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COMPARATIVE ECOLOGY OF MUNTJAC *MUNTIACUS REEVESI* AND ROE DEER *CAPREOLUS CAPREOLUS* IN A COMMERCIAL CONIFEROUS FOREST

PETER FORDE

A thesis submitted to the University of Bristol in accordance with the requirements for the degree of Doctor of Philosophy in the Faculty of Science.

Department of Zoology May 1989

"Although the concept of competition is a central theme in much of modern ecological theory, it has proven to be surprisingly difficult to study in the field and is still poorly understood as an actual phenomenon. Some ecologists consider competition among the most important of ecological generalizations, yet others maintain that it is of little utility in understanding nature."

Pianka (1983)

ABSTRACT

This study describes the ecology and assesses the potential for competition within a community of large herbivores in a lowland coniferous forest. Faecal pellet surveys were used to describe the distribution and habitat selection by muntjac, roe and fallow deer, hares and rabbits throughout the forest. The highest spatial and habitat overlap occurred between muntjac and roe deer.

Over 11,000 radio fixes from adult muntjac and nearly 3,000 radio fixes from adult roe deer were used to describe the ranging behaviour and activity patterns of sympatric muntjac and roe deer in the south-east corner of the forest. Muntjac showed no significant seasonal changes in home range size or daily range length and did not show diurnal or seasonal range shifts. In contrast, roe deer showed significant seasonal changes in home range size and daily range length and did show diurnal and seasonal range shifts.

Muntjac were active for an average of 69% and roe deer for 56% of each twenty-four hour period, with approximately five active periods per day for both species. Muntjac and roe deer both showed crepuscular peaks of activity with lower levels of activity during the day and at night. Outside of dawn and dusk, muntjac were more active during the day and roe deer more active at night.

Faecal analysis was used to describe the diets of muntjac and roe deer. The diets selected by the two species were similar, with lowest dietary overlap between sympatric muntjac and roe deer during winter and higher overlap during the rest of the year.

The ecology and social organisation of muntjac and roe deer are discussed in terms of their functional positions within the Cervidae and multidimensional niche overlaps between sympatric muntjac and roe deer are presented.

ACKNOWLEDGEMENTS

Deer studies in the King's Forest were initiated by Norma and Donald Chapman and my thanks must go to them for selecting such an ideal study site and for setting up, along with Kath and Mick Claydon and Stephen Harris, the muntjac side of this study. Norma has allowed me unlimited access to her unpublished data, was a faithful companion in the forest and helped in many other ways. Kath and Mick assisted with jobs in the forest, kept me sane with their weekend visits and through long discussions greatly improved my knowledge of muntjac biology. Tony Reeman, the King's Forest ranger, who always found me, no matter what part of the forest I was hiding in, was always helpful and provided much valuable information. Although too numerous to mention, I would like to thank all those willing volunteers, who have spent numerous days catching muntjac and roe deer in the King's Forest. My mountain bike provided sturdy transport around the forest and did not fall to bits too often! Audrey and Peter Smith were ever helpful landlords, allowed me to borrow transport and helped make life bearable in many other ways!

In Bristol, members of the ever growing research group have provided help and encouragement during the preparation of this thesis. Dave Rogers, Alan Blackman and George Gooding at the Computer Centre have written the FORTRAN programs used in the analyses and spent innumerable hours sorting out my computing queries. Sue Evans and Margaret Irish also at the Computer Centre have helped with various pieces of statistical advice. Alex and Stephen kindly put me up while I was commuting between Suffolk and Bristol.

Last, but by no means least, I would like to thank my mother for support throughout my "learning days", The Department of Education for Northern Ireland for funding the project, the Zoology Department at Bristol for providing facilities and my supervisor Dr Stephen Harris for setting up the project, for helping to make my job easier and for his support and encouragement throughout.

DECLARATION

Muntjac studies in the King's Forest started in 1979, with radio-tracking studies commencing in 1982. My own involvement with the study began in 1985, when the radio-tracking studies of roe deer were initiated. Thus some of the analyses are based on raw data collected by others. With these exceptions, I declare that the work contained in this thesis is my own, undertaken under the supervision and guidance of Dr S. Harris. No part of this work has been submitted for consideration for any other degree or award.

Peter Forde

Peter Forde

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CHAPTER ONE: GENERAL INTRODUCTION

1.1 INTRODUCTION

Chinese or Reeves' muntjac *Muntiacus reevesi* were introduced to Woburn Park and the surrounding woods in Bedfordshire at the beginning of this century (Chapman, *in press*). They were first reported outside this area from 1922 onwards and are now well established throughout much of southern England (Figure 1.1a).

Roe deer *Capreolus capreolus* had become extinct throughout England by the beginning of the 18th century and the current roe deer population of southern England is derived from introductions (Staines & Ratcliffe, *in press*). Roe of unknown origin were introduced into Milton Abbas, Dorset in 1800, and have colonised an area from west Kent to Cornwall. Deer of German stock were introduced into East Anglia in 1884 (Chapman *et al.*, 1985) and now form a population distributed through Norfolk, Suffolk and Essex (Figure 1.1b).

During the 1950s and 1960s, muntjac colonisation of the Midlands, in the absence of any other medium sized herbivore, was extremely rapid and they appeared to be occupying a vacant niche. More recently, the spread of roe deer north and westwards and of muntjac south and eastwards has meant that in some areas the two species are now sympatric (Figure 1.1c).

Hofmann (1985) has classified both muntjac and roe deer as 'concentrate selectors' on the basis of their small body size and gut morphology, which is adapted to a rapid throughput of high quality and easily digested food items. Muntjac and roe deer would thus be expected to have similar habitat requirements and in the areas of overlap some degree of competition may be expected. This could have important effects for forest management; for example removal of browse at ground level by muntjac could cause an increase in browsing damage to tree crops by roe deer. Any reduction in roe numbers due to the presence of muntjac is also undesirable from a sporting point of view (Prior, 1983).

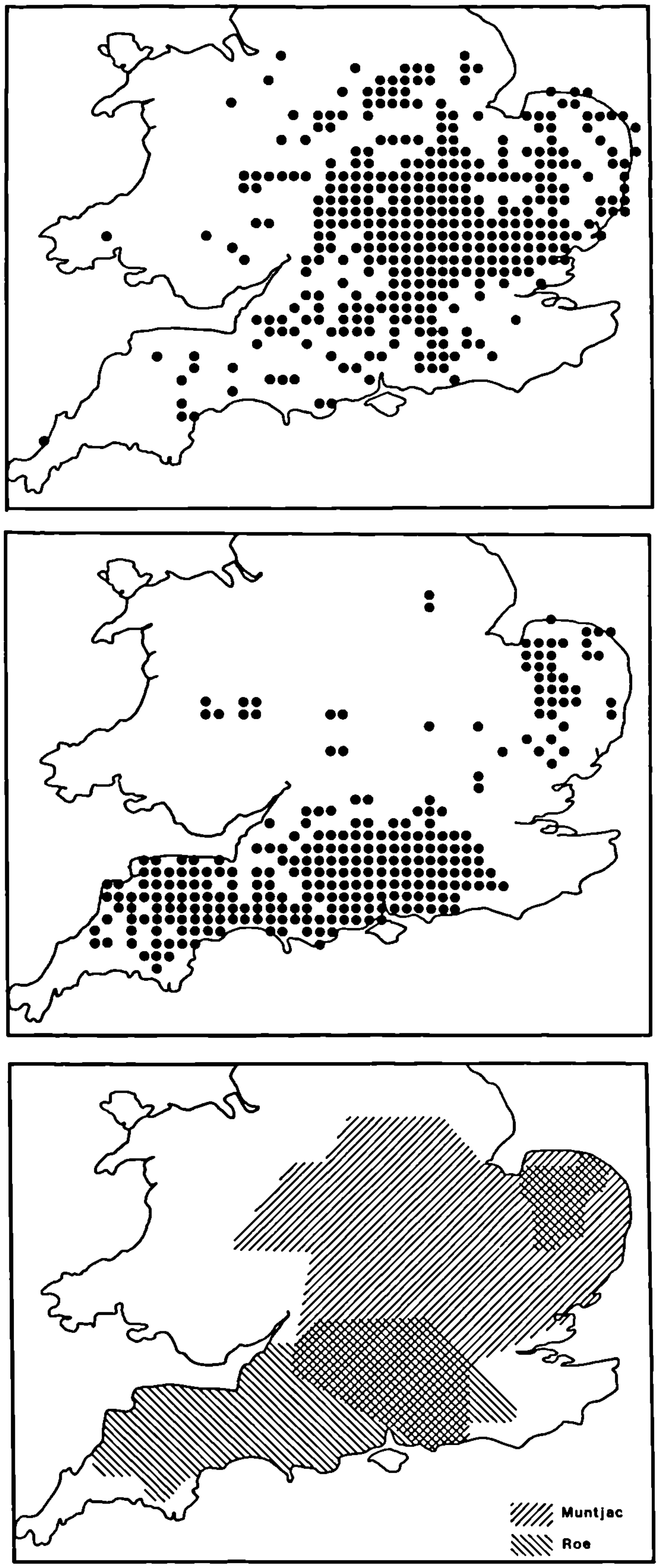
The King's Forest in Suffolk was probably one of the first areas in southern England to have sympatric muntjac and roe deer populations; muntjac colonised the forest, which already contained roe deer, during the early 1960s (Chapman *et al.*, 1985). It is therefore an ideal study site to examine interactions between the two species, since the populations have probably reached some level of stability. In this study, a comparative approach was used to

Figure 1.1a-c Distribution of muntjac and roe deer in southern England (after Arnold, 1984; Tee *et al.*, 1985; Harding, 1986).

Figure 1.1a Muntjac distribution.

Figure 1.1b Roe deer distribution.

Figure 1.1c Overlap in muntjac and roe deer distributions.


Muntjac
Roe

examine the hypothesis that there are competitive interactions between muntjac and roe deer.

1.2 MUNTJAC AND ROE DEER BIOLOGY

Detailed reviews of the origins and biology of muntjac and roe deer in Britain are given by Chapman (*in press*) and Staines and Ratcliffe (*in press*) respectively. A few of the salient details not given in later chapters of this thesis are presented here.

Reeves' muntjac is the smallest of the wild British deer. They stand between 45 and 50 cm at the shoulder and average weights in southern England are 14.8 kg (n=105) for bucks and 12.2 kg (n=124) for does (Chapman, *in press*). Muntjac breed throughout the year with no obvious peak in births, and therefore does can be pregnant or lactating during any month of the year (Chapman *et al.*, 1984). There is a post-partum oestrus and so conception is usually within a few days of parturition. Thus once a female becomes sexually mature at seven or eight months of age, she will then be almost continually pregnant. Although females show no seasonal reproductive synchrony, both bucks and does do have a seasonal moult cycle and adult bucks have seasonal cycles of antler growth and testicular activity (Chapman & Chapman, 1982). Adult bucks cast their antlers between April and July, the new antlers are grown during the summer, with the velvet shed between August and October.

In its native habitat in south-east China, the sub-species *M.r. reevesi*, which was introduced to Britain, inhabits scrub and dense forest between 200 and 400m. Harding (1986) reports that in relation to the climate in southern England, the climate within their range in south-east China is wetter throughout the year. Temperatures are comparable between December and February, but warmer between March and November.

Roe deer stand at between 60 and 70 cm at the shoulder and average weights for roe deer in Thetford Forest are 27.5 kg for bucks and 21.2 kg for does (carcass weights from Staines & Ratcliffe, *in press*, converted to live weights using the formula in Prior, 1968). They show a typical temperate birth pattern, with most births between mid-May and mid-June. Oestrus is not immediately post-partum, but occurs during the rut from mid-July until the end of August. Roe deer exhibit delayed implantation; the blastocyst does not implant into the uterine wall until late December - early January (Short & Hay, 1966).

Roe deer are unusual compared to other temperate deer; the antlers are cast between October and December, new antlers are grown overwinter and the velvet is shed in April. There is a seasonal moult cycle and a seasonal testicular cycle. The testes are active from mid-May until mid-November and regressed between December and March (Short & Mann, 1966; Bramley, 1970).

1.3 COMPETITION AND NICHE THEORY

Pianka (1976) defined competition as occurring when two or more organisms, or groups of organisms such as populations, interfere with or inhibit one another. This will arise when populations use the same resources and these resources are in limited supply (Pianka, 1983). This review is in no way an attempt to summarize all the current thinking in what is a very contentious and wide ranging field, rather it attempts to set out some of the basic principles so that the comparative approach to competition used in this study can be put into context. More detailed reviews of competition and niche theory can be found in Pianka (1976, 1983), Putman & Wratten (1985) and Arthur (1987). In this review and throughout this thesis, competition refers to interspecific competition, i.e. competition between individuals belonging to different species.

Three kinds of inhibitory effects between populations have been noted. Interference competition arises from direct interactions e.g. interspecific territoriality, exploitative competition from the joint use of resources and apparent competition results from a predator consuming individuals of both species (Holt, 1977, 1984). These are not distinct categories since to satisfy both conditions of competition, i.e. that populations use the same resources and that these are limited, some kind of exploitative competition is probably a prerequisite for interference competition (Pianka, 1976).

Inevitably discussions on competition will include definitions of the way a species uses resources - the niche of that species. Pianka (1976, 1983) and Arthur (1987) discuss the historical derivations of the niche and conclude that it is best described by two formal definitions involving resource utilization functions (RUFs). Hutchinson (1957) defined the niche as an n-dimensional hypervolume, each of the dimensions corresponding to an independent variable influencing the life of a species. Each of these dimensions can be equated with MacArthur's (1970, 1972) view of the niche as a RUF, i.e. a plot of utilization against some quantitative resource variable (e.g. the size of seeds eaten by granivorous birds). The best description of the niche probably falls somewhere between the two, as a series of RUFs each occupying a different niche axis.

The fundamental niche of a species refers to the range of conditions along the resource axes that could be exploited if abiotic factors alone influenced distribution. The realised niche is what is left of the fundamental niche once biotic factors are taken into account. The difference between the fundamental and realised niches reflects the effects of interspecific competition (Pianka, 1976). Niche overlap describes the overlap in RUFs for a pair of species along a resource gradient. It is often quoted as evidence for competition, but this will only be true if the resource being exploited is in limited supply.

When sympatric populations interact, there are two possible competitive outcomes: - either at least one of the species may become extinct or the species may evolve to allow coexistence. Gause (1937) formally described how the effects of competition could lead to extinction in the 'competitive exclusion principle'. His own experiments with *Paramecium aurelia* and *P. caudatum* (Gause, 1934) and other laboratory experiments (Park, 1948; Arthur, 1980; Bellows & Hassell, 1984) have all supported this principle, where in mixed cultures one of a pair of species becomes extinct. These laboratory experiments have been criticised as being oversimplistic; the niches available are limited, the environments are stable, and intrinsically unstable *r*-selected species are used. Arthur (1987) concludes that in natural populations there is probably no single conclusive case for the existence of competitive exclusion. For instance, throughout much of England and Wales, introduced grey squirrels *Sciurus carolinensis* have replaced native red squirrels *S. vulgaris*. Kenward & Holm (*in press*) suggest that in deciduous woodland grey squirrels may have a competitive advantage through more efficient utilization of nut crops. However, Reynolds (1985) noted that red squirrels sometimes disappeared before the appearance of grey squirrels, possibly due to disease epidemics (Keymer, 1983), while Harris (1973/74) showed that in parts of Essex, red and grey squirrels coexisted for periods of up to 25 years.

Coexistence of sympatric species has been demonstrated in laboratory experiments, such as Gause's later experiments with *Paramecium caudatum* and *P. bursaria* (Gause, 1936, 1937), and also seems to be the normal situation in natural ecosystems. Niche shifts, character displacements and resource partitioning have all been put forward as evidence that coexistence in natural communities results from competitive interactions.

If the niches of two species A and B overlap less in sympatry than in allopatry, then this may be a response to competition. Behavioural or ecological changes in sympatry are referred to as niche shifts, while morphological changes in sympatry are described as character displacements. Competition can only be inferred from these niche changes if the niche dimension in question is limiting and if the niche changes are heritable. Niche shifts have been demonstrated by experimental manipulation of winter foraging flocks of European tits *Parus spp.* and goldcrests *Regulus regulus* (Alatalo, 1981, 1982; Alatalo *et al.*, 1985). Reductions in the density of one species caused the remaining species to forage in parts of the tree canopy from which they were formally excluded.

The proposed mechanism whereby competition causes character displacement in sympatry can be explained as follows. If the use of different sized seeds by two species of granivorous birds is invisaged as two overlapping RUFs along an axis of seed size, and the size of seed eaten is related to bill size morphology, then in sympatry, selection should result in the bill of the species with the smaller bill becoming smaller and the bill of the species with the larger bill becoming larger, thereby reducing niche overlap. Examples of this phenomenon are widespread and have been reviewed by Grant (1972, 1975). In a recent example, Malmquist (1985) compared skull measurements of sympatric and allopatric populations of pygmy shrews *Sorex minutus* and common shrews *S. araneus.* He found that skull size of *S. minutus* was always reduced in sympatry. Although character displacement is a common phenomenon, before competition can be inferred as the driving force, three initial assumptions must be satisfied. Firstly the character distributions must reflect RUFs, secondly the characters must be heritable, and thirdly there must be exploitative competition in sympatry. Few studies have examined all these assumptions and Grant (1972, 1975) further points out that environmental differences between allopatric and sympatric study sites can account for many of the observed instances of character displacement.

Within communities, competitive interactions will be most intense between species at the same trophic level, or within more restricted community units usually referred to as guilds. Root (1967) defined the guild as a group of species that exploit the same class of environmental resources in a similar way. Membership of a guild implies niche overlap but does not infer competition; this also requires that commonly exploited resources are limited. Competition has been thought of as allowing coexistence within guilds, by being the driving force behind resource partitioning. So long as two species within a guild are separated along at least one limiting resource axis, competitive exclusion will be prevented. In all guilds so far studied, resource partitioning between sympatric species has been found along at least one niche axis. Species either exploit different habitats/microhabitats, eat different foods, or are active at different times of day. Some examples of resource partitioning within guilds are given below.

Emmons (1980) examined habitat selection by nine species of African rain forest squirrel. Two species were separated by occurring in different locations. The remaining seven species were all found in mature rain forest, but within this habitat they were separated vertically. Four species were arboreal, while three species foraged at ground level. In addition, within these foraging groups, differences in body size could be related to partitioning of fruit resources by size and hardness.

Dietary resource partitioning has been described as a mechanism that allows coexistence of large African herbivores (Lamprey, 1963; Bell, 1970, 1971; Stewart & Stewart, 1971; Hansen *et al.*, 1985; McNaughton & Georgiadis, 1986). Wildebeest *Connochaetes taurinus*, zebra *Equus burchelli*, and buffalo *Syncerus caffer* feed exclusively on grasses, eland *Taurotragus oryx* and impala *Aepyceros melampus* are mixed feeders, while giraffe *Giraffa camelopardalis* and dikdik *Madoqua kirkii* feed extensively on browse. Further partitioning occurs within dietary groups due to species using different growth stages of grasses and by browsing at different heights.

Differences in the timing of activity can only reduce competition between two species if they are exploiting the same resource (usually food) and this resource is rapidly renewed (or only slowly depleted), so that the quantity of resource at time t equals that at time t + Δt. Reduction in competition is not a good explanation for some examples of temporal partitioning, such as swallows and bats, since different species of insect fly by day and at night. Temporal partitioning may be more important amongst groups of herbivores, since plant resources are depleted slowly and resource availability, in the short term, is not influenced by the time interval between visits to a food patch. Amongst herbivores that use the same food resources, temporal partitioning should operate by reducing interference competition.

An example of temporal partitioning in herbivores, is the study by Glass & Slade (1980) of cotton rats *Sigmodon hispidus* and prairie voles *Microtus ochrogaster*. During the breeding season, the two species are spatially separated, while outside this period they coexist sympatrically. In allopatry, both species are largely nocturnal, whereas in sympatry voles shifted their activity to become largely diurnal.

It should be stressed that within guilds, resource partitioning seldom occurs along a single resource dimension. Instead, separation occurs along several dimensions so that species pairs with a high overlap along one dimension have a low overlap along another. For example, lizards of the genus *Ctenotus* in western Australia forage at different times, in different microhabitats, and/or on different foods (Pianka, 1969).

Many studies have inferred competition from patterns of niche overlap and resource partitioning found by studies of comparative ecology. However, this will only be true if:

1. Niche divergence has actually occurred.
2. If competition was responsible for these niche changes.
3. If the niche changes have a genetic basis.

These assumptions are seldom tested and Connell (1980) has put forward an alternative view of how niche partitioning might arise. He suggests that species might have diverged as they evolved separately, so that when they later came together, they coexisted because of adaptations to different resources. Thereafter competition might keep them apart, but it was not the initial cause of resource partitioning.

Connell (1983) and Schoener (1983) have both reviewed the evidence from field experiments for interspecific competition as a force in the shaping of natural communities. The majority of studies reviewed by both authors found evidence of competition, although there were reservations about lack of suitable controls with some experiments. The present evidence suggests that competition probably is important in the shaping of ecological communities, although many authors still infer competitive effects from studies of resource partitioning and niche shifts, in the absence of adequate experimental testing. Studies of comparative ecology and resource partitioning will certainly reveal information about community structure and can be used to suggest potential competitive effects, but they must be backed up by carefully controlled experiments if competition is to be confirmed as the driving force behind the observed patterns of resource partitioning.

The aim of this study is to describe the interactions and assess the potential for competition within a sympatric population of muntjac and roe deer in the King's Forest, in Suffolk. This was carried out within the framework of an overall project, began in 1979, whose primary aim was to describe the ecology and social organisation of feral muntjac in a commercial coniferous forest. Competition is assessed through a comparative ecological approach, using a combination of extensive studies throughout the forest and intensive radio-tracking studies of a marked population of muntjac and roe deer in the south-east corner of the forest. The extensive studies have also included the other three forest herbivores, fallow deer *Dama dama,* brown hares *Lepus europaeus* and rabbits *Oryctolagus cuniculus,* so that the ecological relationships between muntjac and roe deer can be put into context.

1.4 STUDY AREA

The study was conducted in the King's Forest, a mainly coniferous commercial forest, 2360ha in area, situated to the south of the main Thetford Forest, in the Breckland region of north-west Suffolk. It is surrounded on all sides by heathland, pasture and cultivated land growing cereals (wheat *Triticum aestivum* and barley *Hordeum vulgare*), sugar beet *Beta vulgaris var. altissima* and carrots *Daucus carotta*. There are a number of small copses and shelter belts scattered through the surrounding farmland.

The climate is more continental than most of southern Britain, with a wide annual temperature range, above average sunshine and low rainfall (Trist, 1979). Breckland soils are sandy and formed as superficial deposits on chalk-sand drift. The soils are complex in nature and changes in acidity and moisture retention, which affect vegetation growth, can occur over distances of less than one metre. Therefore, most soils have been mapped as soil complexes (Corbett, 1973). In the King's Forest, brown calcareous complexes and river valley gravel soils are both calcareous, whereas brown earth complexes are leached neutral to acidic deposits. Calcareous soils predominate in the south and east of the Forest, with acidic soils more common on the slightly higher ground to the north and west.

1.4.1 FOREST STRUCTURE

When the Forestry Commission acquired what is the present King's Forest in 1934, approximately 10% of the area was woodland (Second Edition Ordnance Survey map 1905, scale 1:10,560), largely as a result of plantings in the 18th and 19th centuries. Part of the remaining area was heathland and small areas of arable land, but most consisted of species-rich grassland.

Planting began in 1936 and has continued at intervals to the present. Initially both Corsican pine *Pinus nigra var. maritima* and Scots pine *Pinus sylvestris* were planted, although higher yields have meant that Corsican pine has been the predominant species planted during the last 25 years. Small areas have been planted with other conifers such as European larch *Larix decidua*, Douglas fir *Pseudotsuga menziesii* and more recently Norway spruce *Picea abies*. Some of the early plantings have already been clearfelled and restocked; the remainder of the 1936/37 plantings are due to be clearfelled by 1992.

Many of the old coverts and shelterbelts present prior to planting have been retained in the present forest. These consist of broadleaved plantings of oak *Quercus robur*, beech *Fagus sylvatica*, sweet chestnut *Castanea sativa* and sycamore *Acer pseudoplatanus* and coniferous plantings of Scots pine and larch. Along many of the roadside verges are single rows of mature beech, sycamore and horse chestnut *Aesculus hippocastanum*. Some of these old plantings have been felled and restocked with Corsican pine, so that in 1986 only 5% of the forest area was covered with "pre-plantation woodland". Additional broadleaved cover is provided by a number of strips of birch *Betula spp.*, and also some oak and beech planted during the 1950's.

The current composition of the King's Forest is given in Table 1.1. Conifers, mainly Corsican pine, cover 86.4% of the area, broadleaved trees 11.4% and 2.2% carries no tree cover. The forest is divided into 228 mostly square or rectangular compartments (Figure 1.2), ranging in size from four to 20 ha ($\bar{x}$ = 10.3 ha). Most compartments consist of several different plantings or sub-compartments, the basic units of forest management, which usually comprise a single species and age of tree, although some are mixed species plantings. Harris & Forde (*in prep.*) describe the ground vegetation changes through the forest cycle.

1.4.2 FOREST HERBIVORES

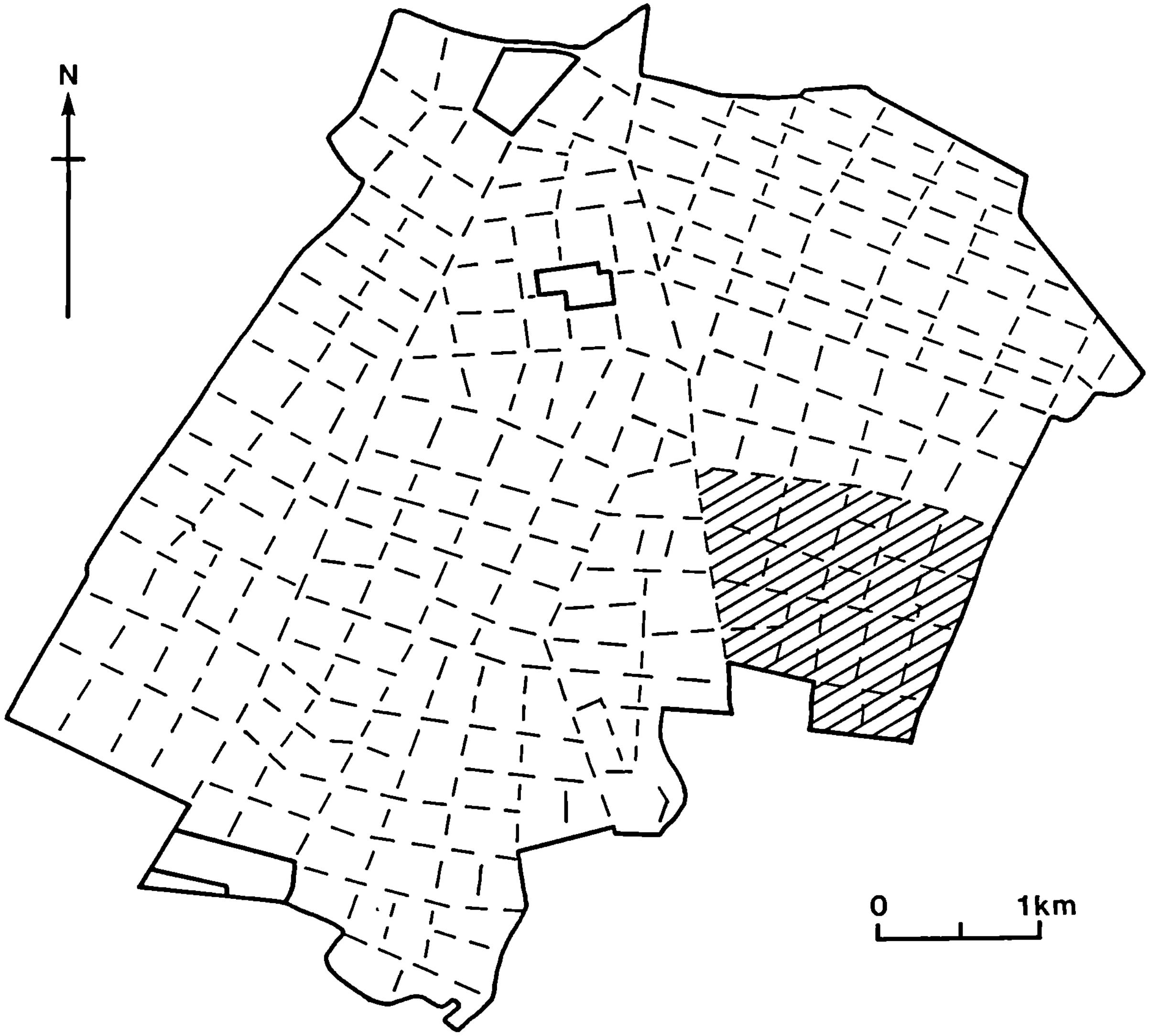
Five large herbivores are present in the forest; muntjac, roe and fallow deer, brown hares and rabbits. Sightings of red deer *Cervus elaphus* have decreased considerably over recent years; they are now only occasional visitors to the forest and so were not considered in the present study. Chapman *et al.* (1985) describe the history of the deer in the King's Forest. Muntjac were first recorded in the forest during 1963, with sightings becoming increasingly common in the later part of the 1960s and throughout the 1970s. Claydon *et al.* (*in prep.*) estimated the muntjac population (± 95% confidence limits) in 1986 at 133 ± 17 deer. This gave a overall density of 5.4 deer km^{-2}, but since muntjac were largely confined to the south and east of the forest, local densities were considerably higher. For example, in the south-east corner of the forest there were 15.0 muntjac km^{-2}.

The roe deer introduced near Thetford in 1884 were present in the area that is now the King's Forest when planting began in the 1930s (J. Brame, *pers. comm.*). The young plantations provided suitable cover and the roe deer population rapidly increased. As the forest structure changed, it seems likely that the roe deer population reduced, although since the early 1970s, the Forestry Commission rangers estimates (A. Reeman & R. Whitta, *pers. comm.*) suggest that the population has again increased as the forest matures. In 1986 Claydon *et al.* (*in prep.*) estimated the roe deer population (± 95% confidence limits) at 269 ±

Table 1.1 Tree cover in the King's Forest in 1986.

		% Total area	
Corsican pine			
	>40 yrs	22.5	
	32-40 yrs	19.0	
	20-31 yrs	9.2	
	10-19 yrs	7.9	
	4-9 yrs	2.4	
	<4 yrs	1.5	62.5
Scots pine			
	>50 yrs	1.6	
	41-50 yrs	9.8	
	34-40 yrs	9.4	
	20-33 yrs	1.6	
	<20 yrs	0.0	22.4
Other conifers			
	<50 yrs	1.5	1.5
Broadleaved nut producing trees			
	>50 yrs	2.5	
	<50 yrs	2.7	5.2
Broadleaved non-nut producing trees			
	>50 yrs	0.9	
	<50 yrs	5.3	6.2
No tree cover			
		2.2	2.2

Figure 1.2 Outline map of the King's Forest, showing the compartment boundaries. The diagonal shading denotes the 206 ha study area in the south-east corner of the forest, where the radio-tracking studies were carried out.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1km

34 deer, giving an overall density of 11.4 deer km^{-2}.

The fallow deer originated from either one or possibly two former park herds that escaped earlier this century. Fallow deer have been present in the forest in low numbers, certainly since 1962, although it was not until the mid 1970s that their numbers started to increase. In 1985/86 the Forestry Commission rangers estimate was 20 bucks and 37 does (A. Reeman & R. Whitta, *pers. comm.*).

Hares were present on the heathland and species rich grassland that dominated the area that is currently the King's Forest (D. Brame, *pers. comm.*). There is no information on their status during the development of the forest, although their present abundance seems to be unusual compared to other lowland conifer forests.

Prior to planting the King's Forest, the principle land use of the area was the cropping of large numbers of rabbits (Macdonald, 1939; D. Brame, *pers. comm.*). When the forest was established, fencing and control operations reduced the rabbit population (J. Brame, *pers. comm.*), although rabbits remained common on areas of open ground within the forest until recent years (A. Reeman, *pers. comm.*). There are now few such areas and the small rabbit population is now largely confined to areas of young first rotation plantings and to the forest edge where it adjoins heathland.

1.5 THESIS STRUCTURE

The remainder of this thesis is organised as follows: Chapter 2 describes the results of two faecal pellet surveys, carried out throughout the forest. The results are used to describe the distributions of the five forest herbivores, to assess interactions between them and to determine habitat selection at the forest level using multiple regression analyses. Multiple discriminant analysis and niche overlap indices are used to describe habitat partitioning by the five herbivores.

The radio-tracking studies of sympatric muntjac and roe deer in the south-east corner of the forest are described in Chapters 3 and 4. The approach used in both these chapters is to compare males and females of the same species and then to compare the same sexes interspecifically or both sexes combined interspecifically as appropriate. Seasonal and annual home range size, internal range structure, diurnal variation in range use, seasonal range shifts and daily range length are presented in Chapter 3. Activity patterns are presented in Chapter 4, using a combination of data from routine radio-tracking, twenty-four hour radio-tracking sessions and automatic activity recordings.

Chapter 5 uses the analysis of plant epidermal fragments in faecal samples to determine muntjac and roe deer diet from a number of sites spread throughout the forest. Firstly muntjac and roe deer diets from all the sites combined are presented, then roe deer diet is compared between sites with and without sympatric muntjac and finally muntjac and roe deer diets from sympatric sites are compared.

Chapter 6 compares the ecology and social organisation of muntjac and roe deer with that of other small forest herbivores. Overall measures of niche partitioning are presented and the evidence for competitive interactions between muntjac and roe deer is discussed.

The multivariate statistical analyses in this thesis were carried out using SPSS^{X} (Norusis, 1985; SPSS^{X}, 1986) initially run on an ICL S39 L80 at the South-West Universities Regional Computer Centre and laterally on an IBM 3090 at the Bristol University Computer Centre. The univariate statistics were carried out using both SPSS^{X} on the above computers and Minitab (Ryan *et al.*, 1985) on the Bristol University Geography Department SYSTIME 8750 computer.

CHAPTER TWO: HABITAT SELECTION

2.1 INTRODUCTION

This chapter describes the use of faecal pellet surveys to determine the distribution and abundance of muntjac, roe and fallow deer, hares and rabbits throughout the King's Forest. A variety of multivariate techniques are used to assess the factors influencing these distributions and to describe the ecological relationships between the five herbivore species.

Habitat selection by roe deer has been studied at Chedington Wood in Dorset and at Porton Down in Wiltshire by Johnson (1984), at Hamsterley Forest in Co. Durham by Henry (1981), and in Scotland by Batcheler (1960), Loudon (1979), Staines & Welch (1984), and Hinge (1986). Harding (1986) has studied habitat selection by muntjac in Rushbeds Wood, near Oxford and Chapman *et al.* (1985) have already described the distribution of the deer species and some aspects of habitat selection by muntjac and fallow deer, but not roe deer, in the King's Forest, using a visual survey technique. Very little is known about habitat selection by lagomorphs in coniferous forests and their relationships with sympatric deer species.

Faecal pellet surveys have been used extensively to measure herbivore population size (Dasmann & Taber, 1955; Ratcliffe, 1987; Claydon *et al.*, *in prep.*) and to assess habitat selection (Henry, 1981; Brusnyk & Gilbert, 1983; Kirchhoff *et al.*, 1983; Loft & Menke, 1984). Putman (1984) and Staines & Ratcliffe (1987) have described some of the uses and limitations of faecal pellet counts for the study of herbivore populations.

Faecal pellet densities can either be measured as the standing crop of faeces (faecal standing crop or FSC) or as the rate of accumulation of faeces over a known period of time (faecal accumulation rate or FAR). The FSC technique has the advantage that only one visit is required. However, because rates of pellet decomposition differ between habitat types (Wigley & Johnson, 1981), pellet counts will need to be corrected for differential rates of decomposition. The FAR technique also requires some knowledge of decomposition rates to select an appropriate time interval between clearing and sampling. Both techniques require measures of findability of faecal pellets in different habitat types and assessments of identification accuracy when more than one species is present. In this study, so that every sub-compartment in the forest could be surveyed, FSC counts corrected for differential rates of decomposition and findability were used and identification accuracy was also assessed.

Habitat partitioning has been described in sympatric ungulate communities in Africa (Lamprey, 1963; Hirst, 1975), in Britain (Batcheler, 1960; Staines & Welch, 1984; Hinge, 1986; Chapman *et al.*, 1985; Putman, 1986), and extensively in North America (Hudson, 1976; Anthony & Smith, 1977; Hayden-Wing, 1979; Wydeven & Dahlgren, 1985; Wiggers & Beasom, 1986; Smith, 1987; Jenkins & Wright, 1988). Generally, these studies have shown that sympatric ungulates partition resources so that species occupy different habitats, or the same habitats at different times or in different places. This general relationship is also found when sympatric ungulates of similar body size are examined (Anthony & Smith, 1977; Wiggers & Beasom, 1986; Smith, 1987). Many of these studies have suggested that resource partitioning is the result of coevolution by sympatric species to reduce interspecific competition, although Jenkins & Wright (1988) found temporal changes in the degree of resource partitioning that were inconsistent with this hypothesis.

Previous studies of habitat partitioning by ungulates have relied on the use of various niche overlap indices to assess the degree of resource partitioning. More recently, multivariate analyses, in particular multiple discriminant analysis (MDA), has been suggested as an alternative technique (Green, 1971, 1974; Hudson, 1976; Dueser & Shugart, 1979; Van Horne, 1982). MDA partitions species along independent resource dimensions and thus ecological separation more closely approximates to the Hutchinson (1957) view of the niche as a series of independent niche axes forming an n-dimensional hypervolume. In this study, both niche overlap indices and MDA are used to examine resource partitioning.

2.2 METHODS

2.2.1 VEGETATION SURVEY

Every sub-compartment shown on the Forestry Commission stock map was surveyed during October and November 1983. Any sub-compartments that had been felled and restocked between 1983 and 1986 were resurveyed during May 1986, as were any plantings less than 10 years old in 1986. Additional features such as rows of mature trees and areas of open ground, not marked on the stock map, were designated as additional sub-compartments, giving a total of 692 sub-compartments. The initial survey was undertaken by Stephen Harris for a previous study of deer distribution and habitat selection in the King's Forest (Chapman *et al.*, 1985), and for uniformity he also carried out the 1986 update.

Each sub-compartment was traversed several times and the following data recorded:

1. The relative importance of the tree species was assessed as % Scots pine, % Corsican pine, % other conifers, % nut producing broadleaved trees and % non-nut producing broadleaved trees. Tree diversity was assessed as the number of conifer species, the number of nut producing broadleaved species and the number of non-nut producing broadleaved species. Spacing of the trees was determined on a scale from one to seven and the age of the trees in 1986 was extracted from the Forestry Commission stock map.

2. Ground cover from vegetation was assessed as % grass, % herb, % bracken *Pteridium aquilinum*, % bush and % bare ground. Herb cover was taken to include all broadleaved plants which were on average less than 100cm in height. On this basis, bramble *Rubus fruticosus agg.* and raspberry *Rubus idaeus*, which were normally less than 70cms in height under the trees, were included as contributing to herb cover, as were Oregon grape *Mahonia aquifolium*, broad-buckler fern *Dryopteris dilatata* and male fern *D. felix-mas*. Climbing species such as ivy *Hedera helix* and clematis *Clematis vitalba* were included as bush cover. In addition, for the grasses and bushes an index of diversity was assessed on a one to five scale, where 1 = one species, 2 = two to three species, 3 = four to five species, 4 = six to seven species and 5 = eight or more species. For herbs the same categories were assessed using the number of families rather than the number of species.

3. Abundance of bramble and abundance of raspberry was assessed on a one to five scale, where 0 = absent, 1 = trace amounts, 2 = scattered occasional clumps, 3 = up to 30% cover, 4 = 31-75% cover and 5 = greater than 75% cover.

4. Ground cover from fallen trees and branches (brashings) was recorded on a one to five scale, where one was very sparse, up to five which was difficult for a person to penetrate.

5. The presence of adjacent farmland and heathland was recorded as zero, one or two, where zero, one or two sides respectively of the compartment containing that sub-compartment adjoined farmland or heathland.

6. Each sub-compartment was allocated to one of three soil types based on the map accompanying Corbett (1973); these were brown calcareous soil complexes, river valley gravel soils and acidic brown earth soils and complexes. The first two categories were combined as calcareous soil types.

7. The area of each sub-compartment was measured from an enlarged copy of the stock map using a digitizing table.

The sub-compartments were grouped using a clustering technique based on squared Euclidean distances following standardisation of the variables (Norusis, 1985). A *'tree type'* grouping was produced by clustering with the variables describing tree cover and age. This assigned sub-compartments to one of 29 clusters, each of which contained not less than four sub-compartments. Eight sub-compartments failed to form clusters and were allocated to an additional 30th cluster.

The sub-compartments were also clustered using the vegetation variables describing both the tree canopy and the ground vegetation. The *'tree type'* clusters were sub-divided into groups of sub-compartments with similar ground vegetation characteristics. This *'ground vegetation'* grouping assigned sub-compartments to one of 37 clusters, each of which contained not less than four sub-compartments. 35 sub-compartments failed to form clusters and were allocated to an additional 38th cluster.

2.2.2 WINTER PELLET SURVEY

Standing crop faecal pellet densities were estimated for muntjac, roe and fallow deer, hares and rabbits in all 692 sub-compartments of the forest between January and April 1986. The faecal pellet density was recorded in a series of 10x4m plots placed at 40m intervals along a transect from the south-west to north-east corner of each sub-compartment. A minimum of five plots were measured in the smallest sub-compartments; if necessary the south-east to north-west transect was also surveyed until five plots had been counted. The mean number of plots surveyed per sub-compartment (± S.E.) was 7.64 ± 0.12. In each plot faeces were identified by species, and the total number of pellets and (for deer) the number of pellet groups counted. Pellet groups were only counted if more than half the group was inside the plot. Since individual or scattered deer pellets are easily overlooked, deer pellet groups containing less than ten individual pellets, as well as those too decomposed to assign to species, were ignored. However, all lagomorph pellets were counted since these do not occur in groups and were generally easier to locate than scattered deer pellets. Lagomorph pellets were easily distinguished both from each other and from the three deer species. Tests showed that pellets of the three deer species could be distinguished with an overall accuracy of 76%. For each sub-compartment, the mean number of pellets and pellet groups per plot was calculated for each species.

Faecal pellet densities were corrected for differential decomposition using the results of a decomposition experiment carried out during January 1988. Decomposition was measured in 10 different *'tree type'* clusters, representing the most widespread types of planting in the forest. Within each cluster, two sub-compartments were selected and five groups of 40 fresh roe pellets were placed at 30m intervals along a transect. The number of pellets visible was counted immediately and after two, four, six and nine weeks.

There was a significant difference between clusters in the number of pellets visible immediately after placement (K-W ANOVA, $H=17.9$, $p<0.05$), indicating that pellet visibility was affected by ground vegetation structure and abundance. There were also significant differences at two, four, six and nine weeks (K-W ANOVA, all $p<0.05$), with a changed rank order suggesting that decomposition differed between habitat types in a different way to visibility.

After four weeks entire pellet groups started to disappear and so the % loss at four weeks was used to correct the faecal pellet densities for both findability and differential decomposition. A mean % decomposition was calculated for each cluster and used to correct pellet densities in other sub-compartments allocated to that cluster as follows;

$$\mathrm{CPD} = (\mathrm{MPD}/100\text{-}d)*100$$

where CPD = corrected pellet density
MPD = measured pellet density
d = mean % decomposition

Sub-compartments allocated to clusters in which decomposition had not been measured, were corrected using the decomposition value from a cluster of similar age and vegetational structure.

All analyses were carried out using the number of individual faecal pellets rather than the number of pellet groups, because the same measure could be applied to all five species and faecal pellet densities were easier to correct for differential decomposition. Kendall's coefficient of concordance (W) was used to examine the relationship between the number of muntjac and roe deer seen during the muntjac and roe deer winter censuses (Claydon *et al., in prep.*) and faecal pellet densities (Table 2.1). There was a significant relationship for muntjac during both winters and for roe deer during the 1986/87 census. The weaker relationship for roe deer may be because the roe deer visual censuses were

Table 2.1 Kendall's coefficient of concordance (w) between the mean number of deer seen per visit to each sub-compartment on the study area, corrected for sub-compartment size, and the mean number of individual faecal pellets per 10X4m plot corrected for decomposition (from Claydon *et al., in prep.*).

	w	p
Muntjac visual census 1985/86	0.768	0.005
Muntjac visual census 1986/87	0.726	0.015
Roe deer visual census 1985/86	0.613	0.116
Roe deer visual census 1986/87	0.725	0.015

confined to the hour before and after dawn (Claydon *et al., in prep.*). Roe deer were usually moving between different parts of their home ranges at this time and thus sightings may not accurately reflect the time spent in different sub-compartments. In contrast, the muntjac visual censuses were carried out throughout the daylight hours (Claydon *et al., in prep.*)

2.2.3 AUTUMN PELLET SURVEY

Standing crop faecal pellet densities were estimated for the five herbivore species in 171 sub-compartments during October 1986. One in four sub-compartments was selected from each *'tree type'* cluster, to give a spread of vegetation types and geographical positions throughout the forest. Faecal pellet density was recorded as above and corrected for findability and differential decomposition using the results of a decomposition experiment carried out during October 1988. There were significant differences in the number of pellets visible immediately after placement (K-W ANOVA, $H=20.1$, $p<0.05$) and after two weeks (K-W ANOVA, $H=33.8$, $p<0.001$). Some pellet groups had already disappeared after only two weeks, and so the mean % decomposition at two weeks was used to correct the autumn pellet data.

2.2.4 ANALYTICAL TECHNIQUES

To examine habitat selection and resource partitioning by the five herbivore species, an array was constructed using the 26 habitat variables measured in each sub-compartment, together with a measure of pellet density for each species (Table 2.2). Examination of the pellet density distributions from both surveys showed a marked departure from normality, an important violation of most multivariate analyses. Log_{10} transformation of the pellet data improved normality considerably, and $\log_{10}$ transformed pellet densities were used in all analyses. The habitat variables did not show marked departures from normality.

Initially correlation matrices were constructed to examine the relationships both amongst the independent variables and between the independent and dependent variables. A sub-set of 13 variables was selected by removing one of each pair of variables when the correlation between them was high (Table 2.2). Relatively large correlations remained between diversity of grasses and % herbs and between abundance of bramble and % herbs. However, all three variables were retained because the univariate statistics had shown their importance in distinguishing biologically between the herbivore species. Reducing the independence between variables was carried out more to aid the interpretation of the multivariate analyses, in particular the multiple stepwise regressions (MSRs), rather than to

Table 2.2 Details of the 26 habitat variables and five dependent variables measured for all 692 sub-compartments in the King's Forest. The sub-set of 13 habitat variables used in the first set of multiple regression models are marked *.

Mnemonic	**Description**
AREA	sub-compartment area (ha)
AGE	age of trees
*FARM	farmland adjacent to n sides of compartment
*HEATH	heathland adjacent to n sides of compartment
*PSP	% Scots pine
PCP	% Corsican pine
*POP	% other pines
*PNPT	% nut producing broadleaved trees
*PNNPT	% non-nut producing broadleaved trees
DP	number species of pines
DNPT	number species nut producing broadleaved trees
DNNPT	number species non-nut producing broadleaved trees
SPACE	tree spacings
*BRASH	brashings
PGRAS	% grass
*DGRAS	diversity of grasses
*PHERB	% herbs
DHERB	diversity of herbs
*PBRAK	% bracken
PBUSH	% bushes
*DBUSH	diversity of bushes
PBGND	% bare ground
*BRAM	abundance of bramble
RASP	abundance of raspberry
*BEAR	presence of brown earth soils
CAL	presence of calcareous soils
	Dependent variables
LCMPELL	$\log_{10}$ muntjac pellet density
LCRPELL	$\log_{10}$ roe pellet density
LCFPELL	$\log_{10}$ fallow pellet density
LCHPELL	$\log_{10}$ hare pellet density
LCRBPEL	$\log_{10}$ rabbit pellet density

satisfy any assumptions of the multivariate techniques. MSR can use intercorrelated variables, but comparison of models between species is difficult, since different models may include either variable from a pair of autocorrelated variables (Hallett, 1982).

The first set of MSRs were carried out using the sub-set of 13 habitat variables as independent variables and log$_{10}$ transformed pellet density as the dependent variable in each case. Examination of residual plots showed that no major assumptions of multiple regression were being violated (Norusis, 1985), and since the aim in this study was to use MSR as a descriptive rather than as a predictive technique no further data transformations were carried out. Such transformations would have improved the percentage of variation explained by the models, but would be unlikely to affect the variables included.

A second set of MSRs were carried out using factor scores for each sub-compartment from a principal components analysis of the independent variables (Brown & Batzli, 1984; Howard & Larson, 1985). These regressions were used to support the findings of the first set of regressions and to confirm that no major sources of variation had been removed when reducing the number of variables. Factor scores are made up of intercorrelated groups of variables, but each factor is independent of any other factor and thus factor scores are appropriate variables for MSR. % Bracken had to be removed from the factor analysis because it was not correlated with any other variable, while the presence of calcareous soils was removed because of a correlation of one with the presence of brown earth soils. A factor analysis on the remaining 24 variables produced for both the winter and autumn surveys eight factors with eigenvalues of greater than one, which together accounted for 69.5% and 71.3% respectively of the total variation. Factor scores for these eight factors were calculated for each sub-compartment and used in the MSRs.

A third set of MSRs were carried out using both the above factor scores and the transformed pellet densities of the other herbivore species as independent variables, to assess any potential competitive effects (Brown & Batzli, 1984). These regressions were only carried out using the winter survey data, since competitive effects are likely to be most important during this period. Residuals plotted for both sets of regressions involving factor scores showed no important violations of MSR assumptions.

Multiple discriminant analysis (MDA) was used to examine the ecological relationships between the five species in canonical space (Hudson, 1976; Dueser & Shugart, 1979; Van Horne, 1982). To obtain maximum discrimination, the MDA was run using all 26 habitat variables, with minimising Wilk's Lamda as the criteria for group separation.

Initially the analyses were run using all the sub-compartments where the pellet density was greater than zero for each species. However, this resulted in poor *discrimination* and so the final analyses were run using only the top 50% by density of sub-compartments for each species. Pianka's (1973) niche overlap indices were also used to examine ecological relationships between the five species.

2.3 RESULTS

2.3.1 DISTRIBUTION OF HERBIVORES

Muntjac were recorded in 351, roe deer in 464, fallow deer in 460, hares in 333 and rabbits in 142 of the 692 sub-compartments surveyed between January and April 1986. No herbivores were recorded in 5.2% of sub-compartments, one species in 15.6%, two species in 24.9%, three species in 32.8%, four species in 18.1% and all five species in 3.5% of sub-compartments.

Figures 2.1a-c and 2.2a&b show the density distributions of the five herbivore species between January and April 1986. Muntjac were largely confined to the south and east of the forest. Roe deer had a more widespread distribution, but were present at high densities in the same parts of the south and east of the forest as muntjac. In addition there was also a central area of high density. Fallow deer also had a widespread distribution, but were found at high densities on the western edge and in the north-east corner of the forest. Hares were found throughout the forest, but only occurred at high densities in the central part of the forest. Rabbits had a very restricted distribution, centred on several areas of high density.

