HABITAT AND SOCIAL ORGANISATION OF ROE DEER (CAPREOLUS CAPREOLUS)

by

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Thesis submitted for the Degree of Doctor of Philosophy

UNIVERSITY OF SOUTHAMPTON 1984

UNIVERSITY OF SOUTHAMPTON <u>ABSTRACT</u> FACULTY OF SCIENCE BIOLOGY <u>Doctor of Philosophy</u>

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Previous studies of roe deer suggested that habitat influences range size, but food abundance has been investigated without conclusive results. This research investigates the influence of habitat on specific aspects of behaviour, and the influence of food abundance and quality on dispersion of roe deer.

Populations were compared between two areas with different vegetation (Porton Down: grassland, woodland, farmland; Chedington Wood: softwood plantation). Individuals in both populations were marked, and a proportion fitted with radio-tags. Food abundance and quality (digestibility, calorific value, nutrients) were assessed in all habitats.

Diel patterns of activity and habitat use occurred in both areas. Open habitats were used more during darkness. Food distribution influenced feeding sites; disturbance influenced when sites were used. Diel changes at Chedington were less pronounced because food and cover were more evenly distributed. Habitat use and diet at Porton changed significantly with season, but were not correlated with food supply.

Social behaviour followed an annual cycle. Group size varied between habitats in winter and spring. Intra-group spacing was related to season, time period, habitat and group size. Group composition varied with month and habitat, but not time period. Marked deer occupied At Porton, adult ranges overlapped: overlap characteristic ranges. between males decreased in spring, but territories were not effectively Within study areas, range sizes of adults were not significantly exclusive. Ranges of both sexes were significantly larger at Porton than at different. Chedington and contained more food. However, they did not contain significantly more available nitrogen, suggesting that available nitrogen is an important proximate factor influencing range size.

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ACKNOWLEDGEMENTS

This research was funded by an S.R.C./C.A.S.E. studentship to the Department of Biology, Southampton University and the Game Conservancy, Fordingbridge, Hants. I wish to thank my supervisors, Dr. Rory Putman and Dr. Stephen Tapper for their help and advice throughout the field work, analysis and writing-up of this thesis.

Thanks are also due to Professor J. L. Hall for providing laboratory facilities in the Biology Department; to the technical staff in the Department for their assistance; to the Director of Porton Down and to Miss J. Rowe for providing access to the study areas; to all those who helped capture and mark deer during the course of this project; and to the Deer Managers at Porton who provided rumen samples from culied deer. I would particularly like to thank Col. A. L. Johnson, who enthusiastically continued radio-tracking at Chedington and generously gave access to the data he had collected.

Dr. Graham Hirons provided many invaluable comments and suggestions. Dr. Margaret Adey gave advice throughout and helped in the final presentation of this thesis, and Dee Gradidge skillfully designed and drew the figures. I am grateful to Karen Kirby for typing the manuscript so quickly.

Finally, I wish to thank my parents, David and Angela Johnson, for their continual support and encouragement.

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CHAPTER 1

Roe deer (*Capreolus capreolus* Linnaeus, 1758) are members of the Cervidae, a family within the order Artiodactyla. Ellerman and Scott's (1951) classification of contemporary cervids recognises five sub-families and includes roe deer in the Odocolleinae. Other British cervids, such as red deer (*Cervus elaphus*) and fallow deer (*Dama dama*) are members of the sub-family Cervinae. Roe deer are widely distributed across Eurasia and three sub-species are usually recognised: C. c. capreolus, which is distributed throughout western Europe from Spain to Scandinavia; C. c. pygargus is distributed from the west of Russia throughout Siberia; and C. c. bedfordII, which is found in eastern China and Korea. Corbet and Southern (1977) give body weights of *Capreolus capreolus* as 26 kg for adult males and 24 kg for adult females, with a shoulder height f 63-67 cm.

Roe deer have been present in Britain since the last ice-age and were abundant in Roman and medieval times (Prior 1968). A change in the forest laws in the 14th century left roe deer unprotected; increased hunting pressure combined with forest clearance probably caused the species to decline, and so by the 18th century, British populations are thought to have been restricted to the Borders of Scotland. Most of Britain has now been recolonised by roe deer, which have spread from successful introductions in the Oth century to Dorset and East Anglia The population increase since the Second World War is (Prior 1968). usually attributed to the islands of suitable habitat produced by the programme of afforestation. Although roe deer colonise young forestry plantations, they are also found in a variety of other habitats including mature woodland (Jackson 1980), moorland (Henry 1978) and upland forest (Cumming 1966), and they now exploit open habitats like farmland (Zejda 1978; Turner 1979). Diet is also varied and has been widely studied (she Section 6.1).

Most temperate cervids rut in the autumn but roe deer are unusual and rut in July/August. Since gestation length is related to body weight roe deer would be expected to mate in mid winter to give birth in spring when conditions favour kid survival. However, their gestation is delayed as the blastocyst does not implant in the uterine wall until January (Short

and Hay 1966, Aitken 1974). Such a long delay is not known to occur in other cervids, but allows roe deer to mate and give birth in summer.

Social organisation of roe deer is unlike that of other British cervids. Most social groups are composed of an adult female with juveniles (Cumming 1966) and large herds are formed only rarely (Zejda 1978). In common with other cervids, adult females occupy characteristic home ranges (Cumming 1966, Bramley 1970a, Strandgaard 1972) which are relatively fixed throughout their reproductive lives (Loudon 1979). However males are territorial. Cumming (1966) found that adult males were more uniformly dispersed than expected by chance, and that male Males occuped the same territory for several territories did not overlap. years and evicted juvenile males, but old or dead males were replaced by Chases between males (both adults, or adult and juvenile) iuveniles. often ended on a fixed line, which Cumming took to signify a boundary. Although males do scent mark, he did not observe boundary scent markings, or boundary patrols.

Cumming performed experiments, removing the adult female from a male's territory. He concluded that males were rot defending females, as dispersion did not change in response to their removal. He also removed territory-holding males and found that female dispersion was unaltered. Bramley (1970a) repeated these removal experiments and the results observed by both authors suggested that adults are replaced by sub-adults and not by less dominant neighbours, as was suggested by Prior (1968).

Firm conclusions about the mating system of roe deer cannot be drawn from removal experiments. Sample sizes were small because of the difficulty in removing a large number of known individuals, and several factors were uncontrolled. For instance, if males were defending territories to gain access to females, the best strategy if females are removed might be to wait for replacements, rather than desert a territory. Since replacement females were allowed to establish themselves, the fact that males remained on their territories is meaningless. It would in fact be very difficult to design and carry out removal experiments whose results could be interpreted clearly.

