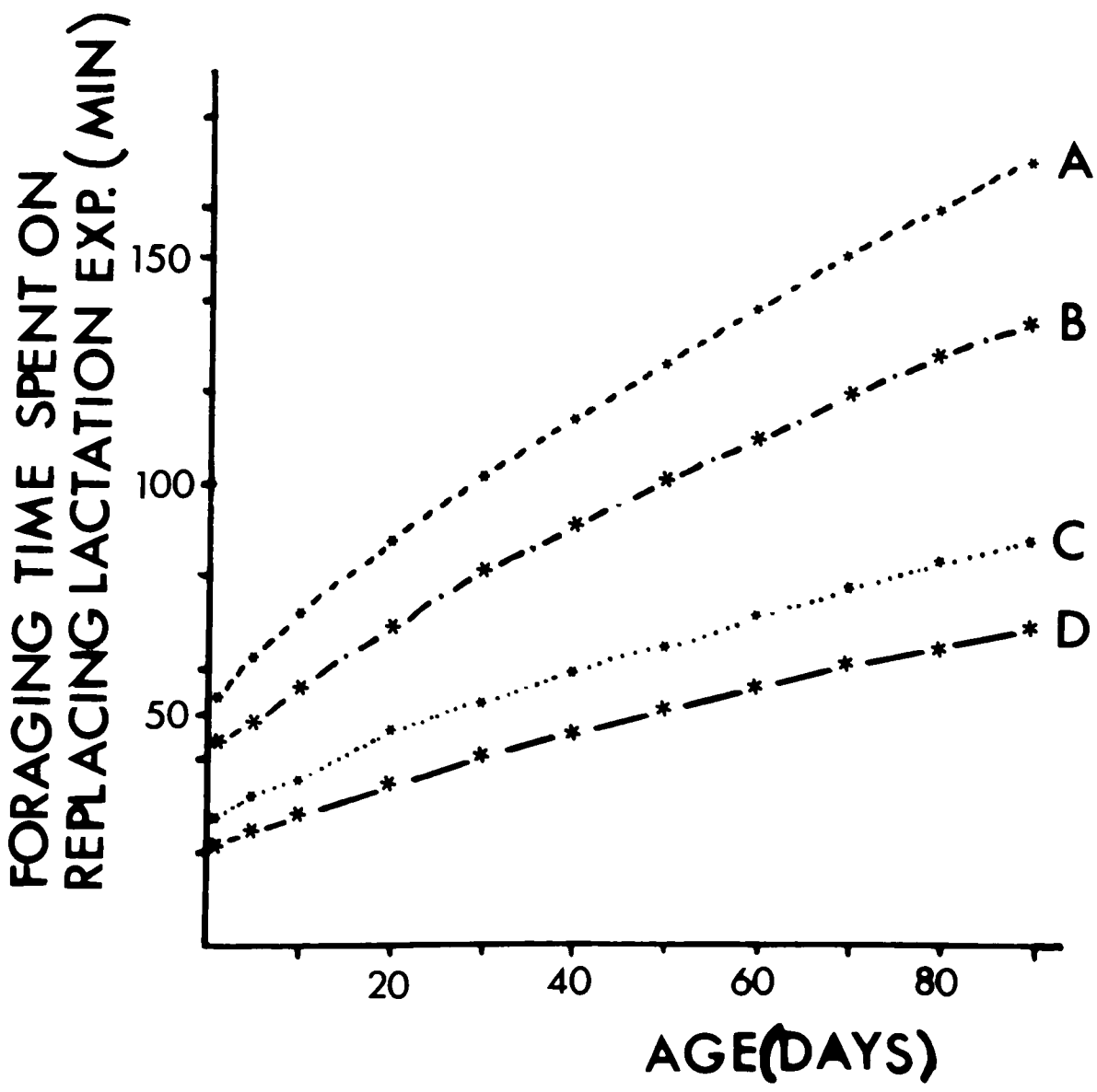
A: high maternal investment & low foraging rate
B: low maternal investment & low foraging rate

C: high maternal investment & high foraging rate
D: low maternal investment & high foraging rate

7-3a


FORAGING TIME SPENT ON REPLACING TOTAL ENERGY EXPENDITURE (MIN)
250
200
150
100
50
A
B
C
D
20
40
60
80
AGE (DAYS)

7-3b.


FORAGING TIME SPENT ON REPLACING LACTATION EXP. (MIN)
150
100
50
A
B
C
D
20
40
60
80
AGE (DAYS)

Cleaning of setts remains an unknown factor, and it is likely that I have underestimated the cost of this activity. Another potential source of error is the numbers of hours spent active. My source (Neal 1977:142) describes average activity during the months concerned (February to May), but it is of course possible that individual badgers may be more or less active. Therefore, my estimates of energy expenditure are minimum estimates and quite likely to be 10 % below the actual value.

Digestive efficiency has not yet been determined for European badgers eating earthworms. Digestive efficiency of fishers for different prey varies between 75 and 90 % (Powell 1982). Lampe (1976) determined digestive efficiency for the North American badger (Taxidea taxus), a strongly carnivorous species, to vary between 72 and 90 % and averaged around 85 % (if preying upon pocket gophers, Geomys bursarius). If I assume a digestive efficiency of 85 % and a TDEE that lies 10 % above the calculated value, then females would need not 255 min/day but 329 min/day at average foraging success and high maternal investment (correction factor of 1.294). If this estimate is more realistic, then foraging time could become a constraint and an additional incentive to the females to secure areas with high resource densities. Note that the above calculations only considers foraging time, but excludes any travelling time or time necessary for other activities.

My discussion of additional foraging effort was based on the concept of a balanced energy budget. However, there is now sufficient evidence that badgers lose 6 to 20 % of their body weight from a winter peak to early summer (Neal & Harrison 1958, Kruuk & Parish 1983, Maurel & Boissin 1983). Fat stored in autumn serves as an energy supply during pregnancy and as additional supply and backup insurance during lactation. The depletion of fat reserves to a minimum in June confirms the suggestion that reproductive effort implies a considerable load for the female.

7.2.2. Development of the young.

Several studies (summarized in Anderson & Trewhalla 1985) point out that mortality during the initial stages of cub development may be considerable. A comparison of prenatal litter sizes and litter sizes at a cub age of 12 weeks have shown a reduction of 25 % which was attributed to respiratory disease, aggressive behaviour by adult badgers and starvation (Stubbe 1970, Anderson & Trewhalla 1985). Thus, at least some females are unable to provide sufficient food either because of insufficient fat reserves or because of poor food availability. Average time of birth is early in the year (at the end of January/beginning of February) and generally coincides with poor food availability, since the soil temperature is too low, and the ground is often covered in snow, so that very few worms are active. Selection should favour females either to give birth later in the year (when food availability is increased) or accumulate sufficient fat reserves in autumn.

An indication of female investment during the lactation period is the average growth rate of cubs. According to Neal (1977), birth dates in South England occur around the beginning of February, and lactation lasts for 90 days. Assuming a birth date of 1st February, I calculated average growth rates for badger cubs caught in Wytham (Table 7.1). Average growth rates of the two cubs caught at the end of lactation are around 40 g day^{-1}, corresponding to the high investment growth rate of section 7.2.1., and decline considerably in the period after weaning, in accordance with other mammals (Koenig 1985). Although the paucity of studies on this aspect of juvenile development precludes any generalizations, the few studies that are available indicate that the period after weaning can be critical for survival, as young animals need to develop predatory skills. Tan & Counsilman (1985) have shown that kittens (Felis catus) require several weeks to become proficient hunters, while pipistrelle bats (Pipistrellus

Table 7.1 Estimated growth rates of badger cubs caught in Wytham Woods in 1982 and 1983, assuming a birth date of February 1st of a year.

Individual	Capture date	Sex	Weight (kg)	Age (days)	Average growth rate ($g\ day^{-1}$)
1	1.5.83	F	4.0	90	43.4
2	2.5.83	F	3.5	91	37.5
	4.7.83	F	3.5	154	29.9
3	6.6.83	M	4.0	126	31.0
4	6.6.83	F	3.7	126	28.6
5	4.7.83	F	4.1	154	26.0

pipistrellus) take at least three weeks to reach a hunting efficiency comparable with that of adults (Racey & Swift 1985). Young badgers (as other carnivorous vertebrates) should have the best chance of developing foraging skills while food is reasonably abundant. However, the weather from middle of May (ie from the time of lactation) onwards is dominated by dry, warm spells of weather detrimental to intense surfacing activity of worms, resulting in a reduction of earthworm consumption by badgers during summer (Chapter 4) and a reduction in the abundance of leaf litter fauna in general (Manns 1967). The young with the highest probability of surviving such lean periods in summer are those that have attained sufficient foraging proficiency before the dry spells are likely to start, since they may otherwise find it difficult to obtain enough food. A comparison of spring versus autumn samples indicates that this is indeed a difficult time; between 48 and 68 % of the cubs of a year may die during this period (Anderson & Trewhalla 1985). Thus, selection should favour a sufficiently early date of weaning and, consequently, an early date of birth which ensures that young badgers achieve a degree of competence in foraging before any extended periods of reduced food availability start. The direction of this selection pressure is opposite to the one favouring a late birth (to avoid a bottleneck in energy supply for the mother), since this implies a date of weaning between middle and the end of April and consequently a date of birth between middle and end of January.

Even if cubs born late survive they may show a greatly reduced development , experience a higher mortality over the winter and not reach adult body size until well into their second spring. In Wytham, one 'late' cub (the male VICIOUS) caught in the JEWS HARP clan on September 11th, 1982, had a body weight of 4.75 kg, implying a birth date in April or May. He was recaught on April 18th, 1983 still weighing only 7.7 kg (average adult body weight in Wytham is around 9 kg, Kruuk & Parish 1983, and my own data). In September, VICIOUS was probably still suckling, since a female of the same

group, JO, was caught one week after him, showing well developed nipples and a belly devoid of hair, signs typical of a lactating female. Thus, if JO was suckling VICIOUS in September, she was incurring a considerable energetic burden at a time when female badgers typically build up fat stores in preparation for winter and to provide reserves for early lactation in the following breeding season.

Thus, if females followed the first option and gave birth later in the year at a time with high food availability (e.g. April), their young may not starve in the early stages of development, but face a reduced rate of development in the summer and perhaps reduced probability of survival over the winter. Females would then follow a high-risk strategy in the sense that they place the time of peak energy expenditure, ie. towards the end of lactation, in June/July, a period with reduced availability of high quality food. Furthermore, opportunities for accumulation of fat reserves in autumn for their own survival may be missed. On the other hand, giving birth early in the year implies the probability of loss of young, since mothers may not have sufficient energy energy supplies at their disposal to suckle the young. The present evidence indicates that the balance is tipped in favour of selection for an early time of birth. Yet the present compromise between the opposing selection forces is not completely satisfactory, since 40-60 % mortality occurs in the summer, presumably due to late weaning, while insufficient food reserves, favouring a late time of birth, account for only less than 25 % mortality.

7.2.3. Factors influencing the future reproductive success of the young.

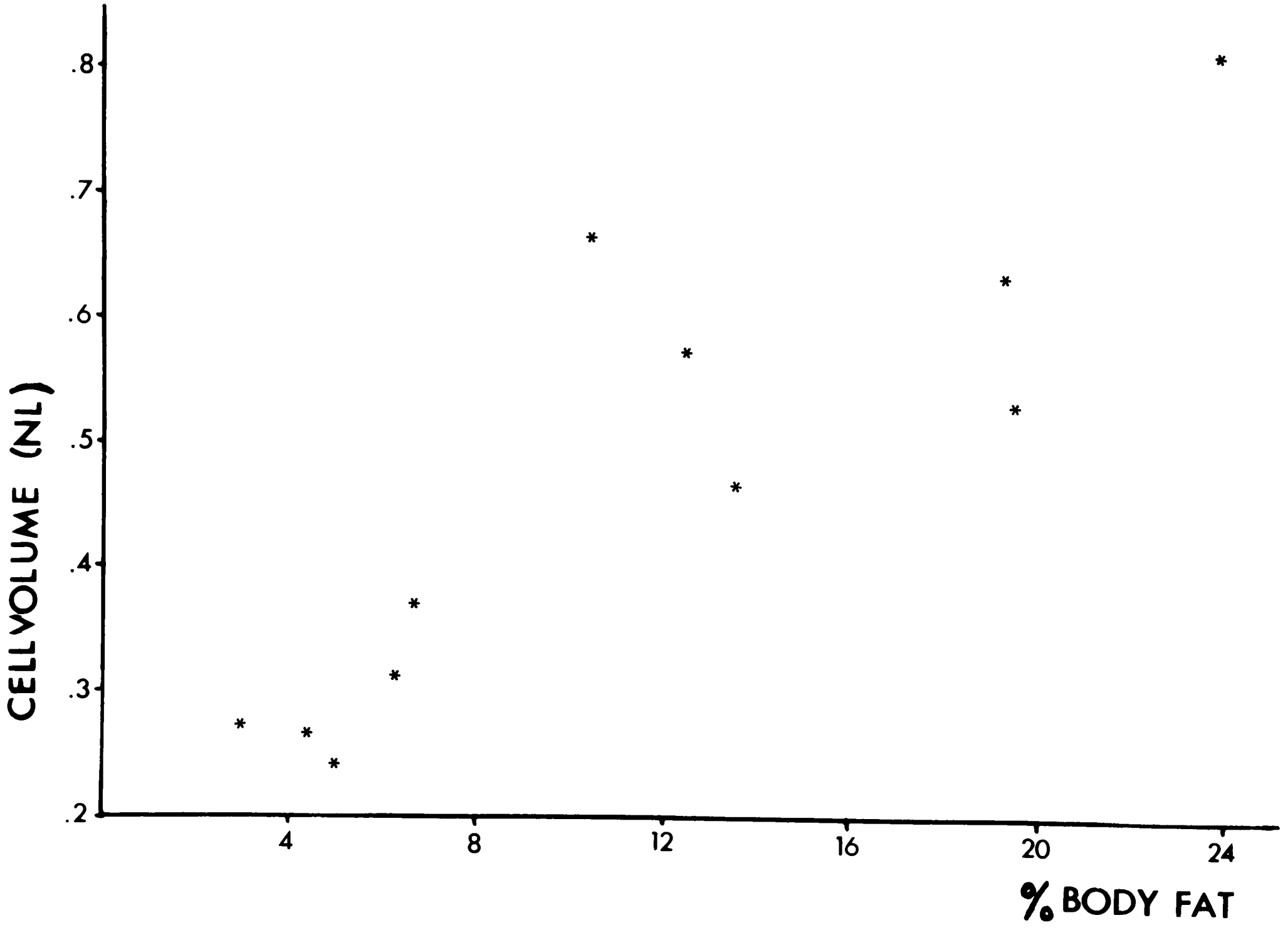
One positive effect of heavy female investment may simply be an increase in body size of the young. If differences in body size amongst cubs are preserved in adult badgers (Gosling & Petrie 1981) and body size is related

to mating success via dominance (e.g. red deer, Cervus elaphus, Clutton-Brock et al 1982), then the growth rate and development of the young will influence a female's fitness. Selection should favour an early date of parturition, thus providing the young with sufficient time to grow and develop foraging skills before the winter inhibits these processes.

A second effect of heavy female investment could be an improved capacity of the young to store fat. Storage capacity of fat is limited by the number of fat cells which seems to be fixed during juvenile development (Pond & Mattacks 1984, Pond 1986). I confirmed for badgers that intraspecific and interindividual variation in obesity must be attributed to variation in cell size, not cell numbers. With the help of Dr. Caroline Pond (Open University) I extracted all fat reserves in 18 different anatomical sites (details of method see Pond & Matacks 1985) of badgers collected from the Oxfordshire/Milton Keynes area. Results are presented in Fig. 7.4. The correlation of average cell volume and obesity expressed as percent fat tissue of total body weight is highly significant (Spearman's rho = 0.827, df=10, $p < 0.01$). Fat storage is important to females for survival through the winter, and for the lactation of cubs in spring (as shown before). Fat storage in males may be beneficial because of increased body size (up to 20-30 % of body mass can be made up of fat) and as energy reserve for the main mating season in February when males range widely and feed little (see below).

Therefore, I suggest that selection should favour female badgers that have sufficient fat reserves to start lactation early in the year and females that have access to high density protein rich food areas permitting a high investment in lactation to enable rapid development of young.

Fig. 7.4. Mean cell volume of fat cells averaged over 18 anatomical sites per animal vs. total obesity per animal. Data from badgers collected in the Oxfordshire/Milton Keynes area. All adipose tissue was quantitatively extracted by dissection.


.8
.7
.6
.5
.4
.3
.2
CELL VOLUME (NL)
4
8
12
16
20
24
% BODY FAT

7.2.4. Summary: direction of selection pressures.

1. Maternal costs of rearing young are considerable. Up to 66 % of the daily energy expenditure of a female may consist of milk provided for the young.

2. Mothers need sufficient high density resource areas at their disposal to cope with the increased energy expenditure during the breeding season. Attaining high density resource areas is more profitable than reducing energy expenditure, e.g. by reducing maternal investment.

3. Mothers need stored fat for their own maintenance during winter when they are largely inactive, as energy supply during pregnancy and as backup during the breeding period. This requires good foraging areas for protein-rich food in autumn when badgers store fat.

4. Cub mortality during the period of lactation indicates that selection should favour a birth date later in the year (March or April) when earthworm availability is high and less unpredictable.

5. Cub mortality after weaning suggests that selection should favour a birth date very early in the year in order to have more time available for the cubs to gain sufficient foraging experience before extended spells of dry, unfavourable weather and associated reduced food availability can lead to high cub mortality.

6. Selection should favour mothers that invest heavily. Higher growth rates of young could lead to a large adult body size, better fat storage capabilities and an increased chance of survival. Large body size and appropriate fat storage capabilities may imply increased reproductive success of the young and thus enhance the mother's fitness.

7.3. Spatial and social strategies of females.

In this section I will examine the kind of spatial and social organization which should be favoured by females in order to achieve maximum reproductive success. Breeding success in badgers seems mainly to be related to maternal care after birth and to the factors promoting it, since Ahnlund (1980) has shown, at least for badgers in Sweden, that there is rather little variation in litter size or regularity of breeding between different adult age-classes. In the previous section I showed that the energetic burden during lactation is considerable and that females should obtain access to high density protein-rich food areas. Before I discuss in detail, how females should go about to obtain such access, I shall investigate constraints on possible forms of spatial distributions of females.

One necessary prerequisite for reproduction is the availability of setts. If suitable sites are rare, then availability of setts is a major factor limiting the local reproductive rate. In one study of badgers in the Bavarian Alps, for instance, females reproduced only if they occupied natural rock cavities on the mountain slopes that could be sufficiently enlarged to provide space for the mother and the young (W. Bock, pers. comm.). Such rock cavities are rare in comparison with other, low quality sites. Males and females without suitable sleeping sites did not maintain stable home ranges but instead drifted through a variety of neighbouring areas. In Wytham availability of setts is high. More than 70 setts and outliers were located in the study area (see also Table 5.7) and many more fox dens and rabbit warrens could be extended to a size suitable for badgers. Due to the distribution of the 'sand-belt' (Kruuk 1978a), the preferred and easy-to-dig soil throughout the area (Killingley 1972, Neal 1977, Long & Killingley 1983), all group ranges have suitable sites at their disposal.