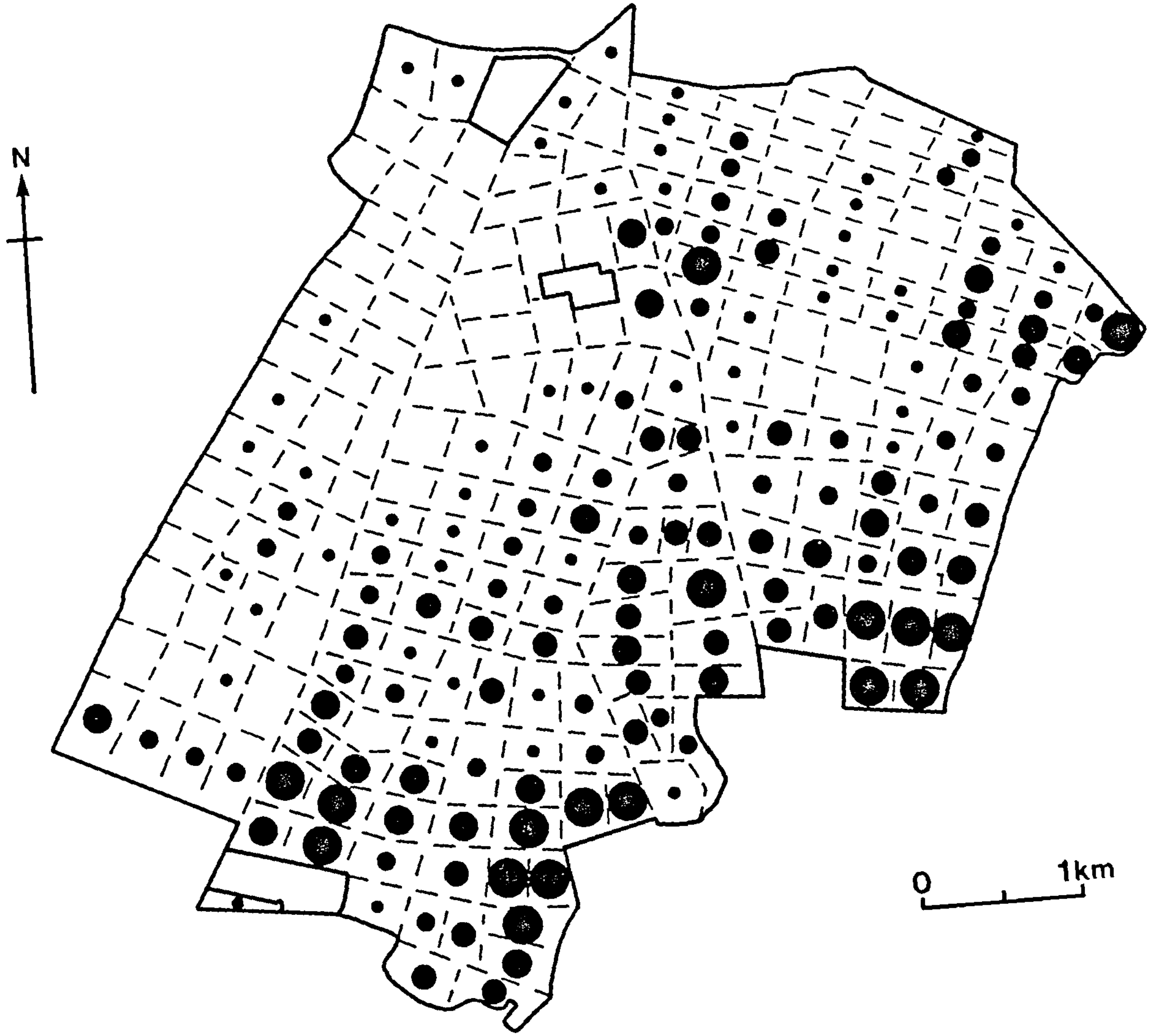
The dispersion parameter 'k' (Southwood, 1978; p. 28) was used to describe the distributions of these herbivores (Table 2.3). Hares had a widespread but even distribution, while rabbits had a highly clumped distribution. Amongst the deer species, the muntjac distribution was most clumped and the fallow deer distribution least clumped.

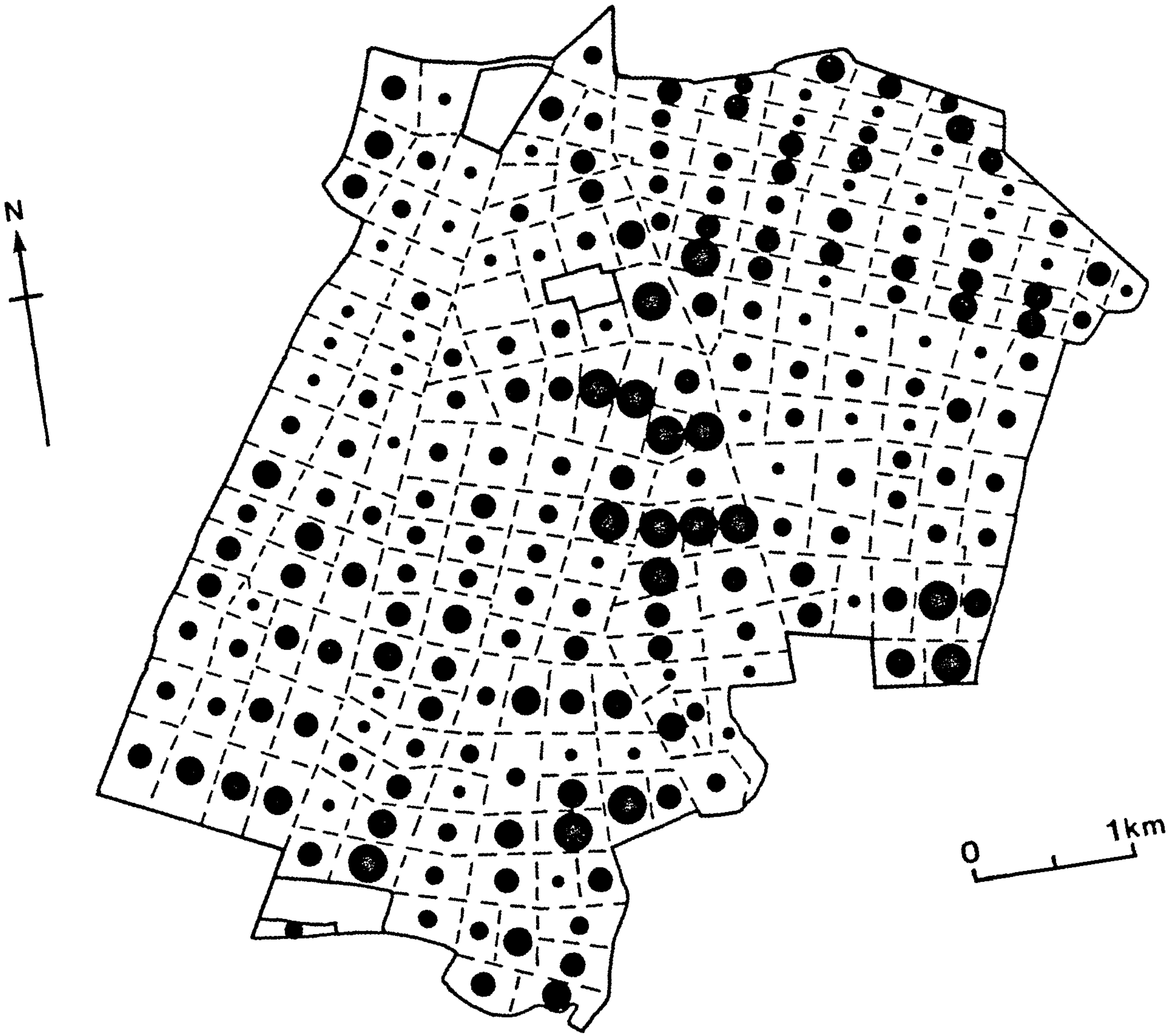
Relationships between the five herbivore species were examined initially using correlation coefficients (Table 2.4). Correlations between the deer species were generally large and positive. Muntjac density was highly correlated with roe deer density and roe deer density was highly correlated with fallow deer density. However, muntjac and fallow deer densities were not significantly correlated, reflecting the low muntjac density in the north-east corner and on the western edge of the forest. The correlation coefficients, although generally not significant, showed a weak negative relationship between the two

Figure 2.1a Distribution of muntjac in the King's Forest, January-April 1986. Symbols denote the mean pellet density for each compartment: ● , <10, ● , 10-30; ● , 30-60; ● , 60-100; ● , >100 pellets per 10X4m plot.

Figure 2.1b Distribution of roe deer in the King's Forest, January to April 1986. Symbols as in Figure 2.1a.

Figure 2.1c Distribution of fallow deer in the King's Forest, January to April 1986. Symbols as in Figure 2.1a.


N
0
1km


N
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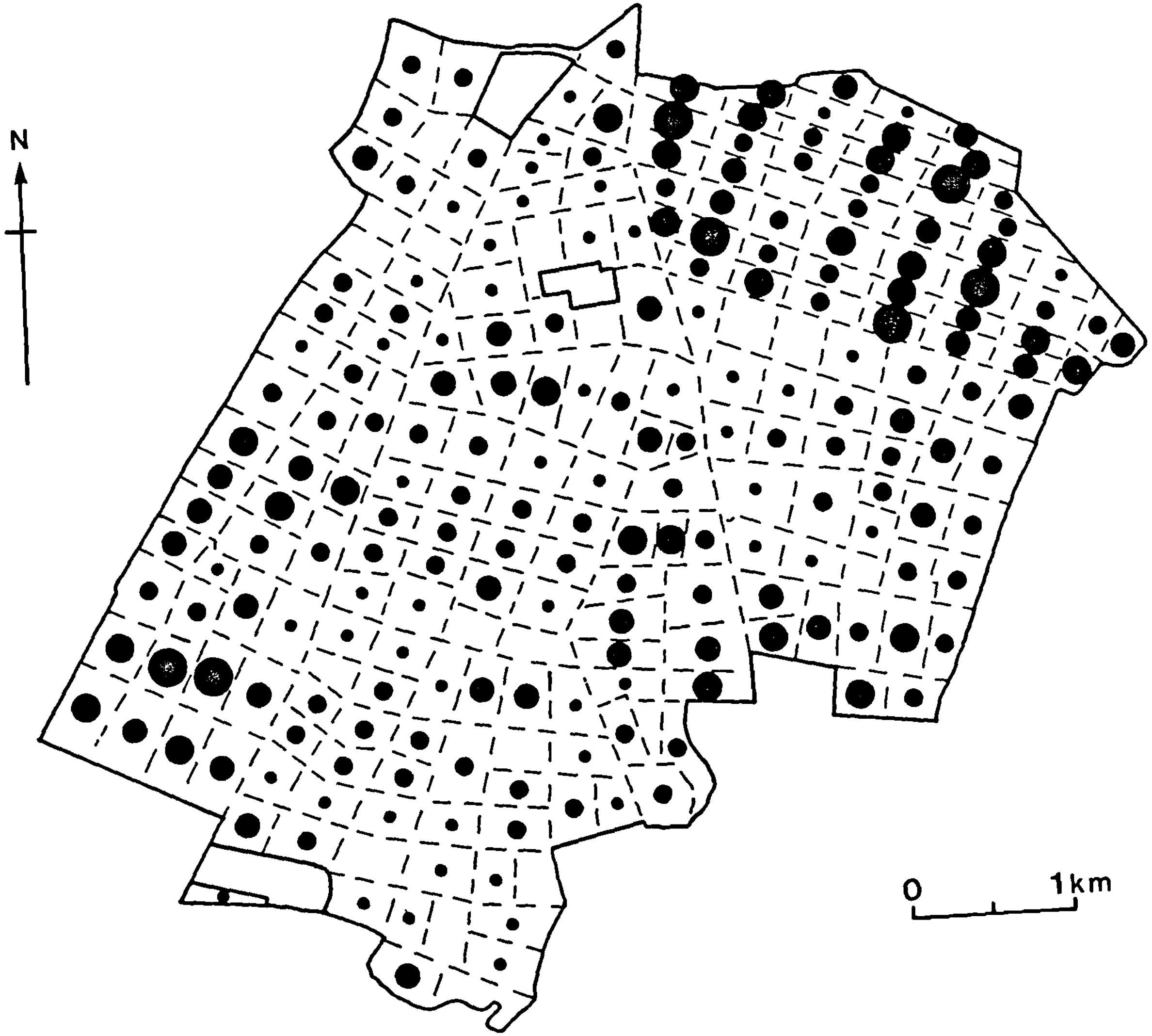
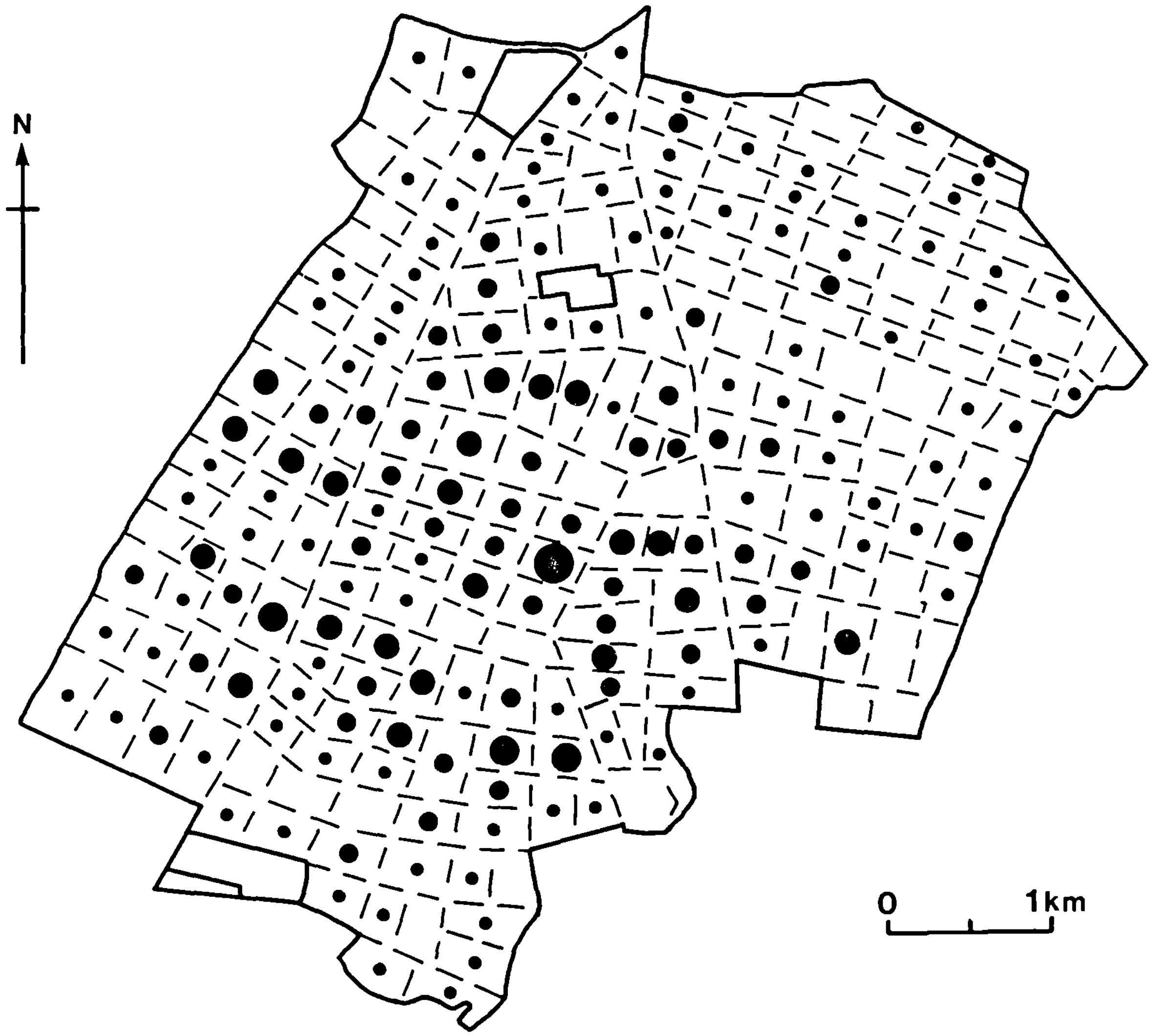

N
0
1km

Figure 2.2a Distribution of hares in the King's Forest, January-April 1986. Symbols denote the mean pellet density for each compartment: ● , <1; ● , 1-5; ● , 5-15; ● , 15-30; ● , >30 pellets per 10X4m plot.

Figure 2.2b Distribution of rabbits in the King's Forest, January-April 1986. Symbols as in Figure 2.2a.


N
0
1km

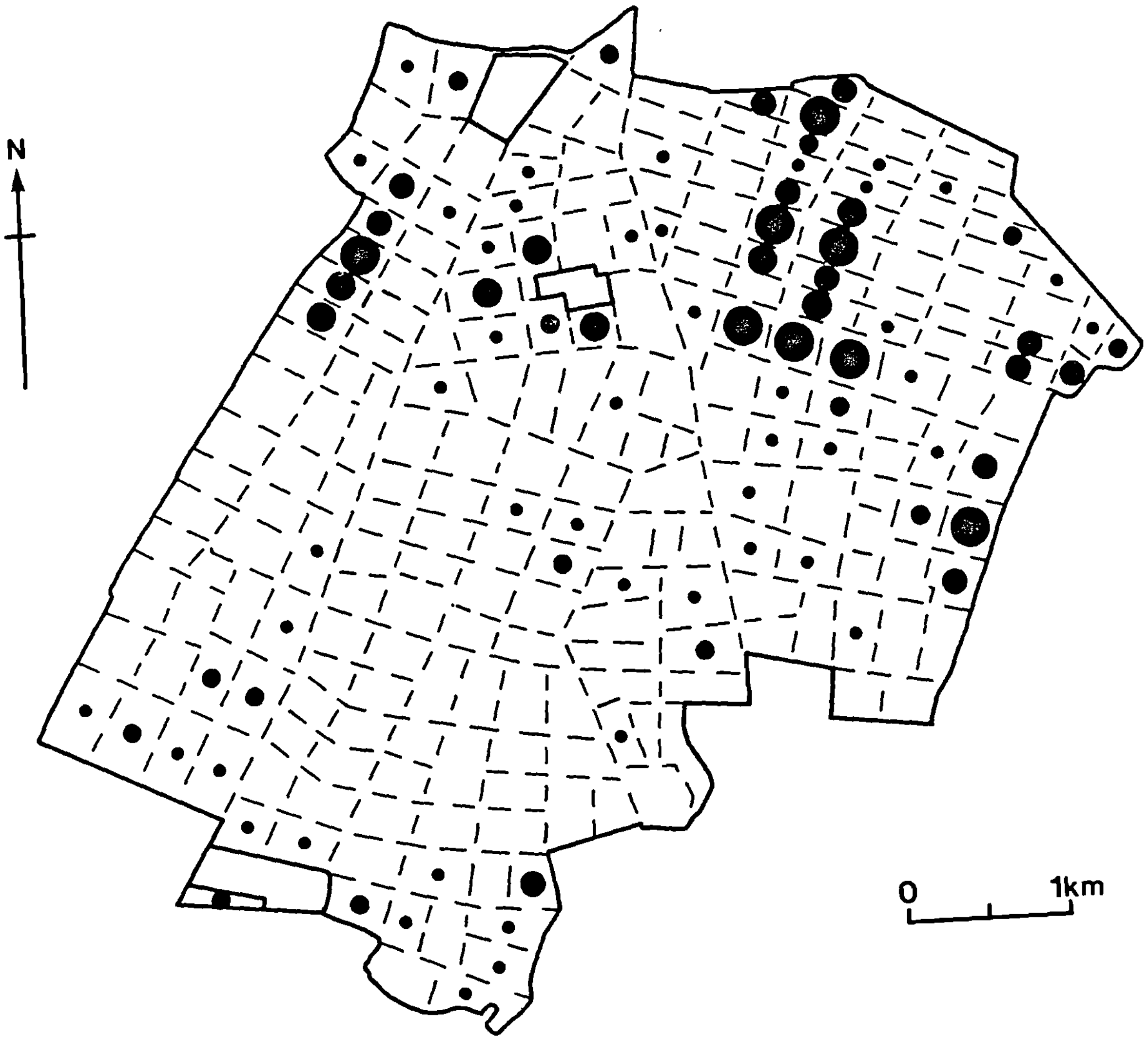

N
0
1km

Table 2.3 Dispersion of herbivore species in the King's Forest, January-April 1986. The dispersion parameter 'k' was calculated across all 692 sub-compartments using the mean number of pellets per plot, corrected for differential decomposition.

'k' was found by iteration using the following formula (Southwood, 1978; p 28);

$$\log_{10} (N/N_o) = k \log_{10} (1+\bar{x}/k)$$

where N = total number of sub-compartments
N_0 = number of sub-compartments scoring zero for that species
$\bar{x}$ = overall mean pellets per plot

Species	**k**
muntjac	0.137
roe	0.226
fallow	0.236
hare	0.300
rabbit	0.047

'k' decreases as the distribution departs from random

Table 2.4 Spearman correlation coefficients (r_s), calculated across all 692 sub-compartments surveyed during the January-April 1986 survey, using the mean number of pellets per plot, corrected for differential decomposition.

	muntjac	**roe**	**fallow**	**hare**	**rabbit**
muntjac	-				
roe	0.353 ***	-			
fallow	0.002	0.245 ***	-		
hare	-0.060	0.087 *	-0.024	-	
rabbit	-0.064	-0.063	-0.075 *	-0.037	-

*** $p<0.001$
* $p<0.05$

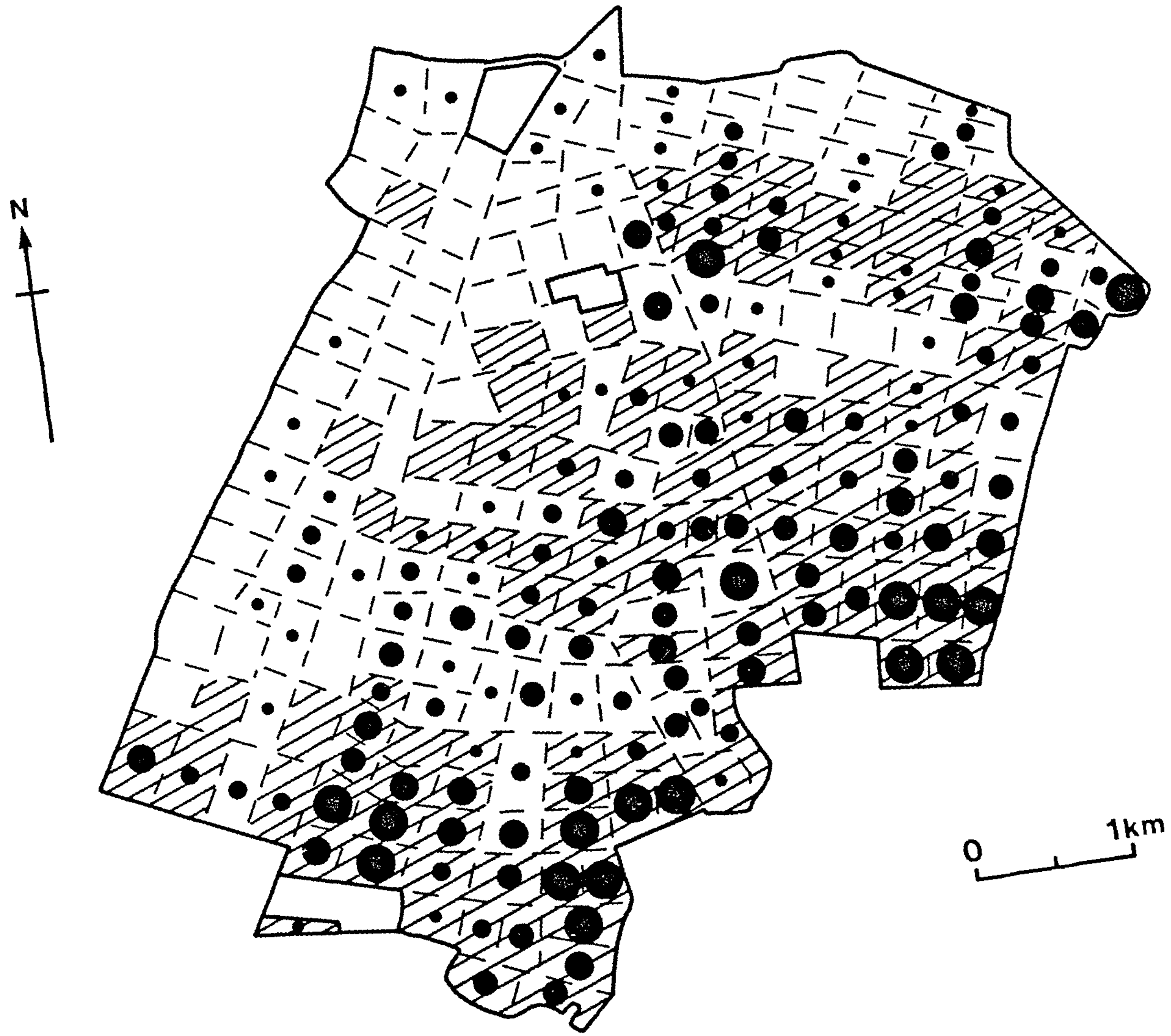
Table 2.5 Pianka (1973) spatial overlap indices calculated across all 692 sub-compartments surveyed during the January-April 1986 survey. The mean number of pellets per plot, corrected for differential decomposition, was converted to the estimated total number of pellets in each sub-compartment.

	muntjac	**roe**	**fallow**	**hare**	**rabbit**
muntjac	-				
roe	0.571	-			
fallow	0.282	0.485	-		
hare	0.105	0.249	0.221	-	
rabbit	0.019	0.024	0.033	0.021	-

$$\text{Overlap}_{ij} = \frac{\Sigma\, p_{ia}\, p_{ja}}{\sqrt{[(\Sigma\, p_{ia}^2)\,(\Sigma\, p_{ja}^2)]}}$$

where p_{ia} is the total number of pellets of species $_i$ in sub-compartment $_a$ and p_{ja} the total number of pellets of species $_j$ in sub-compartment $_a$

Figure 2.3 Distribution of muntjac in the King's Forest, January-April 1986. Symbols as in Figure 2.1a. The shading denotes compartments on calcareous soils.


N
0
1km

lagomorph species and apart from the relationship between roe deer and hares, between the lagomorphs and the deer species.

Pianka's (1973) niche overlap indices, calculated using each sub-compartment as a separate resource unit, gave a measure of spatial overlap between the five herbivore species (Table 2.5). These confirmed the relationships given above, although hares now showed moderate spatial overlap with both roe deer and fallow deer.

The influence of soil type on herbivore distribution was examined by comparing, within species, pellet density from sub-compartments on calcareous soils with that from sub-compartments on acidic brown earth soils. There was only a significant difference for muntjac, with pellet density being significantly higher on calcareous soils (Mann-Whitney U test, $U=45708$, $p<0.001$). Figure 2.3 shows how calcareous soils are largely confined to the south and east of the forest, coinciding with the areas of high density muntjac distribution. There was a tendency for hares and rabbits to be more abundant on acidic brown earth soils, but this was not significant (Mann-Whitney U tests, $p=0.10$-0.05).

2.3.2 WINTER PELLET SURVEY

2.3.2.1 Habitat selection

Correlation coefficients between the $\log_{10}$ transformed pellet densities and all the habitat variables are given in Table 2.6. These were used to confirm the results of the MSRs. Table 2.7 gives the habitat variables selected by the first set of MSRs, using the sub-set of 13 habitat variables as independent variables. All five regression equations were significant ($p<0.001$). The variables selected were in agreement with the univariate correlation analyses. Muntjac were selecting areas with an abundance of bramble, a high diversity of bushes and a low diversity of grasses. Roe deer were selecting areas with abundant bramble and Scots pine, but with a low proportion of nut producing broadleaved trees. Fallow deer were also selecting areas with abundant Scots pine and a low proportion of nut producing broadleaved trees. However, in contrast, abundance of bramble was only weakly selected and diversity of grasses appeared as a weak positive variable. Hares were selecting areas away from farmland, with a high diversity of grasses and abundant non-nut producing broadleaved trees. Rabbits were selecting areas of heathland, with an abundance of the non-bramble components of the herb flora.

The proportion of the observed variation explained by the selected habitat variables was low, varying from only 12% for rabbits and fallow deer up to 38% for muntjac. Much of

Table 2.6 Pearson correlation coefficients (r) between $\log_{10}$ transformed pellet densities from the January-April 1986 survey and habitat variables. Only correlations significant at $p<0.05$ are included; $n=692$.

	muntjac	**roe**	**fallow**	**hare**	**rabbit**
AREA	0.142^{***}	0.282^{***}	0.260^{***}		
AGE		-0.083^{*}	-0.085^{*}	-0.079^{*}	
FARM				-0.141^{***}	
HEATH	-0.109^{**}				0.166^{***}
PSP	0.147^{***}	0.247^{***}	0.232^{***}	-0.139^{***}	
PCP		0.097^{*}			
POP	0.169^{***}			-0.093^{*}	0.078^{*}
PNPT	-0.138^{***}	-0.266^{***}	-0.231^{***}		-0.099^{**}
PNNPT	-0.102^{**}	-0.161^{***}		0.175^{***}	
DP	0.308^{***}	0.256^{***}	0.166^{***}	-0.164^{***}	
DNPT		-0.144^{***}	-0.104^{**}		
DNNPT		-0.115^{**}	-0.085^{*}	0.087^{*}	
SPACE			-0.090^{*}		
BRASH	0.228^{***}	0.207^{***}	0.137^{***}	-0.170^{***}	-0.104^{**}
PGRAS	-0.120^{**}	0.095^{*}	0.148^{***}	0.372^{***}	
DGRAS	-0.108^{**}	0.116^{**}		0.323^{***}	
PHERB	0.150^{***}	0.147^{***}		0.079^{*}	0.169^{***}
DHERB	0.132^{***}	0.141^{***}		0.166^{***}	0.124^{***}
PBRAK		0.126^{***}		-0.103^{**}	
PBUSH	0.149^{***}				
DBUSH	0.364^{***}	0.109^{**}			-0.166^{***}
PBGND		-0.188^{***}	-0.103^{**}	-0.304^{***}	
BRAM	0.415^{***}	0.400^{***}	0.085^{*}		-0.101^{**}
RASP	0.405^{***}	0.301^{***}			-0.098^{**}
BEAR	-0.220^{***}			0.082^{*}	0.103^{**}
CAL	0.220^{***}			-0.082^{*}	-0.103^{**}

*** $p<0.001$
** $p<0.01$
* $p<0.05$

Table 2.7 Multiple stepwise regressions using the sub-set of 13 habitat variables as independent variables and $\log_{10}$ transformed pellet densities from the January-April 1986 survey as dependent variables. The sign indicates the direction of the relationship between each independent variable and the dependent variable.

Species	**Habitat variable**		**EV(%)**
muntjac	BRAM	+	17.2
	DBUSH	+	6.6
	DGRAS	-	3.6
	PNPT	-	3.7
	BEAR	-	2.4
	POP	+	2.4
	PNNPT	-	1.3
	OTHERS(n=2)		1.0
	F=46.64, p<0.001		**Total 38.2**
roe	BRAM	+	16.0
	PNPT	-	6.7
	PSP	+	4.4
	PNNPT	-	0.9
	BEAR	+	0.5
	F=54.51, p<0.001		**Total 28.5**
fallow	PSP	+	5.4
	PNPT	-	4.0
	PBRAK	-	0.7
	BRAM	+	1.0
	PHERB	-	0.6
	DGRAS	+	0.8
	F=16.26, p<0.001		**Total 12.5**
hare	DGRAS	+	10.4
	PNNPT	+	2.9
	FARM	-	2.7
	PBRAK	-	1.1
	BEAR	+	0.9
	BRASH	-	0.8
	F=26.61, p<0.001		**Total 18.8**
rabbit	PHERB	+	2.9
	BRAM	-	3.6
	HEATH	+	2.6
	DBUSH	-	1.4
	BEAR	+	0.7
	POP	+	0.6
	F=15.22, p<0.001		**Total 11.8**

the total explained variation for muntjac and roe deer was due to a single variable, the abundance of bramble. There are several possible reasons for these low explained variations; 1) important sources of variation were removed when reducing the number of habitat variables; 2) important variables influencing herbivore distribution and abundance were not measured and 3) there were non-linear relationships between pellet densities and each independent variable. The third option was not investigated since MSR was being used as a descriptive rather than a predictive technique. The first option was examined by the next set of MSRs using factor scores from a Principal Components Analysis (PCA).

The PCA produced eight factors with eigenvalues of greater than 1.0 and the most important correlations between the independent variables and each of the factors are given in Table 2.8. The results of the MSRs using these eight factor scores as independent variables are given in Table 2.9. Again, all five regression equations were significant ($p<0.001$) and the factors selected confirmed the pattern of habitat selection shown by the previous MSR analyses. The most important variable in both the muntjac and roe deer regression models was factor 3, which is associated with the abundance of bramble and raspberry. In the fallow deer model, factor 5, which is associated with the abundance of Scots pine accounted for the greatest explained variation. Hare density was most strongly influenced by factor 1, which describes the grass and herb components of the ground vegetation, while factor 6, which is associated with heathland was the most important variable in the rabbit regression model.

In both the muntjac and roe deer regression models, the variable explaining the most variation was factor 3. However, overall the factors selected were more similar between roe deer and fallow deer than between muntjac and roe deer, with the first four factors being common to both species and having the same direction of influence. Despite this, because factor 3 accounted for such a large proportion of the explained variation in the roe deer regression model, roe deer habitat selection is best described as being intermediate between that of muntjac and fallow deer.

There was a small decrease in the level of explained variation compared to the previous set of MSRs, for all species except muntjac. This indicated that reducing the number of variables in the previous analyses had not removed any important sources of variation, although the overall low level of explained variation still suggested that either important variables had not been measured or that non-linearity was a problem.

The results of the MSRs using both the factor scores and the densities of other

Table 2.8 Principal components analysis, January-April 1986 survey. The most important correlations between the independent variables and each factor are given together with the explained variation accounted for by each factor. The sign gives the direction of the relationship between the factor and each independent variable.

		EV(%)
Factor 1	- PBGND + DGRAS + PGRAS + DHERB + PHERB	**16.5**
Factor 2	+ AGE + PNPT + SPACE + DNPT	**14.5**
Factor 3	+ AREA + BRASH + DP + BRAM + RASP	**10.6**
Factor 4	+ PNNPT + DNNPT + DBUSH	**6.8**
Factor 5	+ PSP - PCP + PBUSH	**6.1**
Factor 6	+ BEAR + HEATH	**5.6**
Factor 7	+ FARM	**5.1**
Factor 8	+ POP	**4.3**
	Total	**69.5**

Table 2.9 Multiple stepwise regressions using factor scores as independent variables and $\log_{10}$ transformed pellet data from the January-April 1986 survey as dependent variables. The sign gives the direction of the relationship between each independent variable and the dependent variable.

Species	Habitat variable	EV(%)
muntjac	Factor 3	+ 20.1
	Factor 6	- 11.9
	Factor 8	+ 2.6
	Factor 7	+ 2.0
	Factor 5	+ 1.6
	F=84.49, p<0.001	**Total 38.2**
roe	Factor 3	+ 16.3
	Factor 5	+ 3.2
	Factor 1	+ 3.1
	Factor 2	- 2.0
	Factor 4	- 0.9
	Factor 7	+ 0.6
	F=40.44, p<0.001	**Total 26.1**
fallow	Factor 5	+ 4.3
	Factor 2	- 3.3
	Factor 3	+ 3.1
	Factor 1	+ 0.5
	F=21.78, p<0.001	**Total 11.2**
hare	Factor 1	+ 11.0
	Factor 7	- 2.6
	Factor 4	+ 2.2
	Factor 3	- 1.4
	Factor 5	- 0.9
	Factor 8	- 0.6
	F=26.18, p<0.001	**Total 18.7**
rabbit	Factor 6	+ 2.6
	Factor 7	+ 1.9
	Factor 3	- 1.8
	Factor 1	+ 1.3
	F=14.08, p<0.001	**Total 7.6**

Table 2.10 Multiple stepwise regressions using factor scores and $\log_{10}$ transformed pellet density of other herbivores as independent variables and $\log_{10}$ transformed pellet density from the January-April 1986 survey as dependent variables. The sign gives the direction of the relaticnship between each independent variable and the dependent variable.

Species	Independent variable	EV(%)
muntjac	Factor 3	+ 20.1
	Factor 6	- 11.9
	LCRPELL	+ 4.0
	Factor 8	+ 3.0
	Factor 7	+ 1.6
	Factor 5	+ 0.8
	Factor 4	+ 0.5
	F=70.09, p<0.001	**Total 41.9**
roe	Factor 3	+ 16.3
	LCFPELL	+ 10.6
	LCMPELL	+ 3.7
	Factor 1	+ 2.5
	Factor 4	- 0.9
	Factor 8	- 0.9
	Factor 5	+ 0.8
	Factor 2	- 0.8
	Factor 7	+ 0.4
	F=44.29, p<0.001	**Total 36.9**
fallow	LCRPELL	+ 15.3
	Factor 5	+ 2.0
	Factor 2	- 1.7
	LCRBPEL	- 1.2
	Factor 6	+ 0.7
	Factor 7	- 0.5
	F=31.08, p<0.001	**Total 21.4**
hare	Factor 1	+ 11.0
	Factor 7	- 2.6
	Factor 4	+ 2.2
	Factor 3	- 1.4
	Factor 5	- 0.9
	Factor 8	- 0.6
	F=26.18, p<0.001	**Total 18.7**
rabbit	Factor 6	+ 2.6
	Factor 7	+ 1.9
	Factor 3	- 1.8
	Factor 1	+ 1.3
	LCFPELL	- 1.1
	Factor 2	- 0.7
	LCHPELL	- 0.6
	F=10.86, p<0.001	**Total 10.0**

herbivores as independent variables are given in Table 2.10. All five regression equations were significant ($p<0.001$) and other herbivore densities were selected as variables in all regression models except that describing the density distribution of hares. Using both factor scores and other herbivore densities resulted in an improvement in the level of explained variation. This was probably due to improved linear relationships between the independent and dependent herbivore densities, compared to the linear relationships between herbivore densities and the habitat variables. In the deer regression models, herbivore densities were generally selected as important positive variables and the variables selected reflected the correlation coefficients given in Table 2.4, although roe deer density was less important in the muntjac regression model than might be expected. Lagomorph densities were not strongly influenced by the density of other herbivores. These MSRs gave no evidence that there were competitive interactions between the deer species, rather the inclusion of other herbivore densities in these regression models reflected selection of common habitat variables.

2.3.2.2 Niche partitioning

Multiple discriminant analysis (MDA) was used to describe the relationships between the five herbivore species in multidimensional niche space. A test comparing within species variance-covariance matrices was significant (Box's M test, $F=2.960$, $p<0.001$), indicating that the multivariate representations of the species differed significantly in size or shape, regardless of differences or similarities in position. Such a result is to be expected with biological data, merely indicating that niche shape differs between species. Green (1971) and Dueser & Shugart (1979) both suggest that so long as the discriminant functions (DFs) produced are ecologically interpretable, then this is probably not an important violation of MDA.

The analysis produced four significant DFs ($p<0.01$). Correlation coefficients between the habitat variables and the first two discriminant functions, which together accounted for 77% of the total discriminating information available, are given in Table 2.11. Each DF can be represented graphically as an independent normalized ($x=0$, $SD=1$) discriminant axis. These axes can then be interpreted ecologically from the magnitude and direction of the correlations between the DF and each of the habitat variables given in Table 2.11. The pattern of covariance amongst variables on DFI described a gradient from grass dominated ground vegetation under non-nut producing broadleaved trees at one extreme, to a diverse pine canopy with less ground vegetation, but high levels of brash at the other extreme. DFII described a gradient from a diverse bush and raspberry dominated ground

Table 2.11 Multiple discriminant analysis, January-April 1986 survey. Correlation coefficients of habitat variables with the first two discriminant function coefficients used to separate the habitats occupied by the five herbivore species.

Variables	**Function 1**	**Function 2**
PGRAS	-0.537	
DP	0.477	
BRASH	0.435	
DGRAS	-0.412	
PNNPT	-0.372	
PBGND	0.355	
PCP	0.126	
AGE	0.105	
DBUSH		-0.588
RASP		-0.474
HEATH		0.438
SPACE		-0.180
DNPT		-0.167
PBUSH		-0.112
%EV	**54.7**	**21.9**
χ^2	**378.2 *****	**178.7 *****

Table 2.12 Multiple discriminant analysis, January-April 1986 survey. F-matrix for testing the difference between species means across all four discriminant function coefficients (each F statistic has 18 and 852 degrees of freedom). Also given are the percentage of sub-compartments correctly classified by the discriminant function model for each species.

	muntjac	**roe**	**fallow**	**hare**	**rabbit**
muntjac	-				
roe	3.339 ***	-			
fallow	6.292 ***	2.695 ***	-		
hare	11.363 ***	7.768 ***	5.751 ***	-	
rabbit	6.223 ***	4.371 ***	3.866 ***	5.348 ***	-
% correctly classified	**48.3**	**18.7**	**40.4**	**55.0**	**39.4**

Overall correct classification = 39.0%

Figure 2.4 Multiple discriminant analysis, January-April 1986 survey. Species centroids (± 2 S.E.) are plotted in canonical space on the first two discriminant function axes, which have been given biological interpretation as indicated. M = muntjac, R = roe deer, F = fallow deer, H = hares, Rb = rabbits.

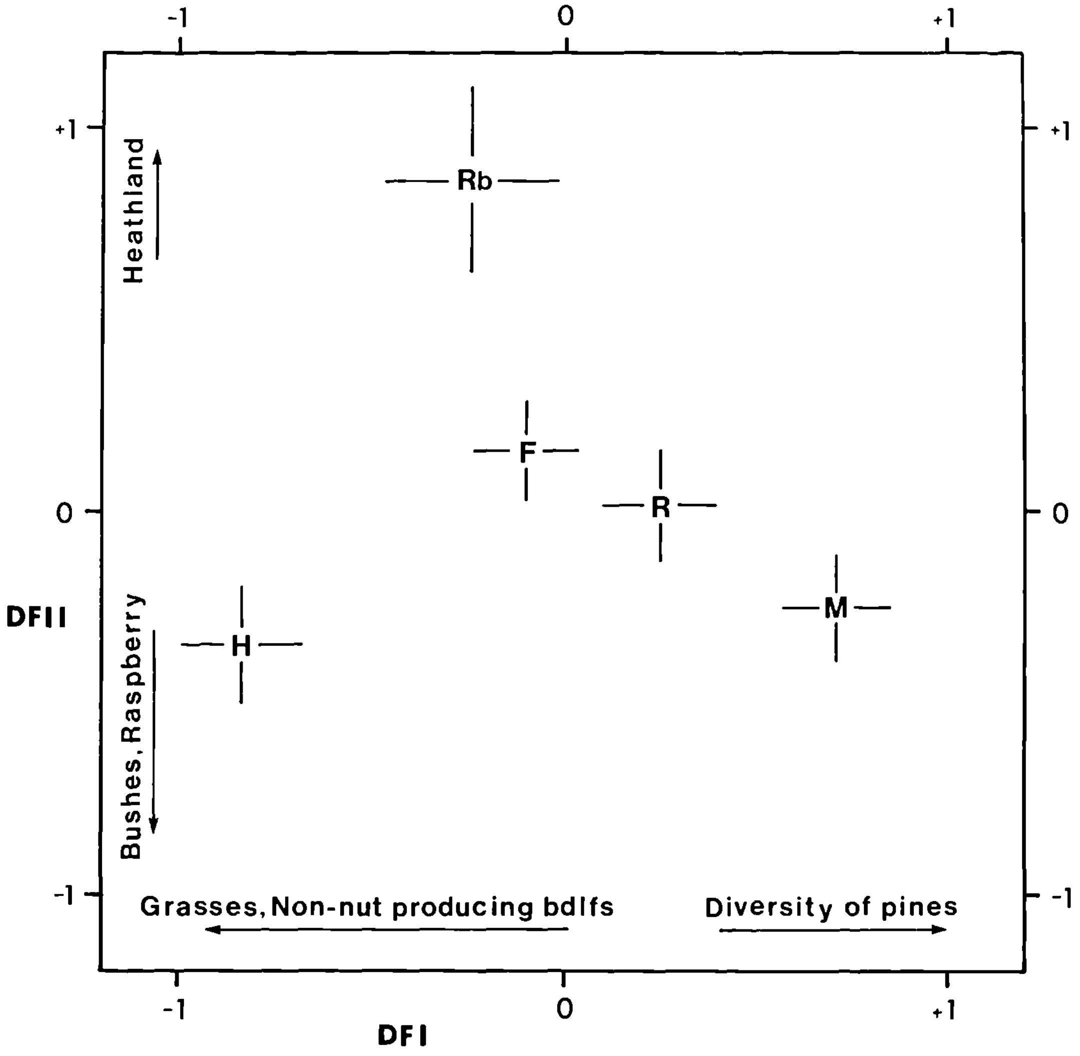

-1
0
+1
+1
0
-1
Heathland
Bushes, Raspberry
DFII
Rb
F
R
M
H
Grasses, Non-nut producing bdlfs
Diversity of pines
DFI

Table 2.13 Pianka (1973) habitat overlap indices for the January-April 1986 survey, calculated using each of the *'ground vegetation'* clusters as a resource unit. The mean number of pellets per plot, corrected for differential decomposition, was converted to the estimated total number of pellets in each sub-compartment and then summed for each cluster.

	muntjac	**roe**	**fallow**	**hare**	**rabbit**
muntjac	-				
roe	0.935	-			
fallow	0.547	0.701	-		
hare	0.449	0.563	0.468	-	
rabbit	0.234	0.317	0.390	0.609	-

$$\text{Overlap}_{ij} = \frac{\Sigma\, p_{ia}\, p_{ja}}{\sqrt{[(\Sigma\, p_{ia}^2)\,(\Sigma\, p_{ja}^2)]}}$$

vegetation at one extreme, to areas of heathland with little bush and raspberry at the other.

The position of the species centroids on the first two DF axes are shown in Figure 2.4. Since DFI accounted for 55% of the explained variation, most separation occurred along this axis. As expected, hares were placed at the grass dominated end of the gradient and muntjac at the diverse pine end. The remaining three species were placed in between, with roe deer towards the brash and pine dominated end of the gradient and fallow deer towards the grass dominated end. Rabbits occupied a position close to fallow deer along DFI. DFII separated rabbits from the remaining four herbivores, placing them as expected at the heathland end of the gradient. There was little separation of the other four herbivores along DFII, although the relative positions of the three deer species were consistent with the results of the MSRs.

Since each DF axis represents an independent environmental gradient, i.e. a niche axis, niche separation of a pair of species is a function of the distance between their centroids in n-discriminant space. Since most of the discriminating information is accounted for by the first two DFs, the relative position of the group centroids along these two DF axes approximates to their positions in n-discriminant space. Ecological separation can also be inferred from the pairwise F-statistics, calculated from the position of cases along all four DF axes, and given in Table 2.12. The smaller F values indicate shorter distances between species pairs in discriminant space. The F values were all significant ($p<0.001$) and therefore the five species occupied significantly different positions in discriminant space, although there was substantial overlap between species. The smallest ecological distances were between roe and fallow deer, and between muntjac and roe deer.

The performance of the DF model in correctly classifying cases was poor; overall only 39% of cases were correctly classified. This was because at least two species were recorded in most sub-compartments, resulting in considerable duplication of the habitat data used to distinguish between species. In particular, the DF model had difficulty in distinguishing the widely distributed roe deer.

Pianka's (1973) niche overlap indices were calculated, using each cluster from the *'ground vegetation'* grouping as a resource unit, to give another measure of niche partitioning (Table 2.13). It must be stressed that while MDA separates species on the basis of presence in a particular sub-compartment (in this case the top 50% of occurrences by density), niche overlap indices compare species using all the available information on species density. This probably accounts for the differences in ecological separation suggested by the MDA and the niche overlap indices.

In contrast to the MDA, the niche overlap indices showed that the smallest ecological separation (highest niche overlap) was between muntjac and roe deer, although there was still a high niche overlap between roe and fallow deer. They also suggested that hares are more closely related to the three deer species than are rabbits, a result expected from the MSRs. The MDA had shown the converse, with rabbits more closely related to the three deer species.

2.3.3 AUTUMN PELLET SURVEY

Muntjac were recorded in 60, roe deer in 86, fallow deer in 75, hares in 60 and rabbits in 25 of the 171 sub-compartments surveyed during October 1986. No herbivores were recorded in 15.8% of sub-compartments, one species in 28.1%, two species in 26.9%, three species in 21.1%, four species in 7.0% and all five species in 1.2% of sub-compartments. Compared to the winter survey, fewer species were recorded in each sub-compartment, reflecting a higher decomposition rate during the summer months.

The dispersion parameter 'k' (Southwood, 1978; p. 28) was again used to describe the distributions of these herbivores (Table 2.14). Roe and fallow deer both had a more even distribution than hares, while rabbits still had the most clumped distribution. Amongst the deer species, muntjac had the most clumped distribution and roe deer the least clumped distribution.

Spatial overlap indices between the five species of herbivores are given in Table 2.15. The highest spatial overlaps were still between muntjac and roe deer and between roe deer and fallow deer, while the overlap between muntjac and fallow deer was increased compared to the winter survey. The spatial overlap between lagomorphs and between lagomorphs and deer remained low

2.3.3.1 Habitat selection

Correlation coefficients between the $\log_{10}$ transformed pellet densities and the habitat variables are given in Table 2.16. Muntjac density was significantly correlated with a number of habitat variables, but for the other four species there were few significant correlations, reflecting a decrease in habitat selectivity compared to the winter survey.

Table 2.17 gives the habitat variables selected by the first set of MSRs using the sub-

Table 2.14 Dispersion of herbivore species in the King's Forest, October 1986. The dispersion parameter 'k' was calculated across the 171 sub-compartments using the mean number of pellets per plot, corrected for differential decomposition.

'k' was found by iteration using the following formula
(Southwood, 1978; p 28);

$$\log_{10} (N/N_o) = k \log_{10} (1+\bar{x}/k)$$

where N = total number of sub-compartments (171)
N_o = number of sub-compartments scoring zero for that species
$\bar{x}$ = overall mean pellets per plot

Species	**k**
muntjac	0.093
roe	0.170
fallow	0.130
hare	0.127
rabbit	0.029

'k' decreases as the distribution departs from random

Table 2.15 Pianka (1973) spatial overlap indices calculated across the 171 sub-compartments surveyed during the October 1986 survey. The mean number of pellets per plot, corrected for differential decomposition, was converted to the estimated total number of pellets in each sub-compartment.

	muntjac	**roe**	**fallow**	**hare**	**rabbit**
muntjac	-				
roe	0.521	-			
fallow	0.340	0.457	-		
hare	0.087	0.158	0.114	-	
rabbit	0.002	0.007	0.008	0.222	-

$$\text{Overlap}_{ij} = \frac{\Sigma\, p_{ia}\, p_{ja}}{\sqrt{[(\Sigma\, p_{ia}^2)\,(\Sigma\, p_{ja}^2)]}}$$

Table 2.16 Pearson correlation coefficients (r) between $\log_{10}$ transformed pellet densities from the October 1986 survey and habitat variables. Only correlations significant at $p<0.05$ are included; n=171.

	muntjac	**roe**	**fallow**	**hare**	**rabbit**
AREA			0.200 **		
AGE	0.216 *				-0.163 *
FARM	0.235 **			-0.162 *	
PSP		0.151 *			
PCP	-0.180 *				
POP	0.224 **				
PNPT	0.246 ***				
DP			0.154 *		
DNPT	0.208 **				
DNNPT	0.179 *				
SPACE	0.163 *				-0.161 *
BRASH	0.206 **	0.304 ***			
PGRAS	-0.229 **			0.192 *	
DGRAS				0.232 **	
PHERB	0.232 **				
DHERB				0.153 *	
PBRAK	0.178 *				
PBUSH	0.206 **				
DBUSH	0.315 ***			-0.188 *	-0.214 **
PBGND				-0.167 *	
BRAM	0.338 ***	0.242 ***			
RASP	0.151 *				
BEAR	-0.253 ***				0.212 **
CAL	0.253 ***				-0.212 **

*** $p<0.001$
** $p<0.01$
* $p<0.05$

Table 2.17 Multiple stepwise regressions using the sub-set of 13 habitat variables as independent variables and $\log_{10}$ transformed pellet densities from the October 1986 survey as dependent variables. The sign indicates the direction of the relationship between each independent variable and the dependent variable.