The mating system of roe deer is still poorly understood. Territoriality causes difficulties in gaining the information required to elucidate their mating system. Because of territoriality rutting individuals are dispersed, and in the habitats occupied by roe deer infrequent events

such as mating are hard to observe. The effects of territory size/position and male age on reproduction success are therefore unknown. Similarly, nothing is known about factors affecting reproductive success of females.

Territory size varies within study areas (e.g. Cumming 1966, Bramley 1970a, Hosey 1974). Bramley (1970b) investigated the level of aggression as a proximate factor influencing territory size. He tried to manipulate levels of aggression in males, by implanting testosterone (to increase aggression) or castrating (to reduce aggression). Implants were unsuccessful in increasing aggression, but a male that was castrated became less aggressive and his territory was taken over by a new-comer. However these results do not show conclusively whether aggression is the proximate factor that controls territory size.

Territory size varies more between localities than within them. Cumming (1966) found a mean territory size of 32.5 ha in upland forest at Glen Dye (Aberdeen) and a mean of 8.2 ha in forestry plantation at Chedington (Dorset). He suggested that territory size was ultimately determined by habitat characteristics.

The relation between habitat and territory/range size was first examined by Hosey (1974) who investigated the influence of food abundance and he calculated food value as the product of abundance, importance and area, concluding that food value per unit area was lower in larger territories. Males defended equal resources regardless of territory size. He found no strong relation between female range size and mean food value.

Hosey's conclusion that total food value of territories was constant despite large differences in size was discounted by Loudon (1979) who found a significant correlation between male territory size and total food value using Hosey's data. These data also show a significant correlation between female range size and total food value (Hosey 1974, Table 8.4, p.227, r = 0.334, N = 13, p < .01). Loudon repeated Hosey's investigation of the relation between food value and range size, using slightly different methods to assess abundance and importance, and working in Peebles rather than Dorset. However, the same conclusions can be drawn from his work as from Hosey's: roe deer of both sexes command more food resources if their ranges are larger.

Although simple measures of food abundance could be misleading if quality of food items varies. Hosey and Loudon concentrated on food abundance. Their work provided a basis for further research and

assessing food quality was a logical progression. Hence one of the main aims of this thesis will be to examine food quality as well as abundance.

Hosey and Loudon only considered annual measures of abundance, relating these to overall territory and range sizes. However it is clear from the work of Cumming (1966), Bramley (1970a) and Turner (1979) that social behaviour changes with season. I decided therefore to try to relate seasonal changes in food supply to seasonal changes in dispersion as this approach would be more sensitive than using annual measures. An additional improvement was to compare dispersion in two study areas, between which food supply might vary more than it would between ranges within a study area. Support for this approach comes from the large differences in range size between different study areas (see Fig. 8.1). Hence Chedington Wood (Dorset) and Porton Down (Wilts) were selected as study areas.

Dispersion is of great interest because it is linked with population density but it was the only aspect of roe deer ecology that had been related to food supply. However, other aspects such as habitat use and diet are important and may themselves influence dispersion. And so I decided to investigate the influence of seasonal changes in food supply on habitat use, activity patterns, diet and grouping behaviour of roe deer. Each topic will be examined in a separate chapter, where the relevant literature and aims will be introduced.

CHAPTER 2 STUDY AREAS

Two areas were used in this study. Most of the research was carried out at Porton Down (Wilts), and ChedIngton Wood in Dorset was used for comparison. Porton Down was chosen because deer could be readily observed in the open habitats, and roe were the only deer species present. Habitats were also relatively simple, making assessments of food abundance easier. Chedington Wood offered a marked contrast in habitats and has a long history of roe deer research (e.g. Cumming 1966; Bramley 1970; Hosey 1974; Loudon 1979; Gent 1983) which provided background information for this study.

2.1 PORTON DOWN

The main study area was on the Ranges at Porton Down (used by the Ministry of Defence since 1916). The Ranges lie to the northeast of Salisbury (S.U. 210370), and are closely related in their geology, flora, history and present land-use to Salisbury Plain which is 9 km to the southeast. The total area of the Ranges is 2752 ha: 1618 ha chalk downland and 264 ha mixed woodland. Wheat and barley are the main crops grown on the surrounding agricultural land.

The southwest part of the Ranges was used in this study (Map 1). The topography is dominated by the secondary chalk escarpment forming Battery Hill (158 m above sea level), which is steepest in the Beech Hanger, (a linear coombe running northwest from Battery Hill). The soil is a shallow, calcareous loam directly overlying chalk; there is no free surface water. The area is bounded by the A30 and Thorneydown roads on the south and east, and by the Porton-Pheasant road to the north. On the west, it runs into farmland lying between the Range and the villages of Winterbourne Gunner and East Gomeldon.

The following habitat definitions are used in this study (details of the cultivation of fields during the study are given in Table 2.1 and the location of fields is shown on Map 1.);



TABLE 2.1 CULTIVATION OF FIELDS AT PORTON DURING STUDY PERIOD

FIELD	1978/1979	1979/1980	1980/1981
			······
A	pasture	pasture	pasture
В	pasture	pasture	pasture
С	pasture	pasture	pasture
D	winter wheat	spring barley	grass
DE	spring barley	winter wheat	spring barley
El	winter wheat	spring barley	grass
E2	seed-grass	winter wheat	winter wheat
E3	spring barley	winter wheat	spring barley
F	seed-grass	winter wheat	winter wheat

1. Permanent pasture.

There were three small fields of permanent pasture adjoining the studyarea. Sheep were regularly grazed on field A. Fields B and C were unfenced and mown for hay.

2. Single-year grass leys

These are referred to throughout as 'seed-grass', but include seed-grass (Timothy grass (*Phieum pratense*) and rye grass (*Lolium sp.*)) and fodder crops.

3. Cereal fields

Winter wheat and spring barley were the only cereals cultivated In the study area.

4. Natural grassland

Six grassland communities were identified by Wells, Sheall, Ball and Ward (1976); three occurred on Battery Hill and were characterised by the following species:

- (a). Oat grasses (Arrhenatherum elatius and Helictotrichon pubescens), and red fescue (Festuca rubra).
- (b). Oat grasses (H. pubescens and H. pratense), and red fescue.
- (c). Sheep's fescue (F. ovina), lesser burnet (Poterium sanguisorba), and bird's-foot trefoil (Lotus corniculatus).

Over 80 plant species were recorded in these communities, including 17 species of moss and one lichen. For simplicity, and because the three grassland types were not readily distinguished in the field, the term 'grassland' refers to these communities throughout the study.

Scrub occurred at varying densities on the grassland. The most abundant was hawthorn (*Crataegus monogyna*) scrub either in single stands with bushes up to 3 m high, or in conjunction with dogwood (*Thelycrania sanguinea*), privet (*Ligustrum vuigare*) and buckthorn (*Rhamnus catharticus*). Juniper (*Juniper communis*) also occurred on Battery Hill. Gorse (*Ulex europaeus*) occurred on small patches of acidic Brown Earth soils.