Setts are probably indispensable for effective protection of the young.

Interspecific predation on cubs by large raptors and possibly large carnivores may have been important in evolutionary times and has been occasionally documented in the present day (eagle owl, Bubo bubo, Uttendoerfer 1952; golden eagle, Aquila chrysaetos, Klotz 1903). Probably more important is intraspecific predation, especially by adult males (Stubbe 1970). Females defend sett entrances leading to nesting chambers with their young against males and scent-mark the entrances (Neal & Harrison 1958). The black and white coloration of the badger's face already shown by very young cubs has also been interpreted as mimicry to protect cubs against predators (see Neal 1977).

Setts are also important resting sites during the winter quiescence. Badgers do not hibernate (Johannson 1956) but show much reduced activity and spend most of their time in setts (Neal 1977). Efficient thermoregulation is achieved by selecting nesting chambers away from the surface and providing them with ample bedding consisting of dry hay and litter. It is important to minimize energy losses due to temperature differences between body and the air, since badgers have no specific metabolic adaptations to the cold. The continuous occupation of specific setts by many generations of badgers may indicate that this condition is not necessarily fulfilled, and setts with good thermoregulatory properties may be rare.

The second constraint concerns the presence of sufficient food resources within the reach of a female. Female body condition, intensity of lactation and the survival and reproductive prospects of the young are all dependent on fat reserves in the female and the presence of high resource density areas. Here, the following questions appear to be relevant:

1. When does it pay a female to maintain exclusive access to a resource (or a habitat), ie. why should a territory owner do better ?
2. What are the costs of holding a territory ?
3. How should, and how do, females cope with compe-

tition from other females, ie. what are the costs and benefits of sharing one's range with other females ?

These questions are discussed in detail with reference to the Wytham badgers. In section 7.3.6 I will then show how differences between populations in the setup of the resource system leads to different types of spatial and social organisation of female badgers.

7.3.1. Why should a territory owner do better ?

Here, a territory owner is defined as an animal with exclusive access to a resource which is actively defended. Territoriality is <u>possible</u>, if the characteristics of the resource, ie. its spatial and temporal occurrence (and in the case of food) productivity permit an economic defense (Brown 1964). Although this is a necessary condition, it is not sufficient to account for territoriality, since a territory owner must do better than if it was without a territory.

Earthworms are the main food resource of badgers in Wytham (Chapter 4) and are a stationary prey with little variation in abundance throughout the year (Phillipson et at 1978) or over longer periods (cf biomass estimates in similar habitats from Kruuk's and my study, Table 3.11). This makes an economic defense plausible. In principle, the status of a badger (whether territory owner or intruder) should, all else being equal, be independent of 'earthworm intake' per time unit. Availability of earthworms is, beyond broad generalizations, essentially unpredictable (Chapter 3). This is mirrored by the fine-scaled utilization distribution of the home ranges (Chapter 6). Good patches are temporarily depleted, if badgers forage there for a long time, since the disturbance and vibrations caused by the badgers on their foraging path will induce the worms to retreat into their burrows and not surface again for some time (at least for ca. 1/2 hour, but may be even longer, Edwards & Lofty 1977). Thus, even though badgers are not likely

to affect earthworm population densities substantially (Macdonald 1983b), the proportion of the available worm population at the surface will be considerably affected by their activities. The number of worms that return to the surface feeding is a function of time (and microclimatic circumstances, Chapter 3). Although the precise shape of the recovery function is not known, it seems plausible to assume that it follows an exponential curve (Davies & Houston 1981), ie. after a threshold time, there is a non-linear increase of worms surfacing until the numbers approach an asymptotic density value which may or may not be equal to the previous level, depending, for instance, on the current microclimatic conditions which may or may not have changed since the worms retreated into their burrows (Fig. 7.5). Hence, the foraging success depends on the time that has elapsed since the last visit of a badger (the renewal period of a given area). Thus, a badger feeding in an area with a short renewal period suffers a depressed feeding rate compared with an animal that enters a patch without any previous depletion; therefore, knowledge of good patches and the renewal time of a given patch is important to achieve a good feeding rate. Due to their energy requirements, badgers are probably energy maximizers (Kruuk 1978b, Krebs et al 1983), thus feeding rate is important. Here territory owners do better, for at least three reasons.

1. Owners can minimize search effort for good patches and travelling time.

As shown in Chapter 3, microclimatic conditions as indicators of possible worm surfacing activity vary considerably within the same habitat, but can be partially predicted for a given location from other sites, provided the knowledge of correlations between different sites is available and occasionally updated. Here, a territory owner with an intimate knowledge of its area is favoured over intruders who cannot usually be expected to have such knowledge.

2. By evicting intruders, a territory owner can enjoy a

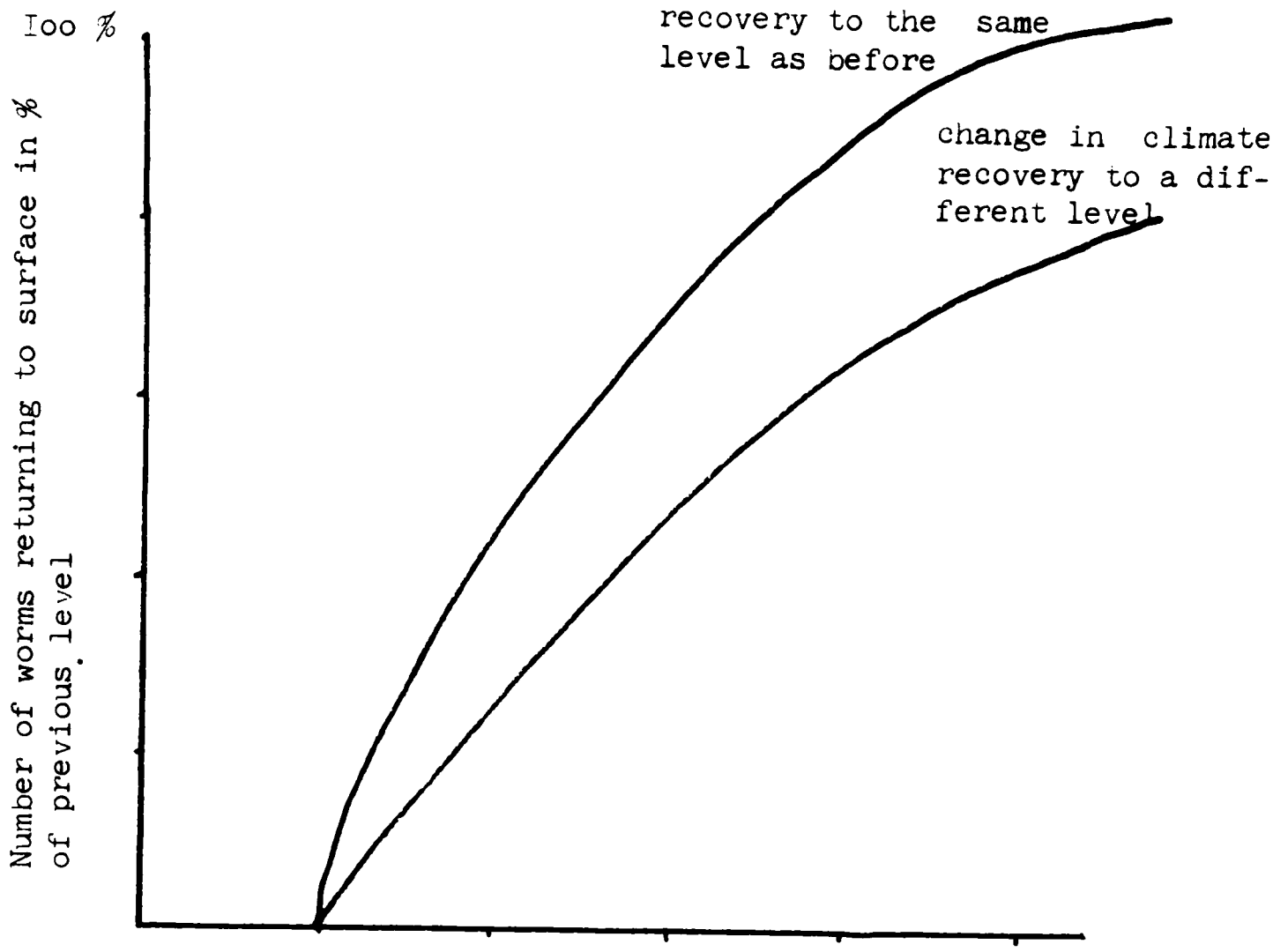


Fig. 7.5 Suggested recovery curve of depleted food patches: number of earthworms reappearing at the surface as a function of the time elapsed since depletion.

higher feeding rate, since the number of patches depleted and the degree of depletion caused by the foraging activities of other badgers is reduced.

Since it pays females to exploit high density resource areas (section 7.2), intruders should concentrate on foraging in patches predicted to be 'rich' for a given night. Even within the same habitat type, variation in microclimatic conditions implies that only a fraction of potentially good sites are actually full of surfacing worms at any instant. Since it pays the owner to forage in the same areas as potential intruders, the probability is high that a resident will come across a depleted patch which has not yet recovered, if only a limited number of sites is available in a given moment. The consequence is a depressed feeding rate; hence, residents should evict intruders to achieve high feeding rates.

3. By exploiting a territory systematically, a resident may benefit itself by increasing the return time to a depleted patch, ie. the time between two successive visits, and simultaneously render it unprofitable to an intruder to come in.

Here, systematic search is defined as any behaviour that maximizes renewal rates of food areas. Systematic search has been observed both on a microscopic scale (within a small food patch, Roper 1983) as well as on a larger scale (Chapter 6). By utilizing patches in a systematic fashion, renewal periods can be increased allowing depleted patches to recover. Examples of renewal periods (Chapter 6) show that residents usually revisit a patch after it is likely to have recovered. The most profitable site, amongst those with high worm availability in a given night, is presumably the site where the time since the last depletion is greatest. If residents search in a systematic fashion, then the most profitable patch should be the one they are about to enter. This, however, is also the place most profitable to an intruder, a place where an intruder could do a maximum of

damage, and where an intruder is most likely to be evicted. If an intruder arrives at other places it can be expected to do worse on average than the owner, since it may not know where the patches with the highest renewal periods are on the territory.

Some observations suggest that foraging badgers frequently scent-mark with their anal glands (Macdonald 1977a, Neal 1977). This could both remind an owner that it has already visited this area, minimizing time spent in recently utilized areas (sections 5.4.3 and 6.3.), and deter an intruder by advertising that the area has already been used. An intruder would then either go somewhere else or start foraging. In the first case, its search time increases, while in the second case it is likely to experience a reduced feeding rate, because the depleted patch may not have recovered yet. It is conceivable that the use of non-border latrines serves as a convention to advertise recent exploitation of a food resource (section 5.4.3., Davies 1981), indicating to a prospective user the unprofitability of the area. Davies & Houston (1981) call this type of territorial defense 'defence by depletion'.

7.3.2. What are the costs of owning a territory ?

Territory owners incur costs prior to any intrusion through activities intended to deter intruders and costs associated with eviction if an intruder has arrived.

Marking of territories is one conventional way of advertisement of territory ownership (Chapter 5). In badgers, it is achieved by scent-marking at latrines (section 5.4.3., Kruuk 1978a, Kruuk et al 1984). The number of latrines maintained is high, if necessary (in spring up to 50 within a range, section 5.4.3), and is apparently adapted to the outside pressure experienced by the range inhabitants (section 5.4.3). Maintenance incurs costs due to the additional distances that have to be covered, digging

activities, and secretion production in the anal and subcaudal glands. Although it is not possible to quantify these costs at present, it seems likely that they are a significant additional burden (cf. Kruuk et al 1984). Additional costs may arise through the need for intruder detection, e.g. patrolling the territory boundary.

Once an intruder has been detected, the owner has to evict him. Intraspecific aggression, has been invoked as one of the major causes of mortality in badgers (Stubbe 1970, Anderson & Trewhella 1985). Although the proportion of injuries or deaths due to territorial fights is unknown, fights observed by Kruuk (1978a) indicate that they can result in severe injuries (cf also Table 5.12). Even if a fight does not result in an injury, chasing an intruder costs time and energy.

After the eviction of an intruder an owner may be displaced from its original site, and may return to a place different from its last place prior to the contest. If the owner had been feeding prior to the contest, returning to an already depleted area will cause a depression in the owner's feeding rate. Finally, an owner also suffers if an intruder remains undetected while feeding, since this reduces the renewal period of the patch which could result in a subsequent depression in the feeding rate of the owner (see above).

7.3.3. Factors affecting intrusion pressure.

Females are most likely to compete with each other at times of peak energetic requirements. As discussed before (section 7.2) these are the lactation period in spring and, to a lesser extent, the feeding periods in autumn when females accumulate fat for the winter and the next reproductive season. In these periods, females should maximize their energy intake (section 7.2). Maximizing energy intake should induce females to strive for access to high density resource areas. Thus, intrusion pressure is expected

to increase with resource density and availability per patch during these periods. Competition (and intrusion pressure) is also likely to increase with population density and is related to the number of females requiring high quality areas and the number of dispersing animals.

Fig. 7.6 illustrates how these factors are expected to relate to intrusion pressure. Evidence for the proposed functional relationships is largely circumstantial. The increased maintenance and marking activities, particularly at border latrines, in spring can be explained as a response to increased intrusion pressure (section 5.4.2). Similarly, latrine activity is low in summer, when energy requirements of females are at their minimum, and when badgers partly switch to other, superabundant foods such as cereals. High resource density areas are preferred by females and visited for long periods (Chapter 6), suggesting that an intruder should also prefer such an area. In a study on the economics of territory ownership on feeding territories of pied wagtails (Motacilla alba), Davies & Houston (1981) also found an increase in intrusion pressure with increased food availability.

The high population density in Wytham, the intensive marking activity, and the occurrence of aggressive encounters suggest that intrusion pressure may be high at certain times of the year. How can a territory owner cope with this ?

7.3.4. Responses of territory owners to high intrusion pressure

In reviews on recent studies of territoriality in relation to resource levels and defense costs, Schoener (1983) and Stamps & Buechner (1985) identified four common responses of owners to elevated intrusion pressures:

1. change territory size;
2. increase the degree of overlap with adjacent territories;
3. accept subordinates in the territory;
4. abandon territorial defense altogether.

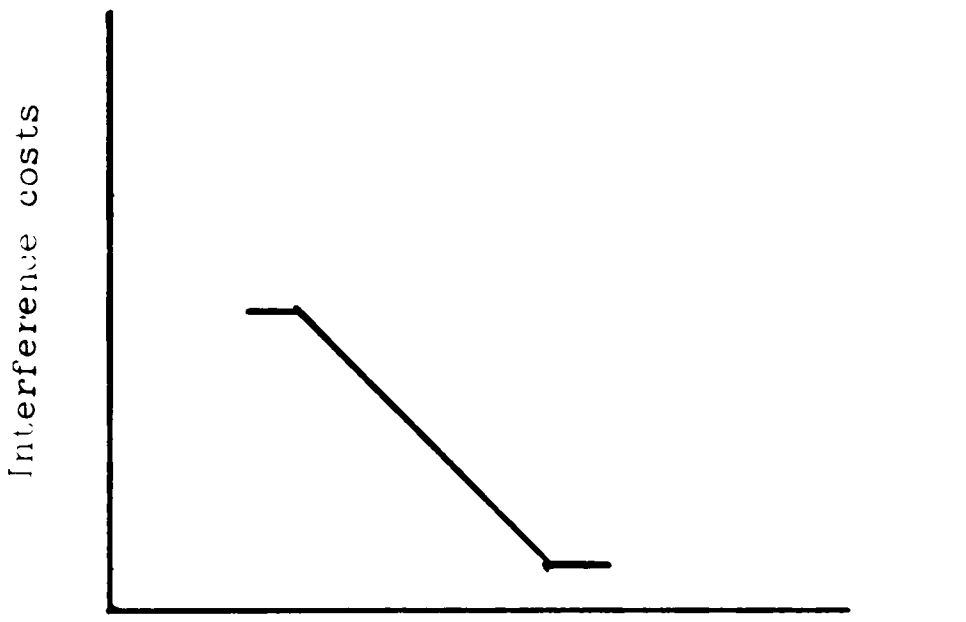
Fig. 7.6. Relationships between resource and social parameters and intrusion and interference pressure. Curves do not represent real data, but are hypothetical (although derived from estimates of the literature for other species).

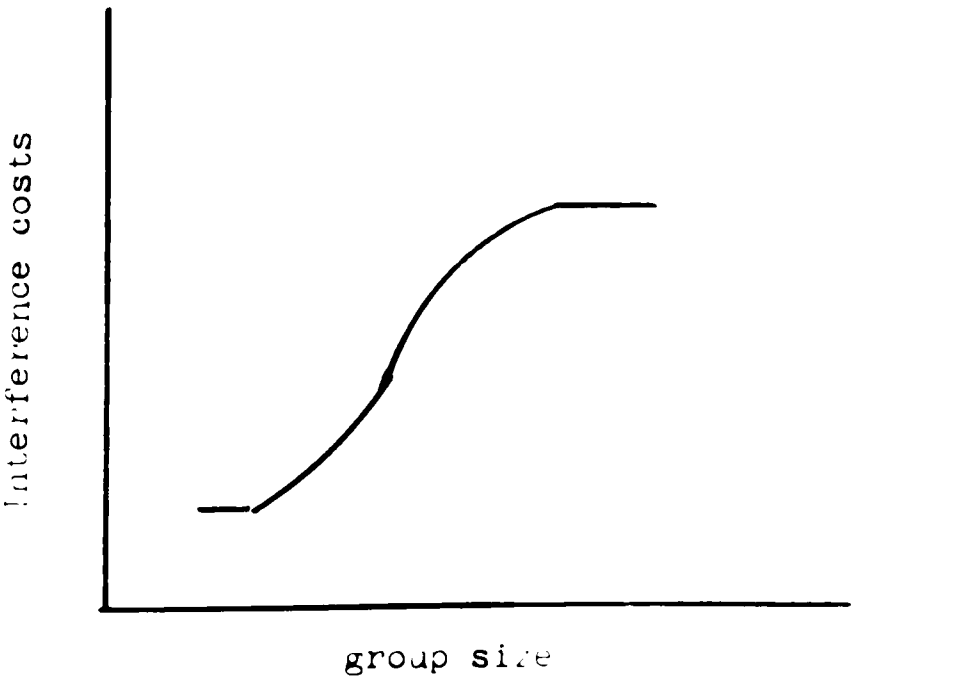
a. defense costs or intrusion pressure on a territory in relation to the productivity or availability of resources. Two thresholds are indicated. Below a lower threshold, a food resource is probably unattractive to intruders as compared with other resources. Beyond a higher threshold, defense costs are so high that territory owners may abandon defense altogether.

b. Interference costs within a group are likely to decrease with total resource availability.

c. Interference costs within a group are likely to increase with group size.