Species	Habitat variable	EV(%)
muntjac	BRAM	+ 11.4
	BEAR	- 5.8
	PNPT	+ 5.5
	POP	+ 4.9
	BRASH	+ 2.7
	PBRAK	+ 2.4
	DBUSH	+ 1.8
	FARM	+ 1.6
	F=11.43, p<0.001	Total 36.1
roe	BRASH	+ 9.2
	BRAM	+ 3.6
	F=12.38, p<0.001	Total 12.8
fallow	-	-
hare	DGRAS	+ 5.4
	DBUSH	- 3.3
	FARM	- 2.2
	F=6.78, p<0.001	Total 10.9
rabbit	DBUSH	- 4.6
	BEAR	+ 3.3
	F=7.21, p<0.001	Total 7.9

Table 2.18 Principal components analysis, October 1986 survey. The most important correlations between the independent variables and each factor are given together with the explained variation accounted for by each factor. The sign gives the direction of the relationship between the factor and each independent variable. The factors are based on the sub-sample of 171 sub-compartments.

		EV(%)
Factor 1	- PBGND + PGRAS + DGRAS + DHERB	**16.5**
Factor 2	+ AGE + PNPT + SPACE + DNPT	**15.1**
Factor 3	+ DNNPT + PNNPT + DBUSH	**10.5**
Factor 4	+ BRAM + RASP + PHERB	**7.5**
Factor 5	+ DP + AREA + BRASH	**6.7**
Factor 6	+ PSP - PCP + PBUSH	**5.4**
Factor 7	+ POP + FARM	**5.2**
Factor 8	+ BEAR - HEATH	**4.4**
	Total	**71.3**

Table 2.19 Multiple stepwise regressions using factor scores as independent variables and $\log_{10}$ transformed pellet data from the October 1986 survey as dependent variables. The sign indicates the direction of the relationship between each independent variable and the dependent variable.

Species	**Habitat variable**	**EV(%)**
muntjac	Factor 7	+ 10.6
	Factor 4	+ 10.2
	Factor 2	+ 5.0
	Factor 8	+ 4.3
	F = 17.80, p<0.001	**Total 30.1**
roe	Factor 4	+ 3.9
	Factor 8	+ 3.1
	Factor 5	+ 2.7
	F = 5.97, p<0.001	**Total 9.7**
fallow	Factor 5	+ 5.8
	F = 10.40, p<0.01	**Total 5.8**
hare	Factor 1	+ 4.7
	F = 8.28, p<0.01	**Total 4.7**
rabbit	Factor 2	- 2.6
	Factor 5	- 2.2
	F = 4.26, p<0.05	**Total 4.8**

set of 13 habitat variables as independent variables. Only four significant regression equations were produced (all $p<0.001$); no variables entered the fallow deer model. The percentage explained variation for the muntjac model was reduced from 38% in the winter survey to 36%. There were greater reductions in explained variation for the other three regression models. In particular, the explained variation for the roe deer model was reduced from 28% to 13%, reflecting the decreased selectivity and increased dispersion of roe deer during autumn.

As during winter, muntjac were selecting areas with an abundance of bramble and a high diversity of bushes. In addition, the abundance of nut-producing broadleaved trees entered the equation as a positive variable. The variables which entered the other three regression models were again those that influenced winter habitat selection. Roe deer were selecting areas with an abundance of bramble, hares areas away from farmland with a high diversity of grasses and rabbits areas with a low diversity of bushes.

The principal components analysis again gave eight factors with eigenvalues of greater than 1.0 and the most important correlations between the independent variables and each of the factors are given in Table 2.18. The factors selected by the MSRs using these eight factors as independent variables are given in Table 2.19. Significant regression equations ($p<0.05$) were produced for all five species, although the level of explained variation was reduced compared to the previous set of MSRs. Generally, the factors selected were in agreement with the MSR analyses using habitat variables. Again roe deer selected factors that were a combination of those selected by muntjac and fallow deer, although roe deer now showed a similar level of explained variation and thus habitat selectivity to fallow deer.

2.3.3.2 Niche partitioning

Although the test comparing within species variance-covariance matrices from the multiple discriminant analysis was again significant (Box's M test, $F=1.655$, $p<0.001$), the analysis was continued since the DFs were ecologically interpretable.

Four discriminant functions were produced, of which only the first function was significant ($p<0.05$). Emphasis should therefore be placed on species separation along DFI, although the other DFs were ecologically interpretable. Correlation coefficients between the habitat variables and the first two discriminant functions, which together accounted for 76% of the total discriminating information available are given in Table 2.20. DFI described

Table 2.20 Multiple discriminant analysis, October 1986 survey. Correlation coefficients of habitat variables with the first two discriminant function coefficients used to separate the habitats occupied by the five herbivore species.

Variables	**Function 1**	**Function 2**
CAL	0.422	
BEAR	-0.422	
BRASH	0.344	
DBUSH	0.308	
PBUSH	0.280	
BRAM	0.148	
POP	0.104	
PGRAS		0.598
FARM		-0.566
PBGND		-0.391
PBRAK		-0.223
% EV	**54.7**	**21.0**
χ^2	**90.1 *****	**43.3 n.s. (0.10-0.05)**

Table 2.21 Multiple discriminant analysis, October 1986 survey. F-matrix for testing the difference between species means across all four discriminant function coefficients (each F statistic has 11 and 138 degrees of freedom). Also given are the percentage of sub-compartments correctly classified by the discriminant function model for each species.

	muntjac	**roe**	**fallow**	**hare**	**rabbit**
muntjac	-				
roe	1.426 n.s.	-			
fallow	2.051 *	0.875 n.s.	-		
hare	4.003 ***	2.337 *	2.521 **	-	
rabbit	3.121 ***	2.613 **	2.146 *	1.657 n.s.	-
% correctly classified	**46.7**	**41.9**	**40.5**	**36.7**	**76.9**

Overall correct classification = 44.4%

Figure 2.5 Multiple discriminant analysis, October 1986 survey. Species centroids (± 2 S.E.) are plotted in canonical space on the first two discriminant function axes, which have been given biological interpretation as indicated. M = muntjac, R = roe deer, F = fallow deer, H = hares, Rb = rabbits.

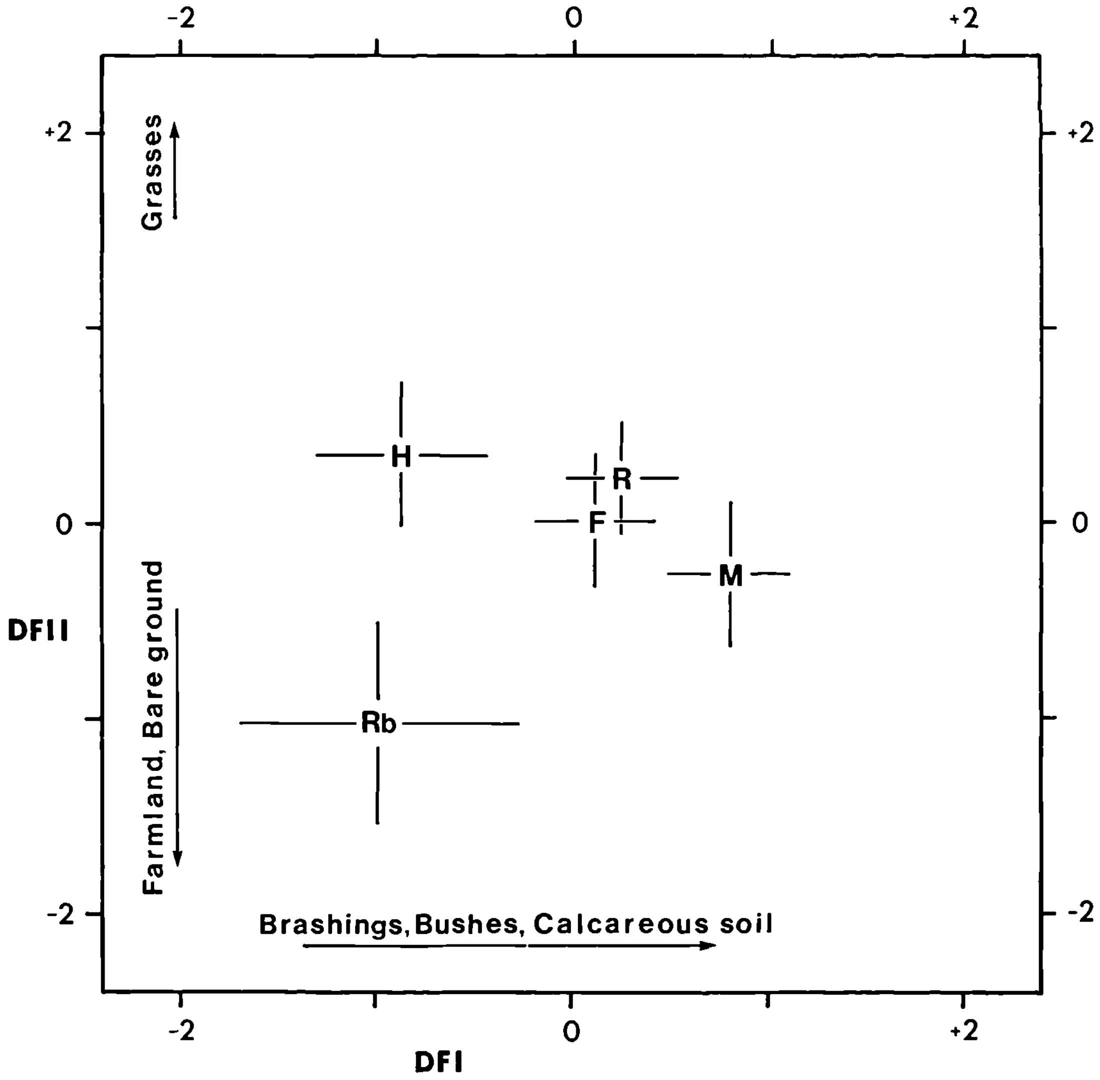

-2
0
+2
+2
0
-2
DFII
DFI
Grasses
Farmland, Bare ground
Brashings, Bushes, Calcareous soil
H
R
F
M
Rb

Table 2.22 Pianka (1973) habitat overlap indices for the October 1986 survey, calculated using each of the *'ground vegetation'* clusters as a resource unit. The mean number of pellets per plot, corrected for differential decomposition, was converted to the estimated total number of pellets in each sub-compartment and then summed for each cluster.

	muntjac	roe	fallow	hare	rabbit
muntjac	-				
roe	0.669	-			
fallow	0.623	0.801	-		
hare	0.437	0.421	0.288	-	
rabbit	0.313	0.221	0.138	0.501	-

$$\text{Overlap}_{ij} = \frac{\Sigma\, p_{ia}\, p_{ja}}{\sqrt{[(\Sigma\, p_{ia}^2)\,(\Sigma\, p_{ja}^2)]}}$$

a gradient from a low abundance of bushes and brashings on brown earth soils at one extreme, to a high abundance of bushes and brashings on calcareous soils at the other. DFII described a gradient from areas adjacent to farmland with high levels of bare ground at one extreme, to areas away from farmland with a high abundance of grasses in the ground vegetation at the other extreme.

The position of the species centroids along the first two DF axes are shown in Figure 2.5. DFI placed hares and rabbits at the brown earth soils end of the gradient, roe and fallow deer at the same position in the middle and muntjac at the calcareous soil with abundant bushes and brashings end of the gradient. DFII separated hares and rabbits, placing hares at the grass dominated end of the gradient.

The pairwise F-statistics comparing the position of species in 4-discriminant space are given in Table 2.21. Three species pairs, muntjac and roe deer, roe and fallow deer, and hares and rabbits, did not occupy significantly different positions in discriminant space ($p>0.05$). Compared to the winter survey, the ecological distance between roe and fallow deer had decreased relative to the distance between muntjac and roe deer, confirming the changes in habitat selectivity and dispersion shown above for roe deer.

The performance of the DF model in correctly classifying cases was still poor, but there was an increase from 39% to 44% of cases correctly classified. In particular, the performance of the model in classifying roe deer and rabbits was improved.

Pianka's (1973) niche overlap indices, using each cluster from the *'ground vegetation'* grouping as a resource unit are given in Table 2.22. These confirmed that the smallest ecological separation (highest niche overlap) was between roe and fallow deer.

2.4 DISCUSSION

The use of faecal pellet counts to determine habitat selection and niche partitioning, assumes that the rate of faecal deposition is a linear function of the time spent in each habitat unit. Collins & Urness (1979, 1981, 1984) found significant differences between the rate of faecal deposition by tame elk *Cervus canadensis* and mule deer *Odocoileus hemionus* and both the total time and the time spent grazing in each habitat unit. They found that defecation rate increased with rate of travel and thus faecal production was higher in less productive habitats, even though the deer spent less time in such habitats. However, Leopold *et al.* (1984) re-examined the data from Collins & Urness (1981) and showed that the rankings of faecal deposition and direct observation did not differ significantly. Similarly, Loft & Kie (1988) found no significant difference between the rankings of habitat use assessed by faecal pellet density and by radio-telemetry. Both authors suggest that faecal pellet counts can be reliably used to estimate the rank order of habitat use, but that they should be used with caution to infer absolute habitat use, especially in habitats that receive similar levels of use. In this study, faecal pellet counts were not used to infer an absolute order of habitat preference (Staines & Welch, 1984), but were used in multivariate analyses that related relative faecal pellet density to a number of habitat variables.

The distribution of muntjac in the King's Forest had changed little from that reported in Chapman *et al.* (1985) for the period 1979-1982. Muntjac have remained confined to the south and east of the forest and it seems unlikely that they will spread further due to lack of suitable habitat. The areas outside their present range are open in structure and have a low diversity of vegetation at ground level. As with the previous survey, roe deer were found throughout the forest, while fallow deer now had a more widespread distribution, a result predicted by Chapman *et al.* (1985). They found that fallow deer were associated with the mature forest sub-compartments and suggested that as the forest matured, fallow deer should become more widespread.

Similar variables influenced habitat selection by the various species during both the winter and autumn pellet surveys, although the abundance of nut producing broadleaved trees switched from being a negative variable to a positive variable in the autumn muntjac regression model. However, habitat selectivity, particularly by roe deer, was lower during autumn. All three deer species selected areas of pine other than Corsican pine, in particular areas of Scots pine. At the ground vegetation level, the three species were placed along a herb/grass gradient. Muntjac selected areas with abundant bramble, raspberry, herb and bush but little grass, roe deer areas with abundant bramble, raspberry, herb and grass and fallow deer areas with abundant grass and bramble but little herb. Hares also selected areas with an abundance and diversity of grass in the ground vegetation, but at the tree canopy level they selected for non-nut producing broadleaves, in particular birch. Rabbits were associated with areas of heathland and with the non-bramble component of the herb cover. Hares and rabbits were associated with the younger forest plantings (Harris & Forde, *in prep.*), while muntjac preferred older plantings such as pre-afforestation Scots pine and in autumn areas of old nut-producing broadleaves.

Chapman *et al.* (1985) used a discriminant analysis to describe the distribution of muntjac in the Kings Forest. On a simple presence/absence basis this analysis also showed that muntjac were selecting areas with a diversity of vegetation at ground level; diversity of bushes, presence of bramble and raspberry, and abundance of nut producing broadleaves giving the most significant correlations with muntjac density. Harding (1986) used radio-tracking data to examine habitat selection in Rushbeds Wood, a very different habitat to the King's Forest, yet here again areas with abundant bushes, shrubs and herbs were preferred over areas with abundant grass in the ground vegetation.

Since roe deer were distributed throughout the forest, Chapman *et al.* (1985) were unable to use discriminant analysis to describe habitat selection on a presence/absence basis. Batcheler (1960), Henry (1981), Loudon (1982) and Hinge (1986) have all examined roe deer habitat selection in upland conifer forests. In upland habitats, areas of younger planting and rides are preferred. In the King's Forest, roe deer also selected areas of young (10-20 years old) conifer planting (Harris & Forde, *in prep.*), although the multivariate analyses do not reflect this because roe deer also occurred at high densities in the mature well thinned conifer plantations that are only found in lowland conifer forests.

In the New Forest, fallow deer, which have access to areas of mature coniferous and deciduous woodland prefer the areas of deciduous woodland (Jackson, 1974; Parfitt, 1985). This is in contrast to the King's Forest, where fallow deer prefer areas of Scots pine even though deciduous woodland is available. Fallow deer were also shown to be selecting the larger sub-compartments and this may explain the difference. In the King's Forest, the areas of broadleaved woodland, both nut producing and non-nut producing, are generally small in extent and may not provide sufficient security from disturbance.

There is very little information about hare and rabbit habitat selection in coniferous forests, although the pattern of habitat selection observed in the King's Forest is consistent with what is known about hare and rabbit diet in other habitats (Bhadresa, 1977, 1987; Frylestam, 1986); in particular rabbits generally have more herb in the diet than hares.

Faecal pellet counts were only carried out within the forest and therefore since all five species make use of agricultural land and copses outside the forest, the assessments of habitat selection will be biased. Radio-tracking has shown that muntjac in the south-east corner of the forest frequently travel between the forest and neighbouring copses, while roe deer make extensive use of both agricultural land and copses (*pers. obs.*). Visual observations have shown that fallow deer and hares move out of the forest onto farmland and rabbits onto adjacent heathland at night (*pers. obs.*). These movements out of the forest may explain some of the observed features of habitat selection. For instance, hare density was negatively correlated with proximity to farmland. Hares were frequently seen in sub-compartments adjacent to farmland during the day, but if most feeding and movement occurs on agricultural land at night, then pellet deposition may be lower than expected in the forest edge sub-compartments.

Competitive effects, if they occur, will be most important during winter, when resources are scarce (Jenkins & Wright, 1988). The winter pellet survey showed that there were high levels of spatial and habitat overlap between the three deer species. The habitat overlap indices showed that the ecological separation between muntjac and roe deer was smaller than that between roe and fallow deer, whereas the MDA placed roe deer approximately equidistant between muntjac and fallow deer in discriminant space. On balance, these results suggest that the highest overlap in spatial distribution and habitat selection, and therefore the greatest potential for competition, occurs between muntjac and roe deer. Previous studies of niche partitioning in similar sized sympatric herbivores have generally found evidence for competitive exclusion, with species densities inversely correlated in the area of spatial overlap (Anthony & Smith, 1977; Wiggers & Beasom, 1986; Smith, 1987). However, in this study, there is little evidence for competitive exclusion. Muntjac and roe deer both occur at high densities in the same parts of the south and east of the forest, although the area of highest roe deer density is in the central part of the forest, north of the main muntjac areas. These central compartments contain similar habitat to the patches of high muntjac density in the south and east. Perhaps then, if muntjac were absent, roe deer might occur at higher densities in the south and east.

Smith (1987), studying sympatric Columbian white-tailed deer *Odocoileus virginianus leucurus* and Columbian black-tailed deer *O. hemionus columbianus*, found that white-tailed deer occupied a specialized niche within the more generalist niche of the black-tailed deer and that within the area of overlap the densities of the two species were inversely correlated. He suggested that although the generalist is more widely distributed and is able to make use of a wider range of resources, within the region of overlap the generalist is outcompeted and excluded by the specialist. A similar situation is seen in the King's Forest, with muntjac as the specialist contained within the more generalist roe deer niche, although there is only weak evidence for the suppression of roe deer by muntjac in the area of overlap. Perhaps either a competitive equilibrium has not yet been established or culling of roe deer (and some muntjac) keeps the populations in balance with the available resources, thereby reducing the strength of any competitive effects.

The autumn pellet survey showed that muntjac maintained the same distribution and habitat selection as in winter, except for an increase in the use of areas of nut producing broadleaved trees. In contrast, roe deer, which during winter were concentrated into the same areas that were preferred by muntjac, became more dispersed and showed less selectivity in habitat selection. In autumn, muntjac and roe deer still had the highest spatial overlap, but roe deer had became ecologically closer to fallow deer, with both the habitat overlap indices and the MDA placing roe deer closer to fallow deer than to muntjac. Since resources are more abundant during the summer months, this temporal change in ecological separation is unlikely to be due to competition (Jenkins & Wright, 1988). More likely, it is a response to summer plant growth in less favourable habitats and to the social factors underlying summer territoriality in roe deer (Bramley, 1970).

These pellet surveys have described niche partitioning by herbivores throughout the King's Forest, and have shown that during winter, when resources are least abundant, muntjac and roe deer are the ecologically closest pair of species. However, there is only weak evidence of spatiai competitive exclusion; in fact, when the two species occur together, they seem to co-exist at high densities. The next two chapters use radio-tracking to examine how sympatric muntjac and roe deer in one such high density area partition resources both spatially and temporally.

CHAPTER THREE: RANGING BEHAVIOUR

3.1 INTRODUCTION

Radio-tracking has been used extensively for more than 20 years to study the ranging behaviour of animals, although in this time, few comparative studies have used the technique. Most workers have monitored a single species by radio-telemetry, or if more than one species has been studied, then the data collected have not been comparable spatially or temporally. Exceptions are the studies of spatial relationships between sympatric coyotes *Canis latrans* and foxes *Vulpes vulpes* by Sargeant *et al.* (1987), sympatric coyotes, bobcats *Felis rufus* and foxes by Major & Sherburne (1987) and of ranging behaviour by sympatric red and roe deer in Scotland by Hinge (1986). In this study, radio-tracking data were collected concurrently from a sympatric population of muntjac and roe deer.

Roe deer ranging behaviour has been studied using radio-telemetry in Britain by Bramley (1970) and Gent (1983) at Chedington Wood in Dorset, by Johnson (1984) at both Chedington and Porton Down in Wiltshire and in Scotland by Hinge (1986). Cederlund (1983) measured both daily and seasonal home ranges of roe deer in northern Sweden and there have been a number of studies in France, at Chizé Forest (Sempéré, 1979a&b, 1980) and also elsewhere (Janeau *et al.*, 1981; Bideau *et al.*, 1983; Vincent *et al.*, 1983; Maublanc, 1986). Ranging behaviour of field roe deer has been studied by visual observation, in Czechoslovakia (Zejda & Bauerova, 1985) and in Poland (Pielowski, 1984). The only study of ranging behaviour in free-ranging muntjac is by Harding (1986), who radio-tracked muntjac in Rushbeds Wood, a neglected coppice wood near Oxford.

To collect radio-tracking data, animals may be monitored continuously, in which case only one individual is followed, or single fixes may be taken at intervals, allowing a number of individuals to be monitored concurrently. When continuously tracking an animal, in addition to recording its position, detailed information may be collected relating to activity, speed of travel and real distance travelled. However, the positional information will contain much redundant data, since the position of the animal may not change between adjacent sampling intervals of say five minutes (Swihart & Slade, 1985). Kenward (1987) suggests that, "If it takes a long time to move between your study animals, then you will probably be constrained to continuous sampling, whereas if you have dense study populations you may be wiser to opt for single fix sampling." Since the aim of this study was to collect positional information from a number of individuals forming a high density population, single fix sampling was chosen. This was also more practical, since the animals had to be monitored throughout the twenty-four hour cycle with limited man power. However, single fix sampling did not preclude the collection of data relating to activity and distances travelled.

Whichever method of data collection is chosen, a large number of fixes or animal locations will be available to describe ranging behaviour. There have been a number of recent reviews concerning the techniques available to measure home range area using radio-tracking data (Amlaner & Macdonald, 1980; Cheeseman & Mitson, 1982; Hinge, 1986; Kenward, 1987; Cresswell, 1988;). It is not my intention to present another review of these here, but rather to discuss aspects of the two techniques chosen to describe ranging behaviour of muntjac and roe deer, the minimum convex polygon and harmonic mean techniques.

The minimum convex polygon technique (Mohr, 1947; Southwood, 1966), is the simplest and most widely used method of measuring home range area. Home range area is calculated by drawing the smallest possible convex polygon around the outermost fixes and measuring the area contained within. This is the only strictly comparable measure of home range area, since there is no ambiguity as to the area enclosed and it also has the advantage of being relatively insensitive to the number of fixes used in the calculation. However, the technique does have disadvantages. Large areas that were not actually visited may be included and there is no indication of intensity of use within the home range. Minimum convex polygons were calculated in this study, to give a simple but robust measure of home range area, which could be compared with a number of other studies.

The harmonic mean method of measuring home range area was first presented by Dixon & Chapman in 1980, with modifications proposed by Spencer & Barrett in 1984. The inverse first areal moment or harmonic mean distance is calculated for each grid intersection and the harmonic mean centre is defined as the grid intersection where this value is minimum. Contours or isopleths are then drawn, based on the harmonic mean distances, to enclose a proportion of the fixes. Thus a 95% isopleth, which is usually used to define home range area, excludes the 5% of fixes with the highest harmonic mean distances. Isopleths, drawn to enclose a lower proportion of fixes, are used to represent areas of concentrated use within the home range. This is perhaps the most realistic of the *'statistical'* techniques available to calculate home range area, since unlike probability circles and ellipses (Harrison, 1958; Jennrich & Turner, 1969) it does not assume that the fixes are independent and distributed normally about the activity centre. Departures from these assumptions, which are usual with home range data, result in the inclusion of large areas containing no fixes, when probabilistic methods are used (Macdonald *et al.*, 1980; Jaremovic & Croft, 1987). The harmonic mean technique is less sensitive to departures from a normal distribution, though highly skewed or leptokurtic distributions will result in inaccurate home range representation (Spencer & Barrett, 1984), particularly when the number of fixes is low. Also, because the data do not have to be normally distributed, it is possible to produce more than one centre of activity, whereas probabilistic methods will always produce a single activity centre. Unfortunately, it is difficult to compare harmonic mean home ranges between studies, since most workers have used different computer programs, each with its own set of algorithms and grid cell size. Harmonic mean home ranges were calculated in this study to give an alternative measure of home range area, although the low number of fixes did cause problems, and also to illustrate internal range configuration, which is less influenced by sample size.

3.2 METHODS

3.2.1 CATCHING MUNTJAC AND ROE DEER

Chapman *et al.* (1987) describe the techniques used to catch muntjac. Sub-compartments were surrounded by a double wall of 2.4m netting, hung from 1.5m bamboo poles, spaced at intervals of five metres. Animals, driven into the nets by a line of beaters, were restrained and placed in wooden holding crates. At a nearby processing area, the animals were transferred to an examination crate, which had a crush and viewing facilities. Adult animals were anaesthetised (Cooper *et al.*, 1986) and fitted with coloured fixed radio collars transmitting on 173 MHz. The design and construction of the radio-collars is as described by Harris (1980) and Cresswell (1988), except that 'C' sized cells were used giving an operational life of 15-20 months. Immature animals were fitted with plastic expanding collars, some of which included a radio-transmitter. All animals were given coloured plastic ear tags, the colour combination allowing individual recognition.

To catch roe deer, the outer wall of netting was hung from 2.5m bamboo poles and the blocks beaten as described above. Animals were restrained with cloth leg ties and fitted with face masks (Cockburn, 1976; Jones, 1984) before transfer to the processing area. Roe deer remained calm during processing and did not require anaesthesia. Adult animals were fitted with coloured fixed radio-collars constructed using 'D' sized cells, giving an operational life of at least two years. Expanding collars were not available for immature animals, but all animals were given coloured plastic ear tags.

3.2.2 RADIOTRACKING MUNTJAC AND ROE DEER

Animals were tracked on foot using a three element "Yagi" antenna with a Mariner M57 receiver for muntjac (Mariner Radar Ltd., Lowestoft, Suffolk, U.K.) and an AVM LA12 receiver for roe deer (AVM Instrument Co., Ltd., Livermore, California, USA). Point fixes were taken at a minimum of two hourly intervals for muntjac and five hourly intervals for roe deer. Fixes collected at these time intervals were considered to be independent. The time interval between roe deer fixes was longer, because larger animals move around their home ranges at a slower rate (Swihart *et al.*, 1988).

The location of an animal was determined by walking along a ride until the position where the peak signal was perpendicular to that ride was found. The distance between this position and the nearest ride junction was measured by pacing; generally a distance of less than 100 metres. This procedure was repeated along another ride, perpendicular to the first, to obtain the second co-ordinate. In addition to noting the date, the time of each fix and whether the animal was sighted, the activity state was assessed as being either active or inactive, based on variations in signal amplitude. Tracking rounds, during which each radio-collared deer was located, were structured to give a spread of fixes throughout the day and night. A minimum of 15 fixes per month were collected for each muntjac and 25 fixes for each roe deer. Included in the monthly totals for each muntjac was a 24 hour tracking session, during which eight fixes were obtained at three hourly intervals. Similarly, there were two roe deer 24 hour tracking sessions each month; five fixes were collected during tracking rounds starting at 0100, 0600, 1100, 1600, and 2100hrs G.M.T.

The pacings were plotted on an Ordnance survey map (Scale 1:1250) and each fix allocated to a 25m square. This grid size was appropriate for the accuracy with which the fixes were collected (Jaremovic & Croft, 1987). Usually the distance between tracker and animal was less than 100 metres and many of the fixes were confirmed by visual observation. The radio-tracking data were entered on a BBC microcomputer and then transferred to the former Bristol University main frame computer, a HONEYWELL L68 DPS, for subsequent analysis.

The radio-tracking analyses in this chapter and in Chapter Four only use data from adult muntjac and roe deer to simplify comparisons between species. Muntjac does entered the adult age category at eight months of age (34 weeks) and bucks on the 1st of June in the year that they cast their first head of antlers (Table 3.1). Both roe bucks and does entered the adult age category at 24 months of age (Table 3.2). At this age roe bucks have just cleaned

Table 3.1 Age categories for muntjac radio-tracking analysis.

1. Fawns:	All animals less than two months old (<9 wks).
2. Immature females:	Females between two and eight months old (9-34 wks).
3. Adult females:	Females over eight months old (>34 wks).
4. Immature males:	Males from two months old (9 wks), up to the age at which they clean the first head of antlers. This occurs at between 46 and 76 weeks.
5. Sub-adult males:	This category is used for animals with their first head of antlers.
6. Adult males:	Bucks enter this category on the 1st June in the year that they cast the first head of antlers and join the adult antler cycle. This occurs at between 51 and 112 weeks.

Table 3.2 Age categories for roe deer radio-tracking analysis.

1. Fawns:	Until 31st July in the year of birth.
2. Juveniles:	From 1st August to 30th September in the year of birth.
3. Immature females:	From 1st October in the year of birth to 30th April in the year after birth (up to 12 months of age).
4. Sub-adult females:	From 1st May in the year after birth to 30th April of the following year (12 to 24 months of age).
5. Adult females:	From 1st May in the second year after birth (>24 months).
6. Immature males:	From 1st October in the year of birth to 30th April in the year after birth (up to 12 months of age).
7. Sub-adult males:	From 1st May in the year after birth to 30th April of the following year (12 to 24 months of age).
8. Adult males:	From 1st May in the second year after birth (>24 months).

their second head of antlers. The younger age categories are slightly different from those used for the population censuses in the King's Forest (Claydon *et al.*, 1986; Claydon *et al.*, *in prep.*), because all radio-collared animals could be sexed at capture.

3.2.3 HOME RANGE SIZE AND STRUCTURE

Adult bimonthly and annual home ranges were calculated using the minimum convex polygon and harmonic mean techniques. The computer program used was written to analyse continuous tracking data (Cresswell, 1988; Cresswell & Harris, 1988) and modifications were required to accommodate the lower density of loci from single fix sampling.

Dixon & Chapman's original definition of a harmonic mean home range was that area contained within the isopleth, whose value in metres (distance from the harmonic mean centre), enclosed 95% of the loci. In the example they used, this isopleth was a single smooth curve. Similarly, Spencer & Barrett (1984) calculated their harmonic mean home ranges by increasing the distance of the outer isopleth from the harmonic mean centre, until they obtained a continuous curve enclosing approximately 95% of the locations. Although Dixon & Chapman (1980) defined the harmonic mean home range in terms of altering the distance of the outer isopleth from the harmonic mean centre, many subsequent workers have defined the home range as that area contained within an isopleth, drawn at a defined distance from the harmonic mean centre, to enclose 95% of the locations, but not necessarily in a smooth continuous curve. This was true of the program used here; the harmonic mean distance of each fix was ranked, the highest 5% were removed and then isopleths drawn to enclose the remaining locations (Jaremovic & Croft, 1987). Running the deer data through the program frequently produced 95% isopleth home ranges that consisted of one or two isopleths enclosing large areas and a number of small isopleths, usually surrounding single fixes. Estimates of home range area calculated from these plots would not fit the Dixon & Chapman (1980) definition of a harmonic mean home range.

To produce an appropriate harmonic mean home range area, the distance of the 95% isopleth from the harmonic mean centre can be subjectively increased or the value of the constant 'k' in the harmonic mean equation altered. Increasing the value of 'k' smooths the harmonic mean distances, so that when there is a low density of fixes, each individual location produces a smaller spike on the profile of harmonic mean distances. The resulting 95% isopleth is then drawn at an increased distance from the harmonic mean centre. The second technique was used, because once a value of 'k' has been selected, all home ranges with an area and density of loci in the same order of magnitude, can be calculated using that value of 'k', rather than altering the distance of the 95% isopleth for each range examined. A 'k' value of 18.0 produced 95% isopleth home ranges for both muntjac and roe deer that fitted the Dixon & Chapman (1980) definition. Figure 3.1 shows the effect of increasing the value of 'k' on harmonic mean home ranges.

Kenward (1987) suggested from a range of studies on badgers *Meles meles* (Parish & Kruuk, 1982), grey squirrels (Kenward, 1982a), goshawks *Accipiter gentilis* (Kenward, 1976) and kestrels *Falco tinnunculus* (Village, 1982), that with single fix sampling of two or three fixes a day, an asymptote minimum convex polygon range size should be reached after approximately 30 fixes, and that the 30 fix range might be a useful standard. Similarly, Hinge (1986) found that roe deer minimum convex polygon ranges reached an asymptote after 20-24 fixes, with four fixes per day. In this study, fixes were collected at intervals throughout each month, rather than concentrated into a few consecutive days, and the concept of asymptotic range size was less applicable. Over a bimonthly period, animals could expand their ranges in a number of different directions and of 30 bimonthly muntjac minimum convex polygon ranges, where at least 50 fixes had been collected, nine failed to reach an asymptote. Out of eight roe deer ranges, with at least 60 fixes, three did not asymptote. With 95% isopleth harmonic mean ranges, which are more sensitive to sample size, over half the muntjac ranges failed to asymptote. Thus the concept of a minimum number of fixes, above which the home range area did not increase, was inappropriate for this data. Instead home ranges were calculated to a standardised number of fixes.

Muntjac bimonthly ranges were calculated as "35 fix ranges". Where more than 40 fixes had been collected, only the first 40 in a bimonthly period were included. When range size was calculated with between 30 and 40 fixes, the estimate of home range area was left uncorrected. When using data sets with between 25 and 29 fixes, the home range area was corrected to a "35 fix range", using a series of regressions calculated from a number of bimonthly data sets with between 35 and 40 fixes, by relating the rate of increase in home range area between 10 and 25 fixes to the range size at 35 fixes. (Village, 1982). These regression equations together with the equation used to correct core area size are given in Table 3.3. Home ranges were not calculated when less than 25 fixes were available in a bimonthly period. Roe deer bimonthly ranges were calculated as "50 fix ranges", using a minimum of 45 and a maximum of 55 fixes, with no corrections applied to the estimates of home range area.

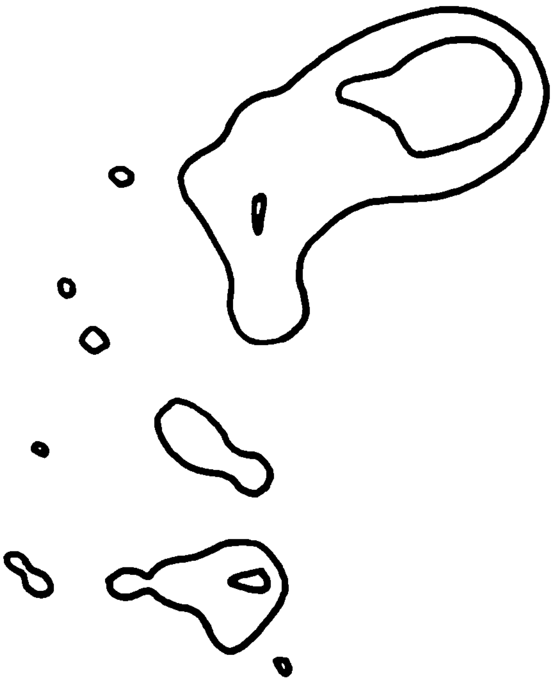
For both muntjac and roe deer, graphs of area enclosed against harmonic mean

Figure 3.1a&b The effect of altering 'k' on harmonic mean home ranges. The contours are 95% and 50% isopleths.

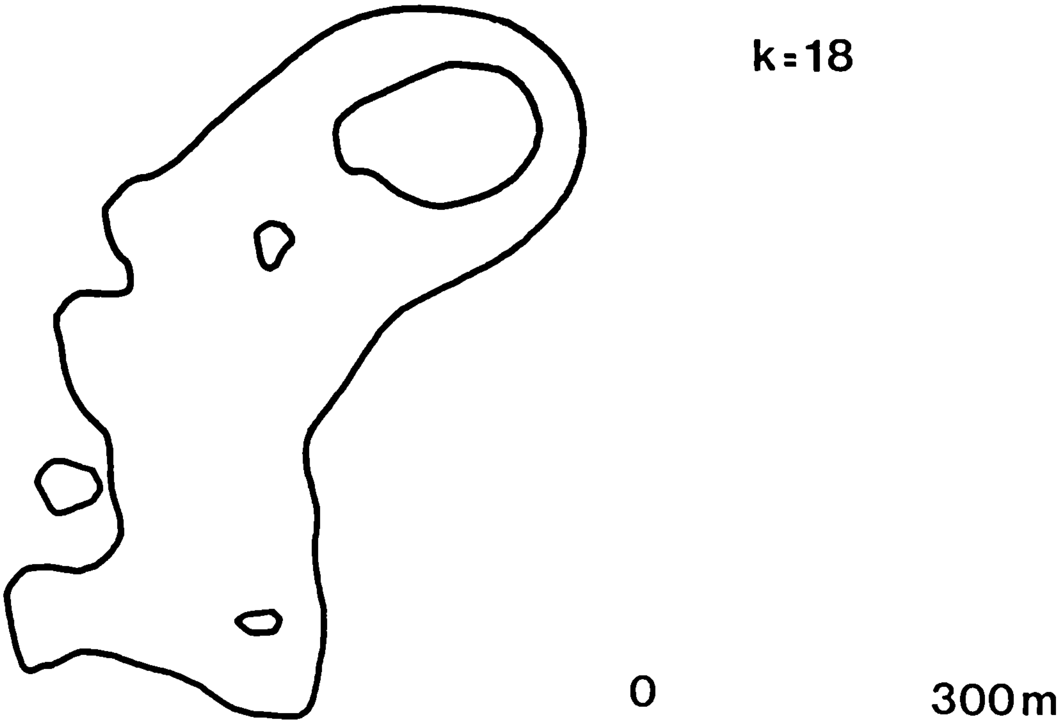
Figure 3.1a (Facing page): Muntjac buck m085 during September/October 1987, based on 40 locations. **Above:** k=9.57. **Below:** k=18.00.

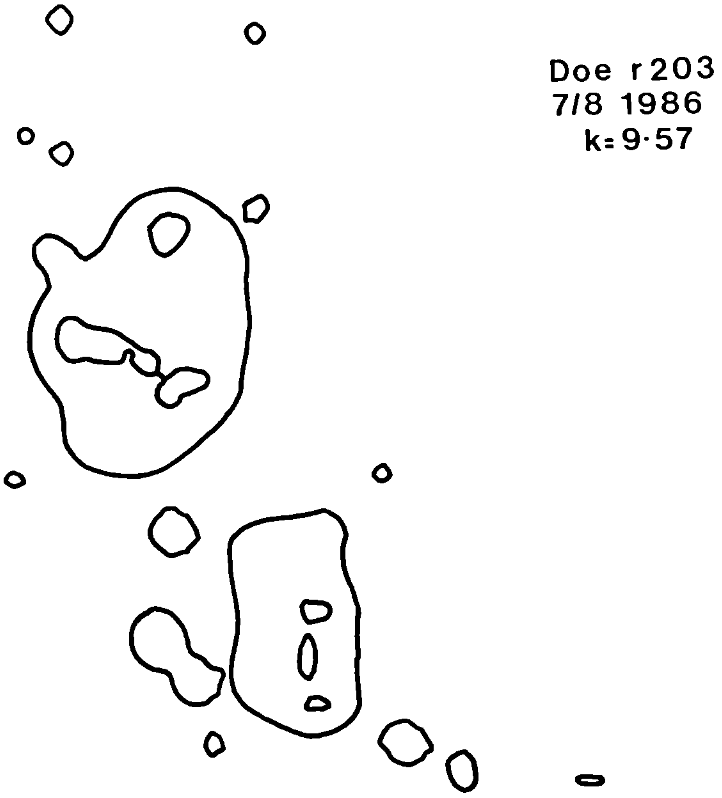
Figure 3.1b (Following page): Roe doe r203 during July/August 1986, based on 53 locations. **Above:** k=9.57. **Below:** k=18.00.

Buck m085
9/10 1987
k=9·57



k=18




Doe r203
7/8 1986
k=9·57

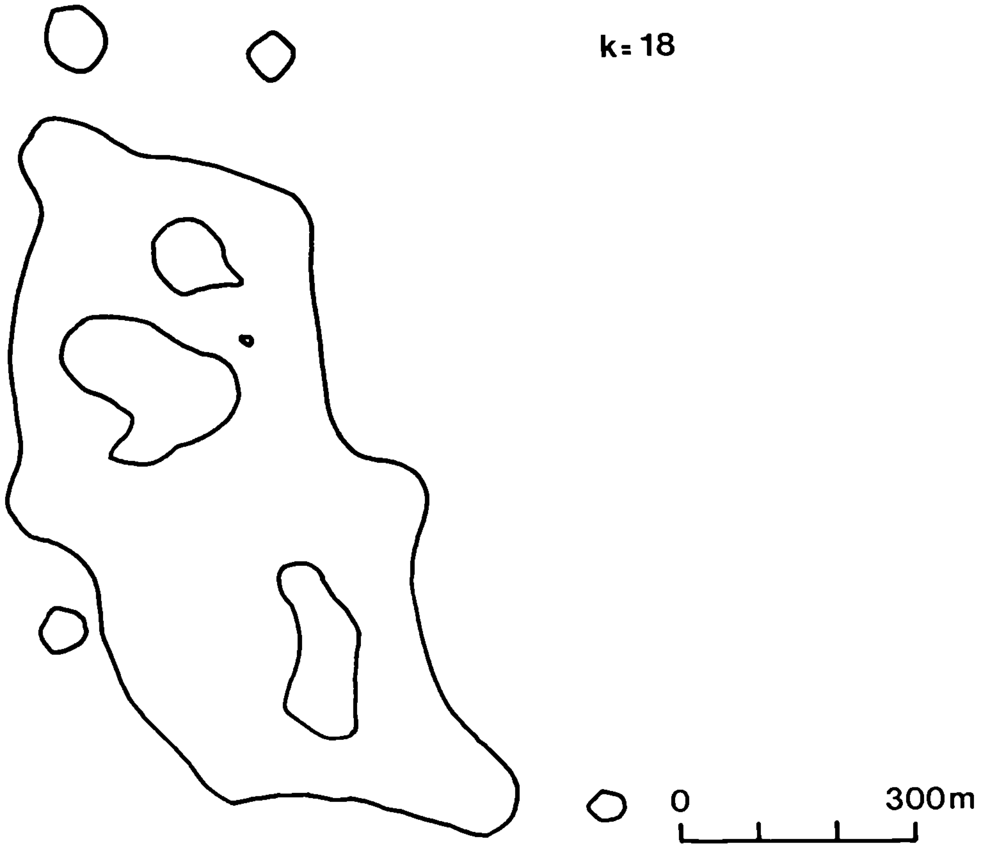

k=18
0
300m

Table 3.3 Regression equations used to correct muntjac home range area and core area size.

		n	r^2	F	p
Minimum convex polygon	a=2.58+27.00b	31	90.2	279.2	***
95% isopleth harmonic mean range	a=2.46+26.81b	34	88.3	248.8	***
50% isopleth harmonic mean range	a=0.69+13.76b	36	59.8	53.0	***

a is the range size at 35 fixes
b is the rate of increase per fix between 10 and 25 fixes

isopleth value, showed maximum deviation from a normal distribution (Clutton-Brock *et al.*, 1982, p. 321; Samuel *et al.*, 1985) at either the 50 or 60% isopleth value and therefore the 50% isopleth was chosen to represent the core area, or area of concentrated use within each home range (Figure 3.2). Core area size was corrected as described above when there were less than 30 fixes in a bimonthly period. 80% isopleths represented an area intermediate between the core area and the 95% isopleth home range. Only areas enclosed by 50% isopleths that contained fixes in at least two different 25m grid squares were included in counts of the number of core areas.

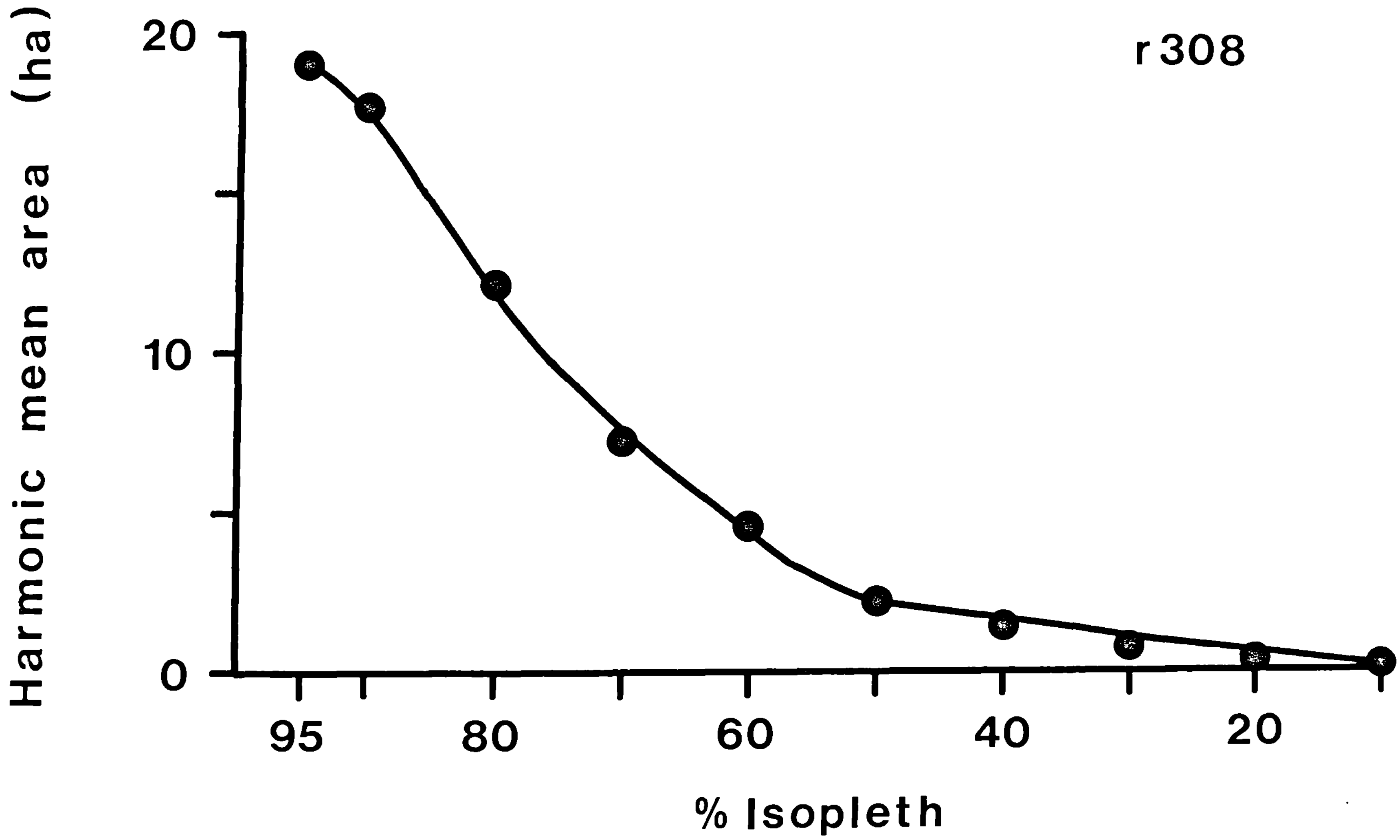
Spencer & Barrett (1984) described how highly skewed or leptokurtic distributions of fixes produced 95% isopleth ranges that enclosed large unused areas. Several muntjac ranges had highly skewed distributions, which resulted in large overestimates of range size and these were excluded from calculations of mean range size.

Home range areas were standardised, to account for different sized ranges, by relating each bimonthly range size to the annual mean range size for that individual. Each bimonthly range size was expressed first as a percentage deviation from the annual mean. To allow statistical analysis, the deviations were converted to a nominal scale where 0-99 represented negative deviations, 100 was equivalent to a 0% deviation and values greater than 100 were positive deviations from the annual mean. For example, 150 was a positive deviation of 50% and 50 was a negative deviation of 50% from the annual mean.

Valid comparisons were possible between muntjac and roe deer home ranges, even though muntjac ranges were calculated as '35 fix ranges' and roe deer ranges as '50 fix ranges'. This was because more fixes were required to describe roe deer ranges with a comparable level of accuracy. Out of the 30 bimonthly muntjac minimum convex polygon ranges with at least 50 fixes, 15 had become asymptotic at 35 fixes, while out of the eight roe ranges with at least 60 fixes, five were asymptotic at 50 fixes, but only one had reached an asymptote at 35 fixes. The 95% isopleth harmonic mean ranges showed a similar comparison.

Annual ranges were calculated, when data was available for at least five out of the six bimonthly periods. For both muntjac and roe deer, approximately 13 fixes per month gave asymptotic minimum convex polygon and 95% isopleth annual ranges. All annual ranges were therefore asymptotic and direct comparisons could be made between the two species.

Figure 3.2 Harmonic mean area plotted against percentage of fixes included (harmonic mean isopleth value). The inflection point was used to define the isoplethic value that enclosed the core area. Roe doe r308 during September/October 1987, based on 50 locations.


r308
Harmonic mean area (ha)
20
10
0
95
80
60
40
20
% Isopleth

3.2.4 DAILY RANGE LENGTH

The 24 hour tracking sessions were extracted from the raw data files using a computer program that selected data sets where there was an interval between fixes of three hours ± 30 minutes for muntjac and five hours ± 60 minutes for roe deer. A second program calculated the distance moved between each fix and the cumulative distance between the first and last fix, for each 24 hour data set. The resulting daily range lengths were standardised as described above.

3.3 RESULTS

3.3.1 HOME RANGES

3.3.1.1 Home range size

Details of the radio-tracking data collected from adult muntjac and roe deer are given in Tables 3.4 and 3.5. The analyses were based on more than 11,000 fixes collected from 36 muntjac and nearly 3,000 fixes from seven roe deer. Two muntjac (m019 and m033) were tracked continuously for more than four years and three of the roe deer for more than two years. Most animals were tracked for at least 12 months.