5. Woodland

There were two woods in the study area: Thornydown Wood on the top of Battery Hill, and Winterslow Firs on lower ground in the east. Both were mixed woodland and, apart from a small area of Thornydown Wood, were approximately 100 years old (Wells et al. 1976). The woodland was composed of oak (Quercus robur) stands with an under-storey of hazel (Corylus avellana) and bramble (Rubus. sp.). Yew (Taxus baccata) was also common in the older region of Thornydown More open areas were dominated by beech (Fagus sylvatica) with Wood. Ground flora elsewhere included (Agrostis a ground flora of oat grasses. sp.), ground ivy (Glechoma hederacea), nettle, (Urtica dioeca) and dog's mercury (Mercurialis orennis), Ferns (Dryopteris spp.) were also common. Woodland edges were mainly hawthorn, privet, bramble,

gorse, dogwood and hazel.

Roe deer established a breeding population at Porton only recently, following vegetation changes that occurred when rabbit densities were reduced by myxomatosis in 1953–54. The successional changes from short-sward grassland to the present mature grassland supporting scrub, provided habitat that was colonised by roe.

Until 1970, the density of deer was low and no systematic records were kept. By 1970 complaints of damage reached an unacceptable level and a census was carried out by ground observers, estimating a population of 36 deer. However, population estimates of roe deer are notoriously inaccurate (Andersen 1953), so this figure and subsequent estimates can only be taken as minimum values. The deer were culled, but complaints of damage increased. Between 1975 and 1980 more accurate annual censuses were conducted, using observers on the ground and in helicopters, to provide information on population Data from these suggest that the population increased to a changes. peak in 1978 of 200 animals and remained above 180 in 1979. The number culled was based on census figures and observation by stalkers, and was adjusted each year.

On Battery Hill, 72 deer were counted in 1978 and 67 in 1979. Census results for 1980 were inaccurate because trees were in leaf and there was no census in 1981.

2.2 CHEDINGTON WOOD

This is a Forestry Commission wood in Dorset (ST 485067) and covers 114 ha; three outlying woods add a further 32 ha. The surrounding farmland is mostly permanent pasture used for hay and gr zing livestock. The soil is a Fuller's Earth clay which retains surface water, and vegetation is generally lush. The southern edge of the wood lies on a ridge (154 m above sea level) and the ground slopes steeply down to 100 m, then more gently to a small stream which drains the area and runs from southwest to northeast.

The wood was originally mature oak and ash (*Fraxinus excelsior*); in the early 1960's these were thinned and under-planted with conifers (mainly Norway Spruce (*Picea abies*), with smaller blocks of Douglas fir (*Psuedotsuga menziesii*), Scots pine (*Pinus sylvestris*) and others). Broad-leaved coppice was removed progressively throughout the 1960's

making the wood more open. By the early 1970's large areas of the planted conifers had reached thicket-stage, mixed with an impenetrable growth of bramble. The areas of thicket increased during the 1970's and observation of deer was restricted to paths, rides and to the southern part of the wood where the plantation was younger. A detailed description of the vegetation can be found in Hosey (1974). The vegetation categories on Map 2 and described below are based on growth stages of the plantation derived from vegetation mapping by Roe (1977).

1. <u>Rides</u>

The network of rides at Chedington is extensive and is kept clear by brashing. The rides vary from narrow paths (approx. I m wide) to hard-core forestry access roads (up to 12 m wide). Species present include sedges, herbs, and a diverse range of grasses.

2. Pre-thicket conifer

The south of the wood contains the youngest and most open Norway spruce. A dense growth of sedges, bracken and herbs develops in spring.

3. Thicket-stage conifer

This category accounts for 57 ha of closed-canopy Norway spruce plantation with a dense growth of bramble and briar (Rosa sp.).

4. Thinned conifer

These areas consist of Norway spruce that was thinned in 1976 by the removal of every other row, or of every fourth row, and are the second largest habitat of wood (50 ha).





5. Pole-stage conifer

There are 7 ha of pole-stage plantation comprising Douglas fir, Scots pine and western hemlock (*Tsuga heterophylla*) interspersed with mixed hardwoods. There is minimal undergrowth and visibility is good.

6. Mature conifer

Only 2 ha of mature conifer occur.

7. Scrub and mature hardwood

The remaining areas of original hardwood cover 11 ha. Nearly half of this is mature oak; the rest is a mixture of ash, sycamore (Acer pseudoplatanus) and alder (Alnus glutinosa), with an under-storey of hazel coppice. This vegetation type also lines streams and gullies.

8. Pasture

Most farmland adjoining the wood is permanent pasture stocked at low densities with sheep and some cattle, and also used for hay and silage.

Roe deer have been caught and marked annually at Chedington since 1961 to gather long-term data on movement, behaviour and population changes during the development of the plantation. Deer are not culled within the wood.

CHAPTER 3 HABITAT USE AT PORTON AND CHEDINGTON

3.1 INTRODUCTION

Roe deer are widely distributed and populations exploit a range of habitats. Members of the population within a locality may have access to several habitats. How individual deer use habitats will depend on a number of factors, including the preference of individuals for each habitat and both inter- and intra-specific competition. None of these factors can be measured in the field without experimental manipulation but population dispersion and patterns of habitat use can be examined.

A number of studies of roe deer have considered population dispersion in relation to habitat (Cumming 1966; Strandgaard 1972; Loudon 1979). These studies show that roe are selective and do not use available habitats equally. However, the major influences on habitat selection remain unclear.

Cumming (1966) investigated the influence of shelter on dispersion and found that roe used the more sheltered areas within habitats. Even so, they could often have found greater shelter by selecting a different Exposure may therefore influence distribution within a habitat altogether. habitat but it is probably not the most important factor determining which habitat is selected. Strandgaard (1972) observed that seasonal peaks in habitat use seemed to coincide with the seasonal abundance of key food species, suggesting that food supply might influence habitat use. Loudon (1979) also made this assertion, but did not relate habitat use to food availability. There is little published information on whether roe favour habitats for particular activities or even on the numbers of deer occupying habitats in different seasons. In addition neither habitat use nor occupation has ever been related to food supply. In this chapter three questions are investigated:

- 1. Does occupation of habitats vary seasonally?
- 2. Is there diel variation in habitat use?
- 3. Are different habitats used for particular activities?

At Porton information was collected largely by direct observation and also by radio-tracking, but at Chedington radio-tracking was used exclusively as vegetation was too dense for observation. Information on habitat occupation was also collected in both areas by measuring rates of faecal accumulation in different habitats.