Defense costs/intrusion pressure
Resource availability (productivity)


Interference costs
Resource availability (productivity)


Interference costs
group size

The choice of response depends on a number of ecological and behavioural factors, including the kinds of resources defended (food, shelter, or mates), the foraging 'goals' (e.g. energy maximizers or time minimizers, Schoener 1971) and the nature of the territory (e.g. temporary feeding territory or permanent multi-purpose territories). I shall now explore which responses are feasible for female badgers and discuss evidence for or against them.

Badger territories in Wytham are all-year multi-purpose territories with infrequent and modest short- and long-term boundary changes (section 5.4.2). Seasonal shifts in range utilization, if present, are modest (Chapter 5). Thus, I do not believe that badgers change territory size as a response to outside pressure. Overlap between ranges in Wytham is virtually non-existent (Chapter 5, Fig. 7.7) and does not seem to be a realized option, but may be applicable elsewhere (see below). Abandonment of territorial defense is difficult to identify, but the circumstantial evidence suggests that the decrease in marking intensity and maintenance of border latrines during the summer is due to a relaxation, not an increase in pressure because of reduced energy demands and increased utilization of alternative superabundant food resources such as cereals (Chapter 4). The solution favoured by Wytham badgers appears to be living in groups where several females (and males) occupy a common range (Table 5.9, 5.10.)

7.3.5. Costs and benfits of satellites.

Davies & Houston (1981) investigated the relationship between territorial pied wagtails (Motacilla alba) and subordinate satellites on winter feeding territories. Their studies identify some necessary conditions for the stability of such a system.

Territory owners were dominant over satellites. Costs of the presence of satellites were reduced feeding rates of owners. However, satellites

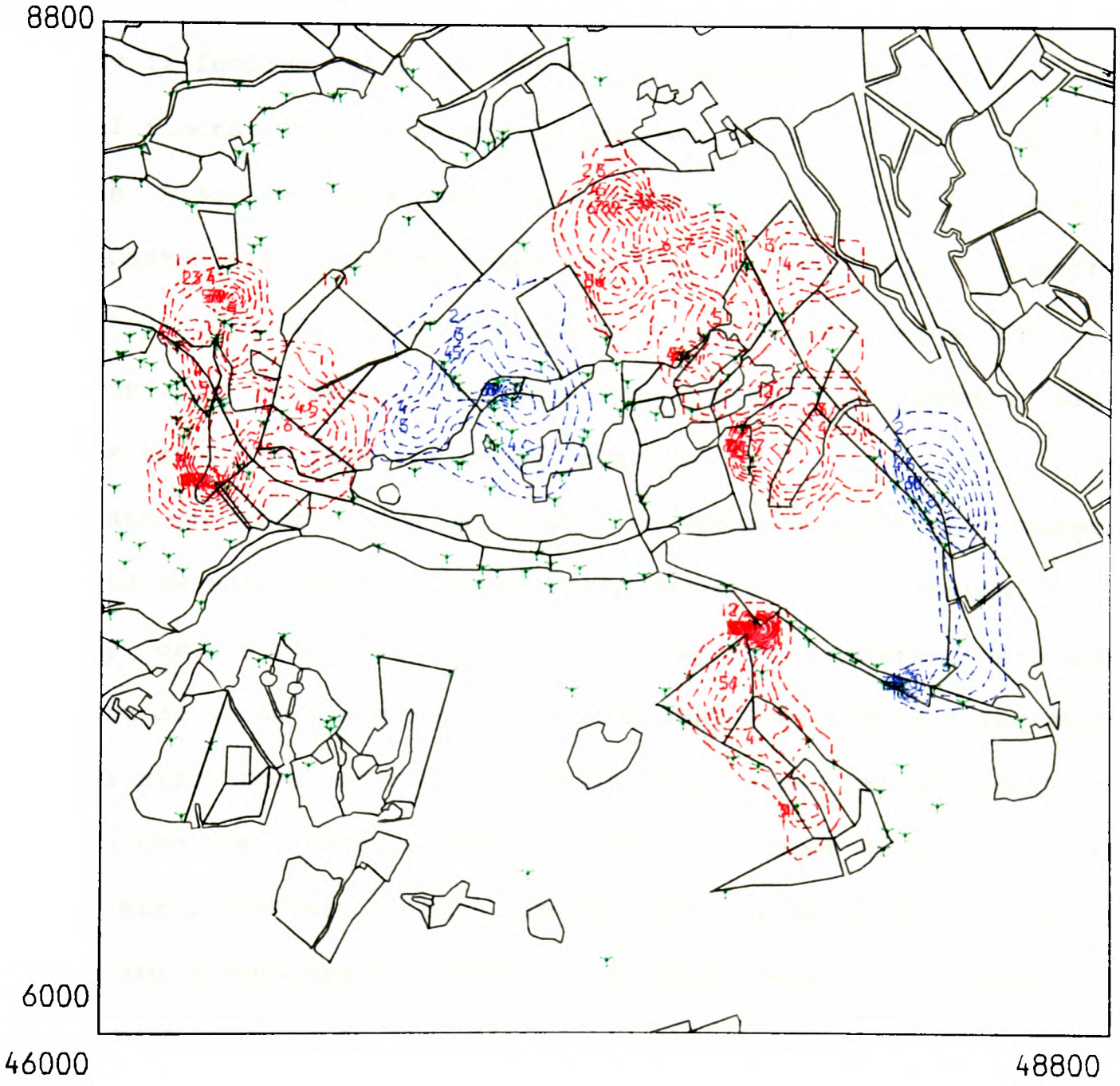
Fig. 7.7. Plot of the ranges of five female badgers, representing five adjacent group territories, on the computerized habitat map. Habitat categories plotted are habitats 7, pasture, and 37, deciduous woodland. Green stars indicate position of latrines.

RED: bottom right - ALI group B2 (UPPER FOLLIES)
upper right - NOEARS group B3 (MARLEY)
left - ELIANE group B5 (SUNDAYS HILL)

BLUE: right - SARA group B1 (BOTLEY)
left - PEACEFUL group B4 (JEWS HARP)

All ranges are plotted as contour plots using 15 min independence interval data. Plots created by program MAPITH, using the GHOST-80 graphics system.

FEMALE BADGERS



foraged in such a fashion that the depression in owner's feeding rate was less than that caused by undetected, feeding intruders. Benefits of presence of satellites to the owner were a major reduction in defense costs against intruders (1/3 to 1/2 of defense costs). Owners admitted satellites only when intrusion pressure and defense costs were high, and evicted them when the costs of the satellite's presence outweighed the benefits. However, if an owner left its territory leaving a satellite behind and did not return for some time, the satellite sometimes took over and successfully expelled the former owner when it returned. Individuals from flocks joined territory owners only if feeding rates in territories exceeded feeding rates in non-territorial flocks. Thus, a satellite may receive both short-term, and, if it persists, also long-term benefits by inheriting a territory. By a similar argument, Gaston (1978) has proposed the 'payment principle', according to which a satellite should take on a share of the defense costs just sufficiently large to make a territory owner accept its presence, ie. the subordinate satellite pays for being tolerated.

The data on group living of badgers in Wytham suggest that badger groups could be modelled on the territory owner/satellite system. Accordingly, groups should form in territories, when defense costs are high. A comparison of group sizes for the period 1982-1984 (Table 5.10) shows that group range sizes remained constant while group sizes varied greatly from one year to the next. Badgers seem to prefer to change group size rather than range size. However, no data are available to show that changes in group size are a response to changes in defense costs. Such changes could be induced by high-ranking females ('owners') that expel subordinates ('satellites'), since studies on captive badgers in Sweden revealed a dominance hierarchy amongst females (H. Oestborn, pers. comm.).

To minimize interference costs for members of the same group, as would be required if satellites are less costly than intruders, group members should somehow coordinate their foraging activities. One possibility is a

dissection of the group range into several areas, each of which is exclusively utilized by one group member. Occasionally, utilization patterns of the group range by several group members seem to fit this pattern (Chapter 5), although there does not seem to be a fixed division in Wytham. However, group members in a study area on the Downs in Sussex are reported to permanently utilize different parts of a group's territory (T. Roper, pers. comm.). A second possibility is the coordinated movements of group members over the group's entire range. Simultaneous radio-tracking of individuals of one group confirmed that group members move in a somewhat coordinated fashion, minimizing disturbance and maximizing renewal periods of food patches (Chapter 6). Interference costs between group members, ie. costs of presence of satellites, therefore appear to be small, at least in the range studied. 'Payment' for residential rights of satellites appears to occur as well, since all group members participate in marking activities and defense (cf Table 5.12, unpublished observations on movements of members of the Jews Harp group to latrines), although dominant individuals carry the main burden (Kruuk et al 1984).

In summary, the formation of female groups in Wytham can be interpreted as formations of defense coalitions as a response to elevated defense costs. Benefits to territory owners (high-ranking females) include the reduction of defense costs. Benefits to satellites (low ranking females) include a place to live, and the prospects of possibly inheriting the territory or some part of it. This is compatible with the developments observed over a period of 8 years (section 5.4.2). All foundations of new ranges can be interpreted as offshoots from existing ranges.

7.3.6. Social organisation in relation to resource characteristics: other studies

Here I present the results of other studies and discuss the differences to Wytham emerging from these studies in relation to changes in the resource system.

Two studies in Britain report an essentially similar situation as in Wytham. Kruuk and colleagues (Kruuk 1978a, Kruuk & Parish 1981, 1982) studied badgers at several study sites in Scotland. Groups occupied exclusive territories, badgers were shown to behave as feeding specialists on earthworms, and group sizes varied between 2 and 11. Territory sizes in Scotland varied between 120 and 309 ha. In Staffordshire, Cheeseman et al. (1985) studied five ranges with group sizes (adults only) ranging from 4 to 11 and territory sizes from 54 to 131 ha. Territories were exclusively used by the residents only.

Two other studies report different results.

In Bristol, Harris (1982) tracked members of 7 group ranges. Here, no distinct territories could be identified. Several radio-tracked females used setts and foraging areas of different groups. Harris therefore defined a 'group-foraging range' as the area in which each individual member of the 'group' spent the majority of its time. Animals were ascribed to a social 'group' according to the setts they 'normally' used as a daytime resting site, but these are not the only setts they may use for this purpose. If he group ranges from his Fig. 1 are taken to calculate the area occupied by the badgers (ca 3.5 km^2), and the number of badgers caught and radio-tracked (31) as a minimum estimate of population density, we arrive at a density of ca 8.9 individuals/km^2. This density is one of the highest recorded (Kruuk 1978a gives a figure for Wytham of 8.4 ind/km^2, Cheeseman et al. 1985 report a density of 6.2 ind/km^2). This is probably an underestimate since presumably not all individuals in the group were caught. He concluded that the

social and spatial setup of this population is remarkably different from those observed in other studies.

Difficulties in interpreting his results arises from the procedure by which he defines group existance and membership, especially since he does not provide any information on latrine distribution or results of bait recoveries. If I had defined my groups solely on the association with certain setts, similar problems as reported by Harris would have arisen. Without any information on marking activity or agonistic encounters, it is difficult to assess to what extent the loose organisation of ranges is 'real' or merely an artefact of the methodology chosen. Assuming that indeed the Bristol badgers show some range overlap I suggest two explanations for the deviation from the normal pattern:

(a) the population reached such a high density that only a core area of the territory can be defended and overlap with neighbouring groups at the periphery cannot be avoided

(b) territory defense is abandoned altogether.

What evidence do we have for either of these suggestions ? This depends to a large extent on the characteristics of resources and the way individuals use them. The results reported by Harris (1982) suggest that resources are probably superabundant and distinct, in their characteristics, from the situation encountered in previous studies. Except for December, when Bristol badgers eat almost exclusively earthworms), they do not appear to exhibit habitat selection. Then, food diversity is high, the food is more scattered, food patches are visited for only short periods (except for periods with high fruit availability) and earthworms, other invertebrates, scavenged items and fruits contribute similar proportions to the overall diet.

This pattern of resource use is distinctly different from that of the studies cited previously. The differences concern (i) abundance of food,

(ii) the importance of renewal rates for foraging rate and (ii) the pattern of resource availability. The Bristol badgers do not suffer from a shortage of food. In contrast to Wytham, for instance, there seems to be a lot of potential scavenge available during the critical periods in spring; they constitute the bulk of the diet from January until May. If the conventional 'bottleneck' in food supply at the end of winter is not present, inter-group food competition can be expected to be much relaxed and hence intrusion pressure is expected to drop considerably. The major prey types are distinguished from earthworms in that their renewal rate is <u>independent</u> of the foraging activities of the badgers. Hence, the likelihood of interference and the benefits gained from a defense are reduced.

Why, then, do Bristol badgers live in groups ? It is not clear to what extent the units identified by Harris actually constitute badger groups in the conventional sense. If it is typical for the population that setts are used in quite a flexible manner, as Harris (1982) described for several females, it may not be justified to call them groups, but rather a system of loosely connected individual ranges, where sometimes several individuals occupy the same resting site. In this respect it is interesting that Harris once observed in one of his 'groups' two breeding units emerge in early 1980 and subsequently split the 'group range' into two <u>separate</u> sections.

In summary, the situation in the urban population in Bristol is quite different from that usually encountered in studies in more natural habitats, but as far as the data permit conclusions, still consistent with the expectations derived from the discussion of territoriality in the preceding sections.

One final study remains to be mentioned. Martin-Franquelo & Delibes (1985) studied the behavioural ecology of badgers in a mediterranean region in Spain. Despite the preliminary nature of the results, some interesting snippets emerge. The main food item are rabbit nests and young rabbits; earthworms are very low in abundance. The dispersion of rabbit nests leads

to large ranges (on average 422 ha) with only one male and one female present per group. Rabbit nests are relatively scarce, but predictable in occurrence; hence the Spanish badgers defend territories. The nature of the main resource and the low densdity of badgers leads to a low level of intruder pressure, hence group sizes are expected to drop to the minimum.

7.3.7. Discussion.

The Resource Dispersion Hypothesis (RDH) put forward by Bradbury & Vehrencamp (1976) and Carr & Macdonald (in press) shows that at very little or no cost to a primary occupant (in foxes and badgers usually a pair) additional individuals may be sustained on a territory under certain circumstances. Given a certain level of heterogeneity in resource availability, a primary occupant has to defend an area larger than it would if food availability was 100 % homogeneous (ie. all food present on a territory is also available). How large the defended area is depends on the chosen level of security, (e.g. in 95 % of all nights there should be a satisfactory energy intake). Then, in a large proportion of nights, resource availability will be higher than what is required to satisfy the primary occupant and other individuals can harvest the 'superfluous crop'. The characteristics of earthworms as main prey fit very snugly to the conditions presupposed by RDH. However, while RDH in principle is certainly applicable to badgers in Wytham, I believe that the foregoing results show that there is at least one additional factor contributing to group formation: under conditions of (a) high energy demands and (b) critical resource availability, intrusion pressure may increase, if suitable high density resource areas are present within a territory, and necessitate the acceptance of additional individuals (satellites) in order to maintain the territory. RDH makes it plausible that presence of a satellite may be less costly than may otherwise be assumed. The 'defense coalition hypothesis' as

described in the previous sections shows that presence of additional individuals may not only be tolerated but actively solicited by a primary occupant. To what extent other processes (e.g. kin selection) play a role in furthering group stability can at present not be decided.

7.4. Male competition and female choice.

In this section I shall first describe some basic features of the reproductive biology of males and females, before I turn to a discussion of the possible incidence of sperm competition, female choice and the evolution of delayed implantation.

7.4.1. Mating seasons and mating success.

In Eurasian badgers, the majority of matings take place in spring, ie. between February and April (Neal & Harrison 1958, Neal 1977); a sizable proportion constitute post-partum oestrus. Ovulation frequency reaches almost 100 % by June (Ahnlund 1980 for Swedish badgers). Not all animals appear to conceive after ovulation, since the ovulation rate increases faster during spring than the incidence of blastocyst formation (Ahnlund 1980). However, renewed ovulation is not restricted to females that failed to conceive but occurs also in pregnant females. This is indicated by the relatively large proportion of females that contain on average 3 blastocysts and 5 corpora lutea ! According to Ahnlund's (1980) detailed analyses, very old and very young (first year or second year breeders) show a higher incidence of renewed ovulations than middle-aged females. Renewed ovulations may usually reoccur until autumn; this explains why males produce fertile sperm from January until autumn, unlike the males of many other species with delayed implantation. Renewed ovulation may occasionally lead to an increase in the total number of blastocysts and hence litter size. This is because

about 15 % of the blastocysts already present survive the second mating period, at least in mink Mustela vison (Johannson & Venge 1951). Superfecundation (several males fertilize eggs during the same oestrus) occurs in the mink (Enders & Enders 1963), and may be possible in badgers, since several males have been observed to mate with the same female (e.g. Paget & Middleton 1974). It is undecided whether female badgers are spontaneous or induced ovulators. The extended periods of copulation frequently observed (Neal 1977), sometimes up to several hours, suggest, however, that badgers similar to other mustelids may belong to the induced ovulators.

In summary, there is a well defined mating season (spring) but females may ovulate at additional times of the year. In the majority of females, formation of blastocysts and pregnancy occur after the first ovulation. Males produce fertile sperm throughout most of the year and may secure additional pregnancies during secondary ovulations. Some of these circumstances of the reproductive biology of badgers are exceptional:

(1) Why do pregnant females come into oestrous repeatedly ?

(2) Why do females exhibit post-partum oestrous, ie. spend a considerable proportion of time on mating while they could spend it on rearing the newly born young ?

(3) Why do females exhibit delayed implantation ?

(4) How do males cope with uncertain paternity that may arise from repeated ovulations ?

7.4.2. Mating behaviour: opportunities for female choice.

Field observations have shown that (i) males may mate with several females and (ii) females may mate with several males. According to observations by Paget & Middleton (1974) and Neal (1977), females do not seem to actively solicit males. In February, the peak mating period in

Britain, the boar calls the sow softly after emergence and patrols around the sett. At this time, females are quite aggressive towards males and decline males access to entrances to the nest chamber of their young. Consequently, mating takes place outside the sett. The male then mounts in typical mustelid fashion gripping the sow by her neck or her ear. The mating pair may stay together for a variable period, between 10 seconds and several hours, but usually matings are of short (less than 5 - 10 min) or long duration (from half an hour onwards). The female usually finishes the copulation by going down a sett entrance, so that the male is forced to let her go. Oestrous lasts for 4–7 days (Neal & Harrison 1958) and during this time mating may occur on and off for hours throughout the period. Mating sites and the female(s) are often scent-marked by the boar after mating.

Despite her apparent passivity, a female has a variety of possibilities to influence the procedure:

(i) termination of copulation can be decided by the female; hence she can decide whether a mating leads to ovulation and possibly conception;

(ii) many males are attracted to a female in oestrous (Neal 1977), since she may advertise her reproductive condition through the latrine system.

(iii) the possibility of repeated ovulations presents her with the opportunity to receive sperm more than once a year, either to exercise positive mate choice or to use it as a 'fail-safe' system (a very high proportion of old females showed renewed ovulations in Sweden, Ahnlund 1980).