Home range size of individual muntjac varied between bimonthly periods (Figure 3.3). There were no obvious seasonal patterns and no evidence from the does, of a cycle in home range size that corresponded to a seven month reproductive cycle.

Mean muntjac minimum convex polygon and 95% isopleth harmonic mean home ranges are given in Tables 3.6 and 3.7. There was little difference between minimum convex polygon and 95% isopleth doe ranges. However, bucks, which had larger average range sizes, had substantially smaller harmonic mean ranges. This was because the minimum convex polygon ranges enclosed areas that contained no fixes; these areas were excluded from the harmonic mean ranges. Generally, the low density of fixes, combined with the skewness contained within most data sets, meant that harmonic mean home ranges did not always accurately represent the distribution of fixes. A concentration of fixes towards the edge of a range would result in the 95% isopleth enclosing part of the area outside the minimum convex polygon. However, the 95% isopleth home ranges were included for comparison with minimum convex polygon ranges and the lower harmonic mean isopleths did reliably describe internal range structure.

Table 3.4 Data used for the analysis of ranging behaviour in adult muntjac. The number of locations was reduced when there were more than 40 fixes in a bimonthly period, while bimonthly periods with less than 25 fixes were excluded.

Animal no.	Sex	Starting date	Finishing date	No.locations
m014	m	11/83	06/85	388
"	m	11/85	12/85	29
m027	m	11/86	06/87	114
m031	m	05/85	04/86	206
m038	m	07/83	04/85	427
m042	m	11/84	10/86	445
m065	m	05/85	06/85	40
m085	m	05/87	12/87	152
m091	m	01/87	12/87	192
m201	m	11/85	06/87	341
m213	m	05/86	12/87	334
m237	m	01/87	12/87	187
m325	m	01/86	08/86	136
m328	m	07/86	12/87	315

				3,306
m004	f	09/82	10/83	230
"	f	07/84	12/84	100
"	f	09/85	02/86	106
m006	f	07/83	12/83	116
"	f	09/84	12/85	298
m019	f	07/82	12/86	935
m029	f	11/84	04/87	507
m033	f	03/83	12/87	1053
m037	f	03/84	04/84	38
m043	f	11/84	12/87	680
m048	f	11/84	12/85	245
m061	f	07/87	12/87	98
m066	f	01/86	12/87	388
m067	f	09/84	12/85	298
m144	f	03/85	06/85	74
"	f	11/85	12/87	446
m202	f	11/86	08/87	162
m216	f	01/86	02/86	40
m217	f	11/85	10/86	174
m221	f	01/85	04/85	76
m302	f	07/86	06/87	182
m307	f	09/87	12/87	60
m309	f	01/87	12/87	198
m310	f	11/86	12/87	226
m329	f	11/86	12/87	217
m430	f	05/87	12/87	136
m512	f	03/84	06/87	712

				7,795

Table 3.5 Data used for the analysis of ranging behaviour in adult roe deer. The number of locations was reduced when there were more than 55 fixes in a bimonthly period.

Animal no.	Sex	Starting date	Finishing date	No.locations
r062	m	03/87	02/88	297
r214	m	01/86	12/87	615

				912
r080	f	03/87	06/87	97
r094	f	01/86	12/87	604
r203	f	01/86	04/87	405
r207	f	01/86	12/87	607
r308	f	05/87	02/88	256

				1,969

Figure 3.3 Minimum convex polygon ranges of individual adult muntjac (m042 is a buck, m019 and m033 are does.).

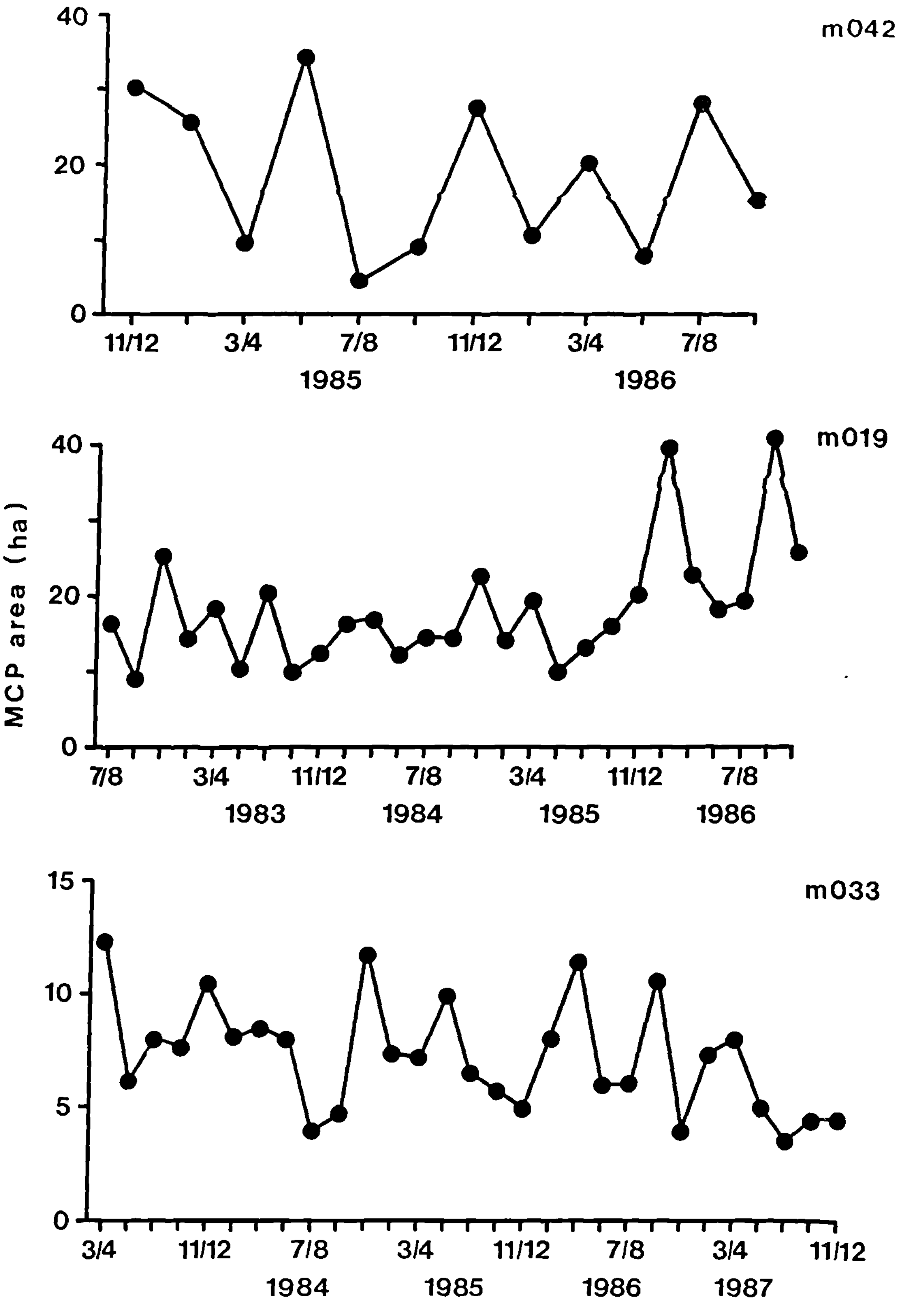

m042
40
20
0
11/12
3/4
7/8
11/12
3/4
7/8
1985
1986
m019
MCP area (ha)
40
20
0
7/8
3/4
11/12
7/8
3/4
11/12
7/8
1983
1984
1985
1986
m033
15
10
5
0
3/4
11/12
7/8
3/4
11/12
7/8
3/4
11/12
1984
1985
1986
1987

Table 3.6 Minimum convex polygon ranges of adult muntjac. A standardised range of 100 is equivalent to a 0% deviation from the annual mean. Figures are means ± S.E., sample sizes are in parenthesis.

	Bucks		Does	
Month	**Area(ha) n=13**	**Standardised area n=9**	**Area(ha) n=24**	**Standardised area n=17**
J/F	28.3±4.9(15)	124.0±20.1(13)	12.7±1.5(34)	102.8±8.1(32)
M/A	27.9±4.9(15)	107.0± 9.8(13)	14.5±1.9(36)	115.9±8.4(34)
M/J	24.0±5.0(17)	100.4±10.3(13)	11.4±1.4(34)	94.2±7.3(33)
J/A	25.8±4.9(15)	100.8±10.6(13)	12.0±1.5(36)	92.2±6.1(34)
S/O	20.8±4.0(14)	87.6± 9.7(13)	12.6±1.9(40)	95.2±8.1(37)
N/D	20.3±4.2(18)	86.6± 9.9(15)	13.2±1.7(45)	101.7±7.2(42)
p	n.s.	n.s.	n.s.	n.s.

Table 3.7 95% isopleth harmonic mean ranges of adult muntjac. Legend as Table 3.6.

	Bucks		Does	
Month	**Area(ha) n=13**	**Standardised area n=9**	**Area(ha) n=24**	**Standardised area n=17**
J/F	17.6±1.9(14)	117.0±15.2(12)	11.1±0.9(33)	104.6±6.3(30)
M/A	14.4±1.3(15)	96.7±11.9(13)	11.9±0.9(35)	111.2±6.8(33)
M/J	15.0±1.8(16)	103.2±10.0(13)	9.6±0.6(32)	92.8±4.4(30)
J/A	17.9±3.0(14)	100.1±12.7(12)	10.5±0.8(36)	99.0±5.0(33)
S/O	15.7±2.4(14)	96.1± 9.6(13)	11.1±1.2(39)	101.0±7.6(35)
N/D	14.6±1.8(18)	89.4± 9.3(15)	10.8±0.9(45)	102.7±6.0(42)
p	n.s.	n.s.	n.s.	n.s.

n.s. not significant, Kruskall-Wallis ANOVA

For both muntjac bucks and does, there were no significant seasonal trends with either minimum convex polygon or harmonic mean home ranges (Kruskall-Wallis ANOVA, all $p > 0.05$). However, there was a trend for bucks to have smaller ranges between September and December and for does to have smaller ranges during the summer months. Bucks had significantly larger minimum convex polygon and harmonic mean home ranges than does at all times of year (Mann-Whitney U tests, all $p < 0.05$).

The size of individual roe deer home ranges changed seasonally, with a regular annual cycle of larger winter and smaller summer range size (Figure 3.4). Mean roe deer minimum convex polygon and harmonic mean home ranges are given in Tables 3.8 and 3.9. 95% isopleth roe deer ranges were markedly smaller than minimum convex polygons, because again the convex polygons enclosed unused areas. Roe deer home ranges were calculated using a higher density of loci and there was less skewness in the distribution of fixes. Therefore, more reliable estimates of harmonic mean home range area were produced. There were significant seasonal changes in home range size for roe bucks and does, using both measures of home range area (Kruskall-Wallis ANOVA, all $p < 0.05$). Bucks had largest ranges during the winter months, and minimum ranges during September/October. This suggested that territory size was maintained until the rut finished in early August, followed by a period of rest and relative inactivity before winter. Does had largest ranges during January/February, and minimum ranges during May/June, when the kids are born. There were no significant differences between buck and doe minimum convex polygon or 95% isopleth ranges at any time of year (Mann-Whitney U tests, all $p > 0.05$).

Roe buck minimum convex polygon ranges were significantly larger than muntjac buck ranges during January/February (Mann-Whitney U test, $U=3$, $p < 0.05$). Also, roe bucks had larger 95% isopleth home ranges between January and April (Mann-Whitney U tests; January/February, $U=0$, $p < 0.01$; March/April, $U=3$, $p < 0.05$). Roe doe minimum convex polygon and 95% isopleth ranges were significantly larger than muntjac doe ranges at all times of year (Mann-Whitney U tests, all $p < 0.01$).

3.3.1.2 Internal range structure

Harmonic mean isopleths enclosing 80% and 50% of locations were used to illustrate internal range structure. The area(s) enclosed by the 50% isopleths, represented the core(s) of each animals range.

Figure 3.4 Minimum convex polygon ranges of individual adult roe deer (r214 is a buck, r094 and r207 are does.).

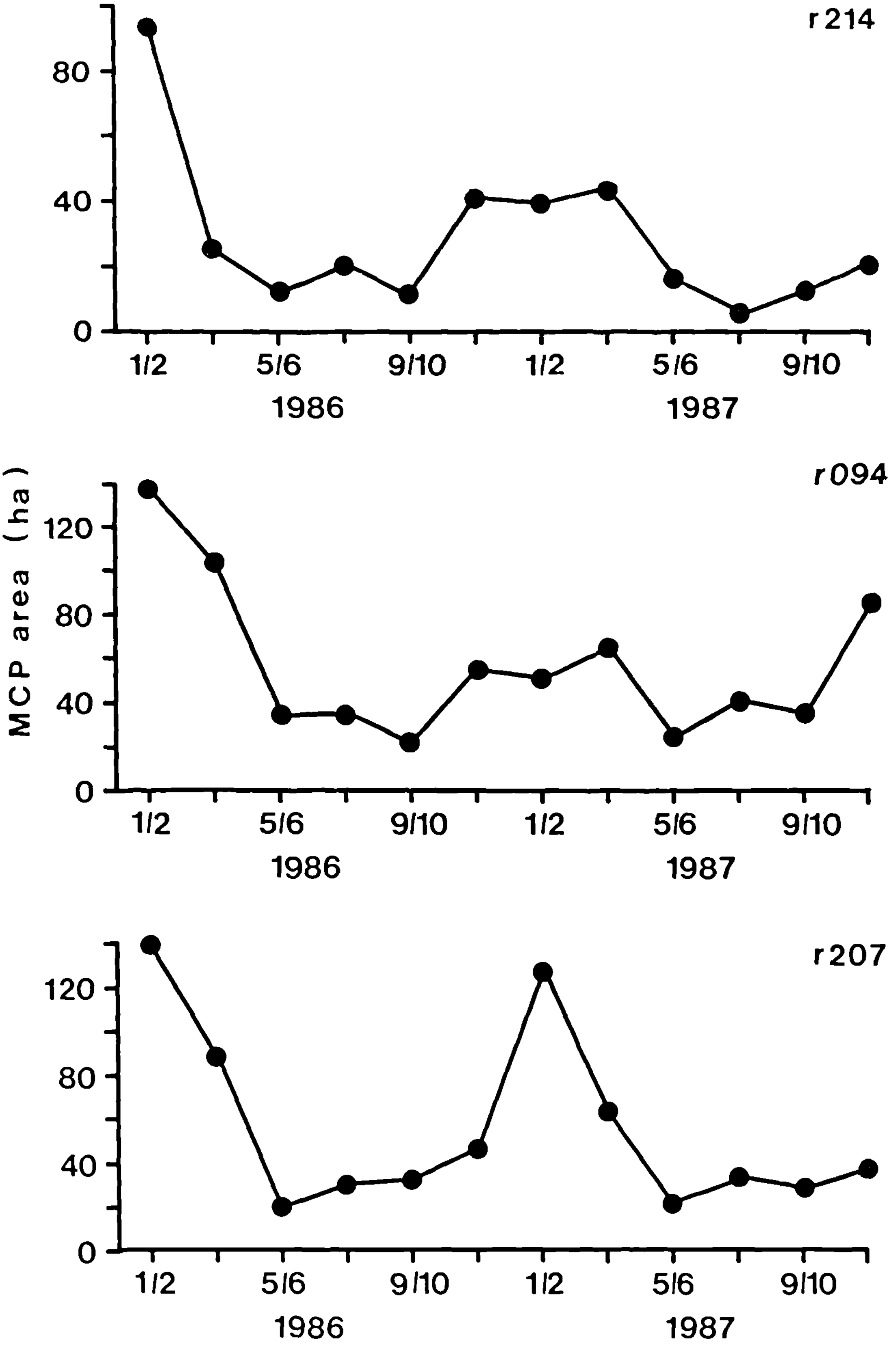

r214
80
40
0
1/2
5/6
9/10
1/2
5/6
9/10
1986
1987
MCP area (ha)
r094
120
80
40
0
1/2
5/6
9/10
1/2
5/6
9/10
1986
1987
r207
120
80
40
0
1/2
5/6
9/10
1/2
5/6
9/10
1986
1987

Table 3.8 Minimum convex polygon ranges of adult roe deer. A standardised range of 100 is equivalent to a 0% deviation from the annual mean. Figures are means ± S.E., samples sizes are in parenthesis.

	Bucks		Does	
Month	**Area(ha) n=2**	**Standardised area n=2**	**Area(ha) n=5**	**Standardised area n=4**
J/F	72.4±16.7(3)	196.8±63.9(3)	114.1±23.0(7)	175.2±28.0(7)
M/A	77.1±42.6(3)	163.0±45.3(3)	67.1±10.4(7)	115.9±19.9(6)
M/J	21.8± 6.8(3)	52.8± 4.4(3)	25.1± 4.9(7)	47.4± 4.2(6)
J/A	18.6± 6.9(3)	45.4±14.7(3)	37.6± 4.3(6)	68.3± 7.6(6)
S/O	17.9± 5.7(3)	43.3± 1.8(3)	35.9± 6.5(6)	64.1± 9.1(6)
N/D	38.3± 9.6(3)	98.6±22.6(3)	74.5±22.6(6)	121.5±19.1(6)
p	*	**	**	***

Table 3.9 95% isopleth harmonic mean ranges of adult roe deer. Legend as Table 3.8.

	Bucks		Does	
Month	**Area(ha) n=2**	**Standardised area n=2**	**Area(ha) n=5**	**Standardised area n=4**
J/F	51.0±10.9(3)	185.8±48.4(3)	60.2±8.8(7)	162.9±21.6(7)
M/A	36.2± 9.5(3)	126.1±25.6(3)	32.5±4.3(7)	91.8±11.6(6)
M/J	20.2± 7.3(3)	67.6±15.1(3)	21.3±3.6(7)	63.5± 5.5(6)
J/A	20.5± 6.5(3)	72.3±23.2(3)	27.4±2.0(6)	81.5± 9.2(6)
S/O	16.1± 3.8(3)	56.2±10.1(3)	25.7±2.4(6)	74.6± 4.6(6)
N/D	25.4± 5.3(3)	92.1±22.8(3)	42.0±6.7(6)	118.0± 9.7(6)
p	*	*	**	***

*	$p<0.05$,	Kruskall-Wallis,	ANOVA	
**	$p<0.01$,	"	"	"
***	$p<0.001$,	"	"	"

There was no seasonal change in core area size for either muntjac bucks or does (Kruskall-Wallis ANOVA, both p>0.05). However, there was a trend for bucks to have smaller cores during September/October and for does to have smaller cores during the summer months. The annual mean core area size (± S.E.) for bucks was 2.0±0.10ha (n=94) and for does was 1.4±0.05ha (n=225); muntjac bucks having significantly larger core areas than does (Mann-Whitney U test, U=6019, p<0.001).

Generally, muntjac does had a single core that was not placed centrally within the range (Table 3.10), while bucks often had more than one core area. There was no seasonal change in the number of core areas for bucks or does (Kruskall-Wallis ANOVA, both p>0.05). The annual mean number of cores (± S.E.) for bucks was 1.8±0.01 (n=94) and for does was 1.5±0.05 (n=225); muntjac bucks having significantly more core areas than does (Mann-Whitney U test, U=8837, p<0.05). Figure 3.5 shows a buck range with two core areas and a doe range with a single core area.

On the study area, groups of does had home ranges that were centred on areas of high quality habitat. Within these groups, minimum convex polygons overlapped, but core areas overlapped less than might be expected. In areas of lower quality habitat, does were usually solitary. Figures 3.6a and 3.6b show minimum convex polygons and 50% core areas for part of the study area during November/December 1986. Two groups of adult does and a number of solitary does are illustrated. In addition there were juveniles, of both sexes, associated with various does. Buck core areas were exclusive from other bucks, although convex polygons sometimes overlapped at the edges. Buck ranges overlapped those of several does, and their core areas often coincided with those of the does.

Roe bucks and does showed no significant seasonal changes in core area size (Kruskall-Wallis ANOVA, all p>0.05), though as with range size, bucks had smallest core areas during September/October and does smallest core areas during May/June. The annual mean core area size (± S.E.) for bucks was 2.2±0.30ha (n=18) and for does was 3.3±0.24ha (n=39); roe does having significantly larger core areas than bucks (Mann-Whitney U test, U=206, p<0.05).

The mean number of core areas for roe bucks and does are given in Table 3.11. Usually, both bucks and does had more than one core area and although there were no significant seasonal differences (Kruskall-Wallis ANOVA, both p>0.05), there was a trend for more core areas during the winter months. Figure 3.7 shows examples of roe buck and doe ranges with multiple core areas. The annual mean number of core areas (± S.E.) for

Table 3.10 Number of core areas within adult muntjac harmonic mean home ranges. Figures are means ± S.E., sample sizes are in parenthesis.

Month	Bucks n=13	Does n=24	
J/F	1.8±0.28(15)	1.7±0.14(34)	
M/A	1.7±0.18(15)	1.5±0.10(36)	
M/J	2.0±0.26(17)	1.4±0.12(34)	
J/A	1.5±0.19(15)	1.4±0.10(36)	
S/O	2.2±0.32(14)	1.4±0.09(40)	
N/D	1.6±0.25(18)	1.6±0.11(45)	
p	n.s.	n.s.	
Annual mean	1.8±0.10(94)	1.5±0.05(225)	*

n.s. not significant, Kruskall-Wallis ANOVA
* p<0.05, Mann-Whitney U test, bucks vs. does

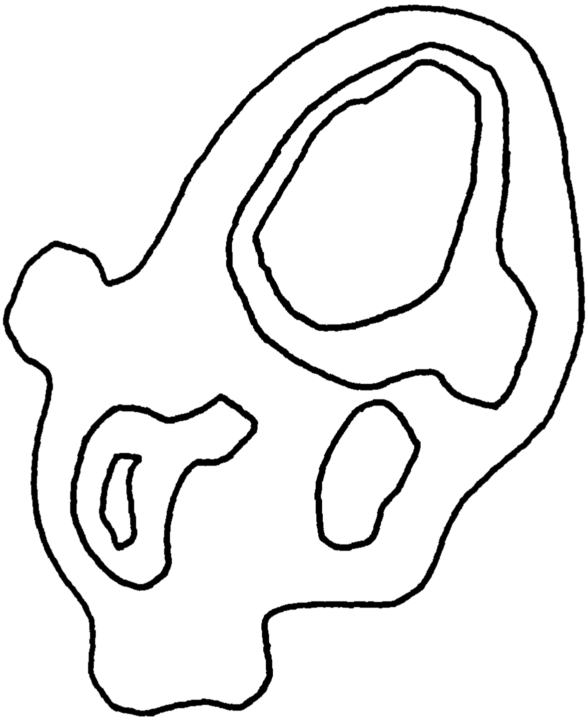
Table 3.11 Number of core areas within adult roe deer harmonic mean home ranges. Figures are means ± S.E., sample sizes are in parenthesis.

Month	Bucks n=2	Does n=5	
J/F	2.3±1.33(3)	2.7±0.47(7)	
M/A	2.0±0.00(3)	3.3±0.52(7)	
M/J	3.0±0.58(3)	2.1±0.40(7)	
J/A	1.7±0.33(3)	2.0±0.51(6)	
S/O	1.3±0.33(3)	1.8±0.48(6)	
N/D	2.3±0.88(3)	1.8±0.40(6)	
p	n.s.	n.s.	
Annual mean	2.1±0.28(18)	2.3±0.20(39)	#

n.s. not significant, Kruskall-Wallis ANOVA
not significant, Mann-Whitney U test, bucks vs. does

Figure 3.5 Internal structure of adult muntjac harmonic mean *home ranges. The contours are* 95%, 80% and 50% isopleths. **Above:** Muntjac buck m014 during March/April 1985 based on 40 locations. **Below:** Muntjac doe m019 during September/October 1983 based on 40 locations.

Buck m014
3/4 1985



Doe m019
9/10 1983

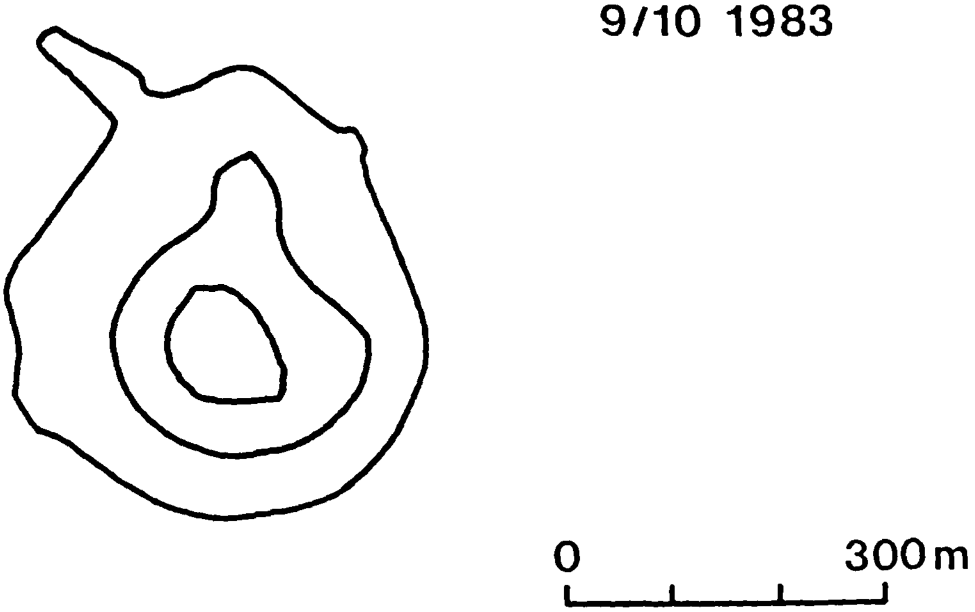
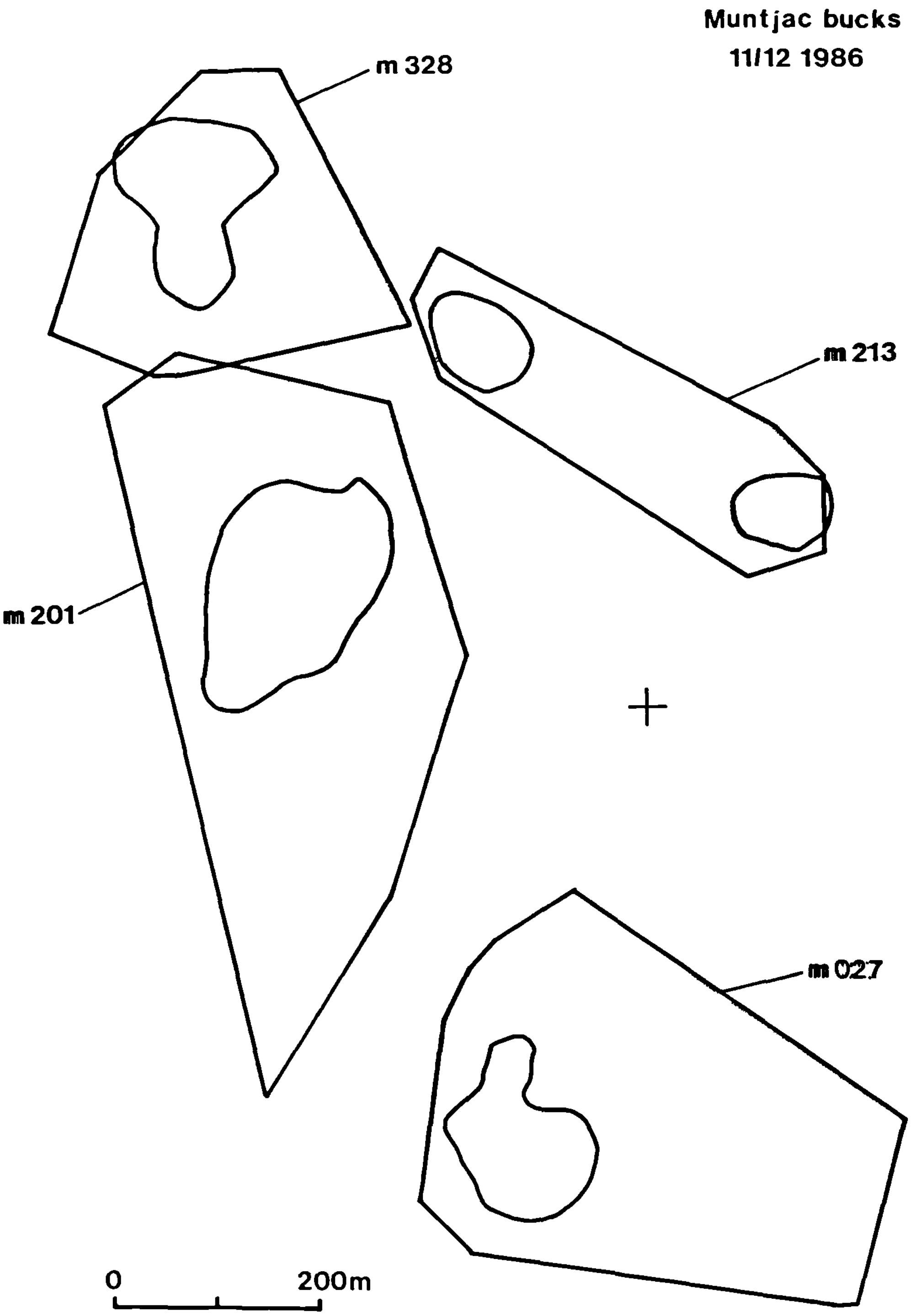


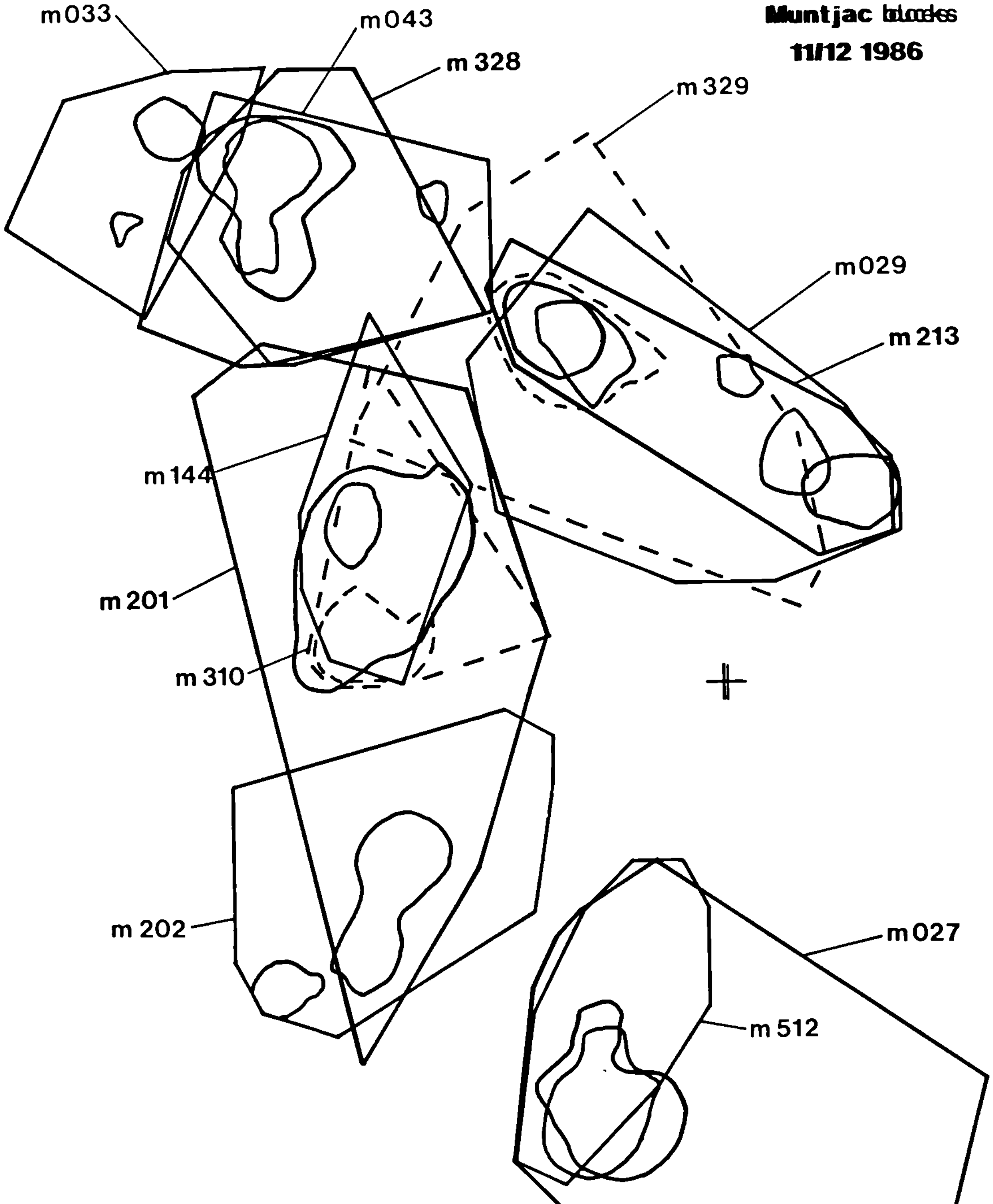
Figure 3.6a&b Minimum convex polygons and 50% isopleth core areas for adult muntjac on part of the study area during November/December 1986.

Figure 3.6a (Overlay): Buck ranges.

Figure 3.6b (Following page): Doe ranges.



Muntjac bucks
11/12 1986



Muntjac blocks
11/12 1986

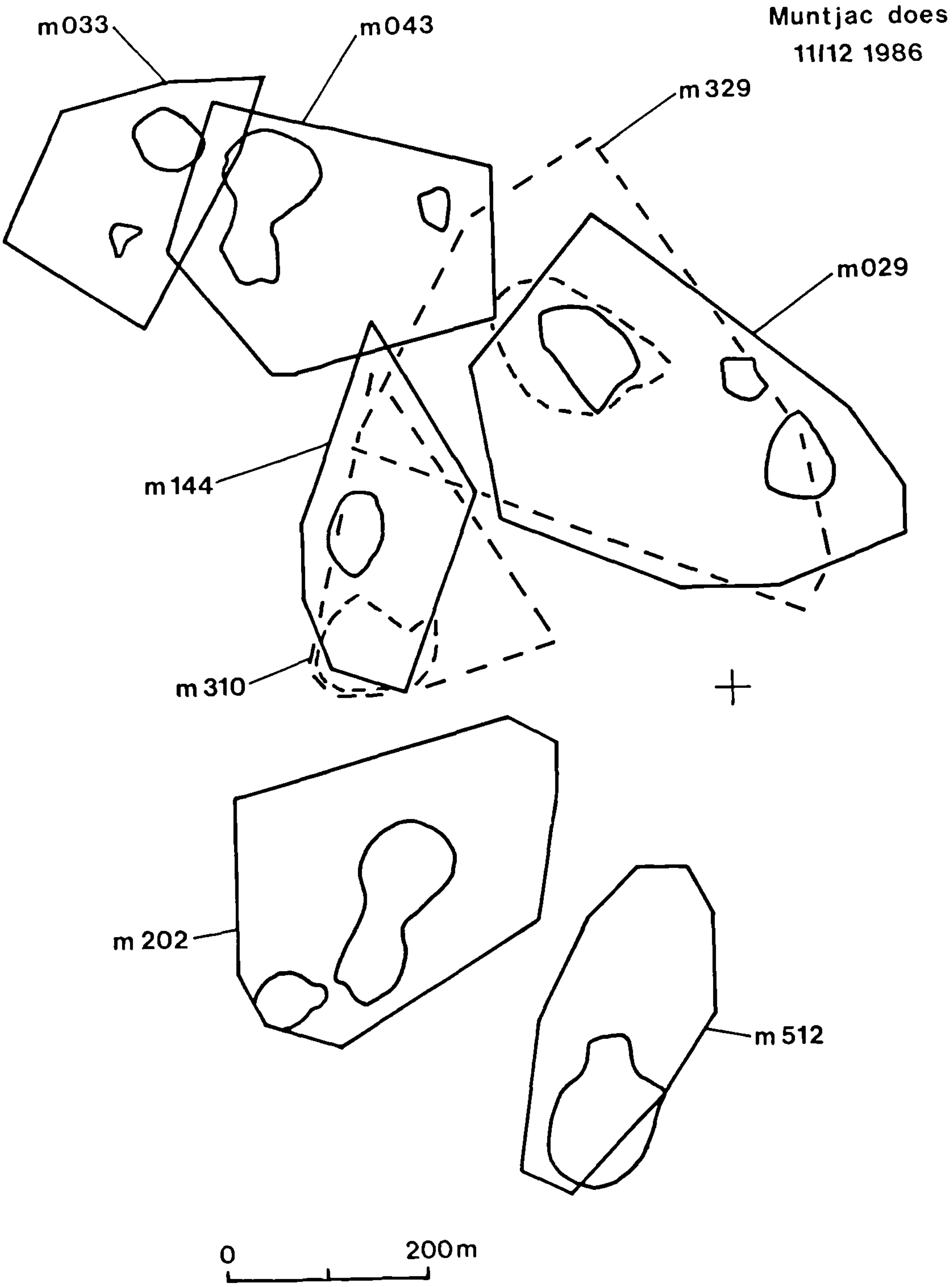
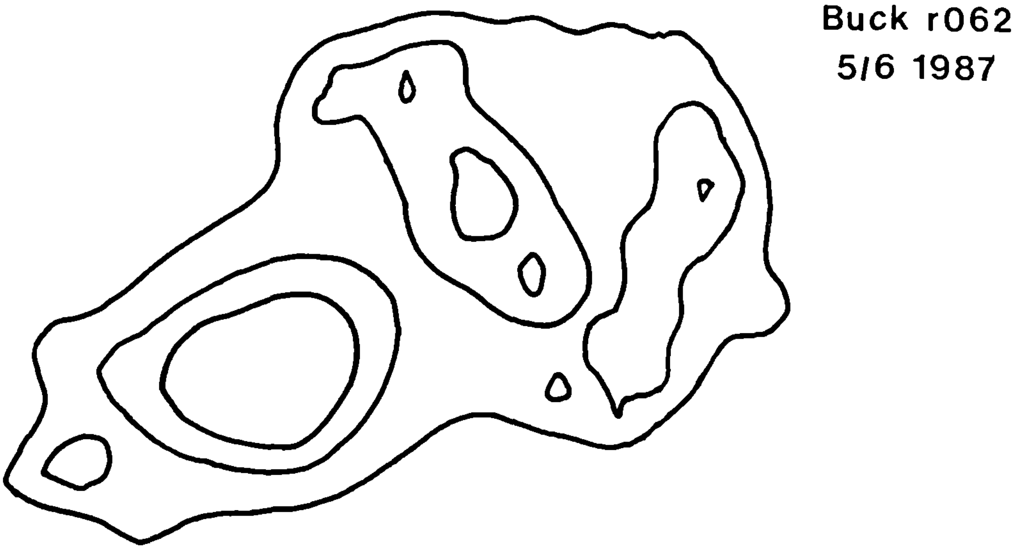

Muntjac does
11/12 1986
m033
m043
m329
m029
m144
m310
m202
m512
0
200m

Figure 3.7 Internal structure of adult roe deer harmonic mean home ranges. The contours are 95%, 80% and 50% isopleths. **Above:** Roe buck r062 during May/June 1987 based on 52 locations. **Below:** Roe doe r203 during July/August 1986 based on 53 locations.


Buck r062
5/6 1987

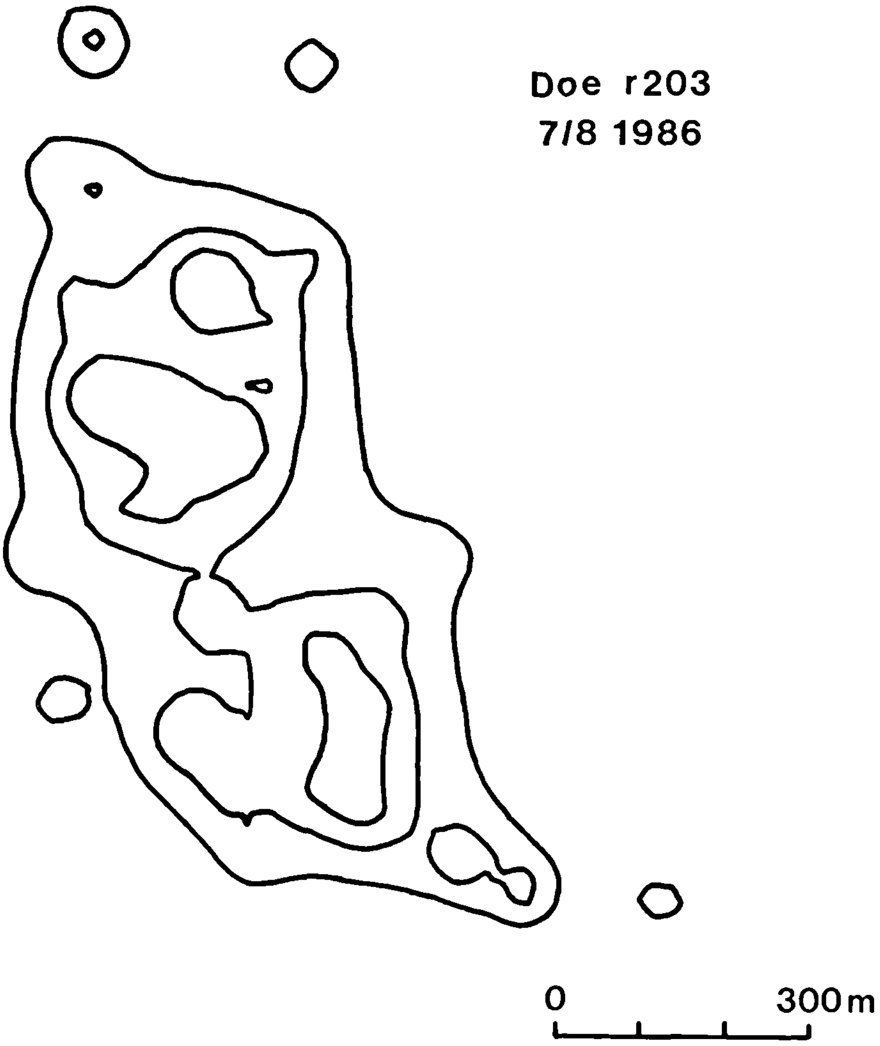

Doe r203
7/8 1986
0
300m

Figure 3.8 Minimum convex polygons and 50% isopleth core areas for adult roe deer on the study area during May/June 1987. Solid lines are doe ranges, dashed lines buck ranges.

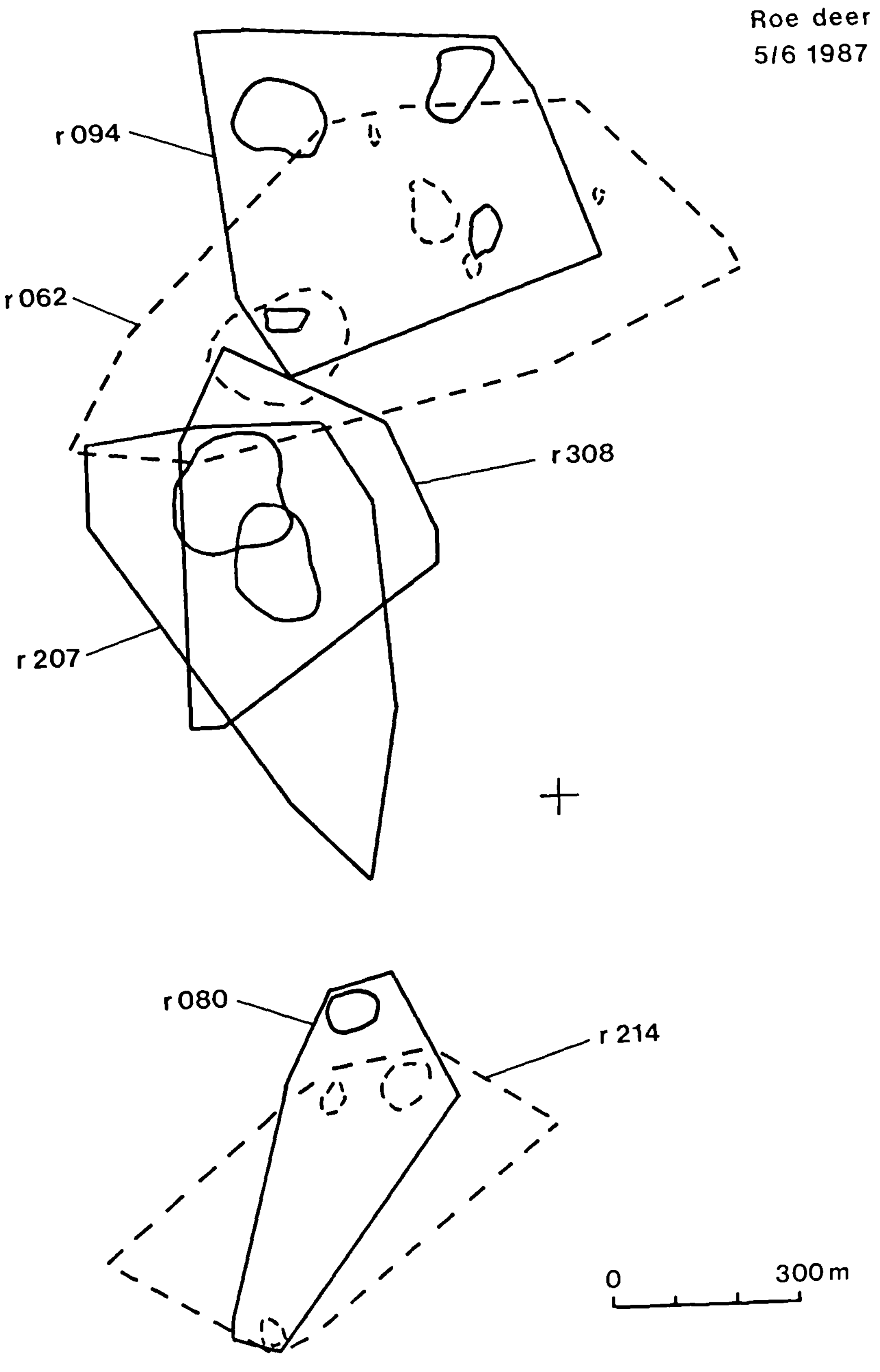

Roe deer
5/6 1987
r 094
r 062
r 308
r 207
r 080
r 214
0
300 m

Figure 3.9 50% isopleth core areas for adult muntjac and roe deer on the study area during March/April 1987. Solid lines are muntjac cores, dashed lines roe cores.


Core areas 3/4 1987
Muntjac
Roe deer
0
300m

bucks was 2.1±0.28 (n=18) and for does was 2.3±0.20 (n=39), with no significant difference between bucks and does (Mann-Whitney U test, n1=39, n2=18, U=312, $p>0.05$).

Figure 3.8 shows the arrangement of roe deer minimum convex polygon and 50% isopleth core areas on the study area during May/June 1987. Although not all the resident deer were being radio-tracked, it was apparent that buck convex polygon ranges overlapped closely with doe ranges, and that more than one doe could share the same range. However, there was little overlap of core areas between does with overlapping convex polygon ranges, or between bucks and does that had overlapping convex polygon ranges. This pattern was not confined to the months of May and June, when doe core areas might represent exclusive kidding territories, although buck and doe cores did sometimes coincide between November and April.

There was no evidence for spatial separation of muntjac and roe deer ranges on the study area; minimum convex polygon ranges overlapped and core areas often coincided (Figure 3.9). Although radio-collared muntjac and roe deer were using the same areas, they were seldom seen in close proximity and interactions between the two species were not observed.

There was no difference in core area size between muntjac and roe bucks (Mann-Whitney U test, U=824, $p>0.05$), although roe does did have significantly larger core areas than muntjac does (Mann-Whitney U test, U=1022, $p<0.001$). There was no difference in the number of core areas between muntjac bucks and roe bucks (Mann-Whitney U tests, all $p>0.05$), but roe does had significantly more core areas than muntjac does between January and April (Mann-Whitney U tests, January/February, U=58, $p<0.05$; March/April, U=20, $p<0.001$).

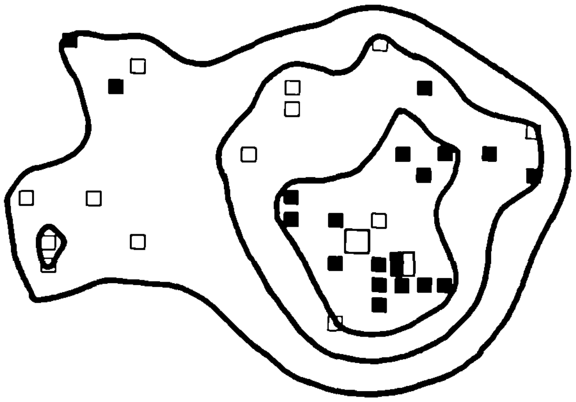
3.3.1.3 Diurnal variation

Diurnal variation in the location of fixes was examined by plotting the location of daytime and night-time fixes. Figures 3.10a and 3.10b show examples for muntjac and roe deer. The location of muntjac fixes within the home range was not influenced by the time of day, even when there were several core areas. However, roe deer frequently used different parts of the home range by day and night. This pattern was most pronounced during the winter months, when some animals selected night-time areas in mature forest with abundant forage, and daytime areas in younger plantations, providing shelter but little forage. During the autumn and winter, an alternative pattern was for animals to visit sugar

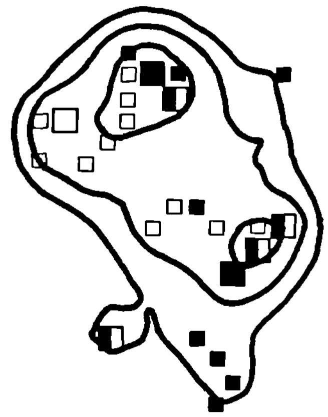
Figure 3.10a&b Diurnal variation in the location of fixes within adult muntjac and roe deer home ranges. The contours are 95%, 80% and 50% harmonic mean isopleths. Filled squares represent 25m squares that contained night-time fixes (beginning of dusk until the end of dawn), open squares 25m squares that contained daytime fixes (end of dawn until the beginning of dusk) and half-filled squares 25m squares that contained both daytime and night-time fixes.

Figure 3.10a (Facing page): Diurnal variation within adult muntjac home ranges. **Top:** Muntjac doe m019 during March/April 1985 based on 39 locations. **Middle:** Muntjac doe m029 during March/April 1985 based on 36 locations. **Bottom:** Muntjac doe m221 during March/April 1985 based on 40 locations.

Figure 3.10b (Following page): Diurnal variation within adult roe deer home ranges. **Above:** Roe doe r203 during March/April 1987 based on 42 locations.**Below:** Roe doe r207 during March/April 1987 based on 47 locations.