3.2 METHODS

3.2.1 Observation of deer at Porton

A transect route was established to sample standardised areas, representative of each habitat. The route was designed to run through all habitat types, covering as much of the study area as possible in a short time to minimise time differences during each sample. The route covered 8 miles and took between 90 and 120 minutes to complete. Deer in the study area were already accustomed to vehicles and so disturbance was reduced by watching from a landrover. Four transects were carried it each week, one at each of four times of day: dawn, mid-day, dusk and mid-night (defined in Appendix 1).

General information on weather, date and starting time were recorded at the beginning of each transect. When deer were sighted the following information was recorded: time, group-size and composition, nearest-neighbour distances within the group, activity (grazing, browsing, inactive standing, moving, disturbed, inactive lying, ruminating lying, or indeterminate lying), grid reference and habitat type. Social interactions were also recorded.

The transect route was followed slowly in a landrover. To reduce disturbance, deer sighted close to the vehicle were passed before stopping to record data (a pair of 8 x 56 Optolyth binoculars were us throughout the study). At night deer could be located by eye-shine at up to 400 m using a powerful spotlamp operated from the landrover.

Data were collected by this method at Porton from March 1979 to Feburary 1980 inclusive and then transferred to computer file. 3.2.2 Marking and radio-tracking individual deer

As roe deer are difficult to recognise individually in the field, individuals were marked so that information on range size, individual behaviour and social organisation could be collected.

The method used to capture deer with long-nets has been described in detail by Cockburn (1967) and Smith (1980). Colour-coded plastic collars were fitted to all captured deer, and were made of 'Darvic' (ICI) by the Forestry Commission Wildlife Branch at Alice Holt, Surrey (from whom full specifications may be obtained). Deer were marked on four occasions at Porton: details of the number, sex and age of deer caught On the first two occasions the method was are given in Table 3.1. modified by using a helicopter to drive the deer into the long-nets. This was very efficient but helicopters were subsequently unavailable and so beaters were used. At the first marking operation at Porton no radio-transmitters were fitted but on other occasions transmitters were attached by the method described below. Radio- collars were fitted to deer caught at Chedington as part of the Forestry Commission long-term Details are given in Table 3.1. marking programme.

Radio-tags were of the AVM SM1 design, transmitting on 104.5 to 105.0 MHz. Early in the study they were powered by 1.5 v. AA-size Duracell batteries (field-life approx. 12 months). Both battery and transmitter were embedded in araldite at the base of the collar. A guitar string antenna (length x/8) was clamped between the collar and the coloured block so that half its length was free. The whip tended to fracture after being repeatedly bent by vegecation; since this reduced signal range drastically, later transmitters were modified by gluing the battery in an aluminium clip at the base of the collar and mounting the transmitter separately in a similar unit riveted to the top of the collar. These later antennae were made of nylon-coated angling trace protected by several layers of heat-shrink tubing, and the connection to the transmitter was surrounded by a silicon-rubber cone to spread bending The antenna formed a horizontal whip lying along the animal's stresses. These transmitters were powered by lithium oxide cells (field life back. approx 22 months). The combined weight of the collar, transmitter and battery was approximately 120 g.

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3	
Ξ.	
4	
F-1	

RECORD OF MARKED DEER

(a) caught and marked at Porton.

Total	18 15 11 10
es	addlfS 6 2 0 0 (1)
Femal Sub-adults	5 5 2 4 (4)
ales adults	0 0 3 (2)
Sub-adults	2000
Date	March 79 Dec 79 April 80 Feb 81

(Numbers in parenthesis indicate radio-transmitters)

(b) fitted with radio-tags at Chedington.

Transmitters functional in March 1983	M1 (NR) M3 F2
March 1982	M3 F2 (NR) F4
March 1981	M1 F1 F3 F3

M = Male, F = Female, NR = new radio

In the field, a directional aerial (3-element Yagi array) and receiver (Model 57 Blotag receiver made by Mariner Radar, Lowestoft, Suffolk) were used to locate signals. The animal's position was determined using three bearings for each triangulation. If bearings did not intersect, the radio-location was discarded; if they did intersect, the animal's position was taken as the centre of the triangle of error. The aerial had good directional sensitivity and because bearings were often taken from within 200 m of the animal the triangles of error were typically under 100 m². Successive locations of the same individual were not made within 60 minutes to reduce auto-correlation.

Signal strength of transmitters fitted at Porton in December 1979 and April 1980 was too weak to locate efficiently and so radio-tracking did not begin until March 1981 when an aerial signal-boost became available from Mariner Radar. From March 1981 to September 1981, deer were radio-tracked over 24 hour periods on weekly visits to Porton. Observations were also collected during this period. Monthly visits were made to Chedington to radio-track over 24 hour periods from March 1981 to September 1981. Radio-tagged deer at Chedington have been located dally since September 1981 by Col. A.L. Johnson.

The following variables were recorded when radio-tracking: date, time, weather conditions, radio-tracker's location, animal code and bearing. Signal strength was also recorded because it provides a valuable guide to the reliability of the bearing and to the proximity of the transmitter. The constancy of the signal was recorded as it indicates whether the animal is active: the signal from a motionless deer is constant whereas movement of the head and neck cause flexing of the antenna and fluctuations in signal strength. This can be demonstrated clearly if a radio-tagged deer is in sight and radio-contact simultaneously. Three categories of signal type were recognised: steady (implying inactivity), fluctuating (implying activity), and indeterminate.

3.2.3 Measuring rates of faecal accumulation

Pellet group counts provide a continuous measure of habitat use independent of observer presence. The number of pellet groups in a habitat are assumed to reflect overall time spent by deer in the habitat, since differences in the rate of faecal deposition of deer engaged in different activities are unknown. This assumption may be incorrect and

there are additional sources of error involved in this technique: the probability of finding groups may depend on habitat type: the rate of disappearance of pellets may differ between habitats, and seasonal changes in either of these factors may differ between habitats; the distribution of pellet groups within habitats may differ. Influencing the efficiency of sampling, and the rate of faecal deposition may vary seasonally or be affected by sex and/or age. Assuming that most pellet groups are unlikely to disappear within a month of being deposited, the effect of different rates of disappearance between habitats can be reduced by clearing plots each month and recording the number of pellet groups deposited during this period. This method is reviewed by lieff (1960).

In both study areas, permanent quadrats (7.1 x 7.1m) were established. At Porton, eight quadrats were located randomly in each habitat. At Chedington, quadrats were placed at 50 m intervals along two transects to facilitate finding them among the dense vegetation.

Initially all pellets were cleared from the quadrats. Then the quadrats were distematically searched at monthly intervals, and the number of pellet groups recorded for each quadrat. A pellet group was defined as ten or more pellets of the same shape, size, colour and age. A group was taken as being within the quadrat if more than 50 % of the group were inside the boundary. In practice, groups were readily distinguished from one another and few groups were bisected by the quadrat boundaries.