I shall now examine costs and benefits of multiple mating from first the male's and then the female's point of view.

7.4.3. Costs and benefits of multiple mating in males.

Males contribute little (Kruuk, pers. comm., observed males in

captivity to provision young with food) or nothing to the rearing of the cubs. Hence, they should, in line with other polygynous and sexually dimorphic males (e.g. Clutton-Brock et al. 1982) strive to achieve maximum reproductive success by maximizing mating success. Mating success is characterized by two aspects:

(i) secure mating success (ie. conception) by monopolizing females and prohibiting other males from access to females;

(ii) maximize the number of matings by mating with as many females as possible.

As Parker (1984) has pointed out, the first aspect poses an evolutionary arms race problem, where adaptations of males to prevent subsequent matings by other males are counteracted by adaptations to produce armament (in a wide sense) to overcome the paternity assurance adaptation. Monopolizing females may be achieved in several ways. Precopulatory and postcopulatory guarding may be an ESS under certain conditions (Grafen & Ridley 1983, Parker 1984). Postcopulatory guarding may not be sensible, if several females in a group come into oestrous simultaneously. Efficiency of postcopulatory guarding is also limited, because it would require the male to guard the female during all oestrous periods. This may be worth only for subdominant males that have little chance to secure other matings (e.g. stoats, Mustela erminea, Sandell 1985). For other males, however, opportunity to mate with other females may represent a higher payoff than guarding (Sandell & Liberg, in prep). Hence, guarding is predicted to be observed occasionally, but not invariably (see Paget & Middleton 1974, Neal 1977). Parker (1984:44) presents a model of sperm competition where he investigates possible ESS solutions to contests between males over mating opportunities with females. If a male has already mated ('resident') and comes across another male without mating ('interloper') then the resident may lose the contest, and hence the interloper gain access to the female, if there is the possibility that more than 2 ejaculates compete for

fertilization.

Males may also restrict other males' access to females by defending a territory encompassing the range of one or several females. Hence, males should defend territories most vigorously in spring during the main mating season, a time when females have a special interest in territory defense due to their increased energy requirements. Work by Kruuk (1978a, Kruuk et al 1984) has shown that males (i) defend territories and sometimes carry the main burden, and (ii) exclude other males from access to females (Kruuk's 1978a 'bachelor clan'). In section 5.4.2. it was shown that the restructuring of the group range arrangements between 1974 and 1982 could best be interpreted as a reorganisation of males' influence spheres. If population density and correspondingly intrusion pressure by other males is high (e.g. Drabble 1970), a single male may not be able to defend his range effectively. Then it is conceivable that a male may tolerate another male in order to share defense costs, in the same way as it pays females to accept other females as satellites, even if this lowers his reproductive success. (By sharing mating opportunities with another male he may still have a higher reproductive success than if he had to give up the territory altogether, or be swamped by intruders !).

Under certain conditions, a male may find himself in the situation of the Prisoner's Dilemma. Consider two neighbours who initially defend territories with their respective females. Their choice is to play cooperative (be 'peaceful'), or form a coalition with another male, because they suspect an increase in pressure from the other territory owner, or because they would like to extend their sphere of influence. This is a 'defection' and makes the second male defect as well, ie. admit an additional male in his area, to redress the 'balance of power'. With additional males on their homeground they are now worse off on average than they would have otherwise been. Hence, the presence of more than one male in a range may not necessarily be beneficial. If the males are related, benefits would accrue to the original

occupant through inclusive fitness, but kin relationships between badgers are not known at present.

The second avenue open to a male is to secure a maximum number of matings. A male should try to maximize the number of matings in his own group and, if possible, also mate with other females. Although the latter may be dangerous (see the results of intraspecific aggression, Table 5.12), there is evidence from tracking in Wytham that this may take place. In Fig. 7.8 and 7.9, contour plots of ranges of neighbouring males and females are plotted on the habitat map. The UPPER FOLLIES male WILF went twice for an excursion into the BOTLEY LODGE Range (Fig. 7.8), where I tracked him once in the same outlier as a female of the local range, SARA. Some overlap is also indicated by GEORGE's movements relative to ALI's range use (Fig. 7.9), but their movements were followed at different times. The occurrence of such excursions emphasizes the necessity of a good and effective territory defense, and confirms that even holding a territory does not suffice to assume perfect paternity for the offspring of your own group.

In summary, males can maximize mating opportunities by restricting access of other males to their own females while at the same time strive to mate with as many females as possible, both inside and outside the group. As a result of specific conditions, males may be required to accept other males in their territory if they want to secure any matings at all.

7.4.4. Costs and benefits of multiple matings in females.

Several authors discussed the costs and benefits of multiple matings for females (Thornhill & Alcock 1983, Schwagmeyer 1984). There are at least four possible kinds of costs:

(i) additional time and energy devoted to courtship and copulation. For instance, female badgers could spend the time used for courtship and mating to concentrate on the rearing of the young.

Fig. 7.8. Ranges of the male WILF (red) from group B2 (UPPER FOLLIES) and the female SARA (blue) from group B1 (BOTLEY) plotted on the computerized habitat map. Lay-out of map and data types identical with Fig. 7.7.

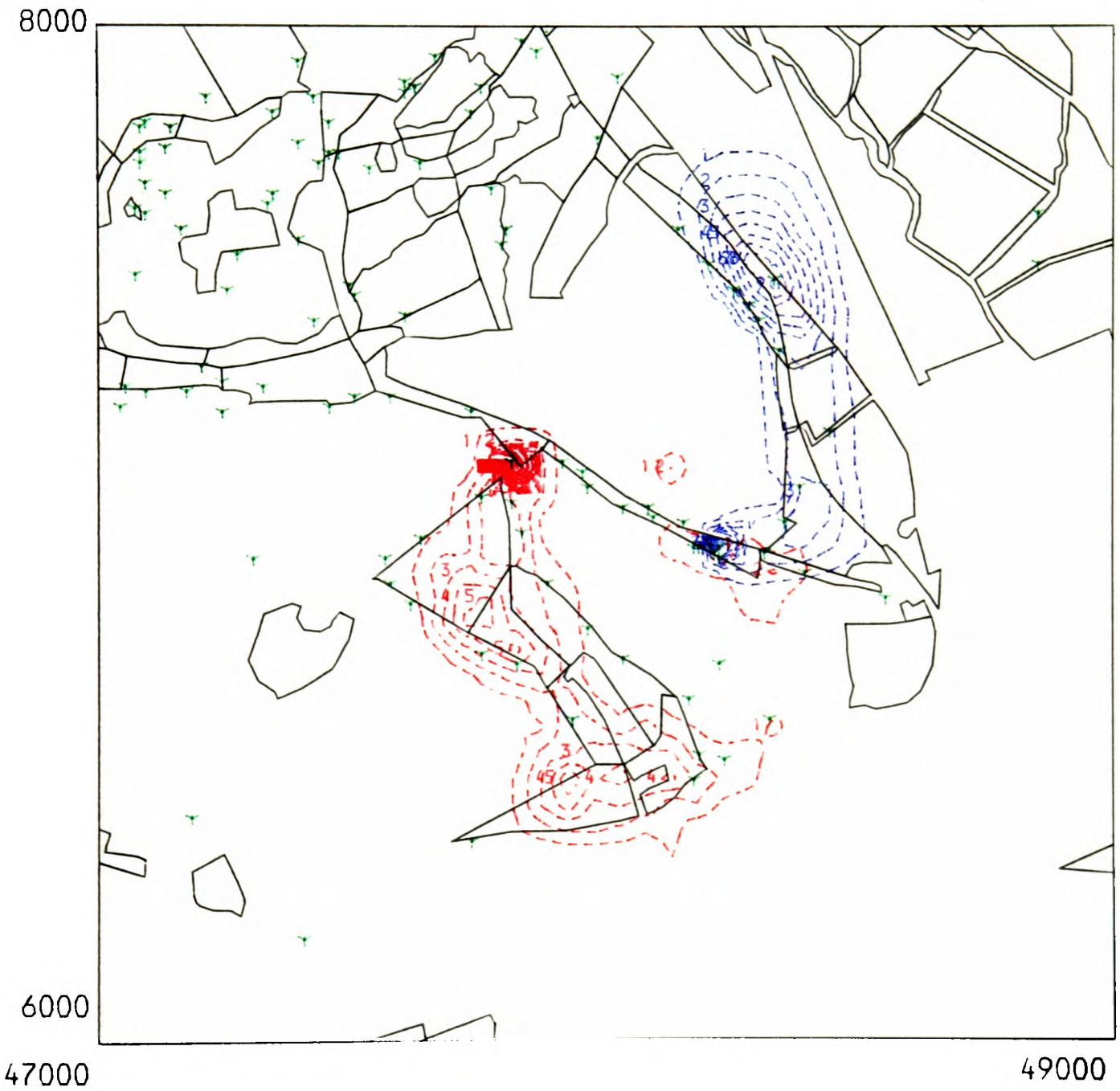
Note that both animals were tracked at the approximately same time. Some of the overlap between SARA and WILF is due to simultaneous presence of both individuals at the same site (an outlier in Range B1).

Fig. 7.9. Ranges of the male GEORGE (red) from group B1 (BOTLEY) and the female ALI (blue) from group B2 (UPPER FOLLIES), plotted on the computerized habitat map. Lay-out and data types identical with Fig. 7.7.

Animals were tracked at different seasons of the year.

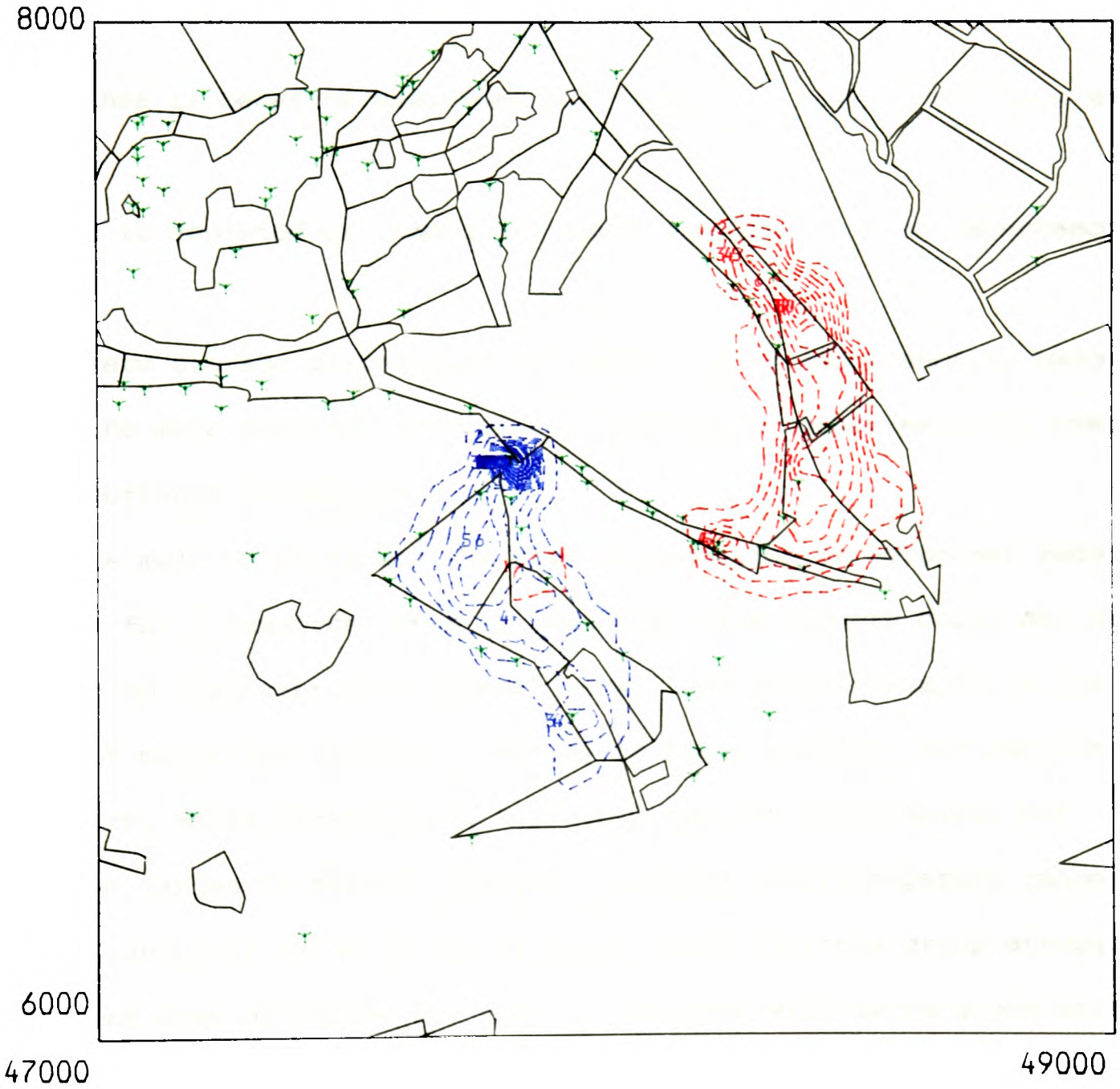
WILF (RED) /SARA (BLUE)

7-8



GEORGE (RED) +ALI (BL)

7.9



(ii) time required to repel unwanted suitors, if in intermediate stages of receptivity. This seems to be a negligible problem for female badgers - all they have to do is to vanish into the sett and emerge from a different entrance, if necessary.

(iii) loss of paternal investment by the male. Accoding to the present evidence unlikely to play an important role in badgers.

(iv) increased vulnerability to predators - this is probably a negligible aspect for badgers.

Altogether 11 benefits have been put forward to explain multiple matings in females:

(i) add to depleted or inadequate sperm supplies - of no importance to badgers.

(ii) sperm storage places cost too much - of no importance to badgers.

(iii) the male provides nutritional benefits or other material resources - of no importance to badgers.

(iv) the male helps reduce the risk of predation or helps her reduce competition for a resource. This is something male badgers could do, but is unlikely to be important on a general level. One counterexample is the situation of males and females in Marley in Kruuk's study (see section 5.4.2): there, males defended the territory against other males, but included the ranges of several females occupying nearly separate ranges and hence were unlikely to be of any efficient help in intra-group struggles. This argument does of course not apply to matings with extra-group males.

(v) the male provides protection from other sexually active males. Since copulating pairs have been observed to be harrassed by other males, this does not seem a very likely possibility.

(vi) replace sperm from a genetically inferior male by that of a genetically superior male. This requires an identification procedure according to which genetically inferior males can be detected. Following

this rule, females should mate at times when maximum distinction between males is possible, e.g. at times when males are in their best condition (Sandell 1985). This seems to be the case for badgers: males reach the highest body weight in February when the mating season starts and are then in prime condition. Sandell (1985) described the conditions that facilitate the evolution of delayed implantation, ie. the decoupling of the time of mating from the time of parturition. Evolution of delayed implantation is then an advantageous development, if opportunities for mate choice are to be maximized, and yet the specific circumstances, e.g. prey availability, prohibit a change in the timing of parturition (section 7.2.4).

(vii) increase genetic diversity of offspring. This is a largely unproven hypothesis which poses all kinds of theoretical problems (Williams 1975).

(viii) avoid the costs of trying to prevent superfluous copulations. This may occasionally be a problem; boars have been observed to drag a female out of a sett to mate with her. One possibility for her is to mate briefly (< 10 min) and then terminate copulation.

(ix) reduce aggression of males. This is especially important, if a new male or a new group of males take over a range. Males would gain from killing young cubs, since females may be able to produce a late litter (see section 7.2). Females should copulate with the new males in order to prevent them from killing next year's litter (which they may already have conceived). The difficulty with evidence for this hypothesis is that, so far, a 'take-over' of a territory by outside males has not been observed. However, infanticide may be a real threat to the young, since females are known to actively defend sett entries to nesting chambers with their young from approaching males.

(x) increase average degree of relatedness of the offspring of all females within a group (Davies & Boersma 1984). This is a suggestion put forward to explain some of the features of lion Panthera leo society. Too

little is known about degrees of relatedness amongst and between badger groups, as that a serious evaluation of this suggestion can be attempted.

(xi) facilitate immigration into a group. The problem with this argument is that even if males will tolerate the new female, it may depend on the female members of the group whether she is accepted. Their 'decision' probably has nothing to do with the incidence of multiple mating.

In summary, with the present data available, three benefits are possible candidates: avoidance of infanticide, mate choice and avoidance of costs of superfluous copulations.

7.5. Conclusions.

In the previous sections, I described how the characteristics of a resource influence the spatial and social organisation of the two sexes. These are summarized in Fig 7.10. Three dependent variables characterise the social and spatial organisation: home range size, territoriality or non-territoriality, and group formation. Resource characteristics determine directly or indirectly all three parameters in a decisive manner. They may exert their influence via the defense coalition path, and/or along the resource dispersion path. For instance, the dispersion of earthworms and the form of recovery of depleted patches determine home range size, defendability of the range and the costs and benefits of group formation. The model applies also for males defending females as a resource. In summary, it points to the success of using resources as an approach for explaining the details of the spatial and social organisation of badgers in Wytham.

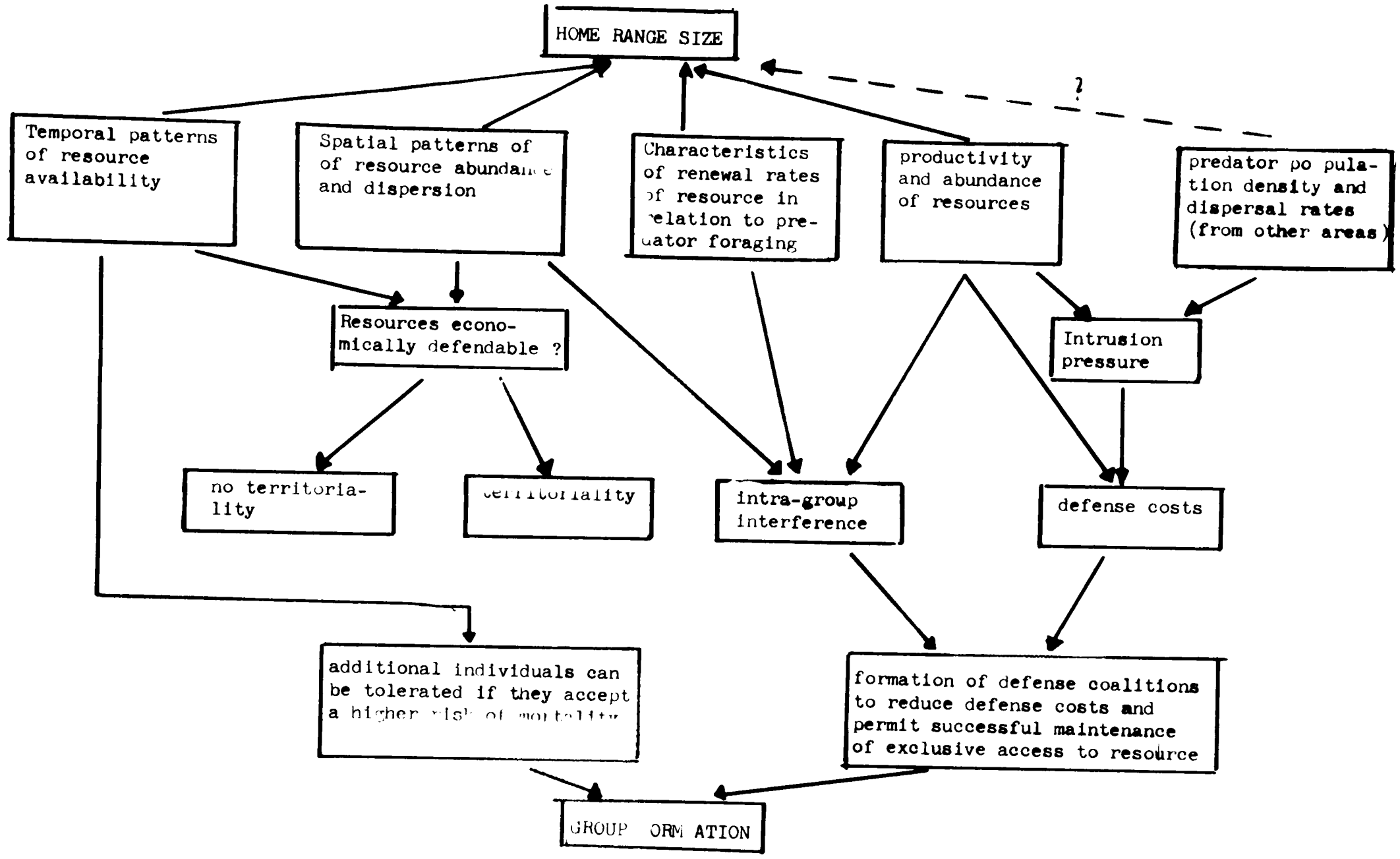
Fig. 7.10. The model that describes the network of important parameters responsible for the shaping of the social and spatial organisation of badgers.