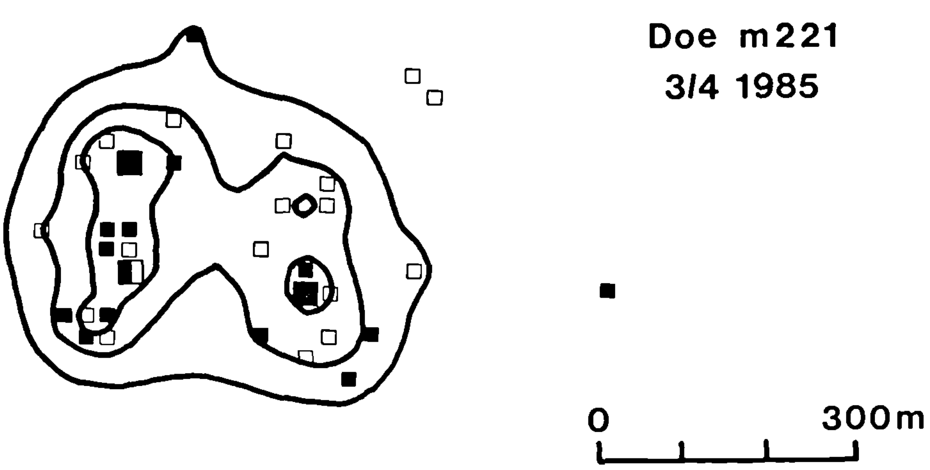


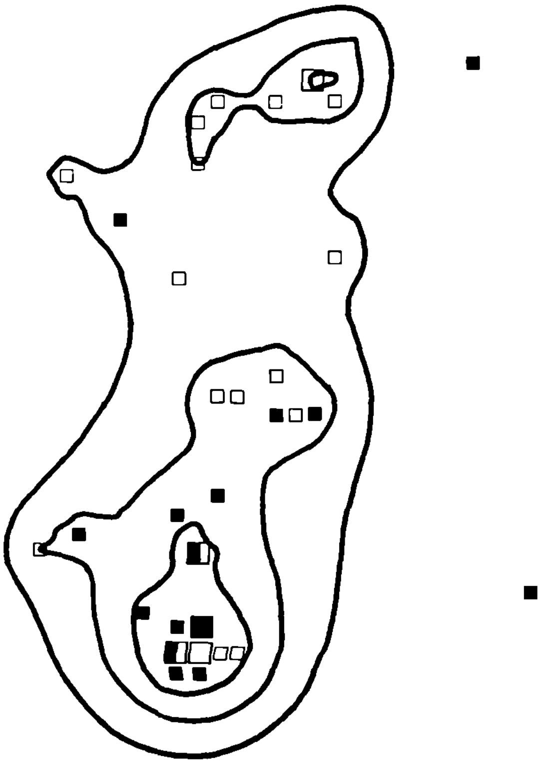
Doe m019
3/4 1985



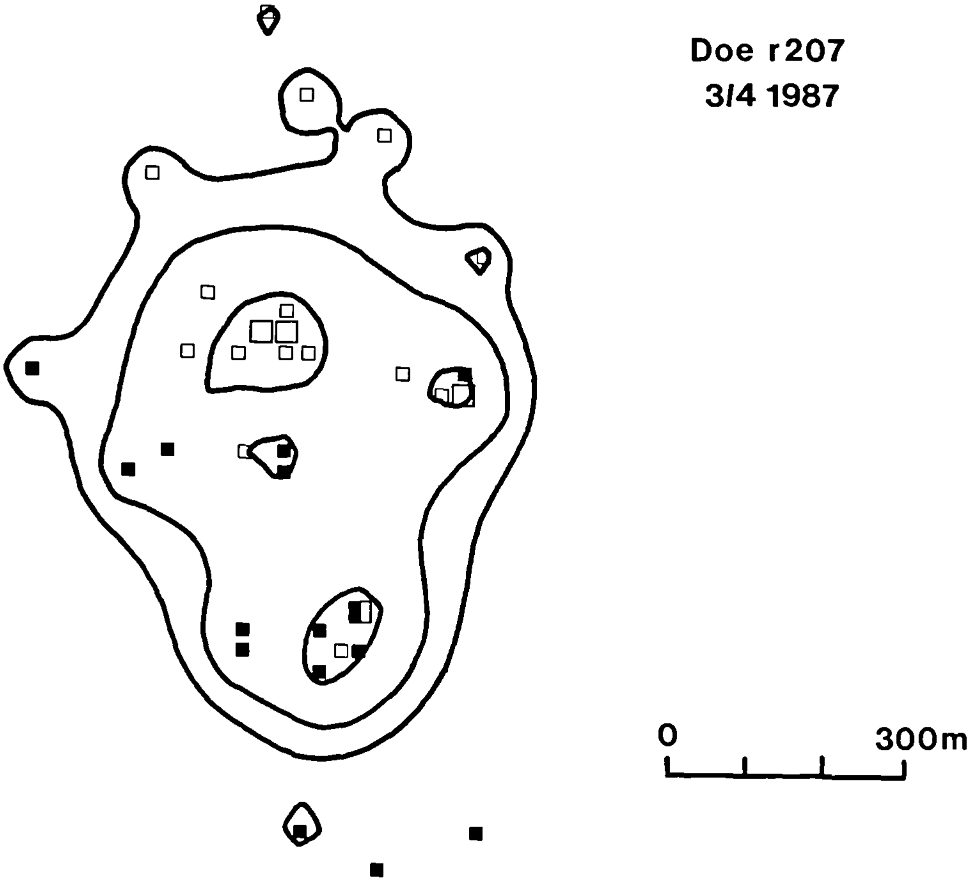
Doe m029
3/4 1985

Doe m221
3/4 1985





Doe r203
3/4 1987



Doe r207
3/4 1987

beet and cereal fields at night, but to remain within the forest during the day.

3.3.1.4 Annual ranges

Annual ranges (Table 3.12) were asymptotic and the high density of loci resulted in accurately defined 95% isopleth harmonic mean ranges. Muntjac bucks had significantly larger minimum convex polygon (Mann-Whitney U test, $U=54$, $p<0.01$) and 95% isopleth ranges (Mann-Whitney U test, $U=46$, $p<0.01$) than muntjac does. There was no significant difference between roe bucks and does (Mann-Whitney U tests, both $p>0.05$), although does tended to have larger minimum convex polygon ranges.

3.3.1.5 Range shifts

The 50% isopleth harmonic mean core areas were used to indicate shifts in the position of home ranges (Figures 3.11a and 3.11b). Out of seven muntjac does and four muntjac bucks tracked throughout 1987, only two bucks showed shifts in core area position. Generally, successive bimonthly muntjac core areas overlapped almost completely. In contrast, out of three roe does and two bucks tracked during 1987, all the deer except one buck showed substantial shifts in core area position. However, both adult muntjac and roe deer had stable annual ranges. When annual 50% core areas were plotted for the seven muntjac does and one muntjac buck, which had been tracked for at least two years, only one of the does showed a shift in home range and this followed three years of stable annual ranges. The two roe does and one roe buck that were tracked for two consecutive years did not shift the position of their annual ranges.

3.3.2 DAILY RANGE LENGTH

Mean daily range lengths for muntjac are given in Table 3.13. There was a significant seasonal change in daily range length for bucks, but only with standardised data (Kruskall-Wallis ANOVA, $H=15.04$, $p<0.05$); buck daily range length was shortest between November and February. There were no significant seasonal trends for does (Kruskall-Wallis ANOVA, both $p>0.05$). Muntjac bucks had significantly longer range lengths than does at all times of year (Mann-Whitney U tests, all $p<0.05$).

Roe deer mean daily range lengths are given in Table 3.14. Standardised buck range lengths showed a significant seasonal change (Kruskall-Wallis ANOVA, $H=16.45$, $p<0.01$), with maximum range length during January/February and minimum range length during September/October. There was a significant seasonal trend for does with both standardised

Table 3.12 Annual minimum convex polygon (MCP) and 95% isopleth harmonic mean (HM) ranges of adult muntjac and roe deer. Figures are means ± S.E., sample sizes are in parenthesis.

Muntjac

	Bucks n=8	**Does n=15**	
MCP	63.6±18.1(9)	27.9±3.5(29)	**
HM	45.5± 9.7(9)	20.1±2.3(29)	**

Roe

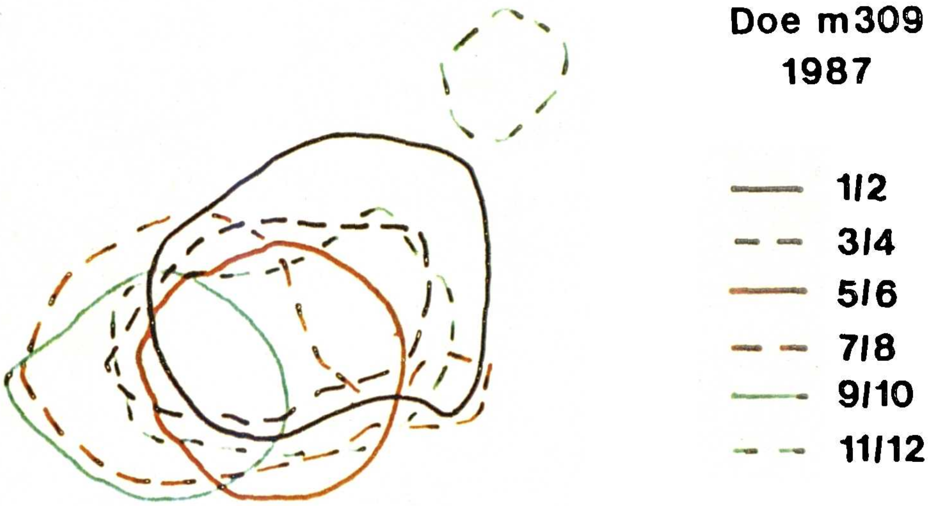
	Bucks n=2	**Does n=4**	
MCP	134.7±42.6(3)	193.2±40.8(6)	n.s.
HM	82.8±42.7(3)	94.2±14.7(6)	n.s.

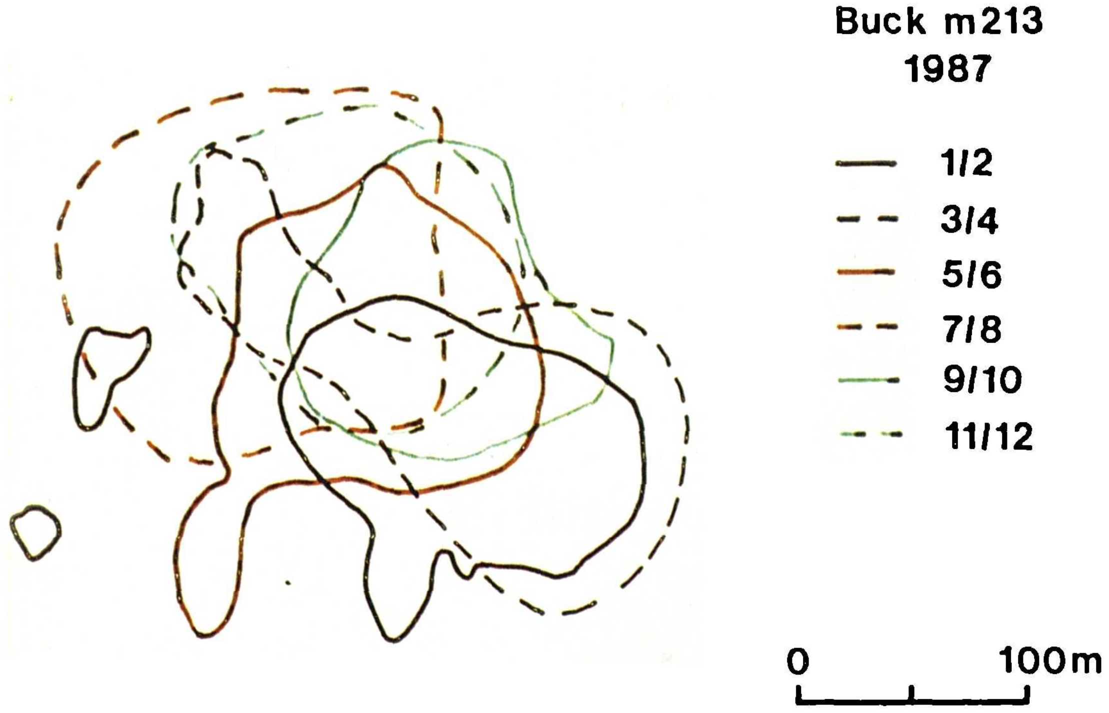
n.s. not significant, Mann-Whitney U test
** $p<0.01$, " " " "

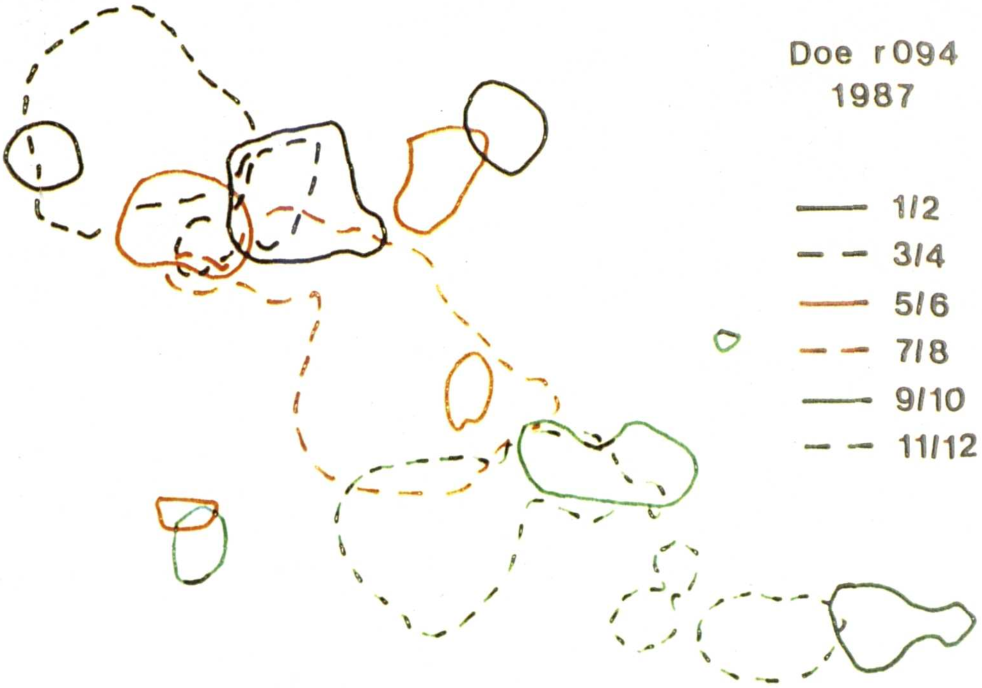
Figure 3.11a&b The position of successive bimonthly 50% isopleth core areas of adult muntjac and roe deer during 1987/88.

Figure 3.11a (Facing page): Adult muntjac, showing successive core areas in the same position. **Above:** Muntjac doe m309. **Below:** Muntjac buck m213.

Figure 3.11b (Following page): Adult roe deer, showing shifting core areas. **Above:** Roe doe r094. **Below:** Roe buck r062 (the core for January/February is 1988 not 1987).


Doe m309
1987
1/2
3/4
5/6
7/8
9/10
11/12


Buck m213
1987
1/2
3/4
5/6
7/8
9/10
11/12
0
100m


Doe r094
1987
1/2
3/4
5/6
7/8
9/10
11/12

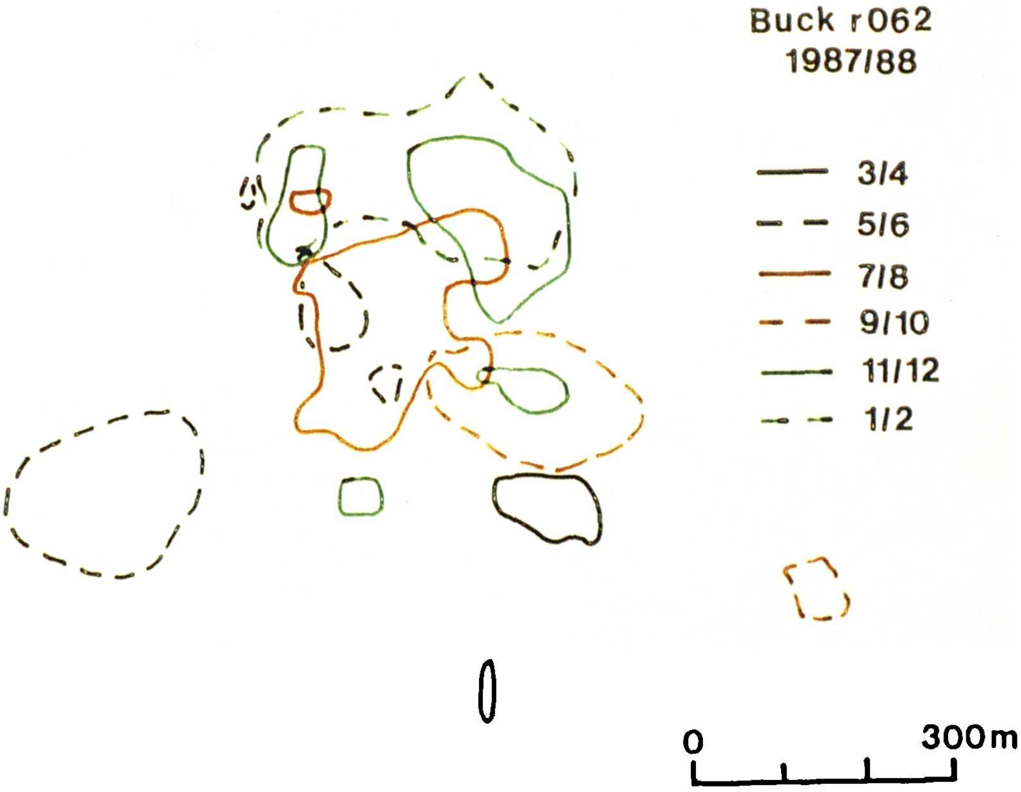

Buck r062
1987/88
3/4
5/6
7/8
9/10
11/12
1/2
0
300m

Table 3.13 Daily range lengths of adult muntjac. A standardised range length of 100 is equivalent to a 0% deviation from the annual mean. Figures are means ± S.E., sample sizes are in parenthesis.

Bucks

Month	**Range length (m) n=13**	**Stand. range length n=6**
J/F	1220.7±158.5(13)	91.1± 9.9(10)
M/A	1332.8±117.0(19)	100.8±10.4(14)
M/J	1267.0± 89.6(14)	106.7± 5.6 (9)
J/A	1270.0±130.3(21)	103.8± 8.1(16)
S/O	1391.0±121.3(22)	117.6± 8.3(18)
N/D	1175.0±152.1(17)	73.5± 6.6(12)
p	**n.s.**	*****

Does

Month	**Range length (m) n=15**	**Stand. range length n=12**
J/F	824.2±52.1(34)	96.0±5.3(32)
M/A	862.9±51.5(42)	103.0±5.1(36)
M/J	920.0±66.5(34)	103.6±6.0(29)
J/A	921.3±66.4(44)	103.2±5.7(36)
S/O	961.9±81.0(44)	99.0±4.6(34)
N/D	836.8±52.3(53)	98.4±5.5(42)
p	**n.s.**	**n.s.**

n.s. not significant, Kruskall-Wallis ANOVA
***** $p<0.05$, " " "

Table 3.14 Daily range lengths of adult roe deer. A standardised range length of 100 is equivalent to a 0% deviation from the annual mean. Figures are means ± S.E., sample sizes are in parenthesis.

Bucks

Month	**Range length (m) n=2**	**Stand. range length n=2**
J/F	1500.1±357.1 (8)	131.6±24.1 (8)
M/A	1266.0±355.6 (9)	125.6±20.8 (9)
M/J	909.9± 91.1(12)	117.4±14.4(12)
J/A	682.2±115.6(10)	87.9±14.1(10)
S/O	542.0±130.1(12)	56.9± 7.4(12)
N/D	832.6±171.0(11)	86.8±10.6(11)
p	n.s.	**

Does

Month	**Range length (m) n=5**	**Stand. range length n=4**
J/F	1856.2±245.9(17)	172.7±19.1(17)
M/A	952.5±118.3(19)	103.4±11.4(15)
M/J	591.0± 68.5(28)	59.1± 5.6(24)
J/A	794.7± 76.7(21)	77.7± 8.5(20)
S/O	834.9±107.2(24)	74.1± 8.0(24)
N/D	1151.2±179.3(20)	104.2±12.0(20)
p	***	***

n.s. not significant, Kruskall-Wallis ANOVA
** $p<0.01$, " " "
*** $p<0.001$, " " "

and unstandardised data (Kruskall-Wallis ANOVA, $p<0.001$). Daily range lengths were longest during January/February and shortest during May/June. There was no significant difference between roe bucks and does, except during May/June, when bucks had longer range lengths (Mann-Whitney U test, May/June, U=81.5, $p<0.05$).

Muntjac buck daily range length was significantly different from roe bucks between May and October, when muntjac bucks travelled longer daily distances (Mann-Whitney U tests, all $p<0.05$). Daily range length of muntjac does was significantly different from roe does during January/February, when roe does travelled longer daily distances (Mann-Whitney U test, U=88.0, $p<0.001$) and during May/June, when muntjac does had longer daily range lengths (Mann-Whitney U test, U=229.0, $p<0.001$). Therefore, roe deer of both sexes had shorter daily range lengths than muntjac during the summer months.

3.4 DISCUSSION

This chapter uses radio-tracking to compare the temporal and spatial organisation of muntjac and roe deer home ranges in the south-east corner of the forest. Radio-tracking confirmed that there was a high degree of spatial overlap between muntjac and roe deer; although there were important differences between the two species, relating to temporal changes in home range size and position, and to the internal structure of the home ranges.

Home range sizes and daily range lengths of individual muntjac were very variable between bimonthly periods, although mean range sizes and lengths showed no overall seasonal pattern. Core areas did not shift seasonally or from year to year; once an adult animal had established a range, it was retained for a number of years. There was no evidence that different parts of the range were used during the day and at night. Bucks had significantly larger bimonthly and annual home ranges, longer daily range lengths and more core areas than does. The social organisation consisted of groups of overlapping doe ranges; buck ranges overlapped with those of the does, but were relatively exclusive from those of other adult bucks. Core areas of overlapping buck and doe ranges coincided, but for does with overlapping convex polygon ranges, the core areas overlapped less than was expected.

In contrast, both individual roe deer and the population means showed a consistent annual rhythm in home range size and daily range length. Ranges were largest during winter and smallest during September/October for bucks and May/June for does. Roe deer ranges had multiple core areas, particularly during winter. These cores shifted seasonally, but the annual ranges of adult animals were stable from year to year. Animals used different parts of their ranges during the day and at night, related to the availability of food and shelter. There were no significant differences between bucks and does in home range size, daily range length or in the number of core areas. The social organisation consisted of overlapping buck and doe ranges, with some doe ranges being shared with other adult does. Generally different core areas were used by bucks and does that shared minimum convex polygon ranges.

Harding (1986) calculated MAP 0.95 home range estimates (Ford & Krumme, 1979) for muntjac in Rushbeds Wood. He found that buck ranges averaged 17.0ha during winter and 13.2ha during summer, while doe ranges averaged 16.0ha during winter and 9.2ha during summer. There were no significant differences within sexes seasonally or between different sexes in the same season. Jaremovic & Croft (1987) calculated that MAP 0.95 indices were on average 26% smaller than 95% isopleth harmonic mean ranges. Taking this into account, doe ranges were larger and buck ranges similar in size to this study. Harding also showed that muntjac ranges had a single core area, though he found that this was usually placed centrally in the range, giving an approximately normal distribution of fixes. He found no evidence for different locations within the range of active and inactive fixes, or of daytime and night-time fixes. Adult home ranges were stable seasonally and from year to year. The spatial organisation of muntjac in Rushbeds Wood was very similar to that found in the King's Forest. Doe ranges overlapped; buck ranges overlapped those of the does, but were relatively exclusive from other bucks.

This study, and that by Harding (1986), have both demonstrated that muntjac populations do not show significant seasonal changes in range size, although the range size of individuals does vary from month to month. The size of home range required by an animal depends on the amount of utilizable energy per unit area, relative to the energy requirements of the individual (Harestad & Bunnell, 1979). During winter, utilizable energy declines and therefore home range area should increase if energy requirements remain constant. However, all temperate deer that have been studied show seasonal cycles of metabolism and appetite (Silver *et al.*, 1969; Drozdz & Osiecki, 1973; Drozdz, 1976; Moen, 1976), so that energy requirements are reduced during winter. In fact, energy requirements appear to decline more rapidly than utilizable energy and so most species actually decrease their home range size during winter (Harestad & Bunnell, 1979). Winter home range size may be further constrained by deep snow in many northern temperate areas, since this restricts movement (Cederlund, 1982; Telfer & Kelsall, 1984). Within this context, muntjac are living in a seasonal British climate, with decreased available energy during winter and yet do not show a winter decrease in range size. Muntjac are aseasonal breeders (Chapman *et al.*, 1984); young are born throughout the winter months and therefore a cycle of decreased winter metabolism and appetite, in does at least, seems untenable. Thus decreasing energy requirements, counteracting a reduction in utilizable energy, would not be a valid explanation for maintaining the same range size between winter and summer. If the climate in south-east China, the natural habitat of Reeves' muntjac, was aseasonal, then this could be a possible explanation for their aseasonality of range size in Britain. However, according to Harding (1986), the climate does have seasonal cycles of temperature and rainfall rather similar to those in Britain. A possible explanation, is that it is advantageous for small ruminants to maintain stable year round ranges, within which they know changing resource patterns intimately (Barrette, 1987).

Seasonal changes in roe deer range size have been found to differ between bucks and does. Bucks have minimum range sizes during the winter, and maximum range sizes during spring and autumn (Sempéré, 1979a&b, 1980; Janeau *et al.*, 1981; Bideau *et al.*, 1983; Cederlund, 1983). This spring increase in range size has been attributed to increased movements in peripheral parts of the range associated with territory establishment (Sempéré, 1979a&b, 1980). Decreased winter metabolism has been shown for roe deer in Poland (Drozdz & Osiecki, 1973; Drozdz, 1979), and Cederlund (1983) suggested that this, together with decreased mobility in deep snow (Cederlund, 1982), explained the winter reduction in range size. Exceptions to this pattern for bucks are Hinge (1986), Zejda & Bauerova (1985) and Maublanc (1986), who all found that range size was maximum during winter and decreased during spring. It is interesting to note that the last two studies were carried out in habitats where the deer had access to agricultural land.

In contrast, most studies of roe doe ranging behaviour have shown that range size is maximum during winter and decreases to a minimum during spring/early summer (Vincent *et al.*, 1983; Cederlund, 1983; Zejda & Bauerova, 1985; Maublanc, 1986). Exceptions are Hinge (1986), who found no seasonal change, and Janeau *et al.*, (1981), who found that doe ranges were minimum during winter and increased during spring. Presumably, differing energetic requirements, and possibly also social behaviour, underlie these differences between bucks and does.

The present study has shown that range sizes of both bucks and does are maximum during winter and then decrease during the spring months to a minimum in May/June for does and September/October for bucks. The two other studies where buck range size decreased from a winter maximum, were both carried out in largely agricultural habitats, and the use these habitats may explain the seasonal changes in home range size shown by the King's Forest roe deer. The dispersion of food resources in agricultural habitats increases greatly during winter, and the only study to show a seasonal change in range size of a similar magnitude to this study, was that by Zejda & Bauerova (1985). Winter range sizes of roe deer in the King's Forest were larger than most other studies, except those of Cederlund (1983) and Zejda & Bauerova (1985), while range sizes during the rest of the year were more comparable.

A number of studies, have demonstrated that roe deer are territorial between April and the end of July (Bramley, 1970; Sempéré, 1979a&b, 1980), and there was no evidence from this study to the contrary. Aggressive behaviour between bucks and barking observations were confined to these months (P.Forde *pers. observ.*). Outside this period, it is generally assumed that no territorial system is in operation, and its breakdown may explain why roe deer are able to shift ranges seasonally and exploit different food resources.

Minimum range size for does during May/June, has been associated with a decreased mobility around kidding (Johnson, 1982; Espmark, 1969). During this time, daily range lengths were particularly small and animals concentrated their activity into a restricted area. The marked post-rut decrease in range size by bucks confirms a well known observation amongst stalkers, who note that bucks are very difficult to observe during this period, leading some authors to suggest that bucks actually leave the area of their territories (Dent, 1985). However, there was no evidence of a marked change in the location of home ranges post-rut, in this study.

The social organisation described here for roe deer agrees with that reported previously by Bramley (1970) and Johnson (1982) at Chedington Wood. Johnson (1982) found that there was a mean annual overlap between territorial bucks of 21% and a much higher overlap between does. Generally at least two does shared a range, though their core areas were often separate. Adult animals had stable ranges that were maintained from year to year.

There have been a number of recent reviews concerning the relationship between home range size and body weight (Harestad & Bunnell, 1979; Damuth, 1981; Lindstedt *et al.*, 1986; Swihart *et al.*, 1988; Reiss, 1988). Since Harestad & Bunnell (1979) calculated their regressions over a range of body weights appropriate to the weights of muntjac and roe deer, their regressions are used here. The relationship for herbivores between annual minimum convex polygon home range area in hectares and body weight in grams, was

$H=0.002W^{1.02}$. Using the body weights given in section 1.2 for muntjac and roe deer in the above equation, the annual home ranges calculated for muntjac bucks and does were 35.9ha and 29.5ha respectively. The calculated doe range size was very similar to that given in Table 3.12, though buck range size was substantially underestimated. Harestad & Bunnell argue that much of the difference in home range size between males and females of a species can be explained by differences in body weight. On this basis, range sizes of muntjac bucks should be approximately 20% larger than does. In fact, the difference is nearer 50%, and so body weight alone does not account for the difference in range size. Perhaps in this study buck home range size was influenced more by the distribution of does than by the distribution of resources.

The calculated annual range sizes for roe bucks and does, using Harestad & Bunnell's relationship, were 67.5ha and 51.8ha respectively. These are almost three fold underestimates, compared to the values given in Table 3.12. Therefore, the relationship between home range area and body weight for roe deer, must be scaling with an exponent substantially greater than 1.02. Harestad & Bunnell suggest that larger animals will use more patchily distributed resources and thus experience lower levels of utilizable energy per unit area. They argue that this explains why home range scales to body weight with an exponent greater than 0.75 (the exponent relating basal metabolic weight to body weight; Kleiber, 1961). In this study, roe deer may have larger ranges than would be predicted from their body weight because they used agricultural habitats, which have an extremely patchy distribution of resources.

Changes in daily range length revealed a similar pattern of seasonal ranging behaviour to the changes in home range size. Swihart *et al.* (1988) showed that larger animals travel around their home ranges at a slower rate and will thus use a smaller proportion of their seasonal range each day. This may explain why although roe deer had larger home ranges than muntjac, daily range lengths were significantly shorter during the summer months and of a similar length during the rest of the year.

The patterns of home range utilization and social organisation of sympatric muntjac and roe deer in this study do not differ substantially from those found by workers studying either species in isolation. Therefore, there is no need to invoke interference competition as the causative agent for any differences in the way muntjac and roe deer use space.

CHAPTER FOUR: ACTIVITY PATTERNS

4.1 INTRODUCTION

Amongst sympatric lizards, activity patterns of similar sized species differ (Schoener, 1970; Huey & Pianka, 1983). This reduces interference competition and allows several species to exploit the same food resources at different times of day. It is less clear whether temporal separation of activity should have any benefits for sympatric herbivorous species, where the timing of activity may be more constrained by predator avoidance and the physiological constraints of ruminant digestion, than by the temporal availability of food resources. However, temporal separation of activity will reduce interference competition between species. The previous chapter demonstrated that there was a high degree of spatial overlap between radio-collared muntjac and roe deer. This chapter examines the activity patterns of these same radio-collared deer to determine the extent of any temporal separation of activity.

Radio-tracking has provided a very suitable non-invasive technique for studying the activity patterns of free-ranging animals. Observations are not limited by daylength or by visibility in dense habitats. Two approaches have been used to collect activity data using radio-tracking. Information has either been collected during routine radio-tracking to determine ranging behaviour and habitat usage or by using a number of techniques specifically designed to automatically record activity data from radio-collared animals.

Continuous radio-tracking of individual animals is perhaps the most accurate way of collecting activity data; there is no loss of signal sensitivity through a recording system and close monitoring of the individual contributes to the assessment of activity state. For example, continuous tracking of individual badgers, from leaving their sett in the evening until their return the next morning, was used by Cresswell & Harris (1988) to describe the activity patterns of badgers in suburban Bristol. Such continuous manual monitoring is limited in that only one individual can be followed and it would not be practicable for species such as muntjac and roe deer which require monitoring throughout a twenty-four hour period.

To overcome some of these problems, several automatic tracking systems have been developed which continuously monitor the position of radio-collared animals. The system at Chizé Forest in France (Deat *et al.*, 1980) can monitor the position of 10 animals every four minutes and has been used to study the activity patterns of wild boar *Sus scrofa*

(Mauget, 1980) and foxes (Maurel, 1980). The output from such systems does not give an activity measure for each fix, although computer programs can produce sequences of rest and activity given movement criteria.

Most radio-tracking studies have taken single fixes at intervals ranging from one hour up to several days and although these data cannot be used to calculate total daily activity and the length and number of active periods, they can be used to assess the population level of activity at different times of day (e.g. Novellie *et al.*, 1984; Ferguson *et al.*, 1988).

Automatic recording systems at their simplest consist of a receiver with a short range aerial connected to a chart recorder. This type of system will monitor the presence or absence of an animal from its nest or burrow (Williams & Williams, 1970; Kenward, 1982a; Parish & Kruuk, 1982; Stone, 1987). More than one individual can be monitored concurrently by using a programmable receiver and a stepped chart recorder (Pearson,1986; Kenward, 1987).

Chart recorder systems incorporating a more powerful aerial can monitor activity away from the nest or burrow. Variation in signal amplitude and strength indicates whether the animal is active and its distance from the receiver (Lancia *et al.*, 1980; Hirons & Owen, 1982; Widen, 1982).

Alternatively the receiver can be linked to a tape recorder via either a mechanical timer (Göransson, 1980) or an electronic timer (Harding, 1986; Hinge, 1986). The timer switches on the receiver and tape recorder for a period of usually up to one minute at a specified time interval. Manual transcription of tape recordings may be more sensitive in detecting amplitude changes than visual transcription of chart recordings, although background noise on the tape can cause interpretation problems.

Generally, the above recording techniques have used transmitters with single pulse rates. However, several types of pulse modulated transmitters are available. Mercury switches can be incorporated into transmitters giving alternating fast and slow pulse rates when the orientation of the transmitter changes. Kenward (1982b) studied hunting activity of goshawks fitted with tail mounted mercury switch transmitters. A slow pulse rate was produced when the tail was vertical in a resting bird, a fast pulse rate when the tail was horizontal during flight and an alternating rate when the bird was feeding.

Alterations in temperature change the pulse rate produced by transmitters incorporating thermistors. In particular these transmitters are useful for monitoring the activity of animals that return to warm nests or burrows (e.g. Osgood, 1980; Kenward, 1982a); the rise in temperature when the animal enters its nest alters the pulse rate. An alternative use was demonstrated by Hirons and Owen (1982), who fitted thermistor transmitters under the wing to monitor roding flights of woodcock. When flying the thermistor cooled, slowing the pulse rate. Pulse modulated signals can be automatically recorded by connecting the receiver to either a tape recorder or a data logger which counts the number of pulses and stores the information for direct transfer to computer. By linking a programmable receiver and data logger, a number of animals can be monitored simultaneously.

Roe deer activity has been studied by Cederlund (1981) using a chart recorder system, Hinge (1986) using an electronic timing device and Turner (1978, 1979, 1980) by direct observation. Yahner (1980a&b) described the activity patterns of captive muntjac contained within enclosures that varied from 0.3 to 0.5 ha in size, using direct observation and Harding (1986) activity patterns in a both a free-ranging population of muntjac at Rushbeds Wood and an enclosed, but wide ranging population at Whipsnade Zoo using an electronic timing device. In this study, activity patterns of muntjac and roe deer were investigated using a combination of data from an automatic recording system, routine radio-tracking and twenty-four hour radio-tracking sessions.

4.2 METHODS

The following definitions are used in this chapter:

1. Dawn lasted for 90 minutes either side of sunrise.
2. Dusk was the same interval around sunset. Sunrise and sunset times were taken from Whitaker's Almanack (1986).
3. Day was from the end of dawn until the beginning of dusk.
4. Night was from the end of dusk until the beginning of dawn.

4.2.1 AUTOMATIC ACTIVITY RECORDER

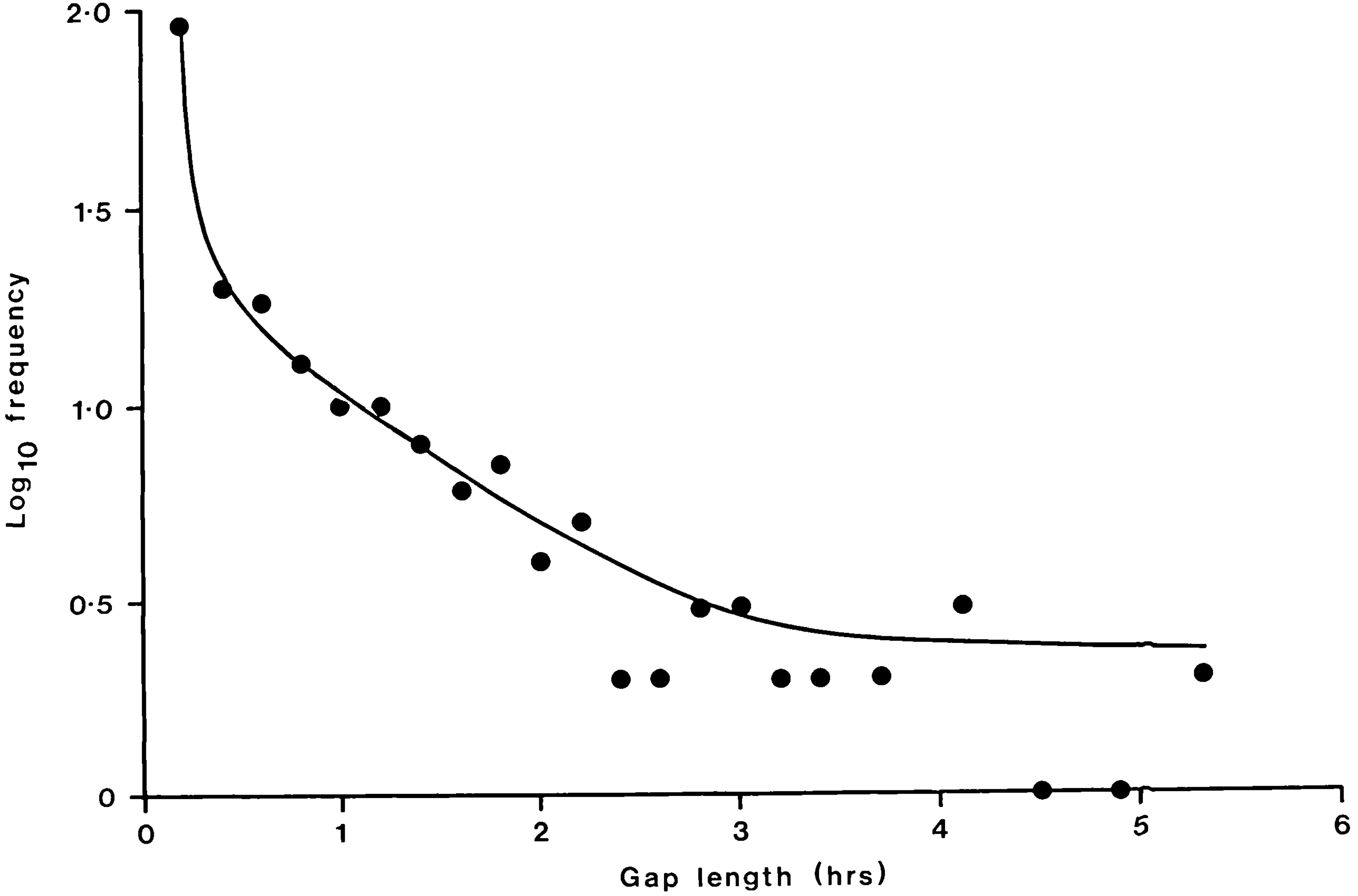
Twenty-four hour activity records were collected using an automatic recording system (Hinge, 1986). This consisted of an AVM LA-12 receiver connected to an electronic timing device (constructed by Mr. M. Hinge) and audio tape recorder. The timer was set to switch the receiver and tape recorder on for one minute in every 12, giving five minutes of recording per hour. Using a C120 cassette, the tape required changing every 12 hours. Often the receiver was checked more frequently, because the signal could drift with temperature. The receiver and timer were powered by a 12 volt car battery, changed every three to four weeks. The tape recorder was powered by internal rechargeable batteries, changed every 48-72 hours. The whole system was housed in a weatherproof, lockable wooden box.

The aerial assembly consisted of a pair of three element "Yagi" antennae, connected by equal lengths of co-axial cable to a Y-connector. The aerials were placed 3-5m above ground level, in the branches of a tree or at the top of a high seat. Signal reception was poor through the trees and as there was no suitable topographical feature above tree height, the system had to be moved around the forest to a suitable position for each recording. During the winter, roe deer ranged over large areas and two automatic recording systems, placed in different parts of the range, were sometimes required to obtain complete twenty-four hour activity recordings. Recordings were always started at 0800hrs or 2000hrs G.M.T.

The tapes were transcribed by playing back at normal speed on a tape recorder fitted with headphones. Each minute of recording could be distinguished by a short break on the tape and was assessed as either active or inactive on the basis of fluctuations in signal amplitude. Assessments were based on visual observations of radio-collared animals. When the amplitude fluctuated, the animal was assumed to be engaged in an activity involving movement such as travelling or foraging. When the signal was constant, it was assumed that the animal was resting. Infrequent amplitude changes through an otherwise constant signal were taken to indicate slight movements of the head during rumination or vigilance behaviour and these signals were assessed as inactive.

Twenty-four hour records were discarded if the signal was missing for more than 120 minutes (10 minutes of recording); although if one of the twelve hour periods (0800-2000hrs or 2000-0800hrs G.M.T.) was complete, then this was included in the analyses where appropriate. Log survivorship curves (Slater,1974; Clutton-Brock *et al.*, 1982; pp. 324-325), were used to determine the minimum length of active and inactive periods (Figure 4.1). The inflection point of curves of active and inactive period length were at 0.4 hours (24 minutes or two minutes of recording) for both muntjac and roe deer. Periods shorter than this (i.e. one minute of recording) were considered to be temporary interruptions and were assigned the activity status of the preceding activity period. Incomplete active periods at the start and finish of a twenty-four hour recording were counted as half periods if shorter than 120 minutes in length and whole periods if longer than 120 minutes. When calculating active period length, incomplete periods of longer than 120 minutes were included, so as

Figure 4.1 Log survivorship curve of the gap length between active periods for adult muntjac between May and August, based on 23 twenty-four hour and 9 twelve hour automatic activity recordings from six animals. The first inflection point is at 0.4 hours (24 mins), i.e. gaps shorter than this are temporary interruptions of active periods.


2·0
1·5
1·0
0·5
0
Log$_{10}$ frequency
0
1
2
3
4
5
6
Gap length (hrs)

not to bias against longer active periods (Clutton-Brock *et al.*, 1982; p. 325).

4.2.2 ROUTINE RADIO-TRACKING

Activity status was assessed for each radio fix as either active or inactive, on the basis of fluctuations in signal amplitude as described above. Often, this assessment was confirmed by subsequent visual observation. A computer program extracted activity data from the radio-tracking files and gave monthly summaries of activity by hour.

4.2.3 TWENTY-FOUR HOUR RADIO-TRACKING

The twenty-four hour radio-tracking data were used to examine how the daily range length was partitioned through the diurnal cycle. Roe deer tracking rounds were at defined times; all animals were located during a period of not more than 90 minutes and there was an interval of approximately five hours between tracking rounds. Therefore, the data were presented as the proportion of the daily range length that was travelled between consecutive tracking rounds.

Muntjac twenty-four hour tracking sessions could start at any time of day and fixes were collected throughout the twenty-four hour period, with a time interval between fixes from each individual of approximately three hours. Therefore, to examine the rates of movement at different times of day, a different approach was necessary. To group the data into time periods, each twenty-four hour period was divided into 12 pairs of two hour periods, the second two hour period commencing one hour after the end of the first. The first pair of two hourly periods was 2200-2359 and 0100-0259 and the twelfth pair of two hourly periods was 2000-2159 and 2300-0059. The proportion of the daily range length travelled between consecutive fixes was allocated to one of these pairs of two hour periods. Where the time interval between fixes did not fit one of these pairs, the data were excluded.

4.3 RESULTS

4.3.1 AUTOMATIC ACTIVITY RECORDER

The number of twenty-four hour and twelve hour activity recordings collected from adult muntjac and roe deer are given in Table 4.1. Twenty-four hour activity records for individual adult muntjac and roe deer are shown in Figures 4.2a&b. For both species, activity occurred as a number of bouts of varying length, dispersed throughout the twenty-four hour cycle.

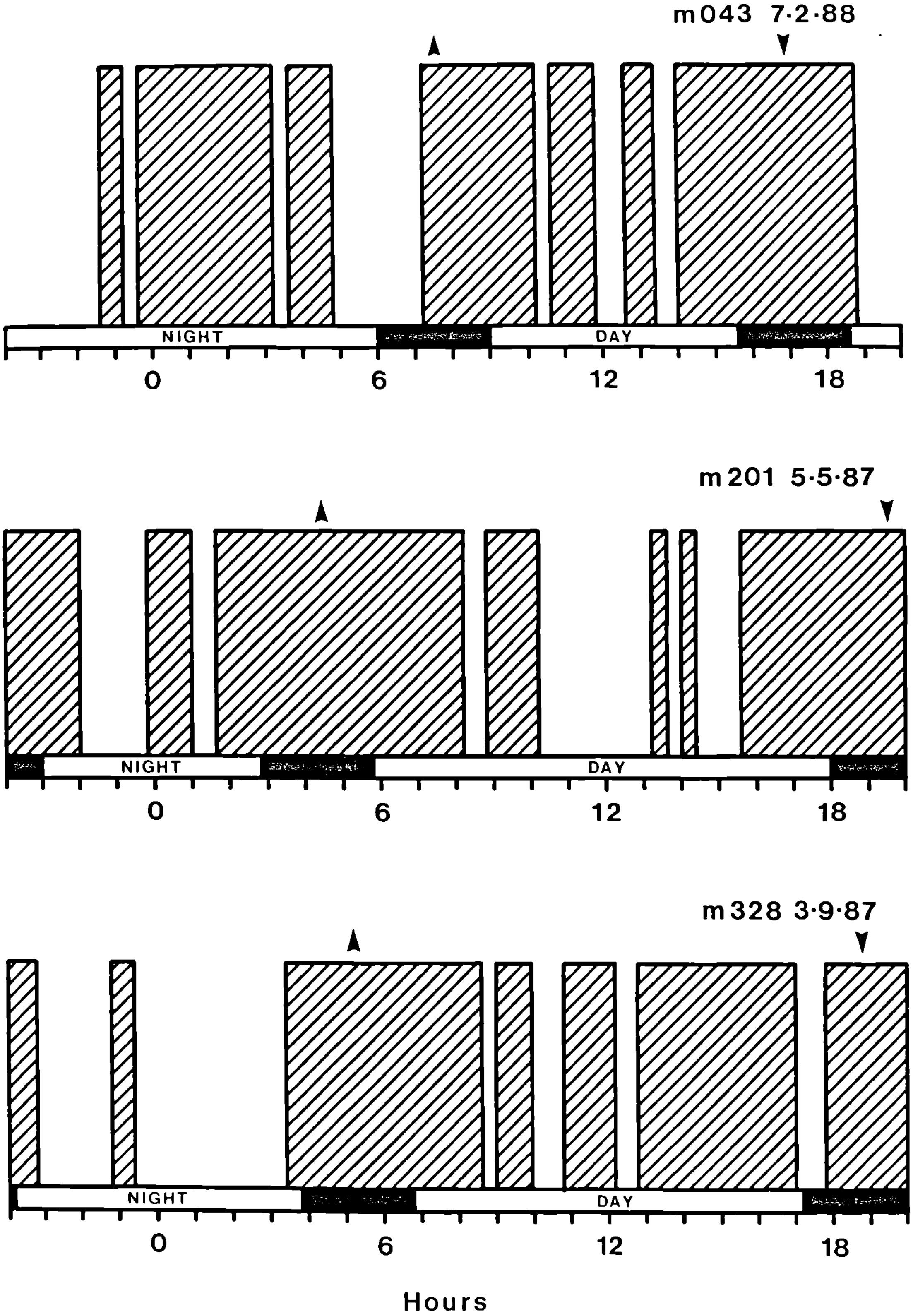
Table 4.1 Number of twenty-four hour and twelve hour automatic activity recordings collected from adult muntjac and roe deer.

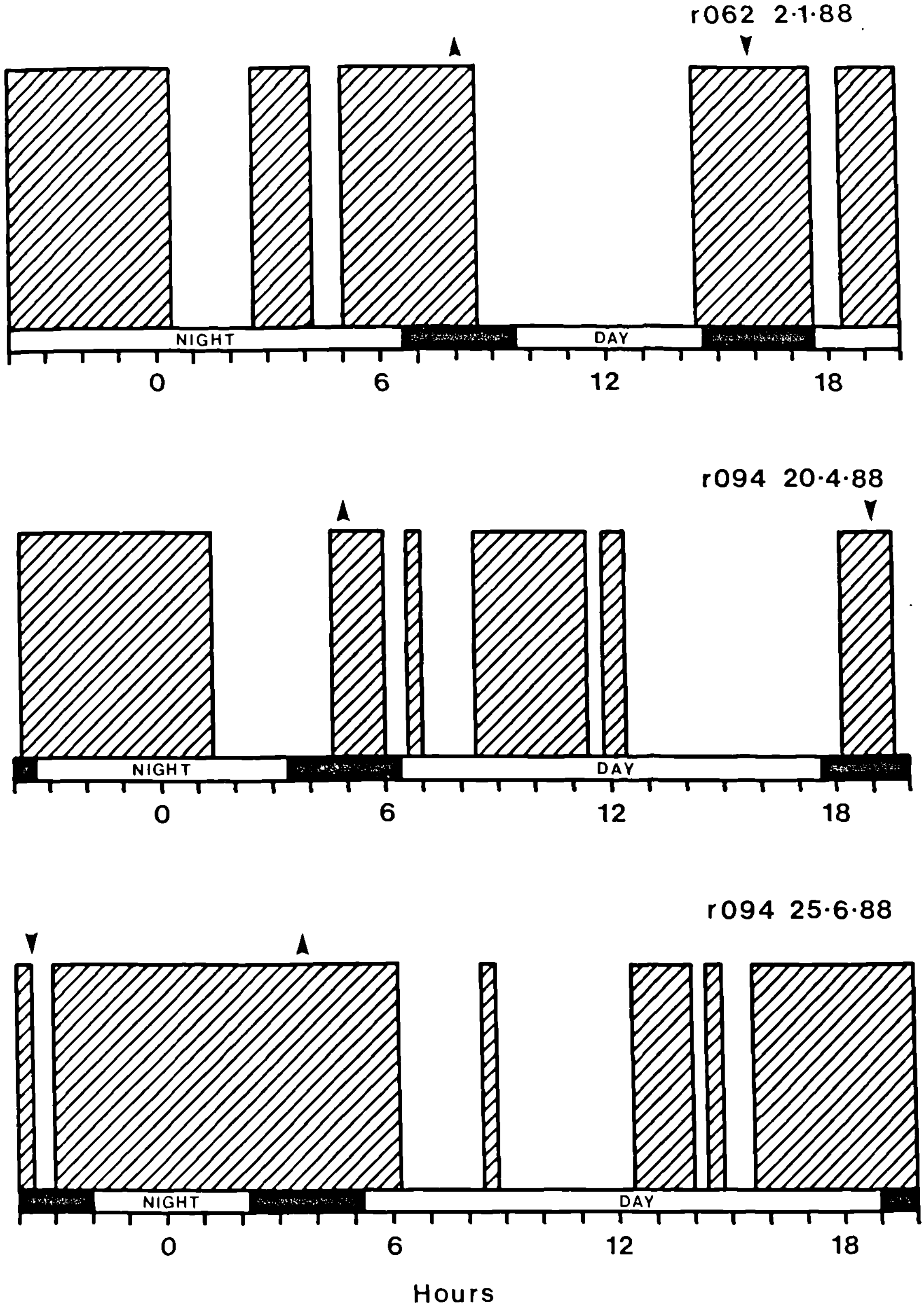
	Muntjac				Roe			
	24 hours		12 hours		24 hours		12 hours	
Month	**Bucks**	**Does**	**Bucks**	**Does**	**Bucks**	**Does**	**Bucks**	**Does**
	n=3	n=3	n=2	n=3	n=3	n=4	n=3	n=5
J/F	4	8	1	1	6	3	2	4
M/A	2	6	1	2	5	4	3	3
M/J	5	6	4	0	5	5	1	2
J/A	5	7	2	2	8	4	0	6
S/O	5	7	1	2	5	5	2	2
N/D	5	4	0	3	5	3	2	1
Totals	**26**	**38**	**9**	**10**	**34**	**24**	**10**	**18**

Figure 4.2a&b Twenty-four hour activity records for individual adult muntjac and roe deer. Hatched areas represent active periods, clear areas inactive periods. The solid parts of the bar are dawn and dusk, the arrows mark the times of sunrise and sunset.