Ten pellets from each group were preserved in 10% alcohol for dietary analysis and the remainder totally removed to avoid recounting on subsequent visits.

3.3 RESULIS AND ANALYSES

3.3.1 Seasonal occupation of habitats at Porton

1. Pellet group counts

Data obtained by this method provide an overall measure of time spent by deer in each habitat.

Over 12 months, 151 pellet groups were found in the quadrats at Porton. 67% of these were found in the woodland quadrats (Fig. 3.1), The data are summarised in Appendix 2, Table 1. In both grassland and



Fig. 3.1. Faecal accumulation rates in grassland (shaded bars) and woodland (clear bars) at Porton, March 1979 to February 1980 inclusive.

woodland the rate of pellet deposition changed monthly, being lowest in summer. The seasonal trends were not significantly different in the two habitats ($r_s = 0.525$, N = 12, p < 0.10) although the rate declined sharply between May and June. The distribution of pellet groups between habitats changed significantly with month ($\chi^2 = 17.344$, d.f. = 7, p < 0.02). High numbers of pellet groups occurred in woodland from January to May and high numbers in grassland during autumn. In other months, observed and expected numbers were similar. No data were obtained on occupation of farmland by this method.

2. Observations collected on transects

A total of 1701 sightings of deer in 860 groups were recorded within 148 transects. The results are summarised in Table 3.2.

The mean number of deer seen per transect varied between time periods, being highest at dawn or dusk and lowest during the daytime. The largest proportion of deer seen were feeding but less than 10% were recorded in any other single activity.

Within all habitats, there was significant monthly variation in the number of deer recorded per transect (Table 3.3). This was examined using the Kruskai-Wallis one-way analysis of variance by ranks. Calculations were carried out using the Statistical Package for the Social Sciences ('SPSS') (Nie *et al.* 1975).

Adjacent months were compared using the Mann-Whitney U tests to determine significant changes in the number of deer seen in each habitat on transects. Significant differences are displayed on Fig. 3.2. (Note, however, that Mann-Whitney U-tests were carried out on the data as given in Appendix 2 (Tables 2-6) not on the proportions shown in Fig. 3.2.)

a) seasonal occupation of woodland

Woodland was occupied more consistently than other habitats (Fig. 3.2). Occupation peaked in spring and declined significantly between May and June U = 32.0, $n_1 = 13$, $n_2 = 13$, p < 0.02). The proportion of deer using woodland increased sharply in late winter. Monthly changes in the mean number of deer seen in woodland were significantly correlated with the monthly changes in rate of faecal deposition in woodland ($r_s = 0.621$, N = 12, p < 0.05).

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SUMMARY OF DATA COLLECTED ON TRANSECTS

-4-2-1 N	11 21 12 13 14 14 14 14 18 18 18	
IODS ons in month Dusk	68 88 94 54 54 54 53 34 54 54 54 54 54 54 54 54 54 54 54 54 54	
TIME PER Observati Day	4 1 1 2 2 1 1 2 4 4 1 2 2 1 1 2 4 4 4 4	60 E
Dawn 7	30 23 46 33 46 12 40 40 40 40 40 40 40 40 40 40 40 40 40	sturbed minate lyi
Social	000000000000000000000000000000000000000	moving, di 1g, indeter :ions
S in month Lying	2100000110001021 10001100011021	& browsing standing, , ruminatir al interact
ACTIVITIE servations Standing	11 16 16 16 15 15 12 12 12 12 12	grazing inactive inactive all soci
% Ob Feeding	74 54 72 62 72 69 74 69 74 69 74 74 74 74 74 74 74 74 74 74 74 74 74	Feeding = Standing = Lying = Social Int =
Mean per transect	12.0 12.0 14.9 9.6 7.3 7.3 7.3 7.3 11.0	
l Total Deer	168 288 194 102 117 74 74 74 74 117 145	
Month	X 4 X 7 7 4 0 0 Z Q 7 B	

TABLE 3.3.

RESULTS OF KRUSKAL-WALLIS 1-WAY ANALYSIS OF VARIANCE ON NUMBER OF DEER PER VISIT TO EACH HABITAT BY MONTH

HABITAT	VALUE OF H	đ.f.	SIGNIFICANCE
Woodland	25.705	11	<i>p</i> < 0.01
Grassland	46.107	11	D < 0.001
Pasture	20.009	11	50°0 > a
Cereals	47.644	11	p < 0.001
Seed-grass	3 8 . 862	11	p < 0.001



Fig. 3.2. Percentage of observations in each month for habitats at Porton: transects, March 1979 to February 1980 inclusive. Stippling indicates significant differences (Mann-Whitney U-test) between adjacent months.

b) seasonal occupation of grassland

Occupation varied more in grassland than woodland (Table 3.3). The number of deer occupying grassland was highest in spring, increasing through the period of leaf emergence, then declining significantly between June and July (U = 30.5, $n_1 = 13$, $n_2 = 14$, p < 0.02). After the rut in July/August the proportion of deer occupying grassland increased again. Seasonal changes in occupation of grassland assessed by observation and by measuring rate of faecal accumulation were not significantly correlated ($r_s = 0.175$, N = 12, ns).

c) seasonal occupation of farmland

On pasture and seed grass, differences in the numbers observed per transect in adjacent months were not significant, (Mann-Whitney U-tests), although there was significant variation overall (Table 3.3). Occupation of pasture declined steadily in spring to a minimum in July, when the crop was mown. The proportion of deer using pasture then increased sharply in autumn. Occupation of seed grass was highest in spring, declining between April and June and remaining low until the fields were resown with winter wheat in the autumn.

The greatest variation in numbers of deer occupying any of the habitats occurred in cereal fields, which were initially mainly winter wheat with small areas of spring barley. There was a small peak in occupation of cereals in spring (on winter wheat), but occupation dropped significantly between June and July as the crop developed (U = 35.5, n_1 = 14, n_2 = 14, p < 0.02). Between July and August occupation increased significantly (U = 36.5, $n_1 = 14$, $n_2 = 14$, p < 0.02), coinciding with the crop ripening and the consequent undergrowth of herbs and grasses. The increase continued in August and September but was not significant. The harvest occurred in early September after which the number of deer using cereal fields peaked. The numbers of deer observed on stubble declined significantly between October and November $(U = 7.5, n_1 = 7, n_2 = 10, p < 0.02)$; at this time the fields were cultivated and resown with barley. Occupation then remained low until December, after which use of the new barley crop increased to a level similar to that on winter wheat in the preceeding spring.

d) correlations between seasonal changes in occupation of habitats

Seasonal changes in occupation of habitats were significantly correlated in the following cases: woodland / pasture ($r_s = 0.698$, N = 12, p < 0.05); woodland / seed-grass ($r_s = 0.759$, N = 12, p < 0.01); pasture / seed-grass ($r_s = 0.841$, N = 12, p < 0.01). There were no negative correlations between seasonal changes in occupation of habitats.