Three dependent variables, RANGE SIZE, TERRITORIALITY, and GROUP FORMATION, are described and determined by the qualities of the resources and intrusion pressure.

Two pathways lead to the formation of groups in badgers:

(i) the 'resource dispersion pathway' explains why individuals may stay on the territory of a primary occupant at little or no cost to the primary occupant (left arrow to 'additional...').

(ii) the 'defense coalition pathway' indicates that group formation may benefit territory owners through sharing defense costs with satellites (right portion of the figure).


HOME RANGE SIZE
Temporal patterns of resource availability
Spatial patterns of of resource abundance and dispersion
Characteristics of renewal rates of resource in relation to predator foraging
productivity and abundance of resources
predator population density and dispersal rates (from other areas)
?
Resources economically defendable ?
Intrusion pressure
no territoriality
territoriality
intra-group interference
defense costs
additional individuals can be tolerated if they accept a higher risk of mortality
formation of defense coalitions to reduce defense costs and permit successful maintenance of exclusive access to resource
GROUP FORMATION

APPENDIX 1: Statistical considerations for sampling design

The accuracy and the results of habitat records depend on the sampling design. Hence, emphasis was placed on a careful sampling scheme. There is a considerable body of literature dealing with sampling problems. There are both general introductions (notably Cochran 1977, Payandeh & Beilhartz 1978, and Green 1979) and studies dealing specifically with problems encountered in vegetation, land use or habitat classification (e.g. Kuechler 1967, Mueller-Dombois & Ellenberg 1974, Howard 1981, Johnson 1981a, Karr 1981, Gauch 1982a, and Greig-Smith 1983). Gauch (1982a), amongst others, lists the following criteria for the development of an appropriate sampling design:

1. APPROPRIATENESS. The type, intensity and breadth of information collected should be adapted to the research purposes and the kind of statistical analysis intended (see also point 3).

2. HOMOGENEITY. Samples should be placed so that the possibility of environmental discontinuity is minimized. The sampling design and the scale on which data are measured should be adjusted to the scale of variation expected for each parameter. Preliminary field observations aid in estimating this. It might not always be possible to develop statistical estimates (Noon (1981)).

3. OBJECTIVITY and STANDARDIZATION. Each parameter should be measured in the same way over all sampling units to make data points comparable. Scoring of data points should be on compatible levels, ie. a variation from continuous data (e.g. a percentage scale from 0 to 100%) to binary data (presence/absence) should be avoided, if possible.

4. EFFICIENCY. There is a trade-off between the number of sampling units that can be recorded and the number of variables and the precision by which they are recorded due to the limited amount of manpower and time available. A successful compromise preserves sufficient accuracy in scoring

while providing for a large number of sampling units.

Particular sampling requirements to consider are:

1. TYPE OF SAMPLING UNIT. The two possible alternatives are transects and plots. The decision of which one to choose will depend on the kind of variables, their expected variation and the expected error, accessibility of the study area, intended statistical analyses and purpose of study. Syntheses of analytical methods and sampling designs are provided for plots by Greig-Smith (1983) and for transects by Caughley (1977) and Burnham et al. (1980). Both my data and those from Forestry were recorded using plots. Transects were discarded because in woodlands transects are less economical than plots in terms of area of sample that must be obtained for a given sampling error and efficiency of detection (Dawkins 1952). Also, most of my other data (e.g. radiotracking data) are effectively summarized using area units. Compatibility of such data with habitat transects would be low. In addition, initial field trials with transects through woodland showed enormous problems with the location of transect lines and accurate transect walking.

2. DISTRIBUTION OF SAMPLING UNITS. The most common schemes are random, stratified random and systematic (regular) sampling (Cochran 1977). Statistical considerations demonstrate both advantages and disadvantages for all three methods. Systematic sampling was selected for the forestry data because the sampling units were intended as the first stage of a long-term Continuous Forestry Inventory System. For such a scheme, regular spacing forms an efficient grid within which future samples, possibly random, can be placed. As Dawkins and Field (1978, their Appendix 1) showed, the probability of detection of rare and unusual events is higher for systematic than for random sampling. The most likely alternative, stratified random sampling, has the disadvantage that the bases of stratification (statistical and ecological considerations) might change with time and therefore render

the initial stratification procedure inefficient or meaningless. I adopted systematic sampling to comply with the Forestry data and to ease comparison with possible future work. It also facilitated accurate location of plots in the field and reduced the time needed to complete field work, thereby increasing sample size.

3. SHAPE OF SAMPLING UNITS. Either square plots or circular plots are usually used. Squares were used in both studies as their perimeter is easier to determine and potential subsampling facilitated.

4. SIZE OF SAMPLING UNITS. Generally the plot size should correspond to the scale of variation expected. However, this is often difficult to predict. Depending on the size of the sampling units, a positive, negative or no correlation can be detected for the association of e.g. two plant species (Greig-Smith 1983). As possible solutions to this problem, a variety of measures have been suggested, e.g. sampling with different plot sizes (Greig-Smith 1983), sampling in concentric plots with expanding aureoles (Bunce & Shaw 1973) etc. A summary can be found in Greig-Smith (1983). Statistical advice on how to deal with results from differently sized plots can be found in Mead (1974). Forestry data were recorded on a 10 by 10 meter square to comply with the unit of area basic to European forest site-quality assessment. I adopted two plot sizes: a 5 by 5 meter square ('central area'), which I judged to be the maximum plot size for which I could record reliable vegetation scores, was located in the centre of the 'base area' of 50 by 50 meters where information on resources, badger and fox presence was recorded.

5. FREQUENCY OF SAMPLING UNITS. Theoretical considerations made it necessary to sample at least 100 plots for the forestry records (Dawkins & Field 1978:11). The final forestry data set comprised 164 plots spread over 326 ha of woodland and covered 0.5 % of their study area. I sampled altogether 441 plots at two sites that covered together 110.25 ha. The data on vegetation covered 1 % of the study area while I tried to sample as much

of the study sites as possible (at least 75%) for data on resources and fox and badger presence.

The number of possible sampling schemes is infinite. There are many different investigative purposes; a researcher interested in bird habitats will emphasise different aspects than a mammalogist or a forest scientist. Also, schemes need to be adapted to the local situation. However, there is enough scope for more general surveys. "General" variables might reveal the patterns for a specific purpose just as well as variables dealing specifically with it, at least for plant communities (Shute & West 1982). Suggestions for alternative recording procedures can be found in Bunce and Shaw (1973), James and Shugart (1970), Cody (1968), Wiens (1969), Noon (1981), Hirst (1975), Burnham et al. (1980), Sabo (1980), and Kling (1980).

APPENDIX 2: Statistical considerations for data analysis of habitat data

The habitat records are a typical case of multivariate data: many variables (also called parameters, variates or attributes) were recorded for many samples (also called sample units or cases). Multivariate methods are particularly suited for these kind of data (see discussion by Gauch 1982a:12, Johnson 1981b, and Shugart 1981). A first task is to summarize the raw data efficiently and reduce the number of dimensions (each variable can be viewed as one dimension) from many to few, revealing the systematic patterns of variation while losing little of the detailed information contained in the raw data. This is necessary because raw data are bulky, difficult to access and contain a lot of redundant information: the number of samples is usually far greater than the number of 'pattern units' (e.g. communities or habitat types) to be discovered. Another task is reduction of 'noise' in the data, ie. the random variation from one sample to another.

The class of techniques that are commonly used for this is called ordination. Many of them have been developed, particularly in the fields of psychology and plant community ecology. A suitable ordination technique is a technique with underlying assumptions that are not violated by the data or are at least robust against slight to moderate deviations. In recent years, a number of studies have been published that provide comparisons of the performance of several ordination techniques using either real data or artificial data sets with exactly known properties (Gauch et al. 1977, Pimentel 1981, Gauch 1982a, 1982b, and Shute & West 1982). In my discussion of the techniques and performance criteria I will draw mainly on these studies and then justify the methods chosen for the analysis.

In principle, ordination techniques work as follows: the data set is canvassed and a series of ordination axes extracted that represent the 'new' variables, along which the variation inherent in the data set is summarized.

Usually these new axes are extracted in a hierarchial fashion with the first axis summarizing most of the variance, the second axis then summarizing most of the variance remaining, and so on. Ordination techniques differ in the ways in which they extract these axes, how they combine the original variables to create new axes, and how they define the relationship between new axes. This is particularly effective if most of the original variables are somewhat correlated: if they were perfectly uncorrelated, an ordination of the data would lead to no significant reduction in the dimensionality of the data set as defined by the number of new axes created. The new axes are called the principal components in Principal Components Analysis, factors in Factor Analysis, and so on. Their virtue lies in the fact that not only do they help to reduce the number of original dimensions but can also be uncorrrelated with each other and thus useful for further analysis. However, the new axes have only a precise mathematical, but no intrinsic biological definition. Therefore it is important to know the limitations of the technique employed in order to decide whether an axis has a biological meaning or not.

The ordination techniques can be characterized by the assumptions they make about the distribution functions of the variables and the relationship between variables. Most of the ordination techniques assume a normal distribution of the variable values (e.g. Principal Components Analysis, Principal Coordinate Analysis, Factor Analysis), if tests for significance of relationships are to be made, but some do not (e.g. the group of multidimensional scaling techniques; cf. Colgan & Smith 1978, Frey & Pimentel 1978, Spence 1978, Pimentel & Frey 1978, Bhattacharyya 1981, and Williams 1981). Also, all ordination techniques make assumptions about the relationships between variables; most of them assume a linear relationship between all variables. There are thus two main questions to consider when a choice of an ordination technique is to be made:

1. How realistic are the assumptions of the distribution functions of

variables and the relationship between variables for the data set in question ?

2. Given a data set that is appropriate for the ordination techniques under consideration, how well do the techniques reduce the noise in the data and reveal the systematic patterns of variation ?

DISTRIBUTION FUNCTION OF VARIABLES. Ecological data, such as data on plant communities or habitat data, are likely to have skewed distributions. It has however been shown that multivariate techniques are quite robust against this kind of violation (Gauch 1982a), usually more robust than common univariate and bivariate parametric methods.

RELATIONSHIP BETWEEN VARIABLES. A more severe problem is the kind of relationship between variables. Most ordination methods assume linearity, e.g. the commonly used Principal Components Analysis. This, however, may be inappropriate, if variables have any kind of non-linear relationship. There are many kinds of non-linear relationships possible, e.g. quadratic, negative quadratic, Gaussian, cubic, etc. A whole school of plant community ecologists work with the premise that plant species show a Gaussian response to environmental factors and to each other (Whittaker 1975). In general, the possibility of ecological data exhibiting Gaussian or other non-linear behaviour has not been sufficiently recognized (for an appraisal see e.g. Westman 1980), and zoological studies investigating nonlinear responses are few (Meents et al. 1983, Phillips 1978). Ordination techniques permitting nonlinear relationships are Principal Components Analysis on suitably transformed data (see Gnanadesikan 1977), parametric mapping (Noy-Meir 1974), Gaussian ordination (Gauch et al. 1974), multidimensional scaling (Anderson 1971) and correspondance analysis or reciprocal averaging including detrended correspondance analysis (Hill 1973b, 1979, Hill & Gauch 1980).

PERFORMANCE OF ORDINATION TECHNIQUES. Gauch et al. (1977) and Gauch (1982b) developed a set of criteria by which to judge the performance of ordination

techniques.:

1. Noise reduction.
2. Recoverage of underlying gradients (e.g. coenoclines).
3. Response to random sampling errors.
4. Behaviour in case of outliers.
5. Reaction to partially disjunct data sets.

Gauch et al.'s (1977) results with simulated data demonstrated superior performance of reciprocal averaging over another technique commonly used in plant ecology, Bray-Curtis polar ordination (Bray & Curtis 1957), and various kinds of principal conponents analyses. They used a data set with 'plant species' responding in a Gaussian fashion to underlying one- and two-dimensional gradients. Reciprocal averaging recovered much of the original gradients, but principal components analysis involuted the gradient ends at high levels of 'species' diversity, resulting in a sequence reversal. In all cases, the expected outcome was a straight line.

Pimentel (1981) used a set of nonlinear taxonomic data to compare principal components analysis, principal coordinate analysis, nonlinear mapping and nonmetric multidimensional scaling. He found that non-linear mapping showed consistently poor results. Good results were achieved using nonmetric multidimensional scaling based on Gower's general similarity coefficient (Gower 1971). Principal components analysis on a correlation matrix showed best, but still inaccurate results. A consultation of these studies shows that reciprocal averaging and standardized principal components analysis (ie. performed on a correlation matrix) show superior performance to other techniques, but are still inadequate for data exhibiting a strong nonlinear tendency.

The two main problems of reciprocal averaging and principal components analysis are the 'arch effect' and the compression of axis ends. These problems result from a discrepancy in the underlying models and the mathematical properties of non-linear data (Gauch 1982a:150, 1982b). Their

effect can be demonstrated using simple data sets of simulated data. If a data set is arranged so that the variation is along one gradient only, the perfect ordination technique would plot all points along a straight line, ie. all points should have the same value on the second axis. Both reciprocal averaging (RA) and principal components analysis (PCA) show an arch distortion (see Gauch 1982a:151, his Fig 4.11) with the points in the centre of the first axis separated from the points at both ends. This is due to a quadratic distortion which results from the condition that two successive axes should merely be uncorrelated (a stronger condition would be that axes should exhibit no systematic relation of any kind with each other). This can lead to ambiguous results when strongly non-linear data are ordinated: the second axis, being merely a quadratic distortion of the first axis, accounts for more of the 'variance' (ie. has a higher eigenvalue) than the third axis with proper representation of the 'real' biological variation deferred to the third axis. The second problem involves compression of the first axis ends in RA relative to the axis middle, so that a given distance of separation in the ordination does not carry the same meaning in terms of implied differences between samples or variables.

As a consequence of these undesirable effects, Hill (1979, Hill & Gauch 1980) introduced a modified version of reciprocal averaging called detrended correspondance analysis (DCA). DCA was specifically designed to correct the two main faults of RA and PCA described above. Tests with simulated and real data show that it actually does what it is meant to and indicate a far superior performance over any other ordination technique (Gauch 1982b).

As a conclusion I decided to use detrended correspondence analysis (DCA) as my main ordination technique. In summary, DCA avoids the main problems of PCA and RA, permits handling of non-linear data and ordinates variables and samples simultaneously on axes that have a meaningful dimension.

APPENDIX 3: Data selection procedures and statistical techniques for diet analysis.

For the analysis of the diet of fox ranges, droppings had to be assigned to each range. As the vast majority of droppings could not be assigned reliably to known individuals, I had to use the information on the location of each dropping and compare this with the information available on the spatial configuration of the ranges. There are at least two potential errors that can lead to a wrong association of dropping and range based on spatial information:

1. Overlap of ranges (see detailed discussion in Chapter 5) prohibits a reliable assignment of droppings collected within overlap zones. Inclusion of droppings from a neighbouring range may introduce a bias.

2. Itinerant and migrating individuals traversing a range might leave scats which distort the results. This problem is intractable and probably has equal effect on each range.

Both these sources of noise will tend to work against any conclusions to the effect that diets differ between the foxes in different ranges. Probably the more influential error is the possible bias introduced by an inclusion of droppings from neighbouring individuals. I therefore developed a procedure to exclude droppings from zones of overlap.

In program SCATCELL a reference map with a 50 meter base grid was established. The program tagged each cell according to which of 14 selected foxes were located at least once therein. In this way a list of all observed combinations of individuals which shared cells was prepared. For each group range a list of 'admissible' combinations of foxes was drawn up (see Table 5.22). For each range program CODESEL compared the list of admissible combinations of foxes with the observed combination in each cell of the base map; the program selected only grid cells with an admissible combination. Finally, program TURSEL tagged each dropping in this heavily

filtered subsample with the appropriate range number by comparing the map coordinates of the dropping with the list of grid cells of each range as determined by program CODESEL.

This procedure is a very strict one in that it excludes all cells where individuals from different groups were located, without regard to the frequency of such events. However, I feel that this is necessary in order to have confidence in the analyses of correlations between habitat and diet characteristics of fox ranges (Chapter 5). The possibility remains that other, not radiotracked, members of each group may have trespassed into neighbouring ranges even further than the radiotracked animals.

The test statistic generally used for comparisons of different temporal and spatial units (months, seasons, ranges) was the Kruskal-Wallis test, a non-parametric equivalent of the one-way analysis of variance. Initial checks with the F_{max}-test (Sokal & Rohlf 1981) indicated that the variances were too heterogeneous for a normal analysis of variance. Where the Kruskal-Wallis test statistic was significant, ie. differences between the means could not be accounted for by chance alone, a multiple comparison procedure was possible (Conover 1980, p.23) in which each mean was compared with each other mean to test whether the means differed. Thus it was possible to work out which range differed from which others without altering the overall level of significance (ie. without an increase in type I errors).