Figure 4.2a (Facing page): **Top:** Muntjac doe m043 for 7.2.88. **Middle:** Muntjac buck m201 for 5.5.87. **Bottom:** Muntjac buck m328 for 3.9.87.

Figure 4.2b (Following page): **Top:** Roe buck r062 for 2.1.88. **Middle:** Roe doe r094 for 20.4.88. **Bottom:** Roe doe r094 for 25.6.88.


m043 7·2·88
NIGHT
DAY
0
6
12
18
m201 5·5·87
NIGHT
DAY
0
6
12
18
m328 3·9·87
NIGHT
DAY
0
6
12
18
Hours


r062 2·1·88
NIGHT
DAY
0
6
12
18
r094 20·4·88
NIGHT
DAY
0
6
12
18
r094 25·6·88
NIGHT
DAY
0
6
12
18
Hours

4.3.1.1 Total activity

There was no significant difference at any time of year in the total activity per twenty-four hour period between muntjac bucks and does or roe bucks and does (Mann-Whitney U tests, three monthly, all $p>0.05$) and therefore the sexes were combined for further analysis. Muntjac and roe deer showed no seasonal change in total activity (Kruskall-Wallis ANOVA; muntjac $H=4.03$, $df=5$, $p>0.05$; roe deer, $H=5.02$, $df=5$, $p>0.05$), although muntjac activity did decrease and roe deer activity increase during May/June (Figure 4.3). While both bucks and does contributed to the decrease in muntjac activity, the increase in roe deer activity was mostly accounted for by a change in the level of activity by bucks. Annual mean activity (± S.E.) per twenty-four hours was $69.3\pm1.5\%$ for muntjac and $56.4\pm1.8\%$ for roe deer. Muntjac were significantly more active than roe deer at all times of the year except during May/June (Mann-Whitney U tests, excluding May/June, all $p<0.05$; May/June, $U=50.5$, $p>0.05$).

4.3.1.2 Number of active periods

The mean number of active periods per twenty-four hours are given in Table 4.2 for adult muntjac and roe deer. There was no significant difference at any time of year between muntjac bucks and does or roe bucks and does (Mann-Whitney U tests, three monthly, all $p>0.05$), or between seasons for either muntjac or roe deer (Kruskall-Wallis ANOVA; muntjac, $H=1.82$, $df=5$, $p>0.05$; roe deer, $H=2.68$, $df=5$, $p>0.05$). The annual mean number of active periods per twenty-four hours (±S.E.) was 5.1 ± 0.1 for muntjac and 5.4 ± 0.2 for roe deer (Figure 4.4); with no significant difference between the two species (Mann-Whitney U test, $U=1677.5$, $P>0.05$).

4.3.1.3 Length of active periods

The mean length of active periods for adult muntjac and roe deer are given in Table 4.3. The only significant difference between bucks and does of either species was for roe deer during May/June, when bucks had longer active periods than does (Mann-Whitney U test, $U=134.5$, $p<0.01$). With the sexes combined, there was no seasonal change in the length of active periods for either muntjac or roe deer (Kruskall-Wallis ANOVA; muntjac, $H=1.37$, $df=5$, $p>0.05$; roe deer, $H=6.39$, $df=5$, $p>0.05$). The annual mean length (±S.E.) of active periods was 3.4 ± 0.2 hours for muntjac and 2.5 ± 0.2 hours for roe deer (Figure 4.5), with muntjac having significantly longer active periods (Mann-Whitney U test, $U=38047.5$, $p<0.001$).

Figure 4.3 Total activity per twenty-four hour period for adult muntjac and roe deer (means ± S.E.). Based on 64 twenty-four hour recordings for muntjac and 58 for roe deer as detailed in Table 4.1.

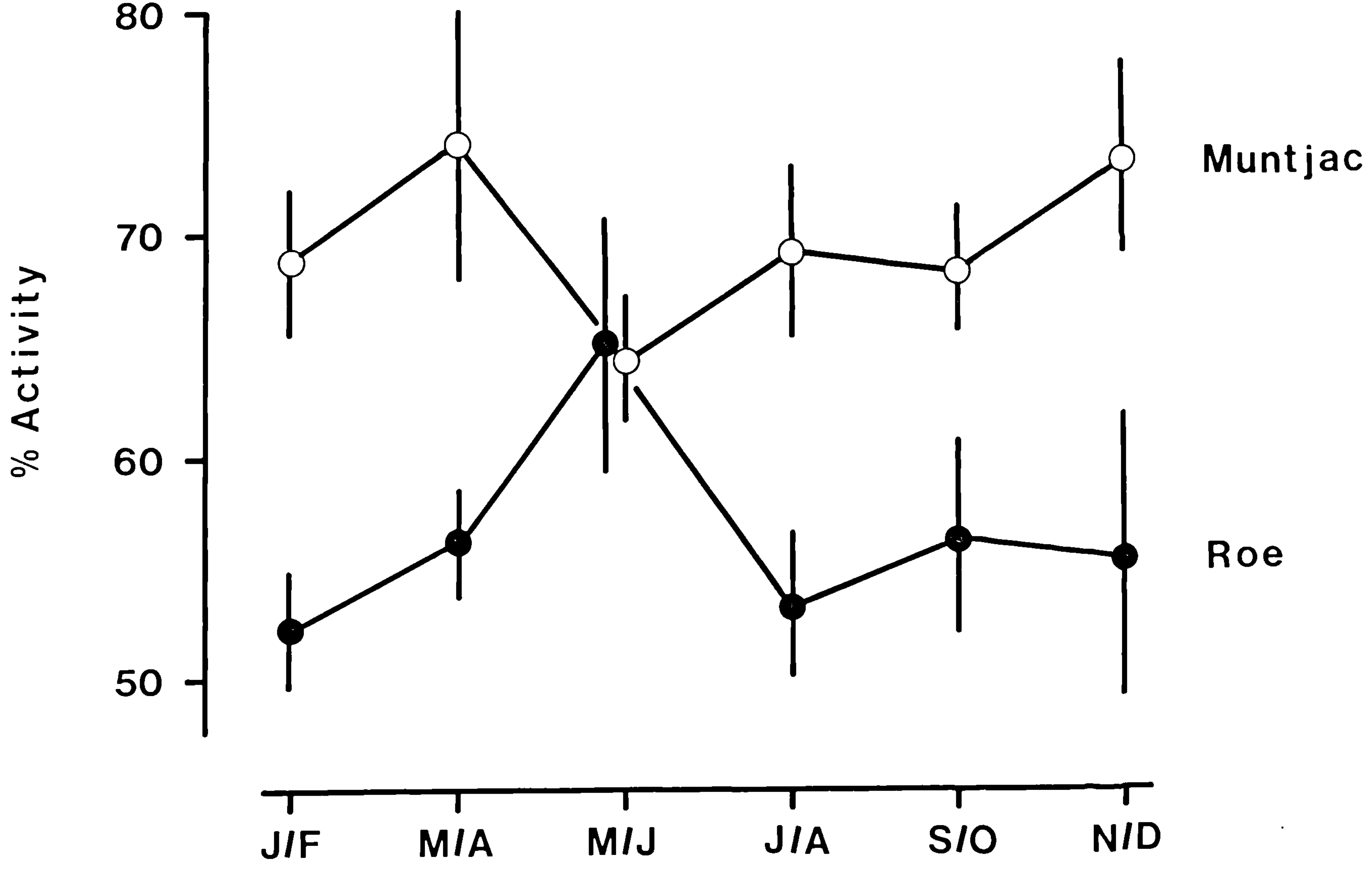

80
70
60
50
% Activity
Muntjac
Roe
J/F
M/A
M/J
J/A
S/O
N/D

Table 4.2 Number of active periods per twenty-four hours for adult muntjac and roe deer. Figures are means ± S.E., sample sizes are in parenthesis.

Month	**Muntjac**		**Roe**		
	n=6		**n=7**		
J/F	5.5±0.40	(12)	5.6±0.53	(9)	
M/A	4.9±0.70	(8)	5.7±0.26	(9)	
M/J	5.3±0.49	(11)	4.9±0.54	(10)	
J/A	5.0±0.39	(12)	6.0±0.68	(12)	
S/O	4.8±0.37	(12)	5.3±0.62	(10)	
N/D	4.7±0.80	(9)	5.1±0.33	(8)	
p	**n.s.**		**n.s.**		
Annual mean	5.1±0.13	(64)	5.4±0.22	(58)	**#**

n.s. not significant, Kruskall-Wallis ANOVA
" " , Mann-Whitney U test, muntjac vs. roe

Figure 4.4 Annual frequency distribution of the number of active periods per twenty-four hours for adult muntjac and roe deer. The arrows mark the mean number of active periods. **Above:** Adult muntjac based on 64 twenty-four hour recordings. **Below:** Adult roe deer based on 58 twenty-four hour recordings.

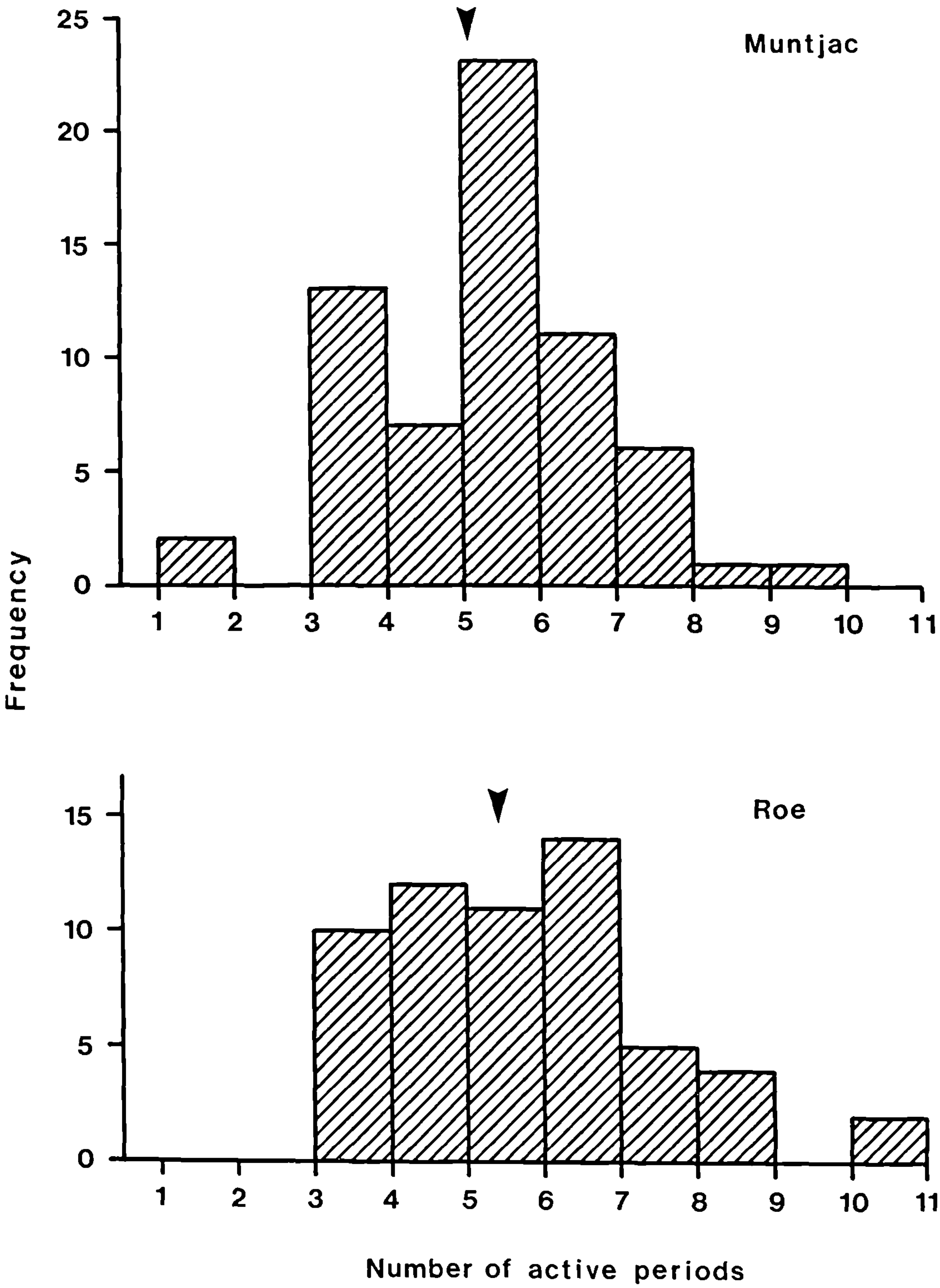

Muntjac
25
20
15
10
5
0
1
2
3
4
5
6
7
8
9
10
11
Frequency
Roe
15
10
5
0
1
2
3
4
5
6
7
8
9
10
11
Number of active periods

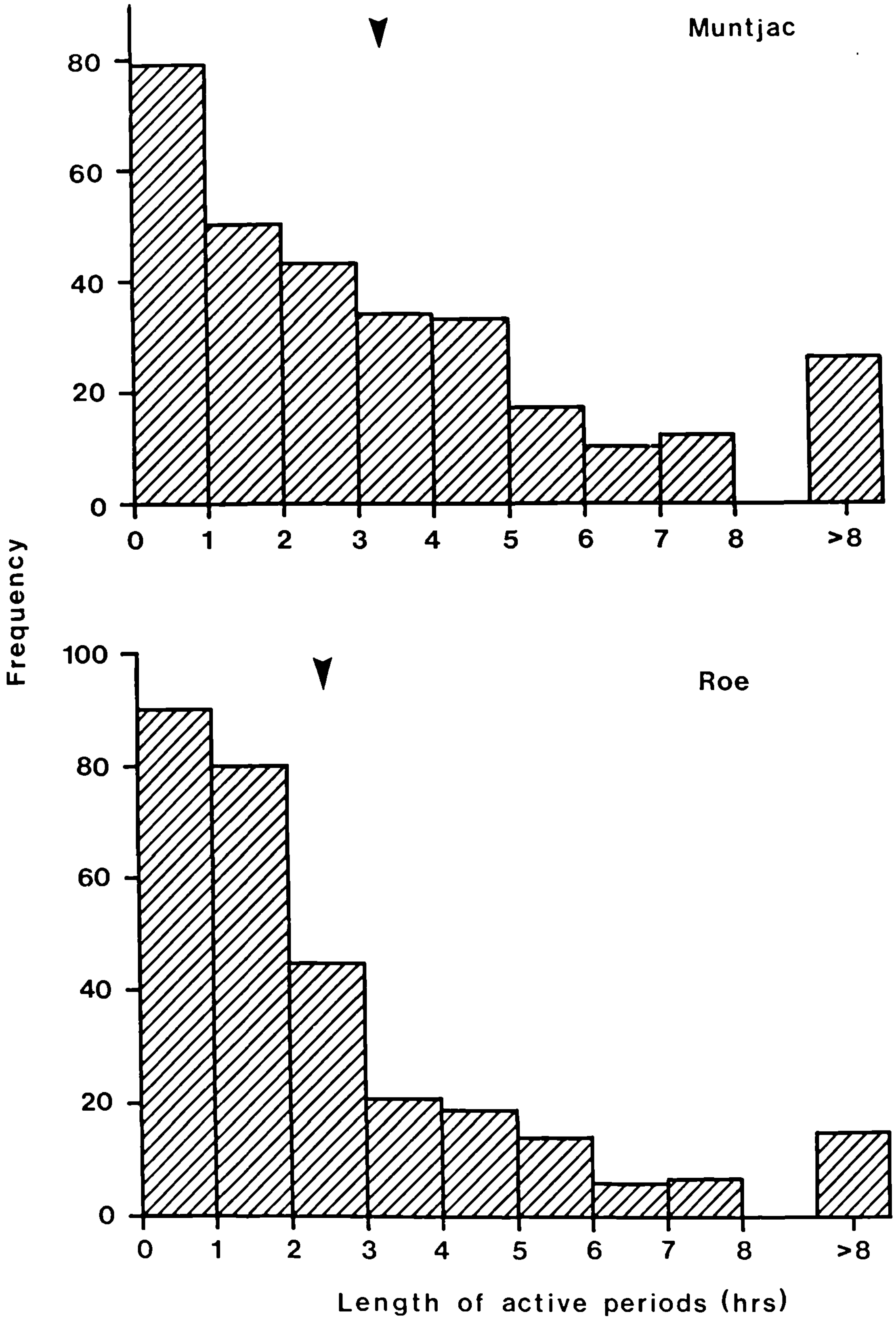
Table 4.3 Length of active periods (hours) for adult muntjac and roe deer. Figures are means ± S.E., sample sizes are in parenthesis.

Month	**Muntjac**	**Roe**	
	n=6	**n=7**	
J/F	3.1±0.39 (60)	2.3±0.27 (47)	
M/A	3.7±0.77 (37)	2.4±0.36 (48)	
M/J	2.9±0.33 (55)	3.2±0.42 (47)	
J/A	3.4±0.35 (56)	2.0±0.25 (65)	
S/O	3.5±0.47 (55)	2.5±0.44 (52)	
N/D	3.8±0.64 (41)	2.6±0.41 (38)	
p	**n.s.**	**n.s.**	
Annual mean	3.4±0.19 (304)	2.5±0.15 (297)	***

n.s. not significant, Kruskall-Wallis ANOVA

*** p<0.001, Mann-Whitney U test, muntjac vs. roe

Figure 4.5 Annual frequency distribution of the length of active periods for adult muntjac and roe deer based on all twenty-four hour and twelve hour activity recordings as detailed in Table 4.1. The arrows mark the mean active period length. **Above:** Adult muntjac based on a total of 304 active periods. **Below:** Adult roe deer based on a total of 297 active periods.


Muntjac
80
60
40
20
0
0
1
2
3
4
5
6
7
8
>8
Frequency
Roe
100
80
60
40
20
0
0
1
2
3
4
5
6
7
8
>8
Length of active periods (hrs)

4.3.1.4 Length of inactive periods

The mean length of inactive periods for adult muntjac and roe deer are given in Table 4.4. There was no significant difference at any time of year between muntjac bucks and does or roe bucks and does (Mann-Whitney U tests; all $p>0.05$) or between seasons for either muntjac or roe deer (Kruskall-Wallis ANOVA; muntjac, $H=4.28$, $df=5$, $p>0.05$; roe deer, $H=8.58$, $df=5$, $p>0.05$). The annual frequency distribution of muntjac and roe deer inactive period length is shown in Figure 4.6. The annual mean length (±S.E.) of inactive periods was 1.55 ± 0.1 hours for muntjac and 1.97 ± 0.1 hours for roe deer, with roe deer having significantly longer inactive periods (Mann-Whitney U test, $U=34946.0$, $p<0.01$). Muntjac inactive periods were significantly shorter than active periods (Mann-Whitney U test, $U=27904.5$, $p<0.001$), while there was no difference between roe deer active and inactive period length (Mann-Whitney U test, $U=39432.0$, $p>0.05$).

4.3.1.5 Diurnal variation in activity

Figure 4.7 shows the diurnal variation in activity of adult muntjac at different times of year. Throughout the year there were peaks of activity at dawn and dusk, with lower levels of activity during the day and at night. During March/April and September/October the level of activity was relatively constant throughout the twenty-four hour cycle, whereas during May/June there was a pronounced diurnal cycle of activity. The dawn and dusk activity peaks followed the seasonal changes in daylength, being closest together during November/December and furthest apart during May/June. Generally, activity was lower at night than during the day, although during November/December, when the nights were longest, there was an additional activity peak around midnight.

The levels of activity for adult muntjac in each of the four diurnal periods (dawn, day, dusk and night) are given in Table 4.5. Activity levels differed between diurnal periods except during March/April and September/October (Chi-squared tests; March/April and September/October, $p>0.05$; all other months, $p<0.01$). Activity was highest during dawn and dusk and higher during the day than at night, except during November/December.

Figure 4.8 shows the diurnal variation in activity of adult roe deer. The overall level of activity was lower than for muntjac and generally the dawn and dusk peaks were more clearly defined. In contrast to muntjac, the diurnal cycle of activity was most pronounced during March/April and September/October and during most months activity was lower during the day than at night. In addition to the dawn and dusk peaks, there was an peak of activity around midday during most months and between September and April there was

Table 4.4 Length of inactive periods (hours) for adult muntjac and roe deer. Figures are means ± S.E., sample sizes are in parenthesis.

Month	Muntjac	Roe	
	n=6	n=7	
J/F	1.41±0.13 (61)	2.21±0.29 (44)	
M/A	1.42±0.17 (34)	2.00±0.20 (46)	
M/J	1.74±0.18 (51)	1.69±0.28 (42)	
J/A	1.63±0.23 (53)	1.87±0.23 (67)	
S/O	1.68±0.19 (48)	1.96±0.25 (49)	
N/D	1.39±0.20 (37)	2.14±0.32 (37)	
p	n.s.	n.s.	
Annual mean	1.55±0.08 (284)	1.97±0.11 (285)	**

n.s. not significant, Kruskall-Wallis ANOVA

** p<0.01, Mann-Whitney U test, muntjac vs. roe

Figure 4.6 Annual frequency distribution of the length of inactive periods for adult muntjac and roe deer based on all twenty-four hour and twelve hour activity recordings as detailed in Table 4.1. The arrows mark the mean inactive period length. **Above:** Adult muntjac based on a total of 284 inactive periods. **Below:** Adult roe deer based on a total of 285 inactive periods.

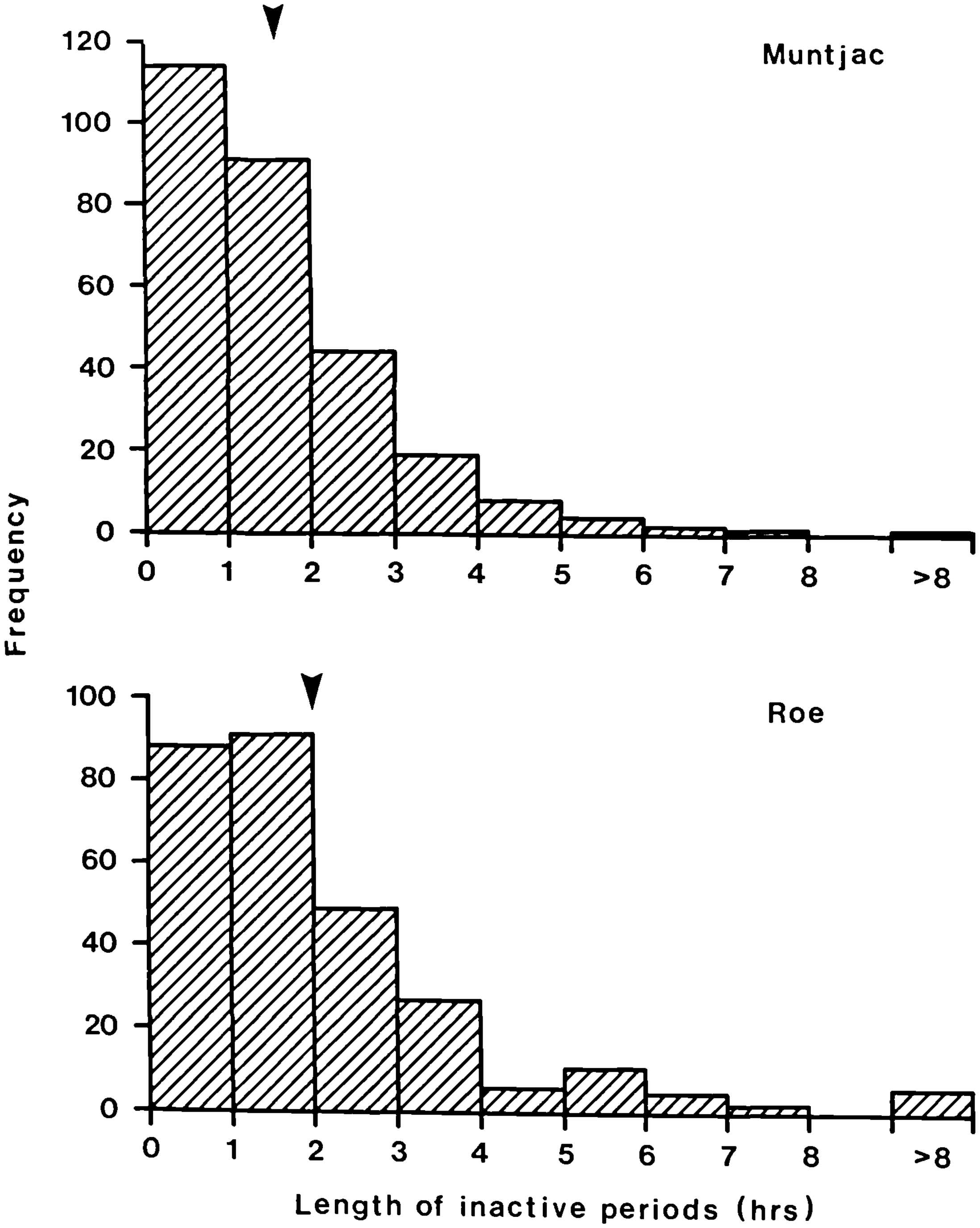

Muntjac
Roe
Frequency
120
100
80
60
40
20
0
0
1
2
3
4
5
6
7
8
>8
Length of inactive periods (hrs)

Figure 4.7 Diurnal variation in activity (running means) of adult muntjac at different times of year based on all twenty-four hour and twelve hour automatic activity recordings as detailed in Table 4.1. The arrows mark the mean times of sunrise and sunset.

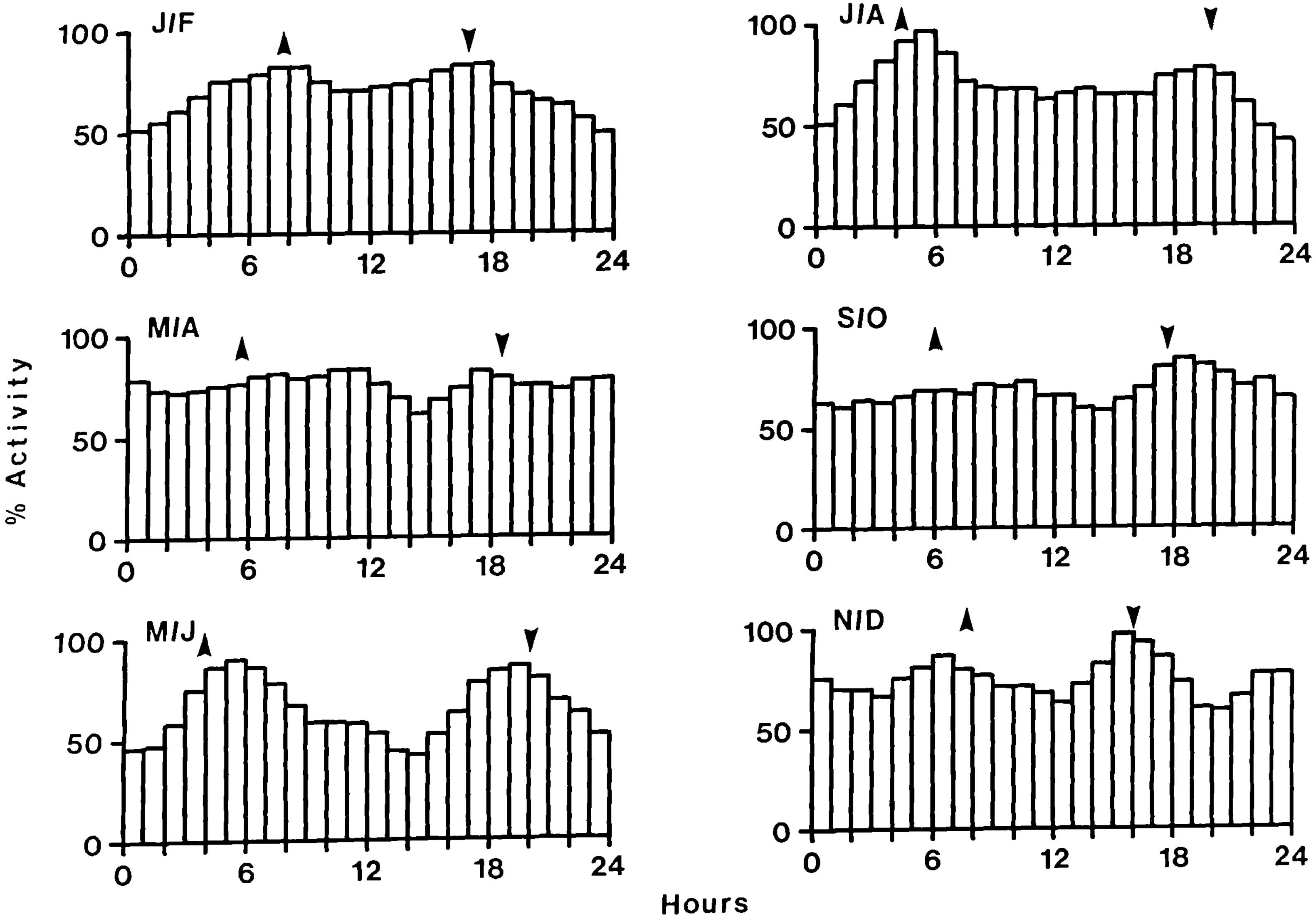

J/F
J/A
M/A
S/O
M/J
N/D
% Activity
100
50
0
0
6
12
18
24
Hours

Table 4.5 Percentage of time spent active as a proportion of total time during dawn, day, dusk and night for adult muntjac. All twenty-four hour and twelve hour activity recordings as detailed in Table 4.1 were used.

Month	Dawn	Day	Dusk	Night	
J/F	81.0	74.2	82.2	61.9	**
M/A	88.9	74.2	80.0	71.8	n.s.
M/J	79.0	63.4	84.2	53.5	***
J/A	87.8	69.4	75.7	54.1	***
S/O	65.1	67.3	82.4	69.1	n.s.
N/D	78.9	69.3	97.3	71.1	**
Annual mean	79.5	68.7	83.0	64.7	***

** p<0.01, Chi-squared test
*** p<0.001, " " "
n.s. not significant, Chi-squared test

Figure 4.8 Diurnal variation in activity (running means) of adult roe deer at different times of year based on all twenty-four hour and twelve hour automatic activity recordings as detailed in Table 4.1. The arrows mark the mean times of sunrise and sunset.

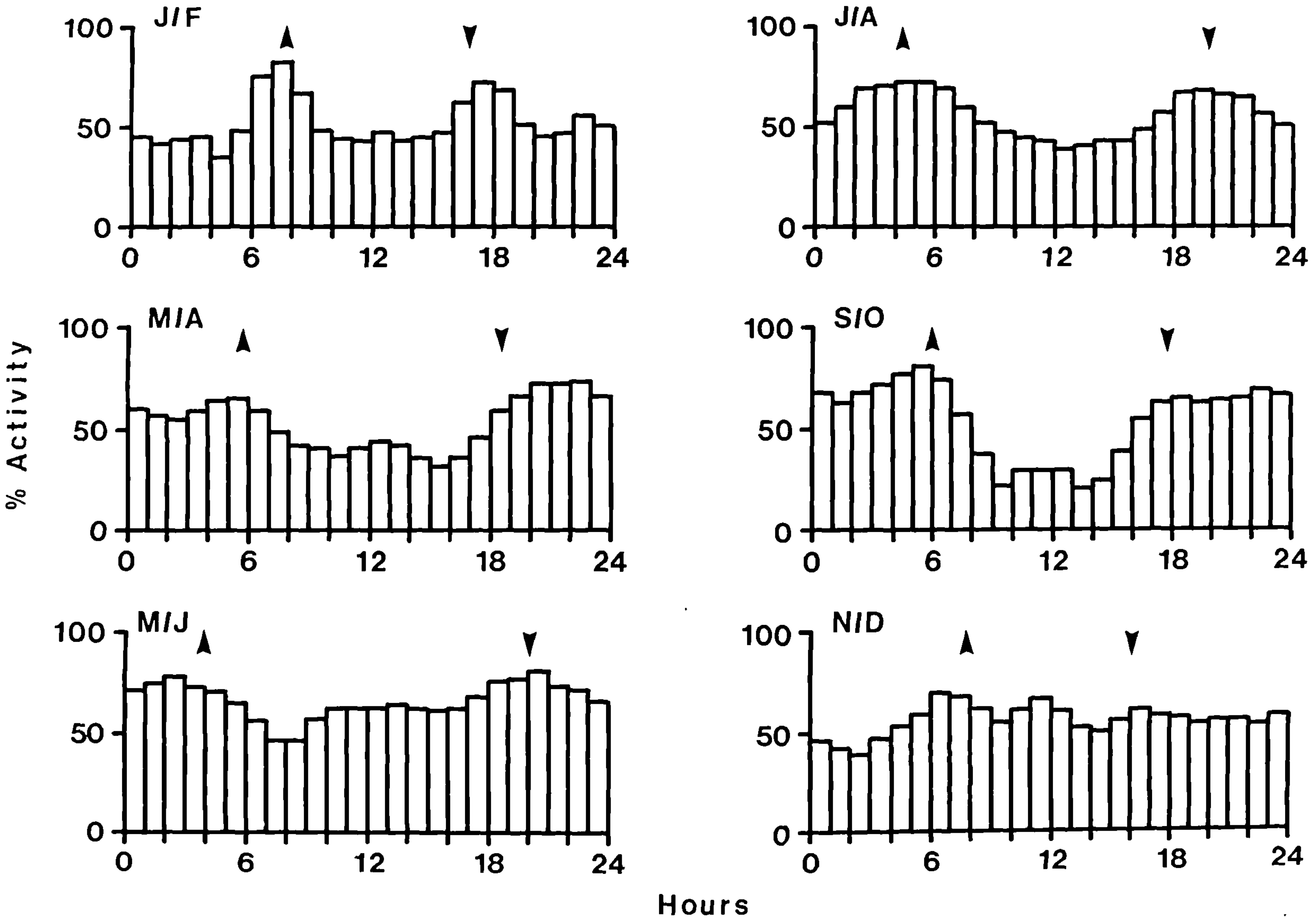

J/F
J/A
M/A
S/O
M/J
N/D
100
50
0
0
6
12
18
24
% Activity
Hours

Table 4.6 Percentage of time spent active as a proportion of total time during dawn, day, dusk, and night for adult roe deer. All twenty-four and twelve hour activity recordings as detailed in Table 4.1 were used.

Month	Dawn	Day	Dusk	Night	
J/F	81.4	45.8	61.7	45.8	***
M/A	81.9	41.0	66.7	68.2	***
M/J	72.1	59.6	80.7	69.1	**
J/A	71.6	49.6	68.4	57.8	***
S/O	73.9	29.7	67.2	66.1	***
N/D	72.7	65.1	61.2	53.4	*
Annual mean	75.7	48.4	67.7	58.3	***

*	$p<0.05$,	Chi-squared test		
**	$p<0.01$,	"	"	"
***	$p<0.001$,	"	"	"

also a small midnight activity peak.

The levels of activity for adult roe deer in each of the four diurnal periods are given in Table 4.6. Activity levels were significantly different between diurnal periods at all times of year (Chi-squared tests, all $p<0.05$). Activity was highest during dawn and also high during dusk. In contrast to muntjac, night-time activity was higher than daytime activity, except for November/December.

Wilcoxon matched-pairs signed-ranks tests (SPSSX, 1986; pp. 820-821) were used to determine whether muntjac activity was consistently higher than roe deer activity during any of the diurnal periods. There was no significant difference during dawn ($Z= -0.94$, $p>0.05$) or at night ($Z= -0.73$, $p>0.05$). However, muntjac were consistently more active than roe deer during the day ($Z= -2.20$, $p<0.05$) and at dusk ($Z= -2.20$, $p<0.05$).

4.3.2 ROUTINE RADIO-TRACKING

Table 4.7 gives details of the routine radio-tracking data used to describe activity patterns of adult muntjac and roe deer. More than 11,000 fixes from 38 adult muntjac and more than 3,000 fixes from seven adult roe deer were used.

The diurnal cycle of activity for adult muntjac is shown in Figure 4.9. As with the automatic activity recorder data, there were peaks of activity at dawn and dusk throughout the year, with lower levels of activity during the day and at night. Again during March/April activity levels were relatively constant throughout the day. However, during the rest of the year the diurnal variation was greater than with the automatic recorder data. Overall the level of activity was lower than shown by the automatic recorder data, though there was still a higher level of activity during the day than at night and also a small midnight activity peak during November/December.

The levels of activity for adult muntjac in each of the four diurnal periods are given in Table 4.8. Activity levels were significantly different between diurnal periods at all times of year (Chi-squared tests; all $p<0.001$). As with the automatic recorder data, activity was highest during dawn and dusk and higher during the day than at night, except during November/December. In contrast, the level of activity during dusk was consistently higher than during dawn.

Figure 4.10 shows the diurnal cycle of activity for adult roe deer. As with the

Table 4.7 Number of fixes for adult muntjac and roe deer used in the analysis of activity from routine radio-tracking data.

Month	**Muntjac**			**Roe**		
	Bucks	**Does**	**Total**	**Bucks**	**Does**	**Total**
	n=15	n=23	n=38	n=2	n=5	n=7
J/F	519	1096	1615	187	459	646
M/A	485	1190	1675	142	337	479
M/J	565	1250	1815	169	393	562
J/A	617	1372	1989	154	319	473
S/O	593	1476	2069	169	383	552
N/D	641	1498	2139	187	433	620
Totals	3420	7882	11302	1008	2324	3332

Figure 4.9 Diurnal variation in activity (running means) of adult muntjac at different times of year based on routine radio-tracking data as detailed in Table 4.7. The arrows mark the mean times of sunrise and sunset.

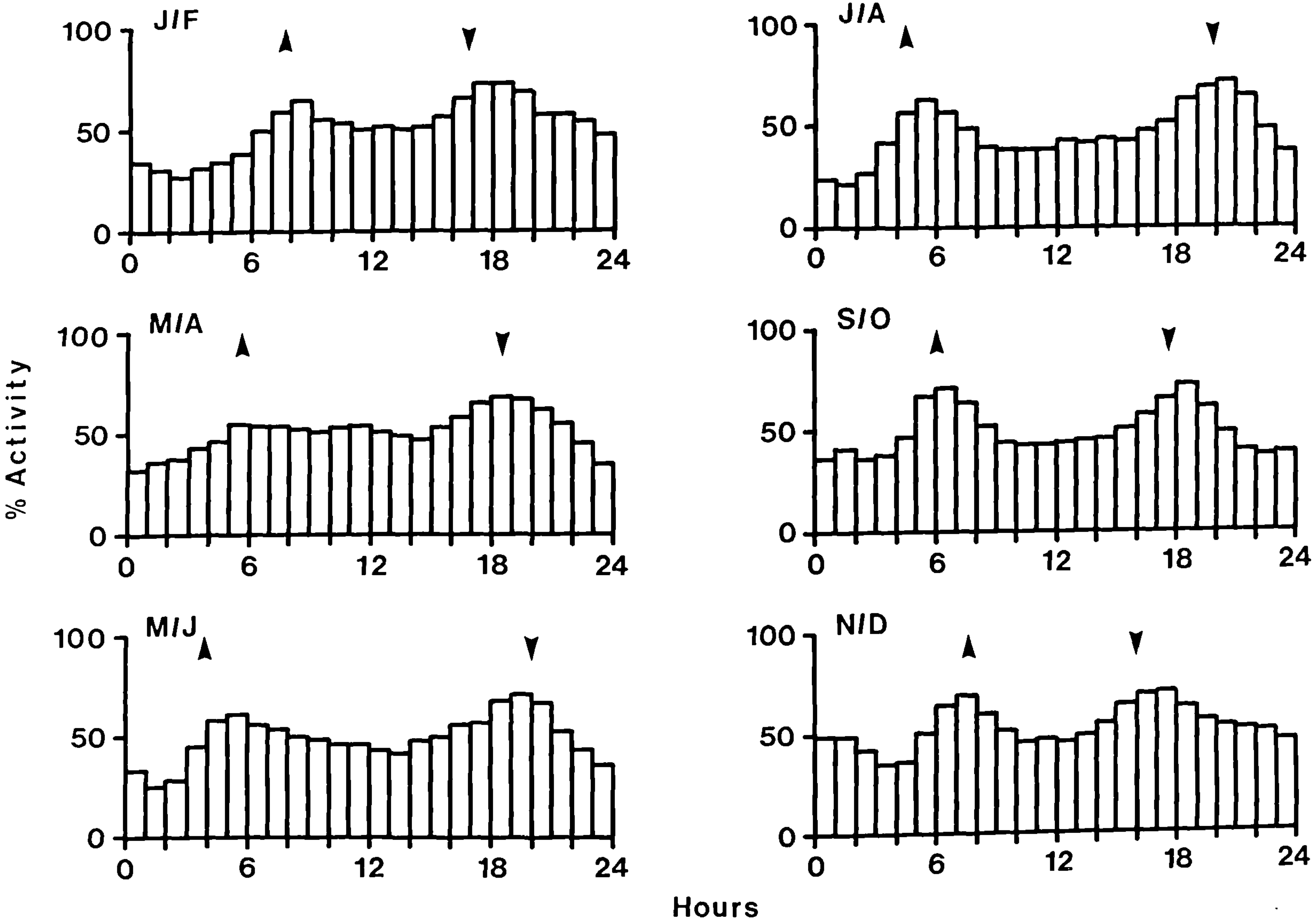

J/F
J/A
M/A
S/O
M/J
N/D
100
50
0
0
6
12
18
24
% Activity
Hours

Table 4.8 Percentage of active fixes as a proportion of all fixes during dawn, day, dusk and night for adult muntjac using routine radio-tracking data.

Month	**Dawn**	**Day**	**Dusk**	**Night**	
J/F	58.9	51.5	68.8	45.1	***
M/A	54.2	51.8	68.2	42.9	***
M/J	49.6	50.0	67.7	36.1	***
J/A	50.0	44.5	70.8	31.4	***
S/O	67.7	45.9	69.4	39.1	***
N/D	69.4	47.0	64.4	50.7	***
Annual mean	59.9	48.0	67.8	43.4	***

*** $p<0.001$, Chi-squared test

Figure 4.10 Diurnal variation in activity (running means) of adult roe deer at different times of year based on routine radio-tracking data as detailed in Table 4.7. The *arrows mark the mean times of sunrise and* sunset.

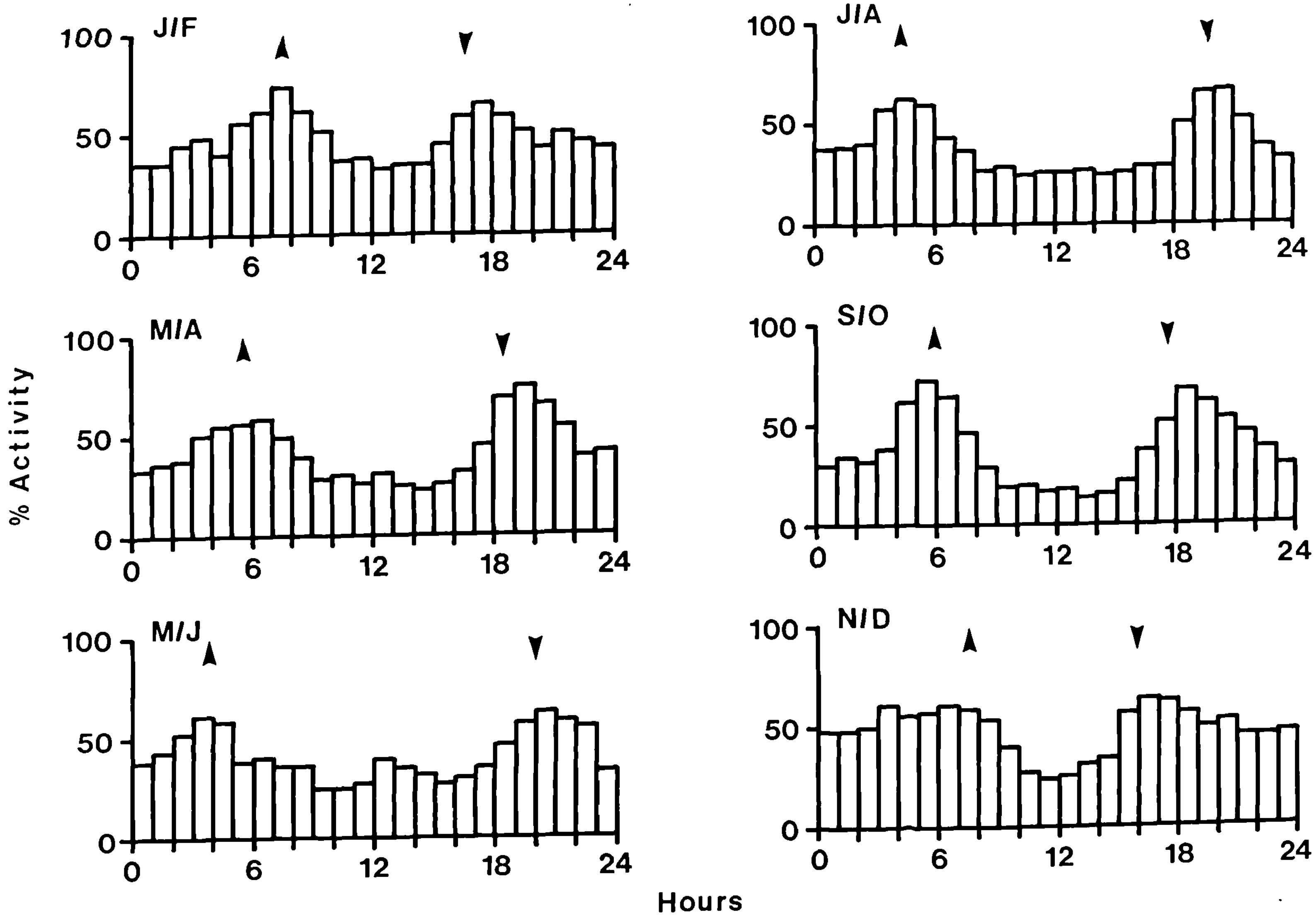

J/F
J/A
M/A
S/O
M/J
N/D
% Activity
100
50
0
0
6
12
18
24
Hours

Table 4.9 Percentage of active fixes as a proportion of all fixes during dawn, day, dusk and night for adult roe deer using routine radio-tracking data.

Month	**Dawn**	**Day**	**Dusk**	**Night**	
J/F	73.1	34.3	65.0	41.9	***
M/A	60.0	29.4	67.8	46.7	***
M/J	58.1	32.6	60.5	43.8	***
J/A	68.8	29.4	67.8	35.5	***
S/O	66.2	20.2	55.3	42.9	***
N/D	59.6	29.5	61.3	49.8	***
Annual mean	64.5	29.3	62.5	44.5	***

*** $p<0.001$, Chi-squared test

automatic recorder data, there were dawn and dusk peaks, which were most pronounced during March/April and September/October, and throughout the year activity was lower during the day than at night. In contrast, a midday peak was only present during May/June, and there were no clearly defined midnight activity peaks. Compared to the automatic recorder data, dawn and dusk peaks were more pronounced and both daytime and night-time activity was reduced.

The levels of activity in each of the four diurnal periods are given in Table 4.9. Activity levels were significantly different between diurnal periods at all times of year (Chi-squared tests; all $p<0.001$), with highest activity around dawn and dusk. As with the automatic recorder data, activity was higher at night than during the day.

Wilcoxon matched-pairs signed-ranks tests were again used to determine whether muntjac activity was consistently higher than roe deer activity during any of the diurnal periods. As with the automatic recorder data, there was no significant difference during dawn ($Z= -1.15$, $p>0.05$) or at night ($Z= -1.57$, $p>0.05$), but muntjac were consistently more active than roe deer during the day ($Z= -2.20$, $p<0.05$) and at dusk ($Z= -2.20$, $p<0.05$).

4.3.3 TWENTY-FOUR HOUR RADIO-TRACKING

Details of the data that were available are found in Tables 3.13 and 3.14. The proportion of the daily range length travelled at different times of day is shown in Figure 4.11 for adult muntjac. Muntjac travelled the largest proportions of their daily range lengths around dawn and dusk. Throughout the year, there were significant differences in the proportion of the daily range length travelled at different times of day (Kruskall-Wallis ANOVA; all $p<0.001$). Although both the automatic recorder data and the routine radio-tracking data showed that muntjac were more active during the day than at night, the twenty-four hour data showed that they travelled a smaller proportion of the daily range length during the day compared to at night.

The proportion of the daily range length travelled between the five tracking rounds is shown in Figure 4.12 for adult roe deer. Throughout the year, there were significant differences in the proportion of the daily range length travelled at different times of day (Kruskall-Wallis ANOVA; all $p<0.01$). Although the daily range length was only divided into four parts, it was clear that the largest proportions were travelled around dawn and dusk. Between November and February the animals remained on the night-time areas of their home ranges until after the second tracking round (0600 hrs), and so a large

Figure 4.11 Variation in the proportion of the daily range length travelled at different times of day for adult muntjac. The twenty-four hour period was divided into 12 pairs of two hourly periods, the second two hour period commencing one hour after the end of the first. The first time period was the pair of two hourly periods 2200-2359 and 0100-0259, the twelfth time period was the pair of two hourly periods 2000-2159 and 2300-0059. The arrows mark the mean times of sunrise and sunset.