3.3.2 Diel occupation of habitats at Porton

1. Diel patterns of occupation across the year.

The number of deer seen on transects varied considerably (Appendix 2, Tables 2–6) and so the following analyses are restricted to considering whether a habitat was used consistently more at particular times of day, firstly over the entire year and secondly within seasons. Differences in use of habitats in time periods within months were not examined.

The mean number of deer seen per transect was calculated for each time period, month and habitat. The variation of the means in each time period was analysed using Friedman's two-way analysis of variance, reating habitats separately. The results of these tests are shown in Table 3.4.

Across the year, all habitats except cereals showed significant variation in mean number of deer seen between the four time periods. The pattern of occupation was different between habitats (cf. mean ranks in Table 3.4). Occupation of both seed-grass and woodland showed less overall variation between time periods (p < 0.04, in both cases) than either pasture (p < 0.01) or grassland (p < 0.001).

Pasture was used mostly at night and least during the day. Deer stopped using pasture at dusk in autumn and winter. Use of cereais was similar overall in all periods except daytime, when numbers were lower. Both grassland and seed-grass were used mainly at dusk. Seed-grass was used least during the day; grassland was used least at night. The highest numbers of deer in woodland were seen at dawn.

2. Diel patterns of occupation within seasons

Months were grouped as shown in Table 3.5, and diel variation tested using Friedman's two-way analysis of variance (Table 3.5).

91	IFFERENCES IN 1	NUMBERS OF DEER	OCCUPYING HAI	3ITATS AT PORTUN B	Y TIME PERIC	Ē
	(Fr:	iedman two-way a	analysis of ve	iriance by rank)		21
HABITAT	DAWN	ДАΥ	DUSK	NIGHT		
	Mean ranks	time period w	ithin habitats	s across year	x, x,	<i>p</i> (d.f. = 3)
Pa sture	3.10	1.50	2.20	3 20		
Cereals	7 / 5	1		•••	11 . 64	< 0.01
	C + • 7	1.75	3.10	2.70	5 70	
Seed-grass	2.60	1.70	3,35	7 35		= 0.i22
Grassland				•••	8.37	< 0.04
	3.20	1.85	3.70	1.25	07 60	
Woodland	3.40	1.95	07 6		ת ד א	< 0.001
) 1	0/•7	L.95	8.73	< 0.04

TABLE 3.4

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TABLE

FRIEDMAN TWO-WAY ANOVA ON MEAN NUMBER DEER SEEN PER

TRANSECT IN EACH TIME PERIOD, BY SEASON

			Mean Rá	ink			
HABITAT	SHTNOM	DAWN	DAY	DUSK	NIGHT	x_r^2	<i>p</i> (d.f. = 3)
Pasture	MAM	2.67	1.0	2.67	3.67	6.6	0.086
	JJASO	3.0	1.5	2.62	0.87	3.375	0.337
	NDJF	3.67	2.0	1.17	3.17	6.9	0.075
Cereals	MAM	2.17	1.50	4.00	2.33	6.1	0.107
	JJASO	2.50	1.75	2.87	2.87	2.025	0.567
	NDJF	2.67	2.00	2.50	2.83	0.70	0.873
Seed-grass	MAM	3.0	2.0	2.67	2.33	1.0	0.801
	JJASO	2.87	1.37	3.37	2.37	5.25	0.154
	NDJF	1.83	1.83	4.00	2.33	5.70	0.127
Grassland	MAM	3.0	2.17	3.67	1.17	6.3	0.098
	JJASO	3.37	1.62	3.62	1.37	9.75	0.021 *
	NDJF	3.17	1.83	3.83	1.17	8.0	0.046 *
Wood Land	MAM	3.0	2.67	2.0	2.33	1.0	0.801
	JJASO	3.75	1.75	2.50	2.00	5.7	0.127
	NDJF	3.33	1.50	3.67	1.50	7.3	0.063

The only habitat in which significant differences occurred between time periods was grassland, where occupation was highest at dusk and lowest at night, during summer/autumn and winter.

3.3.3 Use of habitats at Porton for different activities

Observations have been divided into feeding (grazing and browsing) and non-feeding (all other activities), as sample sizes in many activities were limited. Two analyses have been performed. The first examines whether deer occupying each habitat were primarily feeding. The second uses an index to examine feeding preference for different habitats.

Fig. 3.3 shows for each month the proportion of the deer occupying a habitat that were feeding. Chi-squares were calculated to examine changes in the distribution of numbers engaged in feeding/non-feeding between months (months were grouped where necessary to obtain acceptable expected values).

Pasture was used throughout the year largely for feeding. The proportion feeding was above 70% in all months, and there was no association between activity and month $(\chi^2 = 2.296, d.f. = 3, ns)$. The chi-squares for the other habitats were significant, suggesting that activity changed during the year: cereals $(\chi^2 = 69.386, d.f. = 8, p < .001)$, seed-grass (χ^2 = 38.771, d.f. = 7, p < .001), grassland (χ^2 = 22.904, d.f. = 10, p < 0.05, woodland ($\chi^2 = 34.257$, d.f. = 9, p < 0.001). The proportion of deer feeding on cereals, seed-grass and grassland decreased sharply in summer. in most months, the proportion of deer seen feeding in these habitats was above 50%. In contrast the proportion of deer seen in woodland that were feeding was usually below 50%. in woodland the proportion feeding increased in spring and summer and decreased in autumn.

Feeding preference was examined with the index used by Duncan (1983) (see Fig. 3.4). This index removes the effect of varying numbers of observations in different months and of sampling unequal areas of each habitat. Index values between 0 and 1.0 indicate avoidance of a habitat, while values greater than 1.0 indicate preference. Results are shown in Fig. 3.4. The preferred habitats for feeding were woodland in August and February, grassland in July and October, cereals in September, and pasture in all other months.



Fig. 3.3. Percentage of deer feeding in each habitat at Porton by month: transect data March 1979 to February 1980 inclusive


Fig. 3.4. Feeding preference of roe deer at Porton: transect data, March 1979 to February 1980 inclusive. The preference index follows Duncan (1983) where preference for a habitat is given by P = U/A, U = % observations in habitat and A = % area sampled, occupied by habitat.

i.e. $P = \frac{no. \text{ deer feeding in habitat}}{\text{total no feeding in month}} \frac{\text{total area sampled}}{\text{area habitat sampled}}$

3.3.4 Seasonal occupation of habitats at ChedIngton

Two methods were used at Chedington to obtain data on habitat use. The level of faecal deposition on quadrats was low: only 130 pellet groups were located over the entire year, distributed between 8 habitats. This data set is too small for reliable interpretation, and so radio-tracking data were used to examine habitat use.