Another non-parametric test-statistic was used to investigate whether the directions of temporal fluctuations were synchronized between ranges. For example, this procedure was used to test the significance area of an apparent decrease of the proportion of rabbits taken by foxes from a peak in winter to a trough in summer. Irrespective of the possibility that the representation of rabbits in the diet may vary between different ranges at any time, the test answers the question of whether the changes from one temporal unit to another follow the same pattern for all ranges over all

temporal units considered. The test statistic used is Kendall's coefficient of concordance. Kendall's coefficient of concordance can assume values between 0 (perfect asynchrony) and 1 (perfect synchrony). Computation procedures and hypothesis testing followed Conover (1980) who suggested that the test statistic should be compared with critical values based on a different distribution (the F-distribution) rather than the usual Chi-square approximation. Results of an earlier investigation of the badger's diet (Kruuk & Parish 1981) with published concordance values were used to investigate the effect of Conover's suggestion. The results of the modified tests showed a greatly improved level of significance for all significant effects (ie. synchrony between study areas) and changed one test value from insignificance to significance at a level of alpha = 0.05.

APPENDIX 4: Statistical analysis of telemetric data: the problem of temporal independence

A basic property of telemetric data is the frequent lack of independence of successive data points. By this we mean that within a short time interval a fox or a badger is not equally likely to reach all other locations in its range from a given starting point, hence its subsequent location is partly dependent on its previous location. More formally, statisticians call two events A and B 'independent' from each other if

$$p(AB) = p(A)\, p(B) \qquad (1)$$

with

p(AB) the probability of event A and B occurring together (the joint probability of A and B)

p(A) the probability of event A occurring

p(B) the probability of event B occurring

(Conover 1980:16). The definition implies symmetry, that is if point A is independent from point B, B is also independent from A. The definition is directly derived from the concept of conditional probability. Consider the relationship of the probability of event A and the conditional probability of A given B, p(A/B). This conditional probability is

$$p(A/B) = p\,(AB)/p(B) \qquad (2)$$

Now, if the probability of A, given that B occurs, is the same as the probability of A without any information on the occurrence or non-occurrence of B, one could say that the occurrence of A is independent of whether or not B occurs: the two probabilities would be equal, or p(A/B) = p(A). If p(A/B) is replaced by p(A) in eqn (2), ie. we set A as independent from B, we get eqn (1).

The definition of independence of two events A and B as in eqn (1) implies that the idea of A and B being independent from each other is not an

absolute nor an unconditional statement. The judgement, independence or not, depends on the probability function for events A and B. Naturally, we can not describe the probability function for locations visited by a fox or a badger in advance. However, we know that the probability function depends on the time interval at which we choose to look at events A and B. To demonstrate this by an extreme example, we could choose one second as a suitable time interval for considering two successive events A and B. We know that the highest recorded speeds of foxes are ca 40 km/h (Lloyd 1980) which is equivalent to 11.1 m/sec. The probability that a location B at a distance of more than 12 metres from the present location A would be visited (ie. event B occurs) is practically equal to zero. If you take the same locations but increase the time interval to three days, there is a high probability of event B occurring given a location A - at least with reference to the constraint imposed by the maximum speed of foxes!

Lack of independence of successive data points is important, since a variety of probabilistic home range concepts, whether parametric or non-parametric, assume independence of events. Furthermore, many classical statistical tests require independent data points. Estimates of home range size based on the grid method (Voigt & Tinline 1980) benefit from independent data points. since then the data points are more likely to constitute a representative sample of the animals' movements. There are three ways to cope with this problem:

(1) modify the test statistic to cope with the special qualities of the data

(2) modify the data to create independent data points;

(3) ignore the problem.

As Cliff and Ord (1981) point out (see also Appendix 5), the formally correct procedure is always to modify the test statistic. Since such modified procedures are not yet available, or only for certain problems (e.g. within the context of spatial autocorrelation, Appendix 5), I shall

discuss the second suggestion in more detail.

To date, four procedures have been suggested to look at temporal independence in a data set:

(1) Dunn and Gipson (1977) developed a probabilistic model of home ranges based on the multivariate Ornstein-Uhlenbeck diffusion process. This is a special stationary process based on normally distributed data assuming that a location depends only on its immediate predecessor. With these assumptions, lack of independence decreases exponentially with increased time interval between two locations. This approach is of limited use because of the assumption of bivariate normally distributed data.

(2) Schoener (1981) showed that the ratio of the mean square distance between successive observations to the mean squared distance to the geometric centre should be 2 for independent observations, if the successive observations are identically distributed. However, Schoener did not make any suggestions as to what to do if the observed ratio deviates from his expected value, ie. if the data exhibit dependence (as can be safely assumed for telemetry data).

(3) Newdick (1983), in a study on the ranging behaviour of red foxes in urban Oxford, selected an 'independence interval' by calculating the largest distance across the home range, if defined by all data points, and dividing it by the maximum speed observed for foxes (40 km/h or 667 m/min). One disadvantage of this method is that it produces varying independence intervals if range sizes and configurations vary (in his study he calculated independence intervals of 10 to 30 min for different ranges), so different proportions of the original data set are discarded. The method may also be sensitive to sample size. Doncaster (1985) therefore opted for a consistent independence interval of 15 minutes.

(4) In an extension to Schoener's preliminary analysis, Swihart and Slade (1985) provided empirical evidence that a test statistic can be based on Schoener's ratio and developed an objective, albeit arbitrary criterion to

determine the independence interval. Using data on movements of a female cotton rat (Sigmodon hispidus), they calculated a time interval of 270 minutes, an estimate close to the results Newdick (1983) obtained when he used simpler correlation coefficients in his fox study.

Even though Swihart's and Slade's (1985) procedure may be objective, I doubt whether it is of much use. If only data were admitted for analysis that are at least 4 or 5 hours apart, the bulk of the data would have to be discarded. This renders most problems typical in studies of animal movements totally, and absurdly, beyond analysis.

Newdick's (1983) method of relating the top speed to the largest distance seems most appealing. The resulting interval provides an estimate of the minimum time an animal would require to reach any other point in its range. Since most points in a range are more towards the centre than the periphery of the range, the actual time interval may usually be shorter; thus Newdick's rule provides conservative estimates. Since my ranges were comparable in size with his results, I decided to adopt a standard independence interval of 15 minutes (the mean of the independence intervals for 17 fox home ranges (excluding transient foxes), calculated according to Newdick's procedure, was 15.35 min - S.D. 6.25). The majority of the data points of all foxes will be independent according to this criteria, and comparisons with other studies will be easy.

A second approach considers actual times spent by the animal in an area. If an animal is followed continuously throughout the night, the actual time spent in a patch (or in a grid cell) can be calculated. Home range measures based on actual times spent in area units do not suffer from problems of temporal independence as do measures based on frequencies of visits. If there is still dependence in the data, it mimics non-random behaviour in space (a process we are interested in), but not side-effects derived from the vagaries of a particular sampling regime.

This distinction between unfavourable statistical side-effects of a

particular recording scheme (leading to possible dependencies between successive observations) and the correlations due to the non-random movement patterns of the individual in question has largely been overlooked, but is a vital one: we want to minimize the chance for distortions arising from the sampling procedure while in contrast we are interested in the correlations exhibited by non-random behaviour. Recording of actual times spent in an area unit provides an acceptable solution to this problem. If we record actual times spent in an area, the probability of visiting an area by an individual may also depend on the probability of visiting another area. This is the problem of 'spatial dependence' which will be dealt with in Appendix 5.

APPENDIX 5: Spatial independence of data: the concept of spatial autocorrelation

Consider a habitat which is of no interest to a badger. Let a clump of beech trees be such a habitat. All else being equal, the intensity of usage of this clump of beech trees would be low. Consider a second clump of beech trees which, unlike the first, is situated on a patch leading from one very attractive habitat to another one. As the badgers would pass along the path many times they would naturally also traverse the clump of beech trees (which in a sense is nothing but an obstacle to them). In such a case the intensity of use of this clump of trees can be said to depend on the intensity of use of the two attractive areas. That is to say, the intensity of usage of a habitat (e.g. the clump of beech trees) may solely be a function of its spatial location (e.g. between two attractive sites).

A5.1 Spatial autocorrelation

If the intensity of usage of point A (or, formally speaking, the probability of an animal visiting point A) depends on its spatial location, e.g. on the probability of visits to neighbouring points B,C,..., then the two events A and B, A and C,... are not independent. What is the practical importance of this? If I want to compare the intensity of usage of patches belonging to a selection of different habitats, I cannot be sure that the differences (or similarities) found can solely be attributed to the habitats (e.g. their intrinsic attractivity); it may rather be the case that the result is influenced considerable by the spatial location of the patches considered relative to each other and perhaps to other patches not considered! Unravelling the interplay between habitat selection and spatial inevitabilities might prove interesting per se, but it also means that conventional statistics can be used only in a restricted way - a chi square

test on differences between habitats in the intensity of use would only be admissible under certain conditions (section A5.2). The principle of spatial dependence in radio-tracking data is obvious, but its statistical implications have never hitherto been acknowledged in the vast literature on animal movements.

If a set of data points display interdependence over space, they are said to be spatially autocorrelated. Spatial, because the interdependence is over space, and autocorrelated, because data points of only one variable (e.g. intensity of use) are correlated with each other. The formal definition of spatial autocorrelation is, according to Cliff and Ord (1981:8):

If for every pair of spatial units i and j in the study area the drawings which yield x_i and x_j are uncorrelated, then there is no spatial autocorrelation in this system of spatial units on X;

with X being a random variable (intensity of use) and x_i, x_j the values of X for spatial units i and j. Data with this property are common in disciplines where the analysis of data on their spatial information is required (anthropology, geography, or ecology). In fact, they can be the kind of data that are of special interest to the researcher (Appendix 6). However, the tools for a correct appreciation of the properties of spatially autocorrelated data have only recently become available (Cliff and Ord 1973, 1981). This study is the first to apply them to telemetric data. I shall therefore discuss the properties of spatial autocorrelation in some detail.

The relationship of temporal and spatial independence deserves to be discussed further. We might have achieved temporal independence for the data selected to determine the configuration of the range, but quite apart, there might still be spatial interdependence and thus spatial autocorrelation in the intensity of usage: for the question of spatial

autocorrelation the only aspect of interest is whether the intensity of usage of a given part of the range is due to its location near to or distant from other areas. It is important to realize that temporal and spaial interdependence are different problems and that the solution of one of them does not necessarily imply anything about the state of solution of the other! Should therefore the data be cleansed of temporal interdependence before they are subjected to an analysis of spatial interdependence ? The answer is: there is no need, since there is no requirement for the data to be independent data points in order to calculate the spatial autocorrelation function. In fact, the object of this study is to explore, rather than eliminate, the spatial interdependence that may exist in the data. What is important is not possible temporal independence of data points but their representativity of the true events. Consider the example of the beech trees once more. If the animals take a short time, say 5 minutes, to pass through the beech trees situated between the two attractive sites at which they linger for much longer, and if the decision was taken to collect data every 15 minutes, the badgers might be missed on some or even on all occasions when they walked through this patch of beech trees during the period of data sampling. My sample might then not record their movements through the beech trees and I could therefore not consider this patch of trees in an investigation of spatial use, since in this case the sample would not be representative.

This problem can be generalized by considering the average speed of movement M in relation to the average size of the spatial unit S and relate this to the sample time interval. Four extreme conditions are possible (t = time interval for sampling):

	Speed of movement (M)	
	Slow movements	Fast movements
S small	(1) S < M*t for some intervals	(2) S < M*t for almost all intervals
S large	(3) S < M*t for most intervals	(4) S < M*t for some intervals

The probability of missing a patch visited by the animal would be low under condition (3), moderate under condition (1) and (4) and high under condition (2). If the probability of missing a patch is fairly high, the results of the spatial autocorrelation analysis would be suspect. This would not only affect procedures to investigate spatial interdependence but also bias the picture of range usage! The simplest and best sampling design not affected by this is the continuous recording of the movements of the animal. It is then possible to consider actual durations in a given spatial unit and the spatial units can then be designed independently from considerations of how to sample movements.

As the spatial autocorrelation is defined as the correlation of pairs of values of a random variable mapped onto the study area divided into a system of spatial units, the autocorrelation will depend on the mapping procedure, ie. on the division of the study area into units. For instance, spatial units could be patches of irregular shape (as defined in the habitat map) or cells of a systematic grid placed over the study area. What kind of

unit to choose and the effects on the autocorrelation will be discussed in more detail in section A5.3.

A further point to note is that spatial autocorrelation is defined as the outcome of comparisons of many pairs of spatial units. The rules for building the pairs allow the consideration of points in all directions. This is a fundamental difference to autocorrelation functions found in residuals of regression analysis or the temporal autocorrelation in time series analysis where the pair formation is restricted to one direction. Spatial autocorrelation can be generated by multilateral interactions because of at least two dimensions in space (for the analysis of fox and badger units the third dimension is neglected, but would be important for arboreal species). The direction of interaction is not defined a priori; in fact, the number of possibilities for interaction directions is infinite. As a consequence, a multitude of different kinds of spatial interdependencies occur. For instance, a gradient (trend) may influence the overall pattern; the correlation may depend on the direction (e.g. relative to the earth's magnetic field) of the link between two sites, or the relative strength of the link, e.g. the amount of border line shared by two sites. The scale of dependence can vary as well: on a very local level, as in the example with the clump of beech trees, only immediate neighbours are affected. Effects over large distances are equally conceivable as in animals with symmetrically shaped ranges (e.g. the hexagonal territories of some fishes) visiting the range borders regularly.

These examples show how varied spatial processes can be. Thus, 'spatial interdependence' reveals itself not as a closely defined process but as a summary of a multitude of diverse phenomena - there is not just one kind of spatial dependence but there are many. 'Testing directly for spatial dependence' is rarely possible, or even useful and effective; in most cases this should be read as 'testing for a particular kind of spatial dependence'. We can answer the question 'do the data display spatial

interdependence'?' only via the question 'what kind of spatial interdependence is shown by the data?'.

Thus, investigating spatial interdependence fulfills more than purely statistical considerations. In addition, by setting up and testing spatial models with specified properties (i.e. the hypothesized way spatial location exerts an influence on the dependent variable) we gain an alternative method to complement the usual analytical tools that require independent data points.

A5.2. Effects of spatial autocorrelation on statistical inference

There is general agreement that spatial autocorrelation will affect the outcome of statistical tests (Haggett et al. 1977 p. 336, Cliff & Ord 1981). The following discussion is mainly drawn from Cliff and Ord (1981: 184–196). Conventional methods of hypothesis testing employing statistical inference are based on the assumption that the data points are assumed to be independent. However, the important feature of spatially located data is that the data points cannot necessarily be assumed to be independent. For instance, in the case of positive autocorrelation (values of pairs of spatial units are of similar magnitude), an observation contains less information than an independent observation, since it is partly predictable from other observations located nearby.

So far few studies are available that consider this effect of autocorrelation or that make suggestions of how to modify the conventional procedures to account for the autocorrelation. In principle, there are three possibilities to cope with autocorrelated data:

1. Modify the conventional test statistic to account for the interdependence of observations.
2. Modify the data and filter the autocorrelation out.
3. Ignore the fact that the data contain spatial auto-

correlation.

The formally correct procedure is always to modify the test statistic (Cliff & Ord 1975). This was quite burdensome in all cases investigated so far. There is, on the other hand, only one study that considers the effect of filtering procedures (Martin 1974). Thus I shall concentrate on the modified test statistics.

Studies have been published for the following test procedures:

(1) t-test; (Cliff & Ord 1975)

(2) one-way analysis of variance; (Griffith 1978)

(3) Pearson's product-moment correlation coefficient; (Bivand 1980)

(4) Regression. (Cliff & Ord 1981).

The general message from the results of these studies is quite clear: if autocorrelation is not considered, severe inferential errors are possible. As a rule of thumb, however, it is reasonable to say that if low to moderate levels of positive autocorelation are present and the actual value exceeds by far the critical one (at least the critical one at the 5 percent level) then this result should be significant even if compared with critical values obtained from a modified procedure. If data exhibit negative autocorrelation, the opposite is true - then normal test statistics may be conservative for a given alpha level.

A5.3. Models of spatial autocorrelation

As the previous sections showed, there can be different kinds of spatial interdependence. For the following sections I shall define a model of spatial autocorrelation as a specific scheme of interactions of sites due to their spatial location, ie. a scheme that proposes what specific properties the spatial process in question shows. I emphasize the importance of specificity of models of spatial autocorrelation since the power of the autocorrelation measures is highest, when the factual

autocorrelation pattern corresponds to the hypothesized one (the type II error of accepting a null hypothesis while it is in fact false is then minimized; Cliff and Ord 1981). The power of the various autocorrelation measures is also related to the 'degree of specificity' of the model: if many interactions between sites are considered then the power is potentially lower than if there are few and very specific interactions postulated. In other words, there has to be a compromise between the desire to include as many connections and types of interactions as possible (thus maximizing the chance that the factual autocorrelation pattern is amongst the multitude of included ones) and the loss of power of distinction incurred by the increased generality of possible patterns. These properties of spatial autocorrelation measures have to be considered for a correct appreciation of the results. They also illustrate the importance of a careful decision on how pairs of spatial units (to be compared) are formed, which connections should be of interest and how they are considered. There are then three steps in the procedure of setting up the basic properties of a model:

1. Define the size and shape of area units, ie. the admission to pair formation (how should the areas be defined that are compared?).
2. Determine the admissible connections between area units, ie. the links by which the units are supposed to interact (the formal, or structural pattern).
3. Decide, what influence each connection should exert (the functional pattern of interactions).

Area units are sometimes predetermined by the study in question. If, for instance, the gene frequencies of different populations of a species should be compared and a model is suggested what kind of spatial process is responsible for the pattern found (e.g. panmixis, migration, fission etc.), then the sites, the area units, are already given: they are the places where the different populations are present at the time of the study. On the other hand situations exist where there is a choice amongst competing

systems (maps). Telemetric studies are usually in the latter situation with at least two types of maps of spatial units:

- 'natural units' (e.g. habitat patches on a habitat map) predetermined by their qualities as defined relative to the species of the purposes of the study;
- 'arbitrary units', e.g. a systematic grid of cells of identical properties (size, edge length etc.).

One apparent difficulty with natural units lies in their irregularity of shape: the links between two immediate neighbours (or two distant 'neighbours' through a series of intermittent patches) may vary a lot and are therefore more difficult to account for in a model: the length of the common border line varies etc. In this study I have therefore restricted my discussion of spatial effects on data that are based on a systeatic gid of identical cells. This leads us to the second point, the setting up of connections. It is not necessarily wise to connect every area unit (patch, grid cell) to every other; this is called a maximally connected model. Instead, it may be more appropriate to connect only a selection of area units. The following list presents some examples:

1. Connect only Gabriel neighbours (Gabriel & Sokal 1969). A point (or area unit) B is a Gabriel neighbour of a point A, if no other location lies within the circle with a diameter of the distance AB. This is appropriate for a process where, for example, migration is assumed to play a role and occurs only along the shortest connections in a system of irregularly shaped or placed units.
2. Matern connection (Matern 1960). A connection is established only, if the two members of a pair are within a fixed distance, ie. the second member lies within a circle of fixed circumference that has its central point at the position of the first member.
3. Rook's case. On a systematic grid with cells of identical shape and size (e.g. a chess board), consider only cells that can be connected

horizontally or vertically with each other.