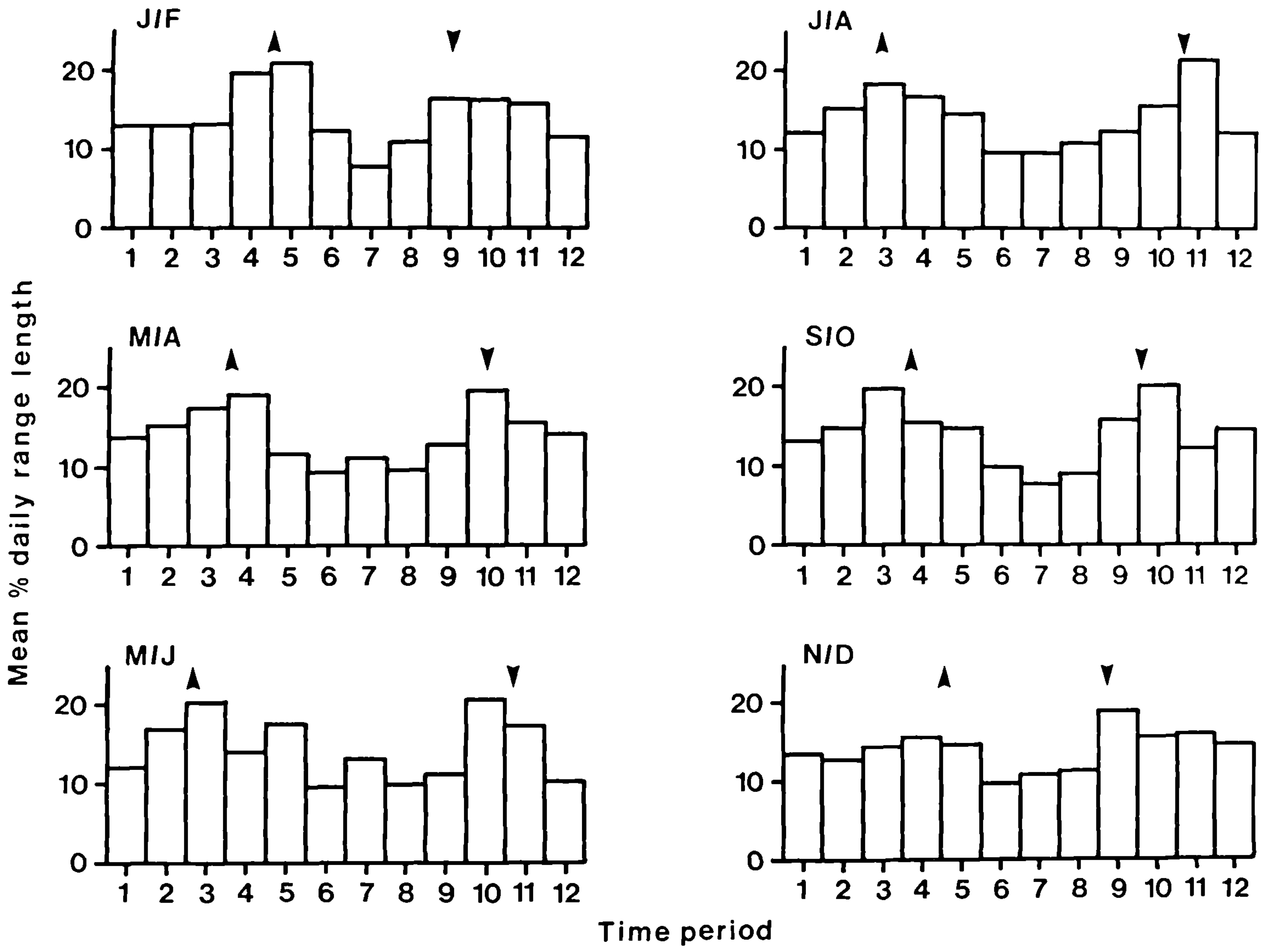
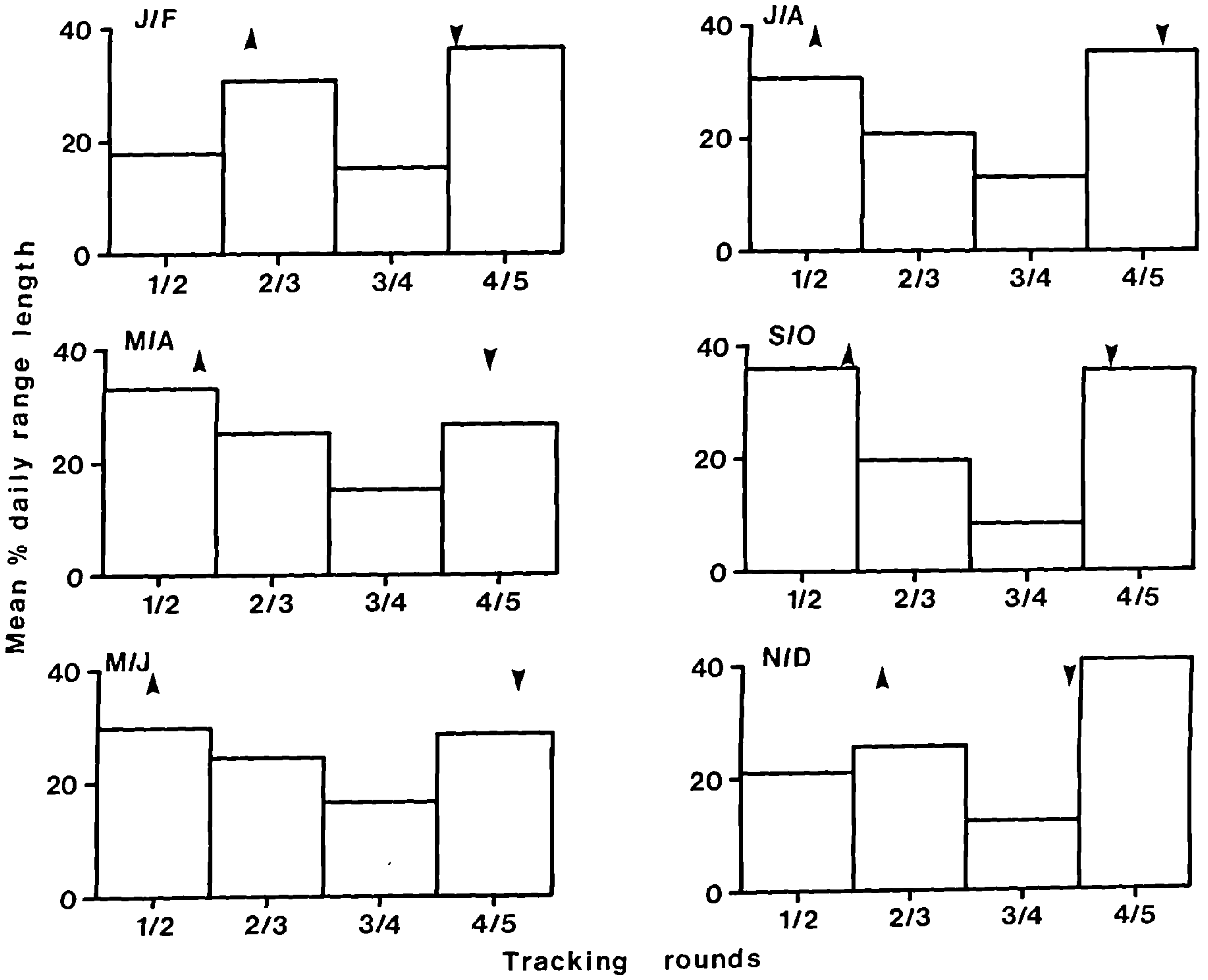

J/F
J/A
M/A
S/O
M/J
N/D
0
10
20
1 2 3 4 5 6 7 8 9 10 11 12
Mean % daily range length
Time period

Figure 4.12 The proportion of the daily range length travelled between tracking rounds for adult roe deer. Tracking rounds one to five started at 0100, 0600, 1100, 1600 and 2100hrs G.M.T. respectively and lasted for not more than 90 minutes. The arrows mark the mean times of sunrise and sunset.


Mean % daily range length
J/F
J/A
M/A
S/O
M/J
N/D
0
20
40
1/2
2/3
3/4
4/5
Tracking rounds

proportion of the daily range length was travelled between the second and third rounds (0600 and 1100 hrs). During the rest of the year, a larger proportion of the daily range length was travelled between the first and second tracking rounds (0100 and 0600 hrs) than between the second and third rounds (0600 and 1100 hrs). The interval between the forth and fifth tracking rounds (1600 and 2100 hrs) always contained the dusk activity peak. Both the automatic recorder data and the routine radio-tracking showed that roe deer were less active during the day compared to at night; the twenty-four hour data also showed that roe travelled a smaller proportion of their daily range length during the day compared to at night.

4.4 DISCUSSION

This chapter describes the activity patterns of sympatric muntjac and roe deer by measuring amplitude fluctuations in automatically and manually collected radio signals and by examining how the daily range length was partitioned through the twenty-four hour cycle. Several studies have examined the reliability of using amplitude fluctuations, either alone or in combination with mercury switch transmitters, to determine activity status (Garshelis *et al.*, 1982; Gillingham & Bunnell, 1985; Beier & McCullough, 1988). Beier and McCullough found that when a combination of amplitude fluctuations and mercury switch pulse rate changes were compared with concurrent visual observations, 98% and 96% respectively of active and inactive sampling intervals were correctly classified. However, their data suggest that if amplitude fluctuations alone are used to determine activity status, then inactivity will be substantially overestimated, because visual observation frequently recorded deer as active when the signals were of constant amplitude. Garshelis *et al.* (1982) compared activity status with distance moved per hour and also found that using a combination of amplitude fluctuations and pulse rate changes gave the most accurate results. In addition they suggested that amplitude fluctuations may become less reliable as the distance between the animal and the receiver increases.

In this study, amplitude fluctuations alone were used to assess activity status. However, it seems unlikely that inactivity was overestimated. The total daily activity for roe deer was similar to that reported for a number of deer species, using various techniques including direct observation, while total daily activity of muntjac was in fact higher than reported previously. Muntjac were active for an average of 69.3% of each twenty-four hour period compared to 56.4% for roe deer. This level of muntjac activity was higher than found by both Yahner (1980a&b) and Harding (1986) and also higher than that reported for other species of deer (e.g. Cederlund, 1981; Risenhoover, 1986). This may be because muntjac spend a smaller proportion of their active periods actually foraging. Yahner (1980a) showed that muntjac grazed for only 45% of the time spent active compared to 76% for moose (Risenhoover, 1986) and 82% for elk (Craighead *et al.*, 1973). The level of roe deer activity was similar to that reported by Cederlund (1981) and Hinge (1986). The pattern of activity was very similar using automatically and manually collected data, although the higher overall level of activity with the automatically collected data suggested that as the distance between animal and receiver increases, constant amplitude signals may be assessed as active, due to problems with interpreting low amplitude signals.

Muntjac and roe deer were both most active around dawn and dusk, whilst outside these periods muntjac were more active during the day than at night and roe deer were more active at night than during the day. The twenty-four hour movement data showed that both muntjac and roe deer travelled the largest proportion of the daily range length around dawn and dusk. Roe deer moved more at night than during the day, while muntjac also travelled larger proportions of their daily range lengths at night, even though they were more active during the day.

According to the "rumen fill theory" (Moen, 1973), which states that ruminant nutrition is not constrained by how fast an animal can ingest food but by how quickly food passes through the rumen, activity patterns should be influenced by the digestibility of forage. Food of low digestibility will be retained in the rumen longer and thus delay the start of the next feeding period. If changes in the digestibility of forage through the year are having an effect on activity patterns, then the length of inactive periods should decrease and the number of active periods increase as the digestibility of forage rises. Neither muntjac or roe deer showed any significant seasonal changes in the length of inactive periods or in the number of active periods per twenty-four hour period. However, there was a tendency for roe deer to have shorter inactive periods during the summer months, which would tend to support the "rumen fill theory". In contrast though, muntjac actually had longer inactive periods during the summer months. Also, time series analysis carried out on the automatically recorded data but not included here, showed no seasonal changes in activity cycle length for either muntjac or roe deer. Thus the activity patterns of muntjac and roe deer were relatively constant throughout the year, with on average just over five active periods per twenty-four hours, and with no clear evidence from the length of inactive periods or from cycle length to support the "rumen fill theory". This was in contrast to Harding's (1986) study, where although muntjac maintained the same total daily activity throughout the year, they responded to decreased forage digestibility by increasing the length of inactive periods and thus in turn increasing activity cycle length. Cederlund

(1981) and Turner (1978) found evidence from roe deer in support of the "rumen fill theory" and also showed that roe deer activity was lower during winter than during summer. Cederlund attributed this winter decrease in activity to energy conservation and decreased mobility due to snow (Cederlund, 1982). It may be that decreased mobility during winter, rather than a lower forage digestibility causes changes in activity patterns that are consistent with the "rumen fill theory". If this was the case, it might explain why in this study, where roe deer were not constrained by winter snow depth, animals did not show changes in activity patterns. Alternatively, changes in the proportion of the active time spent feeding could mask any changes in overall activity. For example, Turner (1979) found that roe deer spent a larger proportion of their active time feeding during winter.

Despite roe deer showing marked seasonal changes in home range size and daily range length, total daily activity did not change seasonally. Thus while roe deer travelled much longer daily range lengths during winter, the total daily activity did not increase, which suggests that using movement criteria as a measure of activity (e.g. Singer *et al.*, 1981; Gent, 1983) should be treated with caution.

Theory also predicts that smaller deer should ingest more digestible food items and therefore have faster gut throughput times, more active periods and shorter intervals between active periods than larger deer. However, this study did not show any difference between muntjac and roe deer in the number of active periods per twenty-four hours, although roe deer did have longer inactive periods.

Active and inactive period length of muntjac and roe deer did not change with season. This was in contrast to Clutton-Brock *et al.* (1982), who found that red deer had shorter grazing bouts during the summer which they attributed to a higher available biomass of forage. For a grazer, the rate of food intake will be influenced by biomass, whereas for browsing species, such as muntjac and roe deer, the rate of food intake will be influenced both by the dispersion and the size of food items. Dispersion and size of browsed food items will change less through the year than will the biomass available to grazers, and this may explain why active period length did not change seasonally for either muntjac or roe deer.

This study showed that muntjac were more active during the day compared to at night. Harding (1986) found the same pattern with free-ranging muntjac at Rushbeds Wood, although enclosed muntjac at Whipsnade Zoo were more active at night than during the day. Yahner (1980a&b) who also studying enclosed muntjac, found that night-time activity was greater than daytime activity and suggested that this was an antipredator response. However, the above comparisons suggest that studies of activity using enclosed animals may be affected by disturbance and that the normal pattern of activity for free-ranging muntjac is greater daytime activity.

Previous studies of roe deer activity have agreed that peak activity occurs around dawn and dusk, but have found different levels of daytime and night-time activity. Cederlund (1981) found that roe deer were generally more active during the day than at night, Gent (1983) found greater activity at night and Hinge (1986) found little difference between daytime and night-time activity. The level of human disturbance influences the timing of activity in roe deer (Van Bemmel & Van den Oord, 1982), and this together with diurnal patterns of habitat use probably determines whether roe deer are more active during the day or at night.

According to the "rumen fill theory", ruminants should have regular cycles of activity and inactivity related to the digestibility of food. Therefore, there should be no synchrony of activity in the population as a whole, although animals occupying overlapping ranges might show synchronised activity cycles for social reasons. This study, as with most other studies of activity in deer, has shown that population activity is synchronised with the times of dawn and dusk. The most likely explanation is that this increased crepuscular activity is associated with a movement between different habitat types at dawn and dusk. Roe deer showed a marked difference in the location of daytime and night-time fixes within the home range and while this did not occur with muntjac, the twenty-four hour data did show an increase in the rate of movement around dawn and dusk. These differences in habitat utilisation between the two species may explain why the crepuscular peaks were more pronounced for roe deer.

Muntjac and roe deer on the study area occupied overlapping home ranges and there was no evidence to suggest spatial partitioning of resources. However, this chapter has shown that there was some temporal separation of activity, particularly relating to differential use of daytime and night-time. The diurnal variations in activity of muntjac were similar to those reported by Harding (1986) from a population of muntjac in the absence of roe deer, and so it seems likely that this is the normal activity pattern of free-ranging muntjac. There is also no need to invoke interference competition as the cause of greater night-time activity in roe deer. A combination of human disturbance and use of more open habitats, including fields at night, is sufficient explanation, although this does not rule out a possible competitive effect. Even so, the observed temporal separation of activity will reduce any potential interference competition between the two species.

CHAPTER FIVE: DIET

5.1 INTRODUCTION

In this chapter, muntjac and roe deer diets are described by examining epidermal fragments in faecal pellets. The influence of the available vegetation and the presence of other species on the diet selected is examined and dietary relationships are assessed at comparable times of year to the pellet surveys used to describe habitat partitioning in Chapter Two.

Roe deer diet has been studied in the south of England by Jackson (1980), Hosey (1981), Hearney & Jennings (1983) and Johnson (1984) and in upland British forests by Henry (1978), Loudon (1979) and Hinge (1986). There have also been extensive studies of roe deer diet in Europe (e.g. Gebczynska, 1980; Helle, 1980; Kossak, 1983; Maizeret & Tran Manh Sung, 1984; Maillard & Picard, 1987). All these studies agree that roe deer are concentrate selectors (Hofmann, 1985), preferring to take nutritious, easily digestible shrubs and herbs when available. In the south of England, bramble is the most important food item throughout the year, with conifers also important during winter and herbs and broadleaved trees and shrubs during the spring and summer.

Less is known about muntjac diet, both in Britain and in China. Helin & Peychao (1976) examined the rumen contents of 15 Reeves' muntjac from south-east China, while Jackson *et al.* (1977) examined 29 rumens collected during February, from south-east England. Harding (1986) described some qualitative aspects of muntjac diet in Rushbeds Wood and Harris & Forde (1986) have already described the diet of muntjac in the King's Forest, using faecal analysis. Hofmann (1985) predicts on the basis of body size and rumen structure that muntjac should also be concentrate selectors, taking nutritious and easily digested forage. Harris & Forde (1986) showed that bramble comprised 30-40% of the diet throughout the year, while Jackson *et al.* (1977) found that bramble and herbs were the most important dietary components during February.

Holechek *et al.* (1982) and Nugent (1983) have reviewed the techniques available for determining herbivore diets. Macrorumen analysis (Jackson *et al.*, 1977; Henry, 1978; Jackson, 1980; Johnson, 1984; Hinge, 1986), microfaecal analysis (Hosey, 1981; Hearney & Jennings, 1983; Johnson, 1984; Harding, 1986; Harris & Forde, 1986), direct observation (Loudon, 1979) and bite count analysis (Harding, 1986) have all been used in studies of roe deer and muntjac diet in Britain.

In this study, faecal analysis was used because it allowed repeated, non-invasive collection of samples from selected sites containing the required combinations of muntjac and roe deer. Also, fewer samples are required to accurately estimate a seasonal diet compared to other techniques. Anthony & Smith (1974) found that only 15 faecal samples were required, compared with 50 rumen samples.

Although faecal analysis has been widely used for many years to determine herbivore diets, there is still much controversy over its accuracy. The major potential sources of error are:

1. Differential digestion of plant species so that the proportion of a species in the faeces differs from that ingested (Dunnet *et al.*, 1973; Pulliam & Nelson, 1979; Smith & Shandruk, 1979).

2. Plant species have different ratios of identifiable to unidentifiable fragments in faecal samples (Westoby *et al.*, 1976; Havstad & Donart, 1978; Gill *et al.*, 1983; Barker, 1986a; Norbury, 1988).

3. Plant species may fragment differently, resulting in different sized fragments, even if faecal samples are milled to constant size (Forde, 1985; Barker, 1986a).

4. Certain species such as legumes (Slater & Jones, 1971) and plant parts such as fruits, nuts, fungi and root crops (Maizeret *et al.*, 1986) may be completely absent or unrecognisable in faecal samples.

Early evaluations of the faecal analysis technique compared the diet from rumen or fistula samples with that from faecal samples for ruminants that were predominantly grazing animals. For such species, the diet determined by faecal analysis agreed closely with that from rumen samples (Stewart, 1967; Todd & Hansen, 1973; Holechek & Valdez, 1985).

More recent evaluations have been for ruminants that feed on a combination of shrubs, herbs and grasses. For such species, significant differences have generally been found between rumen or fistula samples and faecal samples (Dunnet *et al.*, 1973; Vavra *et al.*, 1978; McCullough, 1985), although a few studies have found that faecal samples accurately estimate diet (Anthony & Smith, 1974). When the diet contains a mixture of plant groups, faecal analysis will underestimate the proportion of herbs and shrubs and overestimate the proportion of grasses, ferns and mosses.

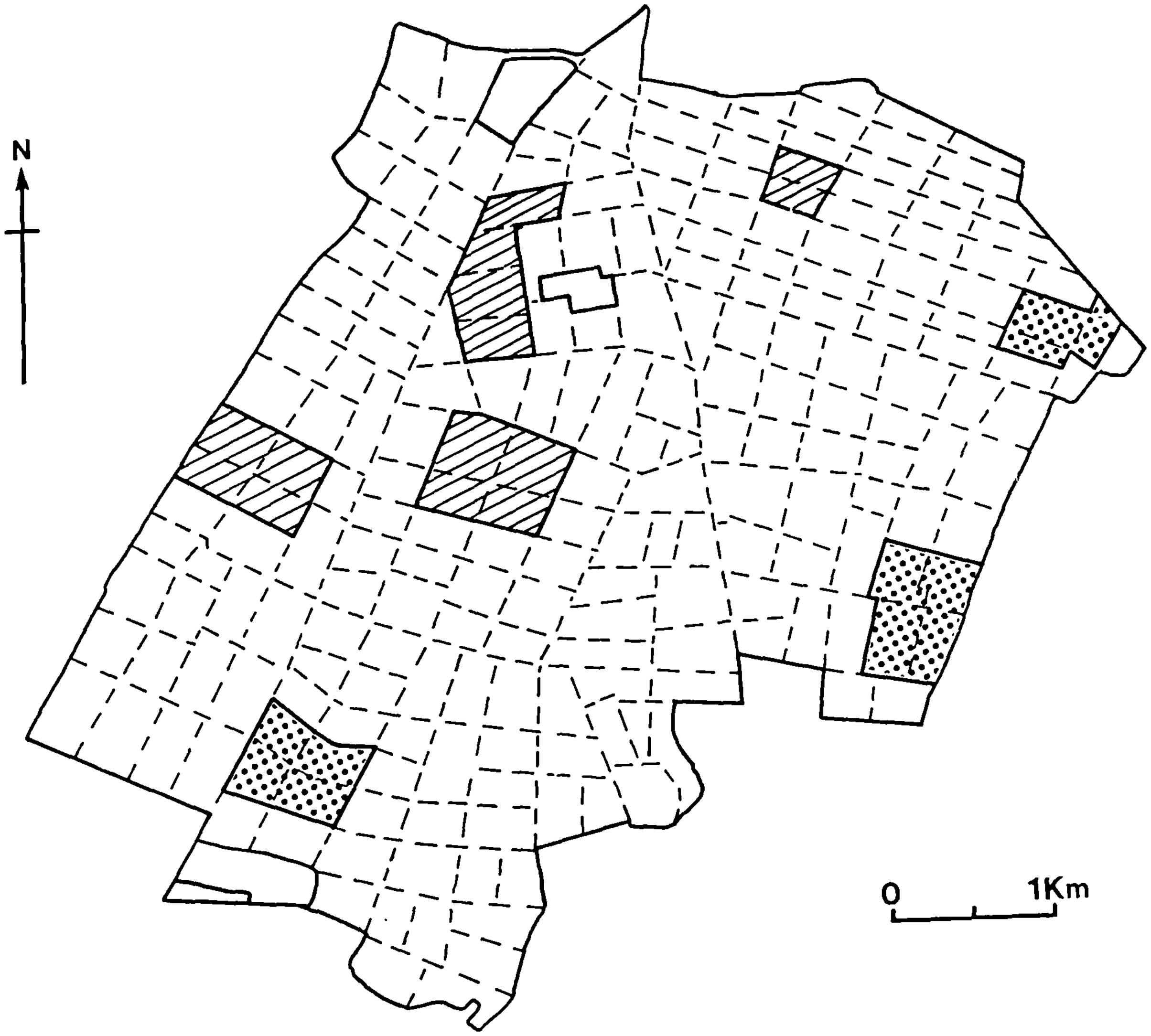
Although differential digestion is usually given as the reason for inaccuracies in faecal analysis, different ratios of identifiable to unidentifiable fragments may in fact be a more important error (Gill *et al.*, 1983). If differential digestion was a major error, then correcting for digestibility should substantially improve the accuracy of faecal analysis. Both Holechek & Valdez (1985) and Forde (*unpubl.*) found that digestion coefficients did not improve the accuracy of faecal analysis, when applied to hand compounded mixtures of known composition. However, Barker (1986b) and Norbury (1988) both showed substantial improvements in the accuracy of faecal analysis when corrected for differing ratios of identifiable to unidentifiable fragments. Grasses, ferns and mosses have higher proportions of identifiable fragments than herbs and shrubs and therefore errors will operate in the same direction as those proposed for differential digestion.

Optimal foraging theory suggests that individuals should forage selectively when food is abundant and opportunistically when forage is of lower quality and less abundant (Westoby, 1974; Nudds, 1980). Alternative theories suggest that species should forage most selectively when food supply is limited, thereby minimising competition (Hobbs *et al.*, 1983). Opportunistic foraging will produce a high dietary overlap, whereas selective foraging will result in a low dietary overlap between sympatric species. Most studies of food partitioning in sympatric ungulates have shown that dietary overlap is lower during periods of resource shortage (Hansen & Reid, 1975; Olsen & Hansen, 1977; Anthony & Smith, 1977; Hobbs *et al.*, 1983). However, a few studies have shown an increased dietary overlap during periods of resource shortage (Staines & Welch, 1984; Hinge, 1986; Putman, 1986; Jenkins & Wright, 1987, 1988), suggesting an increase in the potential for competition. In this chapter, dietary relationships of muntjac and roe deer are examined to assess the influence of resource abundance on dietary overlap.

5.2 METHODS

Faecal pellet groups were collected from seven sites, each consisting of a group of between two and four compartments (six and 13 sub-compartments). Muntjac faecal pellet groups were collected from three sites and roe deer pellet groups from all seven sites, between June 1986 and February 1988 (Figure 5.1). Muntjac were absent or present at low density in the four sites from which only roe deer pellets were collected. Collections of fresh pellets were made during the last week of each month; the aim was to collect four or five roe deer pellet groups from each site and the same number of muntjac pellet groups

Figure 5.1 Distribution of the sites used to collect muntjac and roe deer faecal samples between June 1986 and February 1988. Diagonal shading denotes sites where roe deer faecal pellets were collected, filled circles denote sites where both muntjac and roe deer faecal samples were collected.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from the three sympatric sites. Allocation of pellet groups to a particular herbivore species should have been better than the 76% accuracy reported earlier, since boarderline pellet groups could be ignored. Most of the pellet groups were collected between June 1986 and May 1987, with additional collections made between June 1987 and February 1988 to give a minimum of four pellet groups per species per site for each month. All pellet groups were stored in separate jars containing 10% formaldehyde solution.

A reference collection of plant epidermes was made from more than 100 different plant species collected from the forest and surrounding farmland. Preparations were made of both abaxial and adaxial leaf surfaces, and where appropriate, fruit pericarps and testas from nuts and cereal seeds. Where possible, the epidermis was prepared by placing the required leaf surface face downwards on a microscope slide and scraping off the overlying mesophyll tissue using a sharp scalpel blade, irrigated with hypochlorite solution (Metcalfe, 1960). The epidermis was then washed briefly in concentrated nitric acid to remove any adhering mesophyll cells, before being dehydrated and mounted in euparal, or transferred to water and mounted in hydramount.

Acid maceration (Storr, 1961; Hosey, 1981) was used when the above technique failed to produce a suitable preparation. Small sections of leaf were placed in a petri dish of concentrated nitric acid and gently warmed on a hotplate until most of the mesophyll tissue had dissolved. The leaf sections were then transferred to water, the abaxial and adaxial epidermes separated and mounted in hydramount. Photomicrographs were taken of all reference slides, and these were used to identify epidermal fragments in the faeces.

Each pellet group was examined separately. Parts of two or three faecal pellets were ground in a pestle and mortar with a small amount of water, until a fine paste was produced (Martin, 1964; Hearney & Jennings, 1983). The faecal paste was then made up to 250ml with water and after thorough agitation, two sub-samples of 15ml each were placed in centrifuge tubes. These were centrifuged at 2,500 rev/min for 10 minutes, and then allowed to settle for at least 30 minutes. The supernatant, which only contained loose trichomes and intercostal fragments, was then poured off to leave approximately 1ml of concentrated epidermal fragments. Samples of these were spread on two microscope slides under 22x57mm coverslips.

Slides were analysed by regular traverses at x100, 5mm apart, using a sliding stage microscope (Stewart, 1967). Individual fragments were examined at x400, identified using the photomicrographs and the area of each fragment measured at x100, using a 0.5mm squared graticule. Fragments smaller than 2 units and larger than 100 units in area were ignored. 25 epidermal fragments were identified and measured on each slide, giving a total of 50 fragments per sample. This sample size was found to give an error of less than 10% for species that accounted for more than 2% of the total sample by area (Forde, 1985).

Digestion resulted in the loss of the epidermal cell wall pattern from many broadleaved tree and shrub and herb fragments, particularly during spring and early summer. To prevent biases in the overall diet determination, such fragments were recorded as either unidentified broadleaved trees and shrubs or unidentified herbs, on the basis of epidermal thickness and other characteristics.

For all analyses, the diet was divided into eight plant groups; broadleaved trees and shrubs, bramble and raspberry, conifers, herbs, graminids, ferns, fungi and other foods. Diet diversity was examined using the Shannon diversity index (Magurran, 1988), diets were compared using non-parametric Mann-Whitney U tests, to minimise any effects of differential digestion or different ratios of identifiable to unidentifiable fragments, and by Pianka (1973) niche overlap indices. Multiple discriminant analysis (MDA), with minimising Wilk's Lamda as the criterion for group separation, was used to examine the dietary relationships between muntjac diet, roe deer diet from sites with muntjac and roe deer diet from sites without muntjac (Hanley & Hanley, 1982). The MDAs were confined to two bimonthly periods, January/February and September/October, to correspond to the habitat partitioning described in Chapter Two.

5.3 RESULTS

A total of 161 faecal samples were analysed to determine muntjac diet (Table 5.1 and Figure 5.2). Bramble and raspberry and ferns were important food items throughout the year and showed little seasonal change. The importance of other plant groups in the diet did change seasonally. During winter, bramble and raspberry, conifers, graminids and ferns were preferred. Conifers and graminids were replaced during May and June by increasing amounts of broadleaved trees and shrubs and herbs. Herbs remained a major dietary item until autumn, when they were replaced by increasing use of conifers, graminids and ferns. Broadleaved tree and shrub use was maintained during autumn and winter by ingesting fallen deciduous leaves and evergreen shrubs such as ivy and Oregon grape. Fungi were only ingested in significant quantities during late summer and autumn. The category "other food items", which was mainly mosses, although it contained small quantities of fruit pericarp and nut testa during September/October, accounted for a small proportion of the

Table 5.1 Muntjac diet, based on 161 faecal samples collected between June 1986 and February 1988. Figures are mean % fragment area, ± S.E.

	Mean % fragment area						
Plant group	**J/F**	**M/A**	**M/J**	**J/A**	**S/O**	**N/D**	**Annual**
Broadleaved# trees & shrubs	12.7±2.4	12.2±3.9	27.5±4.1	21.9±3.5	32.4±3.6	22.2±3.3	21.4±1.5
Bramble/raspberry	17.8±3.2	23.8±4.7	24.4±5.5	24.2±3.7	8.1±2.7	20.2±3.5	19.8±1.7
Conifers	6.4±2.0	19.0±3.9	0.4±0.2	0.3±0.2	2.0±0.9	7.3±2.8	5.9±1.0
Herbs	2.2±0.6	9.2±2.0	21.7±2.8	31.9±3.1	25.6±2.1	10.0±1.3	16.9±1.2
Graminids	42.6±4.9	26.0±3.9	8.6±1.9	5.7±1.2	9.0±1.8	16.2±3.4	18.0±1.6
Ferns	16.9±4.7	8.4±3.3	15.9±3.1	11.8±1.9	14.0±2.3	21.8±3.8	14.7±1.4
Fungi	0.1±0.1	0.1±0.1	1.2±0.6	3.6±1.4	7.3±0.9	1.6±0.6	2.4±0.4
Other foods	1.4±0.3	1.4±0.5	0.3±0.1	0.6±0.3	1.6±0.7	0.7±0.3	1.0±0.2
No. of samples	27	27	25	29	27	26	161

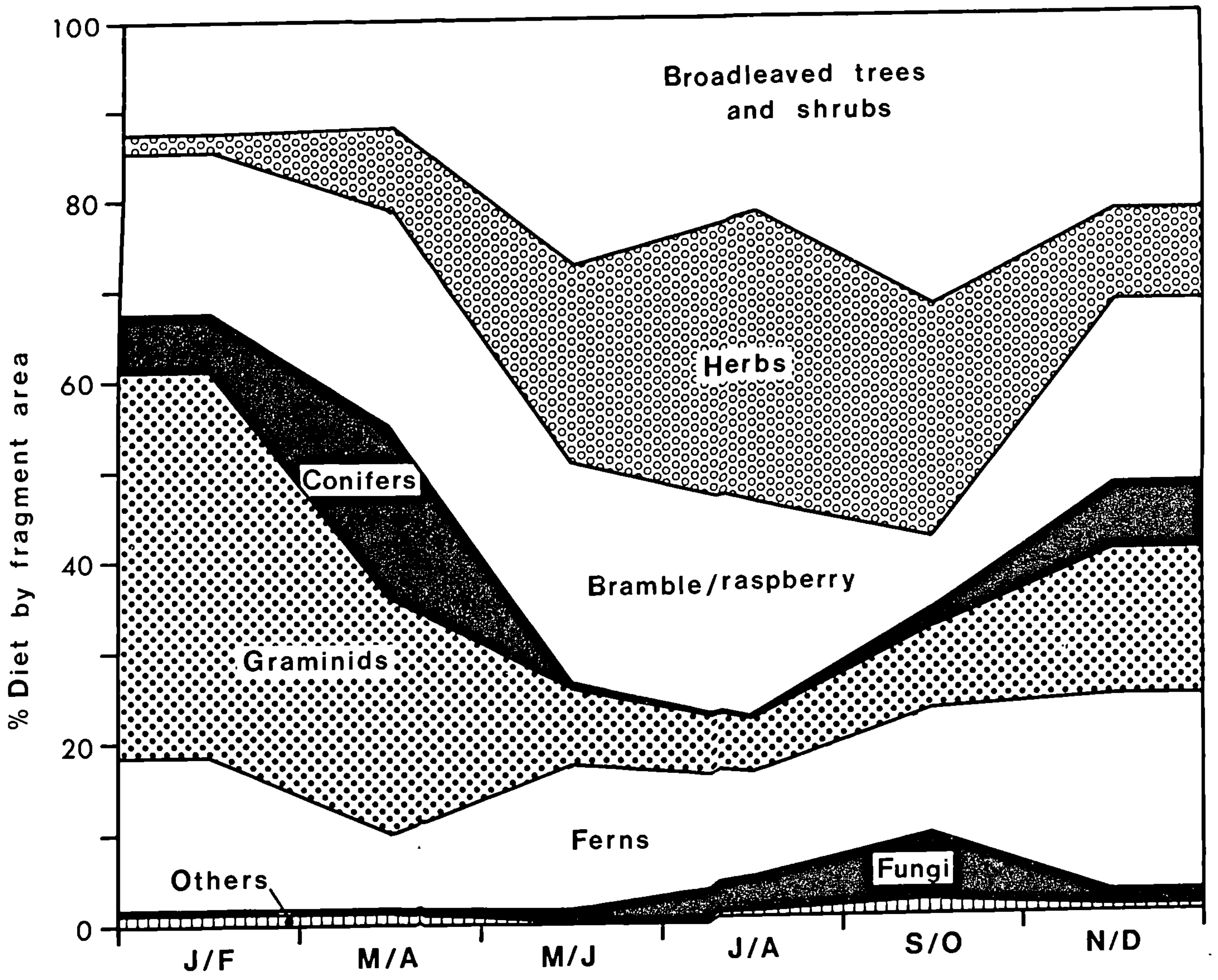
excluding bramble and raspberry

Table 5.2 Shannon indices of muntjac diet diversity, based on 161 faecal samples collected between June 1986 and February 1988.

Month	**n**	**H'**
J/F	27	1.559
M/A	27	1.757
M/J	25	1.626
J/A	29	1.623
S/O	27	1.746
N/D	26	1.806
Annual	161	1.842

$H' = -\Sigma p_i \ln p_i$ (Magurran, 1988)

Figure 5.2 Seasonal variation in the diet of muntjac, based on 161 faecal samples collected between June 1986 and February 1988. The dietary proportions are percentages based on the areas of plant fragments.


Broadleaved trees and shrubs
Herbs
Conifers
Bramble/raspberry
Graminids
Ferns
Fungi
Others
% Diet by fragment area
100
80
60
40
20
0
J/F
M/A
M/J
J/A
S/O
N/D

diet.

The ferns taken were almost entirely *Dryopteris* spp; bracken was only ingested in small amounts. The most frequently recorded broadleaved trees and shrubs were beech, oak, ivy and hawthorn *Crataegus monogyna*. Graminids were mostly forest grasses such as Yorkshire fog *Holcus lanatus* and cocksfoot *Dactylis glomerata*, although some cereals were taken between January and April. With conifers, Scots pine was preferred over Corsican pine and significant amounts of Douglas fir were also taken.

Shannon indices of diet diversity are given in Table 5.2. There was little seasonal change in diet diversity, although diversity was lowest during January/February and highest during autumn and early winter.

A total of 376 faecal samples were analysed to determine roe deer diet (Table 5.3 and Figure 5.3). Bramble and raspberry, ferns and graminids all showed little seasonal change in dietary importance. The importance of other plant groups in the diet did change seasonally. Conifers, ferns, bramble and raspberry and graminids were important during winter. The conifers were replaced by herbs and broadleaved trees and shrubs during summer and autumn, but in contrast to muntjac, graminid use was maintained through the summer months. Again, fallen deciduous leaves and evergreen shrubs such as ivy, Oregon grape and heather *Calluna vulgaris* were taken during autumn and winter. Fungi were only important during late summer and autumn and small quantities of nut testa were taken during September and October.

Again, the ferns taken were almost entirely *Dryopteris* spp., the most frequently recorded broadleaved trees and shrubs were beech, oak, ivy and hawthorn and the graminids were almost entirely forest grasses. As with muntjac, Scots pine was preferred over Corsican pine and significant amounts of Douglas fir were also taken. Roe deer diet contained less broadleaved tree and shrub and bramble and raspberry and more conifer and fern than muntjac diet.

Shannon indices of roe deer diet diversity are given in Table 5.4. Again, there was little seasonal change in diet diversity, although diversity was lowest during January/February and highest during September/October.

Table 5.5 shows the tree canopy and ground vegetation characteristics for the roe deer diet collection sites with and without sympatric muntjac. In the tree canopy, sites with

Table 5.3 Roe deer diet, based on 376 faecal samples collected between June 1986 and February 1988. Figures are mean % fragment area, ± S.E.

	Mean % fragment area						
Plant group	**J/F**	**M/A**	**M/J**	**J/A**	**S/O**	**N/D**	**Annual**
Broadleaved# trees & shrubs	4.7±0.8	6.9±1.6	11.8±1.9	12.2±2.0	25.2±2.9	11.2±2.4	12.0±0.9
Bramble/Raspberry	18.5±3.0	8.5±2.0	13.2±3.1	9.8±2.2	9.5±2.0	10.9±2.1	11.7±1.0
Conifers	28.8±3.2	38.9±4.2	2.6±1.0	0.6±0.2	1.7±0.6	20.2±3.2	15.3±1.3
Herbs	2.0±0.4	5.9±1.9	24.0±2.7	29.5±2.6	16.8±2.0	6.8±1.2	14.3±1.0
Graminids	18.0±2.2	16.4±2.5	16.9±2.5	11.5±1.9	9.5±1.7	8.5±1.4	13.5±0.9
Ferns	27.6±3.3	22.5±3.8	31.0±3.8	33.6±3.5	24.8±3.9	40.0±4.1	29.9±1.6
Fungi	0.3±0.1	0.6±0.2	0.3±0.2	2.2±0.6	9.3±1.7	2.0±0.5	2.5±0.4
Other foods	0.1±t	0.4±0.1	0.4±0.1	0.8±0.3	3.3±0.8	0.5±0.2	0.9±0.2
No. of samples	61	63	65	63	63	61	376

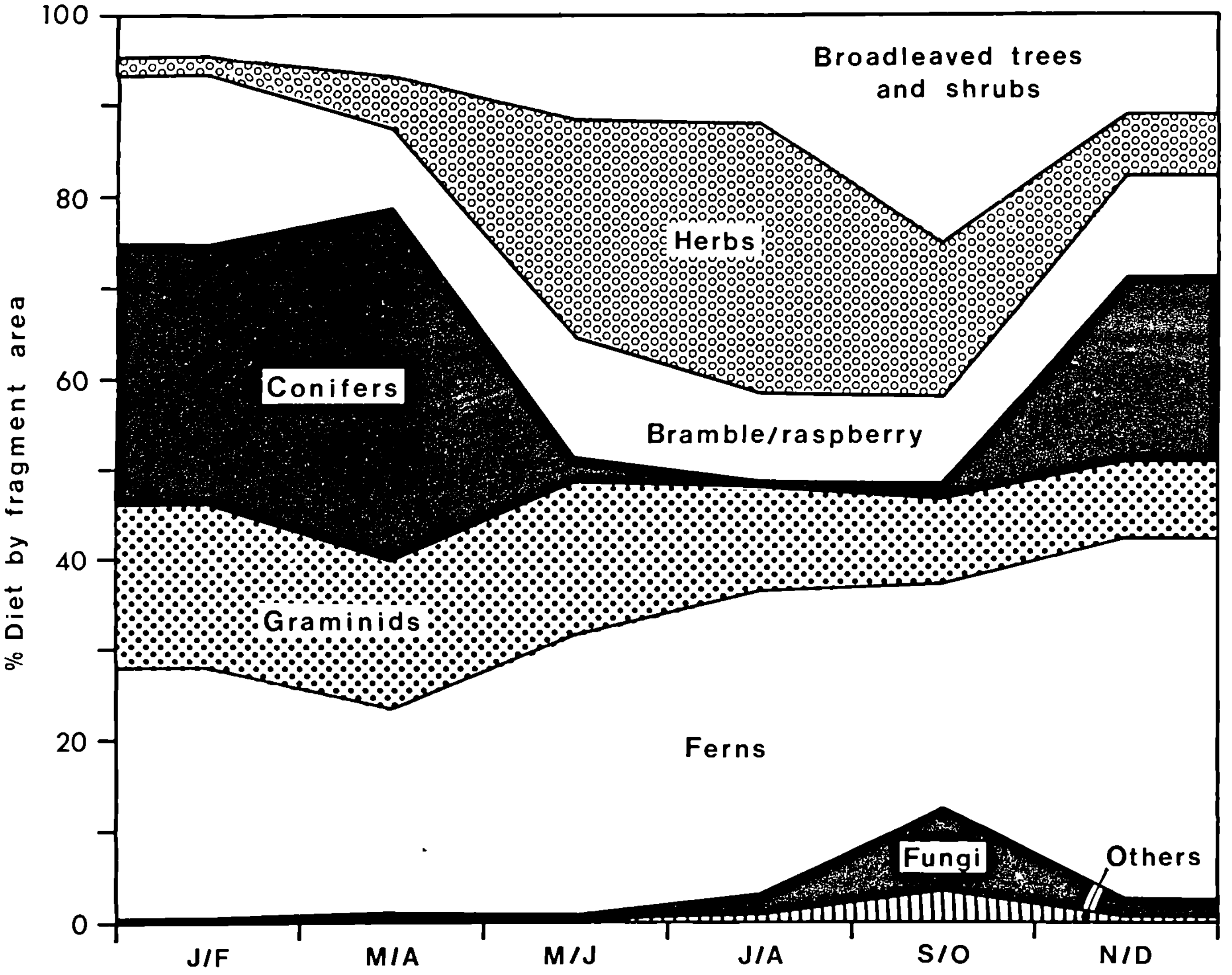
\# excluding bramble and raspberry
t less than 0.05%

Table 5.4 Shannon indices of roe deer diet diversity, based on 376 faecal samples collected between June 1986 and February 1988.

Month	**n**	**H'**
J/F	61	1.581
M/A	63	1.611
M/J	65	1.658
J/A	63	1.609
S/O	63	1.840
N/D	61	1.671
Annual	376	1.835

$H' = -\Sigma p_i \ln p_i$ (Magurran, 1988)

Figure 5.3 Seasonal variation in the diet of roe deer, based on 376 faecal samples collected between June 1986 and February 1988. The dietary proportions are percentages based on the areas of plant fragments.


Broadleaved trees and shrubs
Herbs
Conifers
Bramble/raspberry
Graminids
Ferns
Fungi
Others
% Diet by fragment area
100
80
60
40
20
0
J/F
M/A
M/J
J/A
S/O
N/D

muntjac had significantly more Scots pine, other pines and nut producing broadleaved trees and significantly less Corsican pine. In the ground vegetation, sites with muntjac had significantly more herb and less graminid. Bramble and raspberry were also more abundant at roe deer sites with muntjac.

Mann-Whitney U tests were used to compare roe deer diets from sites with and without muntjac and the results are given in Table 5.6. Broadleaved trees and shrubs, bramble and raspberry, and herbs were significantly more important in roe deer diet from sites with muntjac at most times of year. In addition, on an annual basis, fungi and other foods were significantly more important in the diet from these sites. Ferns were significantly more important at all times of year and graminids were significantly more important on an annual basis in roe deer diet from sites without muntjac.

Diet similarity between sites with and without muntjac, as suggested by the number of plant groups showing significant differences, was greatest during January/February and least during November/December. This is reflected in the diet overlap indices given in Table 5.7. Overlap was highest between January and April and lower during the rest of the year. Diversity indices showed that diet diversity was consistently higher at sites with sympatric muntjac (Table 5.8).

Mann-Whitney U tests were also used to compare muntjac diet with roe deer diet from sites with sympatric muntjac and the results are given in Table 5.9. There were few consistent differences between the two diets. Graminids between November and April, and bramble and raspberry between May and August, were significantly more important in muntjac diet. On an annual basis, broadleaved trees and shrubs, bramble and raspberry and graminids were all significantly more important in muntjac diet, while conifers were significantly more important in roe deer diet.

Diet similarity between the two species, as suggested by the number of plant groups showing significant differences, was lowest during January/February and relatively high during the rest of the year. Diet overlap indices (Table 5.10) also showed a lower overlap during January/February and a consistently higher overlap during the rest of the year. The overlap between muntjac diet and roe deer diet from all seven sites was also lowest during January/February and higher during the rest of the year (Table 5.11).

The multiple discriminant analysis (MDA) between muntjac diet, roe deer diet from sites with muntjac and roe deer diet from sites without muntjac for January/February,

Table 5.5 Vegetation characteristics for roe deer diet collection sites with and without muntjac. The figures are overall percentage cover, corrected for differing sub-compartment size, taken from the vegetation survey described in Chapter 2. The number of sub-compartments used in the analysis is given.

Tree canopy	**With muntjac**	**Without muntjac**	
	n=28	n=40	
% Scots pine	25.47	12.00	***
% Corsican pine	53.39	83.11	***
% Other pines	7.71	0.41	***
% Nut producing broadleaved trees	4.67	0.16	***
% Non-nut producing broadleaved trees	7.83	4.33	
Ground vegetation			
% Graminids	40.75	62.69	**
% Herbs	19.94	10.74	*
% Bushes	4.67	2.27	
% Bracken	7.58	6.77	
% Bare ground	27.06	17.52	

*** $p<0.001$, χ^2 test
** $p<0.01$, " "
* $p<0.05$, " "

Table 5.6 Mann-Whitney U tests to compare roe deer diet from sites with and without muntjac, based on 376 faecal samples collected between June 1986 and February 1988.

Plant group	J/F	M/A	M/J	J/A	S/O	N/D	Annual
Broadleaved# trees & shrubs		**	***	*	**	***	***
Bramble/Raspberry	***	***		**		***	***
Conifers							
Herbs		***	**	**	*	***	***
Graminids				*			**
Ferns	*	**	***	***	***	***	***
Fungi				**			*
Other foods						**	*
No. of samples (with muntjac)	25	25	28	28	28	25	159
No. of samples (without muntjac)	36	38	37	35	35	36	217

\# excluding bramble and raspberry
*** $p<0.001$, Mann-Whitney U test
** $p<0.01$, " " " "
* $p<0.05$, " " " "

Underlined probabilities, plant group significantly more important from sites with muntjac.

Table 5.7 Pianka (1973) roe deer diet overlap indices for sites with and without muntjac, based on 376 faecal samples collected between June 1986 and February 1988.

Month	**With muntjac**	**Without muntjac**	**Overlap**
	n	**n**	
J/F	25	36	0.831
M/A	25	38	0.883
M/J	28	37	0.683
J/A	28	35	0.744
S/O	28	35	0.705
N/D	25	36	0.773
Annual	159	217	0.765

$$\text{Overlap}_{ij} = \frac{\Sigma\, p_{ia}\, p_{ja}}{\sqrt{[(\Sigma\, p_{ia}^2)\,(\Sigma\, p_{ja}^2)]}}$$

Table 5.8 Shannon indices of roe deer diet diversity for sites with and without muntjac, based on 376 faecal samples collected between June 1986 and February 1988.

Month	**With muntjac**		**Without muntjac**	
	n	**H'**	**n**	**H'**
J/F	25	1.559	36	1.511
M/A	25	1.755	38	1.397
M/J	28	1.663	37	1.502
J/A	28	1.701	35	1.400
S/O	28	1.774	35	1.760
N/D	25	1.814	36	1.419
Annual	159	1.910	217	1.672

$H' = -\Sigma\, p_i \ln p_i$ (Magurran, 1988)

Table 5.9 Mann-Whitney U tests to compare muntjac diet with roe deer diet from sites with muntjac, based on 320 faecal samples collected between June 1986 and February 1988.

Plant group	J/F	M/A	M/J	J/A	S/O	N/D	Annual
Broadleaved# trees & shrubs	$\underline{*}$						$\underline{*}$
Bramble/Raspberry			$\underline{*}$	$\underline{*}$			$\underline{*}$
Conifers	***						**
Herbs			*		$\underline{*}$		
Graminids	$\underline{***}$	$\underline{*}$				$\underline{**}$	$\underline{***}$
Ferns					$\underline{*}$		
Fungi		*					
Other foods	$\underline{***}$						
No. of samples (with muntjac)	27	27	25	29	27	26	161
No. of samples (without muntjac)	25	25	28	28	28	25	159

#	excluding bramble and raspberry
***	$p<0.001$, Mann-Whitney U test
**	$p<0.01$, " " " "
*	$p<0.05$, " " " "

Underlined probabilities, plant group significantly more important in muntjac diet.

Table 5.10 Pianka (1973) diet overlap indices between muntjac and roe deer from sites with muntjac, based on 320 faecal samples collected between June 1986 and February 1988.

Month	Muntjac	Roe deer with muntjac	Overlap
	n	n	
J/F	27	25	0.757
M/A	27	25	0.902
M/J	25	28	0.907
J/A	29	28	0.958
S/O	27	28	0.973
N/D	26	25	0.927
Annual	161	159	0.968

Table 5.11 Pianka (1973) diet overlap indices between muntjac and roe deer from sites with and without muntjac, based on 537 faecal samples collected between June 1986 and February 1988.

Month	Muntjac	Roe deer	Overlap
	n	n	
J/F	27	61	0.741
M/A	27	63	0.783
M/J	25	65	0.842
J/A	29	63	0.822
S/O	27	63	0.937
N/D	26	61	0.822
Annual	161	376	0.858

$$\text{Overlap}_{ij} = \frac{\Sigma\, p_{ia}\, p_{ja}}{\sqrt{[(\Sigma\, p_{ia}^2)\,(\Sigma\, p_{ja}^2)]}}$$

showed that within diet variance-covariance matrices were significantly different (Box's M test, F=5.492, $p<0.001$). Therefore, the multivariate representations of the three diets differed significantly in size or shape. However, since the discriminant functions (DFs) produced were related to the dietary plant groups in a manner consistent with the previous analyses, the analysis was continued (Green, 1971; Dueser & Shugart, 1979).

The two DFs produced were both significant ($p<0.001$). Correlation coefficients between the dietary plant groups and the two DFs, which since a three group discriminant analysis only produces two DFs, together accounted for 100% of the total discriminating information available, are given in Table 5.12. The pattern of covariance on DFI described a gradient from diets dominated by graminids, mosses and broadleaved trees and shrubs at one extreme, to diets dominated by conifers at the other extreme. DFII described a gradient from diets dominated by bramble and raspberry at one extreme, to diets dominated by ferns, herbs and fungi at the other. Therefore, both DF axes described gradients from higher quality to lower quality diets.