1. Overall patterns

Results from all radio-collared deer: A total of 809 radio-locations were obtained on 5 adult deer (2 bucks, 3 does) between April 1981 and March 1982 inclusive. In the second six months of this period, data were collected by Col. A.L. Johnson.

Radio-locations were grouped into months and habitats using SPSS. The proportion of each month's radio-locations in each habitat is shown in Fig. 3.5.

Over the year, there were clear changes in occupation of habitats. The distribution of radio-tagged deer between habitats changed significantly with month ($\chi^2 = 179.562$, *d. f.* = 44, *p* < 0.005). There was a clear switch between summer and winter, dominated by a change in the proportion of radio-locations in pre-thicket. This proportion fell steadily from May to July and then increased sharply between September and October, remaining high until the following spring. As the proportion in pre-thicket fell, the proportion in thinned and pole-stage conifers increased. There was also an increase in the proportion in thicket between June and July.

2. Seasonal occupation by individual radio-collared deer.

Females 1 and 2, and Male 1 were all present for the complete year and the number of radio-locations obtained on each was approximately equal. The other two radio-tagged deer have not been considered because sample size were smaller and did not cover the entire year.

Female 1 did not show a significant association between habitat and season ($\chi^2 = 7.741$, d.f. = 6, ns), whereas Female 2 and Male 1 both showed a significant association between habitat and season (Male 1: $\chi^2 = 29.926$, d.f. = 6, p < 0.001. Female 2: $\chi^2 = 27.116$, d.f. = 6, p < 0.001.



Fig. 3.5. Percentage radio-locations in each habitat at Chedington Wood, April 1981 to March 1982 inclusive

3.3.5 Diel occupation of habitats at Chedington

Radio-locations covering the entire year were grouped into habitats and time periods using SPSS. Over the year, radio-tagged deer used particular habitats more at certain times of day. ($\chi^2 = 32.100$, *d. f.* = 15, p < .01). Fig.3.6 shows the proportion of radio-locations in each habitat by period (corrected for differences in the numbers of radio-locations made in each time period). Rides, pasture and mature hardwood/scrub all follow a similar pattern, being used most at night and least during the day. Thinned, thicket and pole-stage/mature conifers were all used more during the day and at dusk, than at dawn or during the night. Pre-thicket conifers were used most at dawn and least at day. Within seasons the distribution of deer between habitats did not change significantly with time period (March-May: $\chi^2 = 17.661$, *d. f.* = 12, ns; June-August: $\chi^2 = 16.050$, *d. f.* = 12, ns; September-November: $\chi^2 = 8.001$, *d. f.* = 9, ns; December-February: $\chi^2 = 11.215$, *d. f.* = 9, ns).

3.3.6 Use of habitats at Chedington for different activities

The only data available on activity of deer at Chedington came from radio-tracking, from which only activity and inactivity could be distinguished. Radio-locations have therefore been divided by signal characteristics and habitat using firstly the entire sample and then separate seasons. The 'indeterminate' category was omitted, because it may be biologically meaningless and it cardot be reliably allocated to either of the other categories. Thus radio-locations have been used only if the signal clearly indicated either an active or inactive animal.

Over the year, there was a significant association between activity and habitat $(\chi^2 = 17,700, d.f. = 6, p < 0.01)$. Fig. 3.7 shows the proportion of radio-locations of active and inactive deer in each habitat over the year. Pasture, rides, scrub and thicket were all used more by active deer. The pole-stage/mature conifer combination was used almost equally by active and inactive deer. Pre-thicket and thinned conifers were used more by inactive deer.



Fig. 3.6. Diel occupation of habitats at Chedington Wood. Radio-tracking data April 1981 to March 1982 inclusive.



Fig. 3.7. Proportion of radio-collared deer that were active (clear) and inactive (shaded) in habitats at Chedington between April 1981 and March 1982.

Within seasons, the only significant association between activity and habitat occurred in winter (December-February: $\chi^2 = 11.102$, d.f. = 5, p < .05). The trends in use of habitats were similar in these winter months to the trends over the whole year. This applied also to other seasons, but differences were not significant.

3.4 DISCUSSION

3.4.1 Porton

At Porton, occupation of habitats by deer changed with season and time of day, and different habitats tended to be used for different activities. There was significant seasonal variation in the number of deer occupying each habitat: least variation occurred in pasture and woodland, most in cereals and grassland. All habitats except cereals show id consistent diel patterns of use: grassland was used least during the night, other habitats least during the day. Pasture was used predominantly for feeding, and deer showed a higher preference for feeding on pasture than elsewhere. Woodland was used least for feeding, and in all habitats is cept pasture the proportion of deer feeding changed significantly during the year.

in early spring, deer were mainly seen on farmland, (nearly 80% of observations in March). There was then a steep decline in the proportion of sightings made on farmland, reaching a minimum of 35% in July. This decline spanned the period of juvenile dispersal (peak in May/June, Loudon 1979), when population density would reach an annual low. During this period there was a sharp increase in the proportion of deer using grassland, suggesting that important behavioural events such as kidding and the onset of territoriality took place in habitats with more cover. The main increase in use of cereals occurred after the end of the rut in August but before the harvest, and use continued at a high level until the fields were re-cultivated.

The decline in use of cereals between October and November was accompanied by an increase in the proportion of deer using grassland and pasture; foraging occurred again on the newly-sown crops once these had emerged. Use of woodland also increased in winter, reaching a maximum in January/February when snow-cover on farmland probably reduced foraging efficiency on the young crops. Although deer were

observed scraping snow away to gain access to young shoots, this process must impose a serious additional energetic cost to foraging in extremely cold conditions.

Clear diel patterns of habitat use were observed at Porton but in the analyses these were obscured by the differential visibility of deer engaged in different activities. Deer tended to move off farmland into grassland or woodland at dawn and return to farmland at dusk. However, all deer using short crops during daylight were visible, whereas few of the deer using woodland or grassland during the day were seen as there was extensive cover, and this would conceal more deer if they were generally less active during daylight. Dividing data to examine diel use of habitats reduced sample sizes, so that it was difficult to distinguish differences in use of habitats between time periods from background variation in the numbers of deer seen per visit. This was compounded by changes in diel use of particular habitats: cereals for instance were used throughout the day in mid-summer but very little in daylight during the rest of the Such changes confused diel patterns when months were lumped to year. accommodate variability between individual transects.

Deer tended to use different habitats for different activities. Pasture was distinctive because over 70% deer seen there were feeding in all months of the year, suggesting that pasture was more important for feeding than for other activities. This is supported by the high preference shown for pasture in winter and spring ween foraging is critical. On cereale, seed-grass and grassland, the proportion of deer feeding decreased in summer during kidding and rutting, as more time was spent in non-feeding activities.