4. Bishop's case. The same situation as with rook's case, but the connection occurs only diagonally.

5. Queen's case. Connections of both the rook's and the bishop's case are admitted.

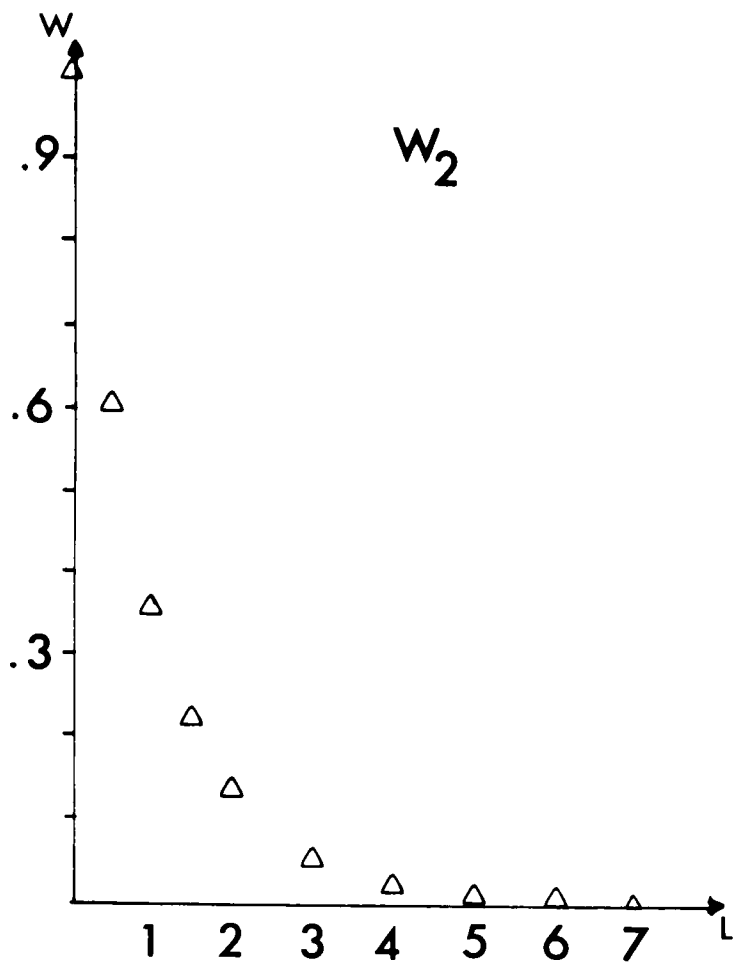
In the first two cases, no restrictions were placed upon the possible direction of the connection while the connections were limited to a certain distance, while it was just the opposite in the latter three cases. It is perfectly conceivable, to construct connection rules that combine restrictions on distance (as in a Matern process) with restrictions on direction. A simple example will demonstrate that the pattern of correlation may depend dramatically on the type of connections considered. If, for instance, on a chess board (with black and white cells) only the immediate neighbour cells are connected according to rook's case, then only pairs with two different colours are formed (black and white in every pair). This is a case of perfect negative autocorrelation. If, however, immediate neighbours are connected according to bishop's rule, a perfect positive autocorrelation would result, since only pairs with the same colour (black - black and white - white) are formed!

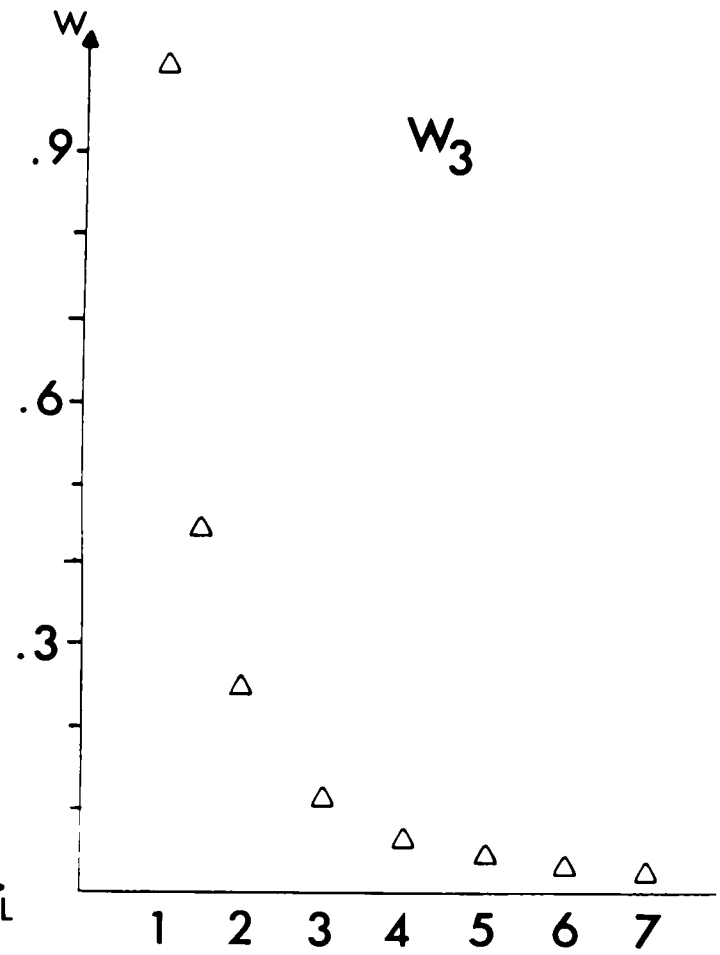
The third step in specifying the model is to decide how the connections should be considered. For instance, if the spatial process in question is assumed to consist of spatial interactions on a very local level, then the connections between close area units should be considered more important than those between distant area units. This concept of assigning values of strength of connection is a weighing procedure, as much important to spatial autocorrelation as it is fundamenetally different from time series analysis. The weights may assume discrete values, e.g. 1 if the connection is according to Matern's rule inside the circle and 0, if the second pair member is outside the circle (in a sense, the distance restriction imposed by the Matern rule can be set equivalent to the weighing procedure).

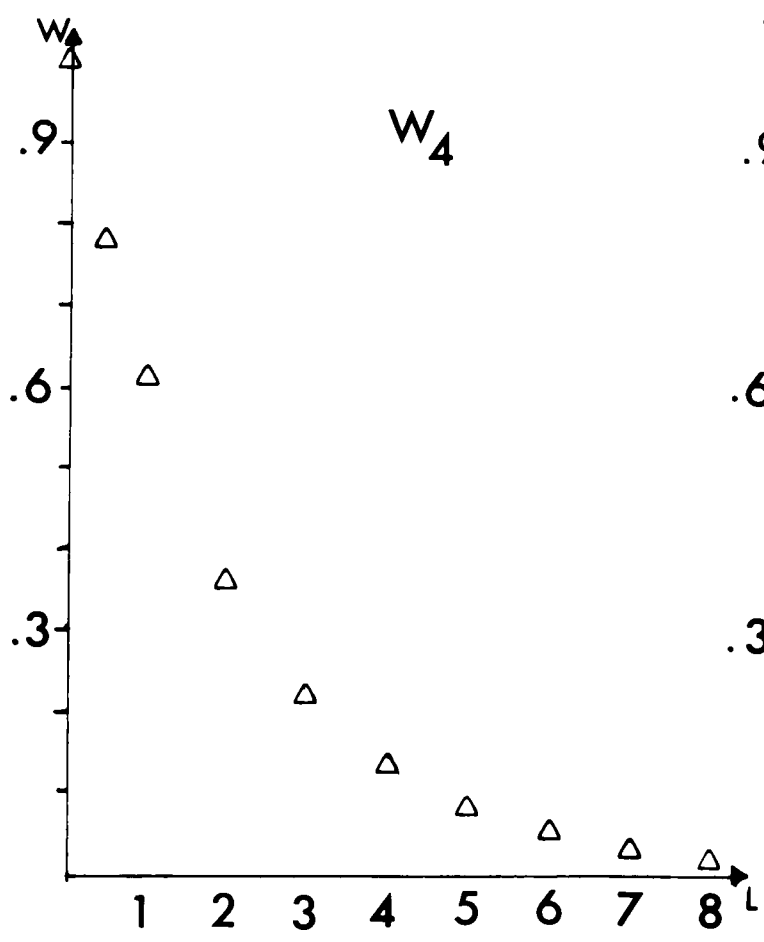
Tobler's (1970) first law of geography (see Appendix 6) may be translated into a parametric weighing function of the kind d_{ij}^{-1} or $\exp(-ad_{ij})$, d_{ij} being the distance between area units i and j, so that nearby points receive a strong weight and distant points have connections with small weights. Fig. A5.1 shows four weight functions (W_2 to W_5 of Appendix 7) that approximately double the influence of distant points each time. W_2 is a weight function that assumes local interactions to be domineering while W_5 assumes interactions to occur over a larger distance.

Cliff and Ord (1981) have shown that it is best to choose the weighing matrix a priori to represent the autocorrelation pattern proposed as an alternative hypothesis. However, the investigator may be unwilling or unable to specify a pattern. In this case, one practical solution is to employ several weighing matrices with increasing consideration of large distance connections, in order to vary the scale over which interaction is hypothesized to take place. Another, complementary method is the construction of a correlogram, analogous to the correlograms in time series analysis. Here, a basic distance is defined (the size of the 'spatial lag') and all connections are considered that fall with their endpoints inside the m-th basic distance, as measured from the first member of the pair. The endpoints of the 1st basic distance are the immediate neighbours (first order neighbours), the endpoints of the second distance are the first-order neighbours of the first-order neighbours, ie. the second order neighbours relative to the first member of each pair (Fig. A5.2). For each multiple of the basic distance, ie. for each order of neighbour, the autocorrelation measure is computed separately. So, in contrast to a model with connections weighed according to a function such as any of W_2 to W_5 <u>where all distances are considered simultaneously</u> for the computation, and weighed according to their value, a <u>series</u> of autocorrelation values are computed. Then, for each order of neighbours all distances receive the same weight but are considered separately, only one distance at a time. The resulting sequence

Fig. A5.1. Shape of weighting functions 2 to 5 used in the fitting of spatial models to radio-tracking data.
W: weight, scaled between 0 and 1, for a given pair of cells, as a function of
L: distance, ie. the spatial lag, in cell size units.


W
.9
.6
.3
W_2
1 2 3 4 5 6 7
L


W
.9
.6
.3
W_3
1 2 3 4 5 6 7


W
.9
.6
.3
W_4
1 2 3 4 5 6 7 8
L

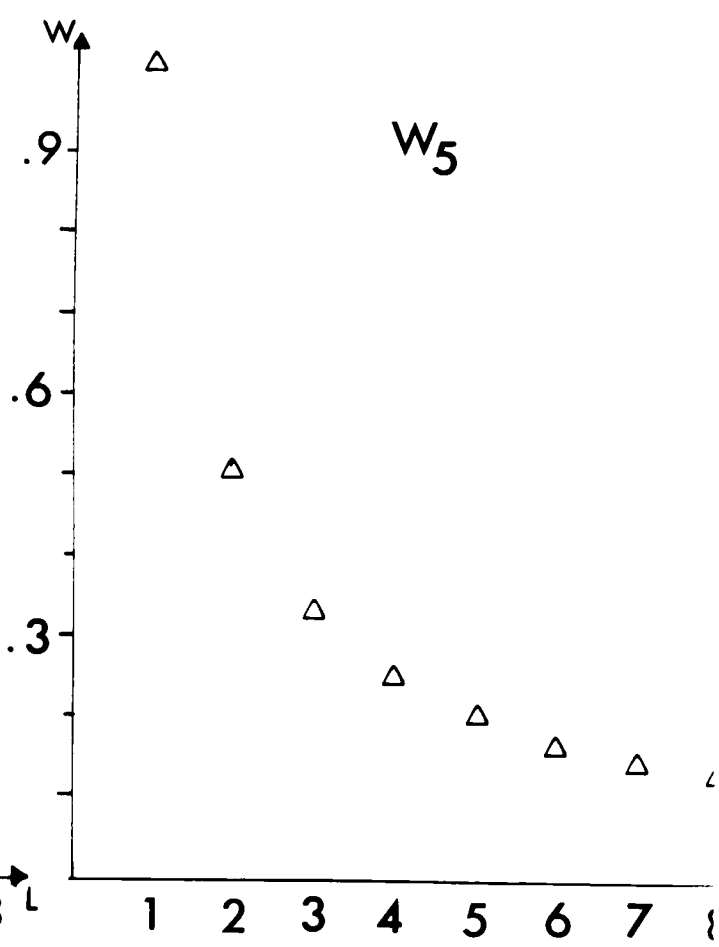

W
.9
.6
.3
W_5
1 2 3 4 5 6 7

Fig. A5.2. Definition of spatial lags and illustration of spatial autocorrelation functions.

a. Definition of spatial lag.
   cell indexed ij: cell in question, in the i-th column and the j-th row.
   other indexed cells: some of the first order neighbours of cell ij.

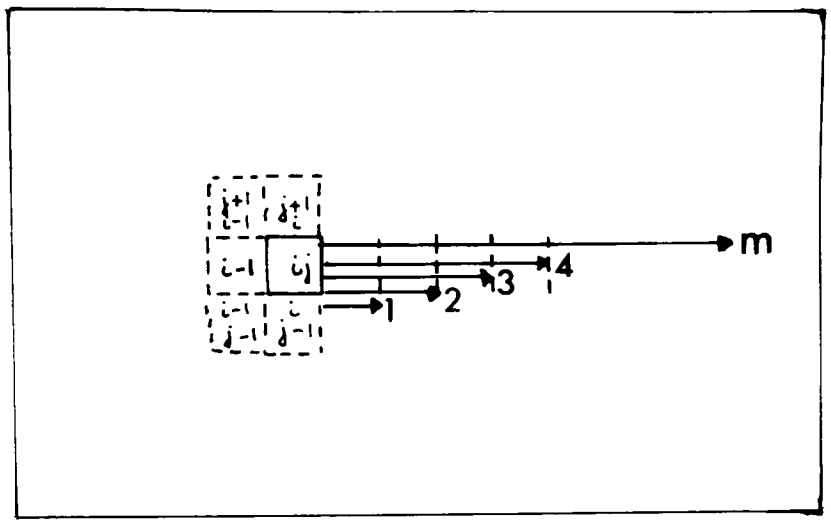
b. Autocorrelation functions are plotted as spatial autocorrelation coefficients versus the spatial lag.

   AF_1 represents a function decaying only slowly with increasing lags, ie. similarity of use of cells at higher lags in comparison with the cell in question is on average high.

   AF_2 represents a function decaying quickly with increasing lags, ie. similarity of use of cells at higher lags in comparison with the cell in question is on average low.

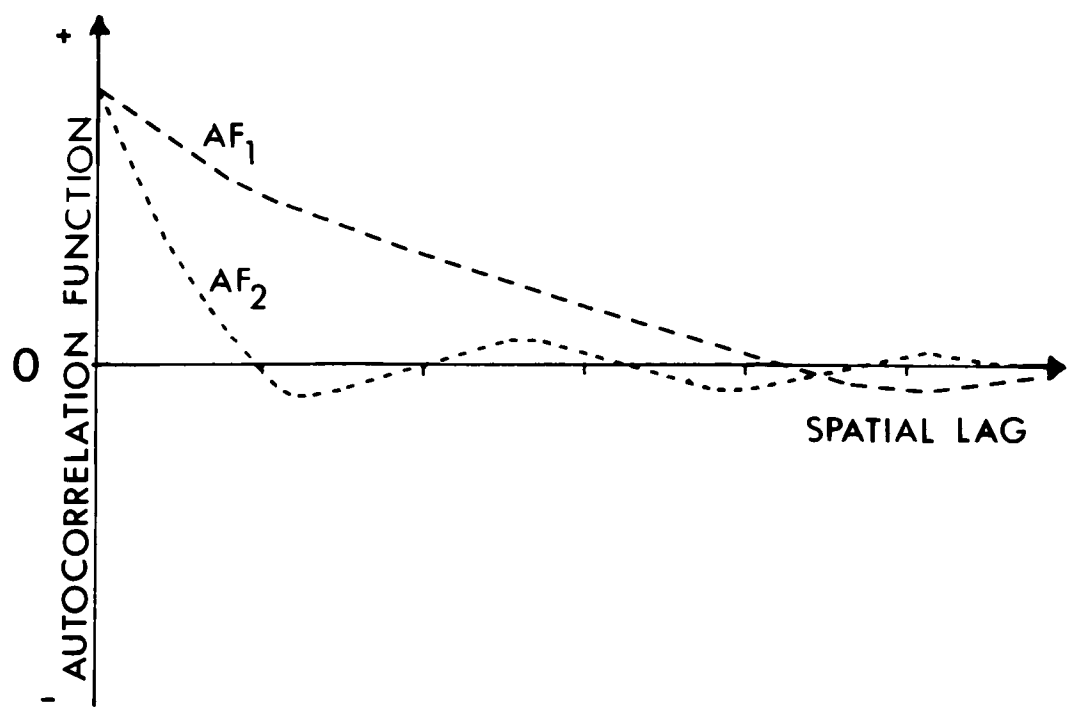
a

DEFINITION OF LAG



1 - FIRST ORDER NEIGHBOUR } OF CELL $_{IJ}$
M - M-TH -"- -"-

b



of autocorrelation values is called an autocorrelation function and is usually plotted against the order of the spatial lags (Fig. A5.2). The slope of the autocorrelation function curve indicates on which scale (at which distance levels) the spatial process under question operates. Steep declining slopes at low lags (ie. looking at the neighbours nearby) indicate that spatial interactions are very locally restricted and that influence fades quickly away, while a shallow slope at low lags indicate a well expressed local interaction that fades away only slowly over larger distances.

Thus, a correlogram can indicate to us some properties, e.g. the scale, of the spatial process under consideration. It does not replace a proper model of spatial autocorrelation, since it does not specify parameters of the model, but it gives a hint which class of models may perform better and which do not.

Since this is the first telemetric study to employ spatial autocorrelation, I used both methods (correlogram and different weighing matrices) to establish a picture of spatial dependence of animal locations.

A5.4. Measures of spatial autocorrelation

Several measures of autocorrelation have been proposed (see Cliff & Ord 1981). Of these, two indices, Moran's I and Geary's contiguity ratio c are the most appropriate for the analysis of telemetric data: they permit the weighing of distances or other measures of connection between two area units and they have been shown to be far superior to other measures (see Chapter 6 of Cliff & Ord 1981). Computation procedures are illustrated for both in Appendix 7.

Although particularly Moran's I bears some resemblance to normal correlation coefficients, it is worth pointing out that the two measures depart from 'normal' correlation coefficients in several aspects. In

Moran's I the expected value is not 0 (as for a normal correlation coefficient) but changes with sample size, and always lies below zero, if only slightly for large samples sizes, while the expected value of Geary's c is 1. Although Moran's I ranges approximately from -1 (perfect negative autocorrelation to +1 (positive autocorrelation), extreme cases are conceivable where these values may not be reached or even surpassed. In the case of Geary's c, perfect positive autocorrelation is at a value of 0 while there is no definite limit for negative autocorrelation (for details see Cliff and Ord 1981). These deviations from the pattern of normal correlation coefficients can also mean that the level of significance may decrease to values as low as 0.1 (for Moran's I) which is not directly comparable to a value of 0.1 of, say, Pearson's coefficient. Tests of significance for both measures are described in Appendix 7 as well. While for Moran's I the test is usually applied in its two-tailed version, Geary's c can be tested only for positive autocorrelation.