The position of the diet centroids on the two DF axes are shown in Figure 5.4. Along DFI, muntjac diet was placed towards the graminid and broadleaved tree and shrub end of the gradient, while both roe deer diets were placed at similar positions towards the conifer dominated end of the gradient. DFII separated the two roe deer diets, placing the sites with muntjac towards the bramble and raspberry end of the gradient and the sites without muntjac towards the fern dominated end of the gradient. Muntjac diet was placed midway along this gradient. These positions were consistent with the previous analyses. The comparison between muntjac diet and roe deer diet from sites with muntjac showed that broadleaved trees and shrubs and graminids were more important in muntjac diet and that conifers were more important in roe deer diet, and DFI described this relationship. The comparison between roe deer diet from sites with and without muntjac had shown that bramble and raspberry were more important in the diet from sites with muntjac and that ferns were more important in the diet from sites without muntjac, and DFII described this relationship.

The F-statistics given in Table 5.13 show that all three diets occupied significantly different positions in discriminant space and also show that the two roe deer diets were more closely related than was muntjac diet to either roe deer diet. This confirms the relationship shown above, where the two roe deer diets had a high dietary overlap index during January/February, whereas the muntjac and roe deer diets showed a low dietary overlap.

Table 5.12 Multiple discriminant analysis between the diets of muntjac, roe deer from sites with muntjac and roe deer from sites without muntjac for January/February, based on 88 faecal samples collected during 1987 and 1988. Correlation coefficients of dietary plant groups with the two discriminant functions used to separate the three diets.

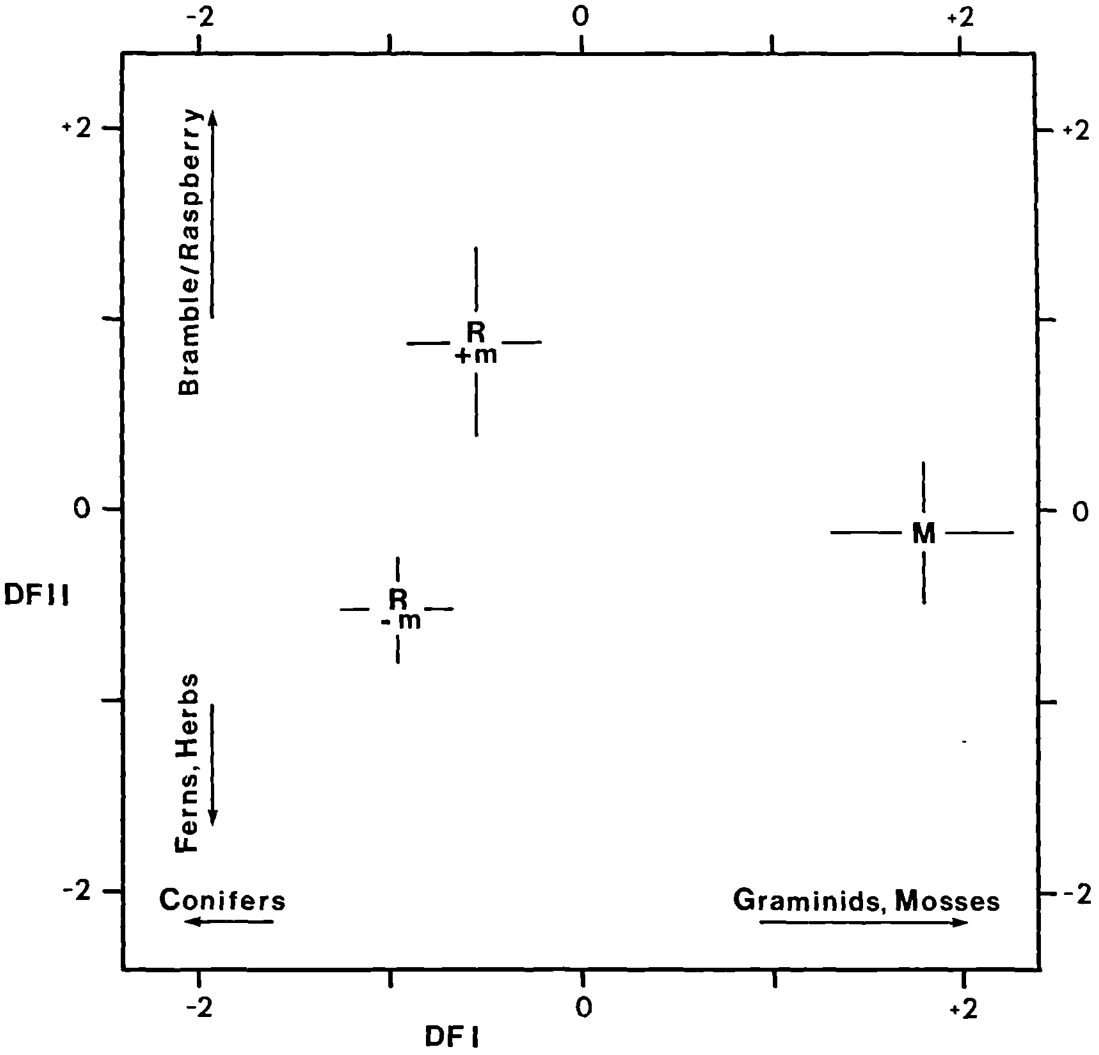
Plant group	**Function I**	**Function II**
Other foods	0.555	
Graminids	0.467	
Conifers	-0.413	
Broadleaved trees & shrubs	0.351	
Bramble/Raspberry		0.853
Fern		-0.382
Herb		-0.234
Fungi		-0.229
%EV	**81.0**	**19.0**
χ^2	**99.2 *****	**24.5 *****

Table 5.13 Multiple discriminant analysis between the diets of muntjac, roe deer from sites with muntjac and roe deer from sites without muntjac for January/February, based on 88 faecal samples collected during 1987 and 1988. F matrix for testing the difference between diet means along the two discriminant functions (each F statistic has 7 and 79 degrees of freedom). Also given are the percentage of diet samples correctly classified by the discriminant function model.

	Muntjac	**Roe deer with muntjac**	**Roe deer without muntjac**
Roe deer with muntjac	11.124 ***	-	
Roe deer without muntjac	15.690 ***	4.173 ***	-
% correctly classified	81.5	68.0	83.3

Overall correct classification = 78.4%

Figure 5.4 Multiple discriminant analysis between the diets of muntjac (M), roe deer from sites with muntjac (R +m) and roe deer from sites without muntjac (R -m) for January/February, based on 88 faecal samples collected during 1987 and 1988. Group centroids (± 2 S.E.) are plotted on the two discriminant function axes, which have been given biological interpretation as indicated.


-2
0
+2
+2
+2
0
0
DFII
-2
-2
Bramble/Raspberry
Ferns, Herbs
Conifers
Graminids, Mosses
R
+m
R
-m
M
-2
0
+2
DF I

The performance of the discriminant function model in correctly classifying cases was good; overall 78% of cases were correctly classified. The model had most difficulty in distinguishing the diet of roe deer from sites with muntjac from the other two diets.

The MDA between muntjac diet, roe deer diet from sites with muntjac and roe deer diet from sites without muntjac for September/October, again showed that within diet variance-covariance matrices differed significantly (Box's M test, F=2.724, p<0.001). However, the DFs were related to the dietary plant groups in a manner consistent with the previous analyses, and so the analysis was continued.

Only the first DF was significant (p<0.001) and emphasis should be placed on diet separation along this axis. However, the second function was retained, since an ecologically interpretable separation occurred along that axis (Green, 1971). Correlation coefficients between dietary plant groups and the two DFs are given in Table 5.14. DFI described a gradient from diets dominated by ferns at one extreme, to diets dominated by broadleaved trees and shrubs at the other extreme. Therefore DFI described a gradient from high quality to low quality diets. DFII described a gradient from diets dominated by herbs at one extreme, to diets dominated by fungi at the other.

The position of the diet centroids on the two DF axes are shown in Figure 5.5 for September/October. Along DFI, roe deer diet from sites without muntjac was placed at the fern dominated end of the gradient and roe deer diet from sites with muntjac was placed at the broadleaved tree and shrub end of the gradient. Muntjac diet was also placed towards the broadleaved tree and shrub end of the gradient. DFII separated muntjac diet from the two roe deer diets, placing it towards the herb dominated end of the gradient. These positions were also consistent with the previous analyses. The comparison between the two roe deer diets showed that broadleaved trees and shrubs were more important in the diet from sites with muntjac and that ferns were more important in the diet from sites without muntjac. Therefore, DFI described this separation. The comparison between muntjac and roe deer diet from sites with muntjac showed that herbs were more important in muntjac diet, and DFII described this relationship.

The F-statistics given in Table 5.15 show that the three diets no longer occupied significantly different positions in discriminant space; muntjac diet was now closely related to roe deer diet from sites with muntjac, whereas the two roe deer diets were most dissimilar. This confirmed the change from high overlap between the two roe deer diets

Table 5.14 Multiple discriminant analysis between the diets of muntjac, roe deer from sites with muntjac and roe deer from sites without muntjac for September/October, based on 90 faecal samples collected during 1986 and 1987. Correlation coefficients of dietary plant groups with the two discriminant functions used to separate the three diets.

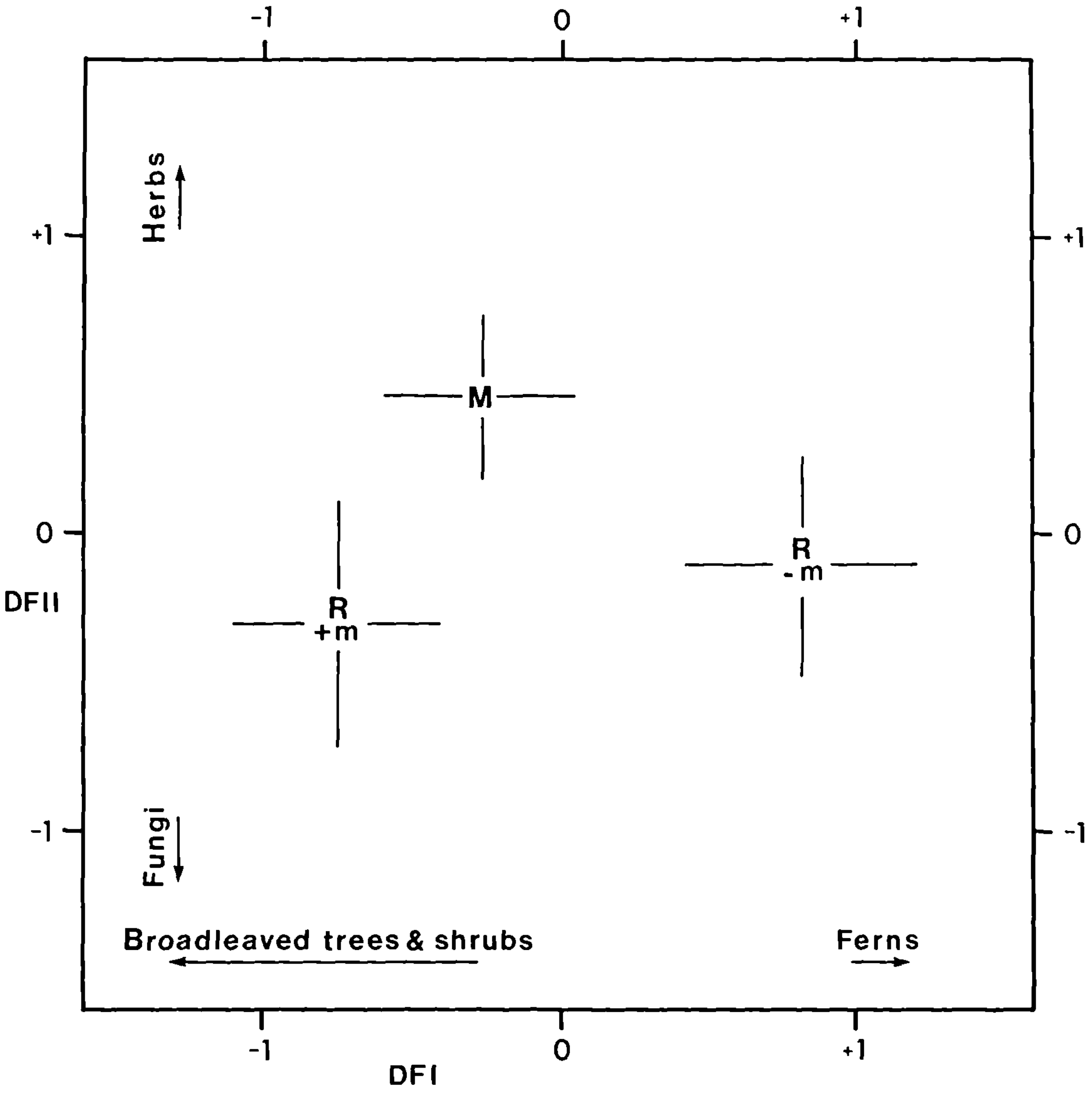
Plant group	Function I		Function II	
Ferns	0.782			
Broadleaved trees & shrubs	-0.602			
Graminids	0.071			
Herbs			0.735	
Fungi			-0.581	
Other foods			-0.304	
Conifers			0.190	
Bramble/Raspberry			-0.081	
%EV	82.2		17.8	
χ^2	40.7	***	8.2	n.s.

Table 5.15 Multiple discriminant analysis between the diets of muntjac, roe deer from sites with muntjac and roe deer from sites without muntjac for September/October, based on 90 faecal samples collected during 1986 and 1987. F matrix for testing the difference between diet means along the two discriminant functions (each F statistic has 6 and 82 degrees of freedom). Also given are the percentage of diet samples correctly classified by the discriminant function model.

	Muntjac	Roe deer with muntjac	Roe deer without muntjac
Roe deer with muntjac	1.784 n.s.	-	
Roe deer without muntjac	3.577 **	6.073 ***	-
% correctly classified	55.6	50.0	54.3

Overall correct classification = 53.3%

Figure 5.5 Multiple discriminant analysis between the diets of muntjac (M), roe deer from sites with muntjac (R +m) and roe deer from sites without muntjac (R -m) for September/October, based on 90 faecal samples collected during 1986 and 1987. Group centroids (± 2 S.E.) are plotted on the two discriminant function axes, which have been given biological interpretation as indicated.


-1
0
+1
Herbs
+1
+1
M
0
0
R
-m
R
+m
DFII
-1
-1
Fungi
Broadleaved trees & shrubs
Ferns
-1
0
+1
DFI

and low overlap between muntjac and roe deer diets during January/February, to high overlap between muntjac diet and roe deer diet from sites with muntjac and low overlap between the two roe deer diets during September/October.

The performance of the DF model in correctly classifying cases was poorer; overall 53% of cases were correctly classified. This reflected the decrease in ecological distance between the three diets indicated by the smaller F-statistics.

5.4 DISCUSSION

Digestibility was determined for the major forage species, using an in vitro pepsin/cellulase digestion (Jones & Hayward, 1975). However, the diet was not corrected using these digestion coefficients because the results produced inconsistent seasonal trends, even though the samples were collected from the same sites, and often the same bush or tree in consecutive months. This demonstrates the difficulty in selecting plant parts of the same quality as those ingested by foraging deer. This, together with problems such as digestibility altering with the proportion of a species in the diet (Milne *et al.*, 1978) and the failure of digestibility coefficients to adequately correct faecal diets (Holechek & Valdez, 1985), makes digestibility coefficients unattractive as correction factors for faecal analysis. A more suitable technique may be to correct for differing ratios of identifiable to unidentifiable fragments (Barker, 1986b; Norbury, 1988).

The diets presented here, based on uncorrected faecal analysis, will contain biases. However, since the diets of the two species are similar, any biases should operate in the same direction and should not adversely affect comparisons between diets. In the diets presented, grasses, ferns, conifers and mosses are likely to be overestimated, while broadleaved trees and shrubs, bramble and raspberry, herbs, fungi, fruit and nuts and root crops are likely to be underestimated. Fruit and nuts and root crops are a particular problem with faecal analysis. Muntjac and roe deer rumen contents from the King's Forest show that acorns and sugar beet in particular, are taken in significant quantities during autumn (P. Forde, *unpubl.*; N.G. Chapman, *pers. comm.*), yet they are rarely detected in the faeces.

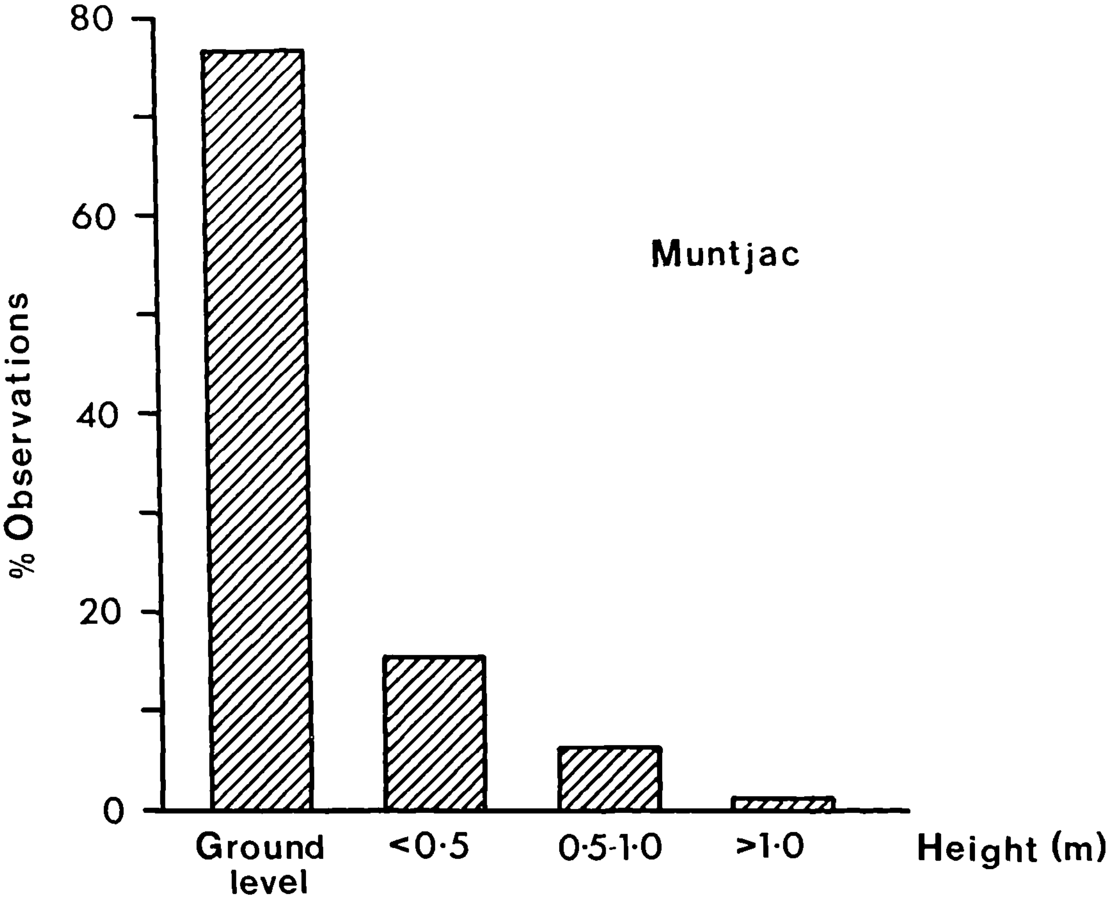
Several changes are apparent in muntjac diet compared to the previous study, which was based on samples collected over the period October 1983 to September 1985 (Harris & Forde, 1986). The importance of ivy, bramble and raspberry, fungi and fruit and nuts has reduced, whereas herbs and graminids have increased in importance. Some of these changes may be due to different collection sites and changes in deer behaviour, such as fewer deer visiting the copses where ivy is abundant, although changes in the structure of the ground vegetation may also have occurred.

Roe deer diet in the King's Forest is similar to that in other forests in southern England (Hosey, 1981; Hearney & Jennings, 1983; Jackson, 1980; Johnson, 1984), although the importance of bramble is lower and ferns higher compared to previous studies. Only the studies by Loudon (1979) and Hinge (1986) in upland British forests have found ferns to be of any importance in roe deer diet. Perhaps the King's Forest is unusual compared to other lowland forests in having a high abundance of *Dryopteris* spp., which are preferred over bracken.

The differences between roe deer diet in the presence and absence of muntjac were entirely consistent with the different vegetation structure of the two sets of sites. Areas of the forest where muntjac were absent are dominated by brown earth soils, where the ground vegetation is less diverse and contains a low abundance of herbs and bushes and a higher abundance of graminids and ferns (Harris & Forde, *in prep.*).

Differences between muntjac and roe deer diet from sympatric sites cannot be explained by differences in available vegetation. Possible causes of the observed dietary differences may be different anatomical or physiological constraints (Hofmann, 1985; Kay, 1986; Kay, 1987) or the effects of competition. Dietary differences are most pronounced during January and February, when food resources are likely to be least abundant, with muntjac diet containing more graminids, mosses and broadleaved trees and shrubs, and roe deer diet more conifers. On the basis of differences in body size and therefore physiological constraints, muntjac diet should contain more high quality, easily digestible food than roe deer diet (Hanley & Hanley, 1982; Hofmann, 1985; Kay, 1987), although gut anatomy suggests that both species should be concentrate selectors (Harding, 1986; Kay, 1987). The presence of more conifer in roe deer diet tends to confirm this hypothesis, yet the presence of more graminid in muntjac diet goes against it. Observations show that there is some separation of feeding heights (Figure 5.6), with muntjac tending to feed more often at ground level (P.Forde, *unpubl.*). However, this does not fully explain the observed differences in diet. Muntjac, feeding more often at ground level, would be expected to ingest more graminids and mosses, yet much of conifer taken by roe deer is from fallen branches, which are also at ground level. The most likely explanation for the dietary differences is a competitive effect, with roe deer ingesting poorer quality forage, though this is offset to some extent by an ability to forage at higher levels. However, in spite of this,

Figure 5.6 Feeding height observations from forest habitats for muntjac and roe deer, based on 78 observations of muntjac and 89 observations of roe deer between April 1986 and April 1988. Feeding height was assessed visually into one of the four categories.


80
60
40
20
0
% Observations
Muntjac
Ground level
<0·5
0·5-1·0
>1·0
Height (m)


60
40
20
0
% Observations
Roe
Ground level
<0·5
0·5-1·0
>1·0
Height (m)

sympatric roe deer still had a higher quality diet than allopatric roe deer.

Differences between sympatric muntjac and roe deer diets decreased during the summer months and the MDA for September/October showed that there was no significant difference between the two diets. Therefore, this study has shown that during winter, when food resources are less abundant and of lower quality, sympatric muntjac and roe deer show a lower dietary overlap than during periods of resource abundance. This is consistent with theories suggesting that species should forage most selectively when food supply is limited, thereby minimising competition (Hobbs *et al.*, 1983).

CHAPTER SIX: GENERAL DISCUSSION

This chapter aims to answer three main questions:-

1. How does the ecology and social organisation of muntjac found in this study compare with other studies of morphologically conservative deer (MCD) and other ungulates of similar body weight?

2. How does the ecology and social organisation of roe deer found in this study and other studies compare with the MCD, and are there sound ecological reasons for not including roe deer with the MCD?

3. What is the multidimensional niche overlap between muntjac and roe deer in the King's Forest, what is the potential for competition between the two species, and what evidence is there that competition is occurring or has occurred.

MCD are concentrate selectors, lead a solitary but social life, are probably non-territorial yet sedentary on a limited home range, are polygamous, have a litter size of one, a gestation of five to seven months and a post-partum oestrus (Barrette, 1987). The ecology and social organisation of Reeves' muntjac seems to fit well with these overall characteristics. In this study, muntjac home range size showed no significant seasonal changes, and core areas did not shift seasonally or from year to year. The social organisation consisted of groups of adult does with overlapping ranges; buck ranges overlapped those of does, but were relatively exclusive from those of other adult bucks. Although home ranges overlapped, 76% of sightings were of solitary individuals (N. Chapman & D. Blakely, *pers. comm.*). Dietary studies showed typical characteristics of a concentrate selector. Muntjac have a litter size of one, a gestation of seven months and a post-partum oestrus.

African antelopes of comparable body size have this same type of social organisation, which corresponds to Leuthold's social organisation (SO)-type 3a or SO-type 4 (Jarman, 1974; Leuthold, 1977). In SO-type 3a species, the social unit is a single adult animal, although the females may be accompanied by immature offspring. Adults of the same sex live in exclusive home ranges, which overlap with those of the opposite sex. The home ranges, particularly of the males, may be defended as territories. The common duiker *Sylvicapra grimmia* (body weight 10-18kg) is a typical SO-type 3a species, where relatively exclusive male territories overlap with those of several females. Although individuals occupy overlapping ranges, Dunbar & Dunbar (1979) found that 86% of sightings were of solitary individuals.

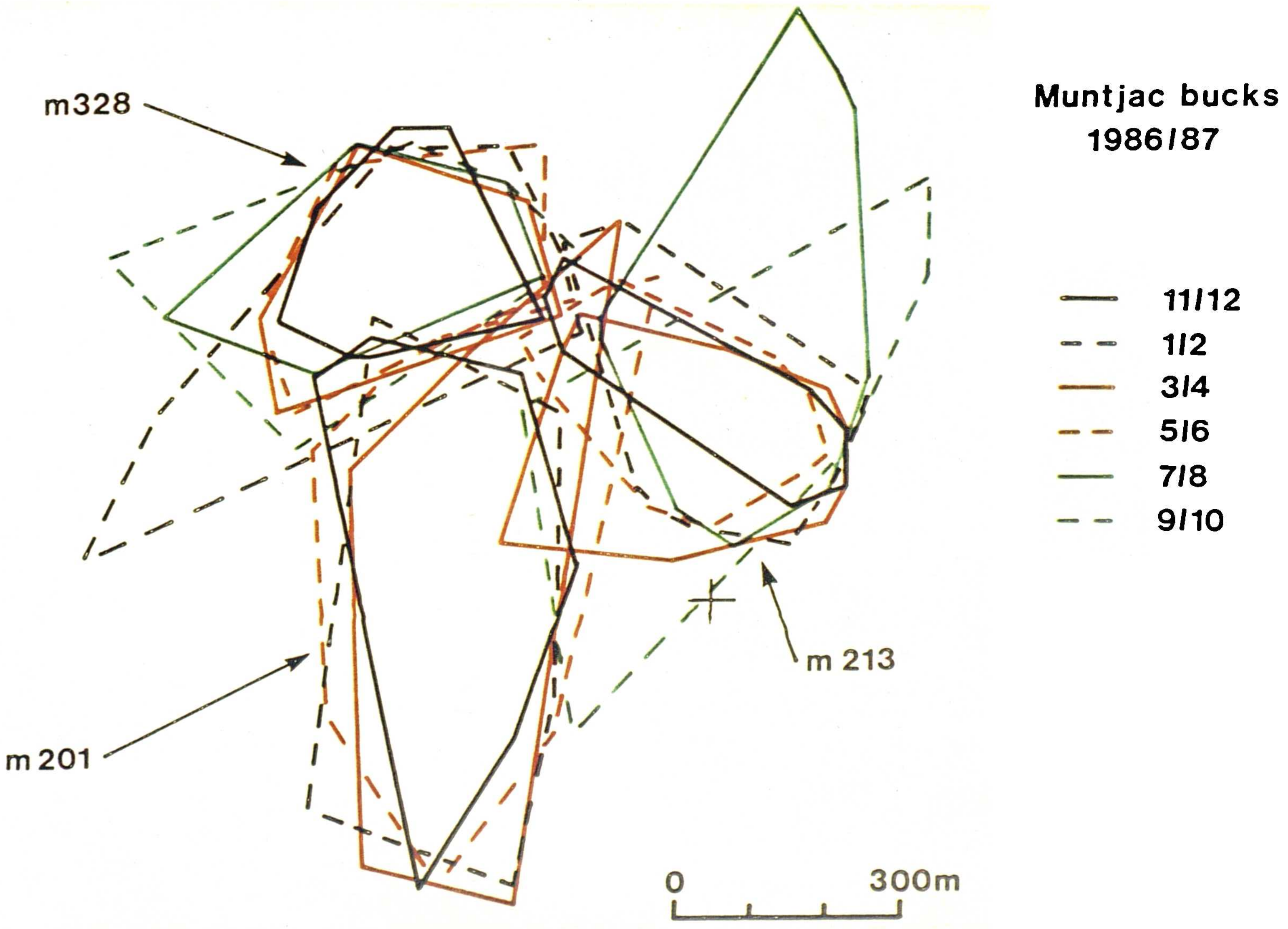
The SO-type 3a system adequately describes the social organisation of muntjac at low density. However, at high density, the female muntjac social unit consists of small groups of adults and their offspring, which is closer to the SO-type 4 system. This type of social organisation has been described for southern reedbuck *Redunca arundinum* (body weight 50-80kg) and gerenuk *Litocranius walleri* (body weight 29-52kg) (Leuthold, 1977). Only the male, which is solitary, defends the home range as a territory. This largely coincides with the home range of a group of females, although the male territory may overlap, at least partially, with several groups of females.

From their studies of African ungulates, Jarman (1974) and Leuthold (1977) both suggest that small ungulates, in particular males, defend home ranges as territories. Jarman (1974) proposed that these should be defended both for access to resources and to females. However, Barrette (1987) found that the few detailed studies of MCD suggested that males were probably not territorial (Dubost, 1978; Feer, 1979), although home ranges were stable seasonally. Home ranges will only be defended as territories when the benefits gained outweigh the costs of defence (Brown, 1964; Mitani & Rodman, 1979). Barrette (1987) argued that the home ranges of small ruminants should not be defensible, because they contain widely scattered and rare food items. However, the costs of defending small stable home ranges as territories may be less than expected, because neighbouring individuals will be known intimately and permanent scent marks can be used to mark territorial boundaries. Also, the benefits gained from territorial defence may be greater than would be predicted, due to an intimate knowledge of seasonally changing resource patterns.

Although the home range size of individual adult muntjac bucks in the King's Forest changed seasonally, range boundaries between contiguous bucks were stable; range expansions or contractions were into areas not occupied by resident adult bucks (Figure 6.1). This, together with the exclusive nature of buck home ranges, suggests that these may be defended as territories.

An alternative interpretation of the data is that males were only defending the core areas of their home ranges as territories. These were stable seasonally and overlapped with the doe core areas. Defence of these core areas would ensure a supply of high quality resources, and access to oestrous females. Although fights between muntjac bucks were rarely observed, examination of carcasses showed that canine wounds were common and

Figure 6.1 Minimum convex polygon ranges of three adult *muntjac bucks* (*m201, m213*, and m328) on part of the study area in successive bimonthly periods during 1986 and 1987.


Muntjac bucks
1986/87
11/12
1/2
3/4
5/6
7/8
9/10
m328
m201
m 213
0
300m

older bucks frequently had broken canines (N. Chapman, *pers. comm.*). However, it was unclear whether fights between bucks were disputes over territorial boundaries or over access to oestrous females (Barrette, 1977a&b). Bucks remain in close attendance with oestrous females and although up to four different bucks have been observed with the same oestrous female over a twenty-four hour period (N. Chapman, *pers. comm.*), it is unclear whether these changeovers are the result of buck/buck interactions, or due to the doe moving into another buck's territory. Therefore, muntjac bucks certainly defend oestrous females and probably also core areas. They may also defend the entire home range as a territory. Hence, they are defending both resource based territories and territories that give access to oestrous females. There was no evidence of antagonistic adult doe/doe interactions; core areas of groups of adult does were centred on patches of high quality habitat, and the availability of these probably determined the spacing of doe home ranges and also the position of buck core areas.

When Barrette (1987) reviewed the ecology and social organisation of the MCD, she included species up to a body weight of 25kg. Roe deer were excluded for rather arbitrary reasons, although on the basis of body weight they could have been included. The reasons given were that roe deer had a wide geographical range and the best comparisons could be made within the species itself and also that so much more was known about roe deer that it would be difficult to compare it with the other species in a balanced manner.

Like the MCD, roe deer are concentrate selectors and have a polygamous mating system. However, in contrast, roe deer are strongly territorial, although only during the breeding season (Bramley, 1970), are not sedentary, frequently have twins and do not have a post-partum oestrus. The social organisation found in this study agrees with that from other studies; adult buck and doe ranges overlapped, and some doe ranges were shared with other adult does. Sightings showed that roe deer were less solitary than muntjac and stable family groups were formed particularly during winter (P. Forde, *pers. obs.*). This type of social organisation does not fit particularly well into Leuthold's (1977) classification. However, depending on the time of year and the number of does in the female social unit, roe deer are probably closest to the SO-type 3a or SO-type 4 system.

During the breeding season, roe bucks defend the entire home range as a territory. These territories contain resources that females require, and does maintain stable home ranges within buck territories for several months. However, mating occurs on a small rutting stand within the territory; this has no obvious resource value and the female only visits it to be mated. Thus, in contrast to muntjac, where the buck defends an oestrous female, the roe buck defends a area of ground, to which the oestrous female comes to be mated.

Therefore, although on the basis of body weight, roe deer ought to be included with the MCD, their ecology and behaviour sets them apart from this group. Presumably, roe deer have exceeded some upper critical body size for concentrate selectors, above which the food resources required throughout the year cannot be viably defended. However, an alternative explanation is that territorial defence in small ungulates arises from the defence of oestrous females rather than the defence of food resources, and the lack of territorial behaviour in roe deer outside the breeding season is a consequence of seasonal breeding.

From the above, it is clear that roe deer lie somewhere between the MCD and the larger deer in their social organisation and reproductive strategy. Depending on the time of year, roe deer may be solitary like muntjac, or grouped together into family units, like some of the larger deer. Roe deer have a gestation period of five months, similar to most MCD, but the interval between conception and parturition is greatly extended by a period of delayed implantation. There is no post-partum oestrus, although the rut starts in mid-July, six to eight weeks post-partum. This compares with approximately three months post-partum in the larger red and fallow deer, which have a gestation period of eight months and no period of delayed implantation. Thus, although muntjac and roe deer are close together on an absolute scale of body weight, they represent different functional positions, a factor that is important when considering potential competitive effects.

Schoener (1974) suggests that the three most important niche axes are those representing habitat, diet and the timing of activity. To represent resource utilization functions (RUFs) along habitat and dietary niche axes, frequency distributions of discriminant function scores along DFI from the habitat and dietary MDAs in Chapters Two and Five were used. Since MDA aims to achieve maximum separation between species, niche width may be overestimated, but the area of overlap along the DF axis will correctly represent niche overlap. The ratio of daytime to night-time activity was used to represent resource utilization along an activity niche axis. The relative positions of muntjac sites, roe deer sites with muntjac and roe deer sites without muntjac along these three niche axes are shown in Figure 6.2 for January/February and Figure 6.3 for September/October.

During January/February, in areas of the forest with sympatric muntjac and roe deer, the frequency distributions along the habitat niche axis showed that sympatric muntjac and roe deer were selecting very similar habitats. In areas where muntjac were at

Figure 6.2 Three-dimensional niche separation of muntjac sites (M), roe deer sites with muntjac (R+m) and roe deer sites without muntjac (R-m), for January/February. The frequency distributions along the habitat and dietary niche axes are the distributions of discriminant scores along DFI from the multiple discriminant analyses in Chapters Two and Five. The arrows give the direction of the higher quality resources along the two DF axes. On the habitat axis, discriminant scores for roe deer sites with muntjac were defined as being from sub-compartments within compartments where the mean density of muntjac pellets was greater than 10 pellets per 10X4m plot between January and April 1986. The position along the activity niche axis represents the ratio of daytime to night-time activity from the routine radio-tracking data given in Tables 4.8 and 4.9. The cross-hatched area is the region of habitat and dietary overlap between sympatric muntjac and roe deer.

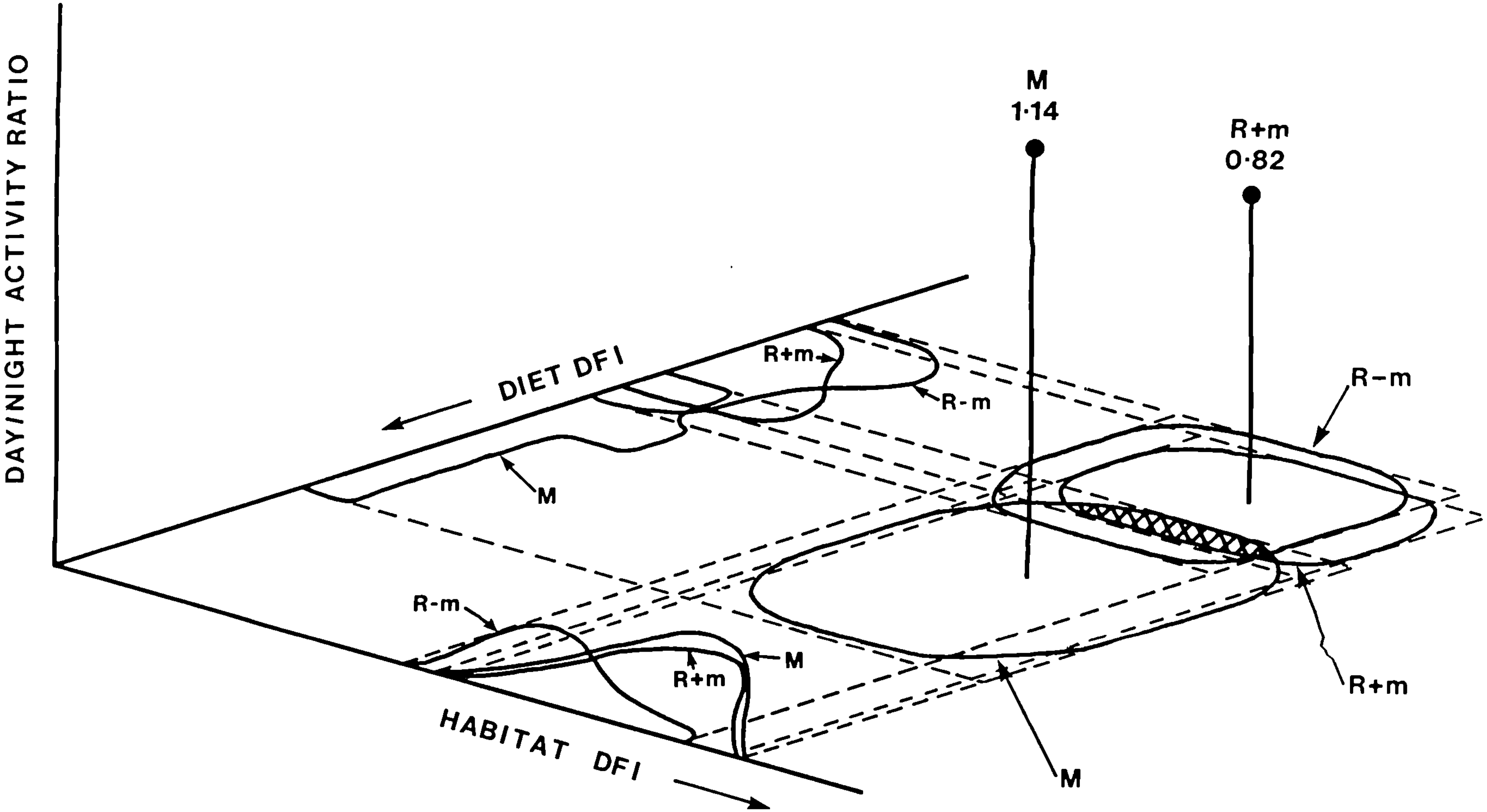
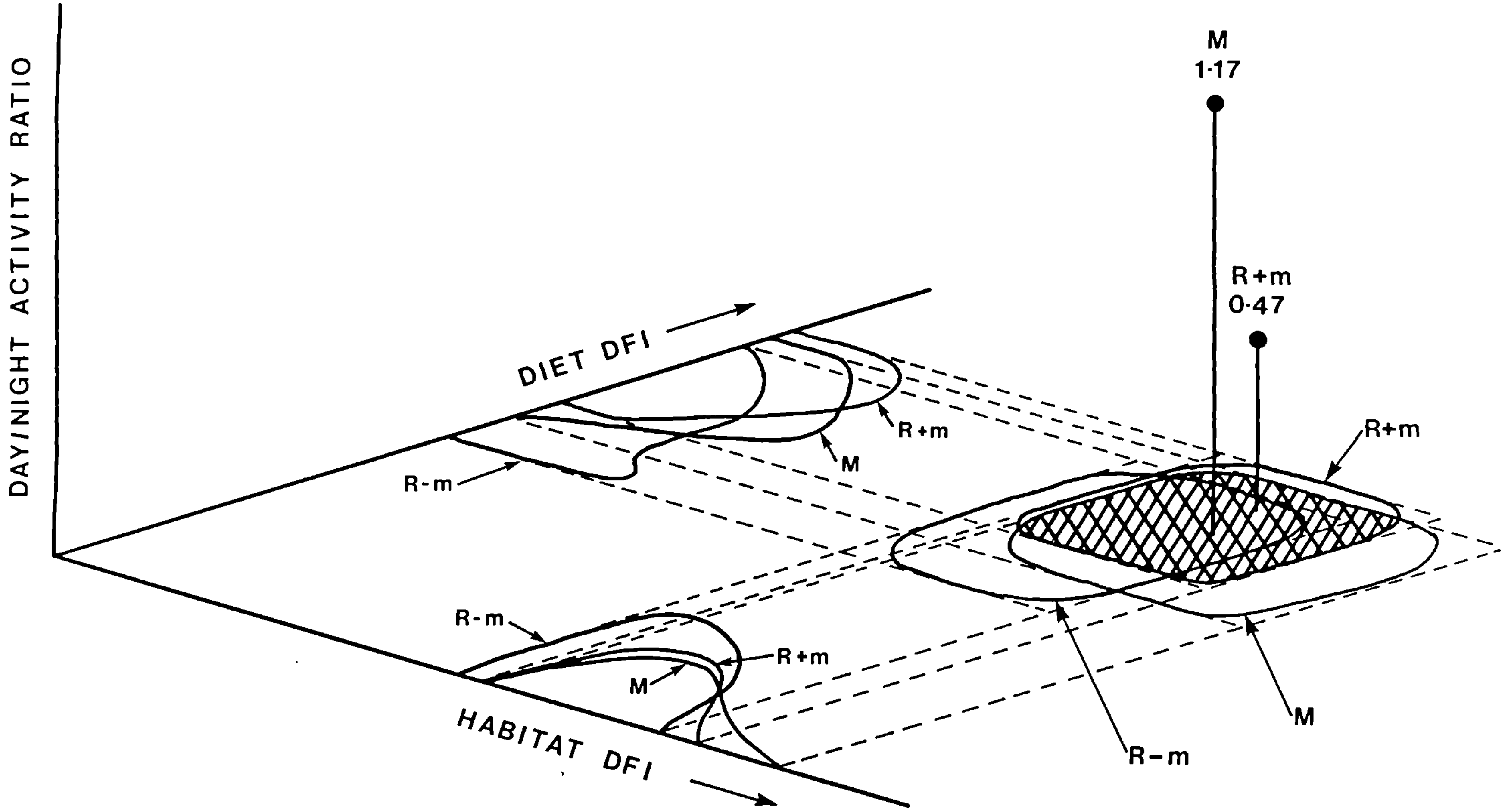

DAY/NIGHT ACTIVITY RATIO
M
1·14
R+m
0·82
DIET DFI
R+m
R-m
M
R-m
R+m
M
HABITAT DFI
R-m
R+m
M

Figure 6.3 Three-dimensional niche separation of muntjac sites (M), roe deer sites with muntjac (R+m) and roe deer sites without muntjac (R-m), for September/October. The frequency distributions along the habitat and dietary niche axes are the distributions of discriminant scores along DFI from the multiple discriminant analyses in Chapters Two and Five. The arrows give the direction of the higher quality resources along the two DF axes. On the habitat axis, discriminant scores for roe deer sites with muntjac were defined as being from sub-compartments within compartments where the mean density of muntjac pellets was greater than 10 pellets per 10X4m plot between January and April 1986. The position along the activity niche axis represents the ratio of daytime to night-time activity from the routine radio-tracking data given in Tables 4.8 and 4.9. The cross-hatched area is the region of habitat and dietary overlap between sympatric muntjac and roe deer.


M
1·17
R+m
0·47
DAY/NIGHT ACTIVITY RATIO
DIET DFI
R+m
M
R-m
R+m
M
R-m
R-m
R+m
M
HABITAT DFI
R–m
M

low density or absent, roe deer were utilising habitats of lower quality. Along the dietary niche axis, the frequency distributions of sympatric muntjac and roe deer diets overlapped little and this resulted in a small area of combined habitat and dietary overlap. Thus high niche overlap along one axis was cancelled by low niche overlap along another axis and therefore there was a low potential for exploitative competition between sympatric muntjac and roe deer, mainly achieved through the selection of different diets. There was also some temporal separation of activity; muntjac were more active during the day and roe deer were more active at night, and this further reduced the potential for competition through a reduction in interference competition.

During September/October there was a high level of overlap in habitat selection by muntjac, sympatric roe deer and allopatric roe deer, though again allopatric roe deer were utilising habitats of slightly lower quality. However, sympatric muntjac and roe deer diets now also overlapped and this resulted in a large area of combined habitat and dietary overlap. Thus during summer and autumn, there was a large potential for exploitative competition, although actual competition was unlikely, because resources are likely to be in excess of requirements during the summer months. In fact, because the pellet surveys were confined to forest habitats, the area of overlap will be overestimated for areas of the forest where deer have access to field habitats. The reduction in daytime activity shown by roe deer during September/October reflects an increase in the night-time use of field habitats, which will reduce the overlap along the habitat niche axis. The increased temporal separation of activity during autumn, when habitat and dietary overlap are highest, may be important in reducing interference competition during the day, when all the roe deer are within the forest.

Although the temporal separation of activity shown by sympatric muntjac and roe deer will reduce interference competition, is this temporal separation the result of competition or does it reflect different ecological strategies? Most studies have found a higher level of night-time activity in small ungulates, although this is always associated with the use of more open habitats at night (Dubost, 1978; Feer, 1979; Novellie *et al.*, 1984; Green, 1987). When small ungulates do not show diurnal range shifts, they are more active during the day (Harding, 1986). Thus, the temporal separation of activity shown by sympatric muntjac and roe deer in the King's Forest is probably due to roe deer using open habitats such as fields at night, and hence showing diurnal range shifts, while muntjac make less use of open habitats and do not show diurnal range shifts. Therefore this is probably not a competition induced effect. However, it is not possible to rule out the alternative hypothesis, that muntjac do not use open habitats at night to avoid interference competition with roe deer. Although greater daytime activity is not the normal temporal activity pattern for small ungulates, Harding (1986), who studied muntjac in the absence of roe deer, also found that muntjac were more active during the day. Perhaps, the higher daytime activity shown by muntjac in southern England is a response to the type of habitat occupied, which allows secure daytime foraging, although it may also be a response to the lack of natural diurnal predators.

Competition will arise when populations use the same resources and these are in limited supply (Pianka, 1983). Therefore, in a seasonal climate, the greatest potential for competition will occur during winter, when resources are least abundant. The discussions above show that trophic overlap between sympatric muntjac and roe deer in the King's Forest was low during January/February, mainly through the selection of different diets. However, from a comparative ecological study, it was not possible to distinguish between the alternative hypotheses that this low overlap was either the result of competition or that low overlap indicated a low potential for competition and that competition had not occurred (Pianka, 1983). To assess which of these hypotheses is correct and to determine whether competition is an important force in shaping this herbivore community, detailed manipulative experiments would be required.

Discussions of the potential for competition are further complicated by the influence of seasonal appetite cycles. These are well documented for roe deer in Poland (Drozdz & Osiecki, 1973; Drozdz, 1979) and for most species of temperate deer (Kay, 1985, 1987). It is likely that roe deer in Britain will also show such appetite cycles. If so, an alternative hypothesis to competition is that sympatric roe deer may be selecting a lower quality diet to reduce gut throughput times in combination with winter inappetence. Very little is known about seasonal cycles of physiology and appetite in MCD, although winter inappetence seems unlikely, certainly for muntjac does, which may be pregnant or lactating throughout the winter months. Studies have been initiated to assess seasonal physiological patterns in the King's Forest muntjac and roe deer, by examining seasonal changes in thyroid gland structure and rumen wall papillae. The results of these investigations should help answer some of the questions relating to the pressure on resources during winter.

Bunnell (1987) has reviewed the reproductive strategies of the Cervidae, and suggests that species with stable seasonal home ranges, poorly synchronised birth seasons and a post-partum oestrus, are characteristic of stable habitats. In contrast, twinning, which is common in roe deer, is a characteristic of unstable habitats or the early seral stages of successions. Such "*r*" selected species are generally poor competitors, but can tolerate a wide range of environmental conditions. This hypothesis fits with the distributions of muntjac and roe deer in the King's Forest, where muntjac occupied a specialized niche within the more generalist roe deer niche. There was also some evidence for the suppression of roe deer density in areas of high muntjac density, suggesting that muntjac are superior competitors. These areas of high muntjac density are centred on areas of mature forest plantings. Although roe deer are probably better adapted to the early stages of a forest cycle, in the absence of superior competitors they may also reach high densities in the later stages of the forest succession. In the King's Forest, it seems likely that roe deer density would be higher in the absence of muntjac.

So far, the potential for competition between muntjac and roe deer has been discussed in isolation from the other herbivore species. While the two lagomorph species have a low spatial and habitat overlap with muntjac and roe deer, fallow deer show considerable overlap, particularly with roe deer. Fallow deer are characteristic of the later stages of seral successions (Batcheler, 1960) and, like muntjac, are probably also superior competitors to roe deer in these habitats. Therefore, roe density may be suppressed by the influence of both muntjac and fallow deer.

The roe deer population is the only deer species regularly culled in the King's Forest. Culling will reduce the potential for competition by reducing pressure on resources. In high density areas, the muntjac population appears to be stable (Claydon *et al.*, *in prep.*), and further population growth is probably limited by social constraints. Therefore, while culling of roe deer probably has little effect on muntjac numbers, it may prevent severe interspecific competition leading to competitive exclusion of roe deer, by keeping the overall deer biomass below the level at which resources become limiting. Thus culling of roe deer may allow muntjac and roe deer to coexist. Alternatively, insufficient time may have elapsed since muntjac density reached its current relatively stable level in the King's Forest, for resources to become limiting and for competitive exclusion to occur. Subjective impressions suggest that in areas of high muntjac density, vegetation quality, particularly bramble, may have reduced in recent years due to browsing pressure. Perhaps then, competitive effects will become more pronounced in the years following this study, and there will be a greater suppression of roe deer density in areas of high muntjac density.

Many of the observed differences in the ecology and social organisation of sympatric muntjac and roe deer shown in this study can be explained in terms of different body sizes and the resulting different functional positions within the Cervidae. However, it is not possible, from a comparative study such as this, to exclude competition as an important mechanism in shaping this herbivore community. The suppression of roe deer density in areas of high muntjac density, and the lower quality diet selected by sympatric roe deer during winter, which results in a low combined habitat and dietary overlap, are both indicators that competition may be occurring. However, in contrast to most studies of sympatric herbivores, there was a high level of spatial overlap between potentially competing species. Subjective impressions suggest that the spread of muntjac through the King's Forest was slower than in areas where muntjac colonised woodland in the absence of roe deer. Therefore, muntjac may have had some difficulty in establishing themselves in the King's Forest, although, once established, they appear to be the superior competitor in areas of mature woodland, which is high quality habitat. However, in a forest such as the King's Forest, with a diverse mosaic of different aged plantings, muntjac and roe deer will always be able to coexist. Indeed, as the forest enters its second rotation, and the proportion of younger forest plantings increases, roe deer density may increase at the expense of muntjac.

In conclusion, when muntjac become sympatric with roe deer, some reduction in roe deer density seems inevitable, because of their similar habitat and dietary requirements. This is particularly true in the later stages of lowland forest cycles, when the ground vegetation becomes more abundant and diverse creating a particularly suitable muntjac habitat. The extent of this reduction may depend on the availability of younger forest plantings within the forest structure. In these early seral stages, roe deer probably have a competitive advantage.

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