The two measures are sensitive to slightly different behaviours of the data (Jumars et al 1977). Moran's I is most sensitive to large deviations from the mean (x_i-x) weighed strongly, while c is most sensitive to the difference (x_i-x_j) independent from the overall mean. In other words, I is most sensitive to a proximity of extreme x_i values, while c is most sensitive to a proximity of similar or dissimilar x_i values, independent from their departure from the overall mean, x.

APPENDIX 6. A sequence of citations from the geographical and anthropological literature on the importance of spatially related data.

(1) Francis Galton (1889) remarked on a paper by Tylor on the historical links between societies through migration and cultural diffusion:

It was extremely desirable for the sake of those who may wish to study the evidence for Mr. Tylor's conclusions, that full information should be given as to the degree in which the customs of the tribes and races which are compared together are independent. It might be, that some of the tribes had derived them from a common source, so that they were duplicate copies of the same original. Certainly, in such an investigation as this, each of the observations ought, in the language of statisticians, to be carefully 'weighted'.

(2) W.R. Tobler (1970) defined the 'first law of geography':

Everything is related to everything else, but near things are more related than distant things.

(3) P.R. Gould (1970) discussed the interest geographers should show for spatially related data:

Why we should expect independence in spatial observations which are of the slightest intellectual interest or importance in geographic research I cannot imagine. All our efforts to understand spatial pattern structure and process have indicated that it is precisely the lack of independence - the interdependence - of spatial phenomena that allows us to substitute pattern, and therefore predictability and order, for chaos and apparent lack of interdependence - of things in space and time.

(4) F.F. Stephan (1934) discussed the nature of geographic data:

Data of geographic units are tied together like bunches of grapes not separate like balls in an urn.

APPENDIX 7. Computation procedure and test on significance of Moran's I and Geary's c. Formulae taken from Haggett et al. (1977), Jumars et al. (1977) and Cliff and Ord (1981).

(1) Basic notation

X a random variable (e.g. intensity of use expressed as hours spent or frequency of visits)

x_i i-th value of X; i = 1,2,...,N; N = total number of observations

each observation is located on a systematic grid with equal cell size, one observation represents the value of X for one cell;

d_{ij} Euclidean distance between cells of observations i and j; by definition the coordinate of a cell was its lower left corner; distance was standardized by division through cell length (50 m)

w_{ij} the weight associated with each pair of i-th and j-th observation; w_{ij} and w_{ji} need not be symmetric but were defined so in all computations, i.e. $w_{ij} = w_{ji}$.

(2) Weighing matrix (W)

the weights w_{ij} were parametric functions of the distance d_{ij} and followed one of the following functions:

$W_1(g) = 1$; if $g < d_{ij} < (g + 0.99)$; g = distance in cell length units

$= 0$; otherwise

$W_2 = e^{-\beta_1 d_{ij}}$ with $\beta_1 = 1$;

$W_3 = d_{ij}^{-2}$

$W_4 = e^{-\beta_2 d_{ij}}$ with $\beta_2 = 0.5$;

$W_5 = d_{ij}^{-1}$

(3) Computation of Moran's I

$$I = N \frac{\sum_{i=1}^{N}\sum_{j=1}^{N} w_{ij}(x_i-\bar{x})(x_j-\bar{x})}{W\sum_{i=1}^{N}(x_i-\bar{x})^2} \quad \text{; with } W = \sum_{i=1}^{N}\sum_{j=1}^{N} w_{ij} \quad \text{with } i \neq j$$

(4) Expected values of mean and variance for Moran's I

For the purpose of testing the significance of the value of I the expected first and second moments have to be calculated. This can be done under two, different null hypothesis:

a) Normality: the x_i are the result of N independent drawings from a normal population or populations; (N)

b) Randomization: the position of the observed value of I is not in any sense unusual in the set of values of I, if all possible spatial arrangements of the x_i (there are n! arrangements) are evaluated (R)

The expected means are identical for both null hypotheses, but not the expected variances.

$$E(I)_N = E(I)_R = -(N-1)^{-1} \quad \text{(expected value of mean)}$$

$$\text{expected variance} = E(I^2) - (E(I))^2$$

$$\text{exp. var.}_N = (N^2 S_1 - N S_2 + 3W^2) / (W^2(N^2 - 1))$$

$$\text{exp. var.}_R = \frac{N((N^2-3N+3)S_1 - NS_2 + 3W^2) - B_2((N^2-N)S_1 - 2NS_2 + 6W^2}{N(-1)(N-2)(N-3)W^2} - (N-1)^2$$

with

$$S_1 = 0.5 \sum_{i=i}^{N} \sum_{j=i}^{N} (w_{ij} + w_{ji})^2 \; ; \; i \neq j$$

$$S_2 = \sum_{i=1}^{N} \left(\sum_{j=1}^{N} w_{ij} + \sum_{j=1}^{N} w_{ji} \right)^2$$

$$B_2 = \left(N \sum_{i=1}^{N} (x_1 - \bar{x})^4\right) / \left(\sum_{i=1}^{N} (x_i - \bar{x})^2 \right)^2$$

(5) Testing the significance of I

If $N \to \infty$ then I can be treated as an asymptotically normally distributed variable, if autocorrelation is zero. Serious inferential error is not likely, unless N falls below 20, in which case correction factors should be used. Thus

$$z = (I - E(I)) \sqrt{\text{exp. var.}} \; , \qquad (1)$$

can approximately be treated as a standard normal deviate. If

$$|z| > z_{\alpha} \qquad \alpha \text{ level of significance;}$$

then the null hypothesis of no autocorrelation is rejected, and the alternative hypothesis of presence of autocorrelation is accepted. Alternatively, it may be asked what value I has to adopt in order to place z in the critical region. For this purpose we solve eqn (1) for I to get $I_{crit,\alpha}$ and the result is

$$I_{crit,\alpha} = z\sqrt{(exp.var.)} + E(I) \qquad (2)$$

since z is identical with $t_{\alpha,\infty}$ eqn (2) can be written as

$$I_{crit,\alpha} = t_{\alpha,\infty}\sqrt{(exp.var.)} + \beta E(I) \; ; \; \beta = 1 \qquad (3)$$

However, the normal approximation to the distribution function of I may be conservative, if

$$N-(N/\sqrt{N}) \; < \; Q/4 \; < \; 2N-3\sqrt{(N)}-1 \qquad (4)$$

with Q being the number of pairs of observations considered. In this case, β modifies to (from eqn (3))

$$\beta = \sqrt{(10\alpha)} \qquad (5)$$

A detailed discussion and derivation of the distribution function is presented in Cliff and Ord (1981). It is worth mentioning here, that for any non-normal populations the $E(I^2)_R$ are particularly unbiased estimators of the moments, ie. they can be validly used whatever the underlying

distribution of the x_i!

(6) Computation of Geary's c

$$c = \frac{(N-1)\sum_{i=1}^{N}\sum_{j=1}^{N} w_{ij}\,(x_i-x_j)^2}{2W\sum_{i=i}^{N}(x_i-x)^2} \qquad i \neq j\ ;$$

(7) Expected values of mean and variance of Geary's c

The null hypotheses (conditions of N = normality and R = randomization) are identical with the hypotheses for Moran's I.

$E(c)_N = E(c)_R = 1$ (expected value of the mean)

$$\text{expected variance}_N = \frac{(2S_1 + S_2)(N-1) - 4W^2}{2(N+1)W^2}$$

$$\text{exp. var.}_R = \text{sum}_1 + \text{sum}_2\ ;$$

$$\text{sum}_1 = \frac{S_1\,(N-1)\,(N^2-3N+3-B_2(N-1))}{N(N-2)\,(N-3)W^2}$$

$$\text{sum}_2 = \frac{0.25S_2(N-1)\,(N^2+3N-6-B_2(N^2-N+2))+W^2(N^2-3-B_2(N-1)^2)}{N(N-2)\,(N-3)W^2}$$

(8) Testing the significance of c

Principles and conditions for conservativity of the normal approximation are identical with Moran's I (see above). The equation for the critical c is

$$c_{crit,\alpha} = 1 - t_{\alpha,\infty}\sqrt{exp.var.} + \beta(N-1)^{-1} \qquad (1)$$

$\beta = 1$; for the normal approximation

$\beta = \sqrt{10\alpha}$; if the conservativity criterium is valid

APPENDIX 8. Asymmetries of transition frequencies between patches as investigated by the Bradley-Terry model of paired comparisons

Here I outline the reasons for selecting the Bradley-Terry model of paired comparisons (Bradley & Terry 1952) to establish whether asymmetries in transition frequencies vary amongst links of neighbouring patches and the origin patch (for a definition see section 6.2.6). The model was adapted from a modified version previously used to assign cardinal dominance ranks to interacting individual animals (Boyd & Sil 1983). The procedure for computing asymmetries in transition frequencies and comparing them was as follows:

Each transition by an individual from one patch to a neighbouring patch was regarded as a 'contest' between the two patches. A Departure was arbitrarily assigned as a win and an Arrival as a loss of the contest. A group of patches consisted of the origin patch of a local window plus all neighbouring patches visited by the individual. A transition matrix was established by entering all the Departures and Arrivals (gains or losses) between the patches of a group. Then, the Bradley-terry model as modified by Boyd and Silk (1983) was used to asign a cardinal 'index of dominance' to each patch based on the transition matrix of a specific group. Patches were assigned cardinal ranks on a straight line in such a way that the distances on the line between patches i and j represented the 'amount' by which i 'dominates' j in terms of the probability P_{ij} that i 'defeats' j in any given encounter. (Here, defeat means that the individual is likely to depart from i to j rather than the reverse). If $P_{ij} > 0.5$, then patch i is said to stochastically dominate j.

Using the Bradley-Terry model to establish such ranks between partners in a contest has several advantages. The possibility of a cardinal dominance index permits a continuous spectrum of transition asymmetries.

Secondly, the Bradley-Terry model can be applied, even if some members of a group never interact, as is the case with two neighbouring patches of an origin patch that lie at opposite sides.

Application of the Bradley-Terry model necessitates the following assumptions:

1. There exists a stochastically transitive hierarchy amongst patches (see Boyd & Silk 1983 for a more detailed explanation). This condition is clearly violated, if none of the links show any asymmetries in transition frequencies or all asymmetries are equal. If this appeared to be the case, then this local window was discarded from further analysis.
2. The probabilities P_{ij} are constant for the period(s) of observations.
3. The outcome of an encounter is probabilistically independent of outcomes of previous encounters (ie. the probabilities of patch i winning n consecutive encounters with patch j is $(P_{ij})^n$).

These two assumptions mean in essence that the sequence of timing of encounters is unrelated to the outcome; they formalize the notion that any transition comprises a deterministic component assumed to be stable throughout the periods of observations, and a random component assumed to vary independently from one transition incident to the next.

Program PATDOMIN selected and compiled all transition matrices and program DOMTESTH (modified from the program listing obtained from Boyd and Silk (1983) and corrected, together with Dr. John Fa, with the help of Dr. FHC Marriott, Biomathematics Department, University of Oxford) calculated the Dominance Indices for each local window for each individual animal from selected periods of intensive tracking.

Since the Dominance Indices are calculated as maximum likelihood estimates, they have the comforting properties of being asymptotically unbiased, efficient and normally distributed (Boyd & Silk 1983). On this basis, methods can be developed to test hypotheses about the relative magnitude and differences of the dominance estimates within and between

groups (Boyd & Silk 1983). The null hypothesis of interest in our case states that:

> the patches belonging to the subset S_1 of a specific local window have the same cardinal dominance rank; where S_1 is the subset of all neighbouring patches except the origin patch.

The alternative hypothesis states that

> at least two patches within the subset S_1 have significantly different dominance indices.

To test the null hypothesis, the generalized likelihood ratio statistic is used which, after suitable modification, is approximately distributed as a chi square random variable with t degrees of freedom, t being the number of neighbouring patches per local window. A significant result would indicate that asymmetries in transition frequencies for different transition directions vary significantly amongst neighbouring patches. Program DOMTESTH was used to calculate the test statistic.

Appendix 9. Estimate of daily energy expenditure of lactating female badgers.

Total energy expenditure ($kcal\ day^{-1}$) = (1) Maintenance energy +
(2) Energy for hunting and searching prey +
(3) Energy for prey capture +
(4) Energy for copulation +
(5) Energy for lactation +
(6) Energy spent on cleaning and preparing the sett +
(7) Energy for thermoregulation

(Powell 1982:176). Thermoregulation is probably negligible during lactation (Powell 1982). Copulation, activities concerning the preparation of the sett, activities related to foraging, and lactation are mutually exclusive activities. Since female badgers do not seem to spend much time to search for a mate and are fairly passive during copulation (see text), the energy expenditure for copulation probably does not exceed that for hunting. Energy spent on cleaning the sett is difficult to estimate and is provisionally assumed similar to hunting energy per time unit. However, since this activity is not very important, if considered over the entire period of lactation (90 days), the error is probably not very important. Since the main item of the badger diet in Wytham is earthworms (Chapter 4), energy spent on capturing prey should be similar to energy spent on searching for and detecting prey ("hunting"). Thus, hunting energy, energy for prey capture, energy for copulation and energy spent on activities concerning the sett are assumed equal per time unit and summarized as "Activity Energy". The modified equation is then:

total energy = (1) Maintenance Energy during sleep and rest +

expenditure (2) Activity Energy during active periods +

(3) Lactation Energy

Ag.1 Maintenance Energy during sleeping and rest

This is assumed to be equivalent to the energy expenditure known as Basal Metabolic Rate (BMR).

BMR (ml O_2 g^{-1} hr^{-1}) = 0.3 (for Taxidea taxus, the American badger, Harlow, 1981)

Assuming that the European badger has a very similar BMR, this correpsonds to 34.56 kcal kg^{-1} day^{-1}. Using Hayssen & Lacy's (1985) empirical relationship of body weight and BMR for Carnivores (exp 0.738) and their conversion factors, we get the characteristic equation

$$BMR\ (kcal\ day^{-1}) = 61.459\ W^{.738} \qquad (1)$$

The average body weight of female badgers caught in early autumn (ie. at a time when they show a similar body weight as during the period of lactation) is 8.5 kg. This gives

298.19 kcal day^{-1}

Using Neal's (1977:142) data, badgers are active on average for

10 hours	at	February, 1st	set as	Day	1	of	lactation
9.5	"	" March, 2nd	"	"	" 30	"	"
9	"	" April, 1st	"	"	" 60	"	"
8	"	" May, 1st	"	"	" 90	"	"

The remainder is spent as rest or sleep. From this the energy spent during sleep can be calculated. Maintenance Energy is then

(hours of rest/24) * 298.19 kcal day^{-1}.

Ag.2 Activity Energy

Energy spent during the active period can be expressed as specific metabolic rate (SMR) while running (Powell 1982, Peters 1983). This is linearly dependent on running speed. From Peters (1983:81) we obtain:

SMR (kcal day^{-1}) = specific basal metabolism (BMR) * postural correction + net transport costs = $73.75\ W^{.738} + 196.55\ W^{.72}V$

with W body weight (kg), V running speed (m min^{-1}), using the BMR from eqn (1) times 1.2, the postural correction (Peters (1983))

Using 8.5 kg as the average body weight for a female badger in Wytham, we obtain

SMR (kcal day^{-1}) = 357.83 + 15.294 V

Using 10.74 m min^{-1} as the average running speed from a typical night of PEACEFUL, we get

522.087 kcal day^{-1}

Ag.3 Lactation energy

From Moors (1974)

lactation energy = (litter size * (kit growth energy + kit maintenance energy)) / (lactation efficiency * milk assimilation efficiency)

Litter size is set as 2.43, the average litter size from several published studies (Anderson & Trewhalla 1985). From Powell (1982)

kit growth = kit growth rate (g day^{-1}) * energy content per

energy unit weight (kcal g^{-1})

(kcal day^{-1})

Kit growth rate is difficult to determine. Peters (1983) suggests to use Case's (1978) empirically determined relationship of the growth rate for the time when the kit grows from 10 % to about 90 % of adult body weight

$$G_{10-90} \text{ (Watts)} = 0.445\ W^{.72}$$

which yields for an adult badger of 8.5 kg body weight 2.0775 Watts or

0.04 kg day^{-1} (1 kg wet mass equals 7 * 10^6 Joules,

Peters (1983))

or 40 g day^{-1}

Successive weightings of two young badgers reared in a Polish zoo yields an average linearized growth rate of 30 g day^{-1} (data from Gucwinska & Gucwinski 1968) and a rate of 39 g day^{-1} for later stages of development, for a reported adult weight of 9 kg which is fairly close to the value Case's. The average linearized growth rate for several badgers reared in captivity by Frank (1940) is ca 56 g day^{-1}. For a reported mean adult body weight 12.5 kg as again closely to the by Case's eqn predicted growth rate of 53 g day^{-1}, : the rate 30 g day^{-1} from the Polish zoo study as 'normal' investment and the (predicted) rate of 40 g day^{-1} as 'heavy' investment.

According to Powell (1982)

energy content per unit weight = 1.647 kcal g^{-1}

so that

kit growth energy (rate 1) = 49.41 kcal day^{-1}

(rate 2) = 65.88 kcal day^{-1}

Following again Powell (1982)

kit maintenance = K * (birth weight + (kit age * kit

energy (kcal day^{-1} growth rate))^B

$$(\text{rate } 1) = 77 * (0.091+(0.03 * \text{kit age})^{.738}$$

$$(\text{rate } 2) = 77 * (0.091+(0.04 * \text{kit age})^{.738}$$

with K = 77 (Powell (1982))

B = 0.738 (Hayssen & Lacy (1985))

birth weight = 91 g (Gucwinska & Gucwinski (1968))

The efficiency of lactation is estimated as 0.90, and the efficiency of milk assimilation as 0.95 (Moors (1974)). Together, lactation energy expenditure (kcal day^{-1}) amounts to

$$\text{Rate 1:}(120.066 + 187.11 * (0.091+0.03 * \text{kit age})^{.738})/0.855$$

$$\text{Rate 2:}(160.088 + 187.11 * (0.091+0.04 * \text{kit age})^{.738})/0.855$$

Ag.4 Summary: total energy expenditure

Using the activity schedules mentioned in Ag.1 and the relationships found in Ag.1, Ag.2, and Ag.3, total energy expenditure per day of a lactating female badger is

Rate 1:

$$(\text{hours asleep}/24) * 298.19 + (\text{hours active}/24) * 522.087 + ((120.066 + 187.11 * (0.091 + 0.03 * \text{kit age})^{.738})/0.855)$$

Rate 2:

$$(\text{hours asleep}/24) * 298.19 + (\text{hours active}/24) * 522.087 + ((120.066 + 187.11 * (0.091 + 0.03 * \text{kit age})^{.738})/0.855)$$

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