Overall, the lowest proportions feeding seen were in woodland. These results are perhaps surprising because cover might be expected to conceal non-feeding deer and increase the proportion feeding; hence the proportion feeding is probably over-estimated. The results suggest that woodland was used for shelter and was less important for foraging than the more open habitats, except in cold weather (e.g. February 1980). Results from faecal accumulation counts lend support to this conclusion as rates of accumulation were normally higher in woodland than in grassland, indicating that deer spent more time overall in woodland.

The index used to assess feeding preference compensates for the effects of sampling different proportions of available habitats. The index is influenced by two factors: the density of deer feeding in the habitat

and the density of deer feeding over all habitats. Thus small-sized habitats tend to score high preference indices: pasture was the most preferred habitat for feeding in seven months of the year (including winter and spring), woodland was the most preferred in two months, and cereals were only preferred in September when they were used by large numbers of deer.

While the index has biological value, it takes no account of the accessibility of habitats. Pasture, for instance, was inaccessible to most deer because the small fields were located on the NW of the study area (Map 1). It was used at a high density but by a small number of regularly visiting deer. Woodland as similar in area to pasture but was located centrally, adjoining all other vegetation types except pasture, and was used regularly by a large proportion of the population.

The index also takes no account of the heterogeneity of habitat use, but observations suggested that deer used all vegetation types patchily. Use of large fields was particularly heterogeneous, although data on this were not presented. The patchy use of woodland and grassland was evident from observations, and from faecal accumulation quadrats some of which regularly yielded higher counts than others. This heterogeneity of h bitat use renders the preference index inadequate except as an overall measure of the use made of different habitats by the deer. Determining the factors influencing heterogeneity of habitat use would indicate proximate factors influencing habitat selection, since patchy use may correspond to topography, potential disturbance or variations in food supply.

3.4.2 Chedington

Radio-collared deer made different use of each habitat. The pattern of occupation of habitats altered in autumn. Thinned, thicket and pole-stage conifers were used mainly in spring and summer, but in autumn deer switched mainly to pre-thicket conifer until the following spring. Different seasonal patterns of habitat use by individual deer reflect access to particular habitats.

Radio-collared deer also sho ed diel patterns of habitat use, although the trends were not strong enough to be significant within seasons. At night, they frequented more open habitats such as rides, pasture and scrub/mature hardwood: habitats in which they tended also to be more

active.

The habitats at Chedington differ in structure, location and potential Rides and pasture offer no cover. The comparatively low disturbance. use of rides may be an under-estimate because of the disturbance created when using them while radio-tracking. A greater use of rides might have been expected as habitat boundaries provide abundant food. The scrub/mature hardwood habitat at the edge of the wood provides cover but was used by people and dogs. The coniferous habitats all provide cover; however food supply varies considerably between them (Section 5.3). For example, the pole-stage habitat was almost devoid of food, as light penetrates only small areas of it; it was most used in July, possibly associated with rutting. During the rut deer seemed to select more open habitats, provided there was no disturbance. For instance, rutting deer were observed in pasture in 1981, but moved elsewhere when cattle were introduced. The thicket stage conifers were mostly used in summer. Thicket comprised the largest proportion of the wood but was used mainly by active deer and never at high density. This habitat was probably used for transit, as the impenetrable vegetation bordering paths through the thickets limited access for feeding and the only escape routes (from dogs, etc.) were paths along which pursuit is Pole-stage and thinned conifers were used more than thicket at easy. kidding time, when deer are particularly sensitive to disturbance; females could naintain vigilance over their kids in these more open habitats, but withdraw from disturbance when necessary.

3.4.3 Factors affecting observational data

Observations are influenced by several factors which cannot be controlled. These include: differences in visibility of deer in different habitats, seasonal changes in visibility within habitats, and differences in the probability of sighting deer engaged in different activities. The number of deer observed will depend on the relationships between these factors, and the patterns of habitat use and activity frequencies of deer.

The observed patterns of habitat use were probably not solely produced by changes in the probability of seeing deer. This is apparent if comparisons are made between habitat use determined by radio-telemetry and observation (i.e. out-of-sight records and in-sight records), using data from the third field season, when radio-telemetric

methods were first successful. During this field season, observations and radio-locations were gathered on the same visits to the Porton study area. To avoid comparing dissimilar groups of animals, the analysis was confined to radio-tracking data and observations on the same individuals. Farmland was excluded during March and April: as visual scans were made first, there were no radio-locations on farmland until crops were high enough to conceal deer.

The differences between patterns of use determined by the two methods were compared using chi-squares (Table 7, Appendix 2). Expected values were compensated as the area sampled visually was smaller than the area sampled by radio-tracking (White, *pers comm*. See Table 7, Appendix 2). The only significant chi-square was obtained in March/April. The largest contribution to the value came from an unexpectedly low number of radio-locations on grassland and an unexpectedly high number of observations in woodland. The direction of these differences does not support the view that visibility was affected by vegetation density.

Seasonal changes in visibility within habitats were apparently unimportant in determining changes in numbers of deer occupying if an increase in cover were important then it would be habitats. expected to affect immediately the number of deer seen in a habitat, and would result in more records of deer engaged in readily observed The major change in vegetation density occurs activities (e.g. feeding). during leaf-emergence in April and May. This coincided with a small decrease in the number of deer seen in woodland, but the significant decline occurred in June. In grassland, numbers of deer actually increased as cover increased in spring, declining significantly in July. The lowest number of deer seen in woodland or grassland occurred during summer, however numbers increased before the autumn (i.e. before leaf-fall). These trends suggest that observed changes in patterns of habitat use were real, and not artefacts caused by changes in visibility.

The proportion of deer feeding in woodland and grassland showed different trends through the year. The proportion feeding in woodland increased during spring and summer, suggesting that cover obscured non-feeding deer. The reverse occured in grassland (note that changes in frequencies of activity may also occur during this period). Observed changes in habitat use therefore cannot be entirely attributed to changes in visibility.

3.4.4 Factors affecting radio-telemetric data

Radio-telemetry data are subject to different bias from observations. The main bias is that the number of individuals sampled is low, although they can be located frequently, regardless of activity or habitat.

Sampled animals may be atypical of the population if they have access to different habitats from the population as a whole. This was avoided by collaring animals from more than one sector of the wood. Sampled deer may also be different from the population in their age This bias was unavoidable as the five radio and/or sex-class distribution. collars were all fitted to adults for two reasons. The non-expanding collars are loose on sub-adults, and on yearling males particularly, the weight of the transmitter could cause excessive rubbing. As deer were caught in March few data would have been collected before juvenile dispersal. All radio-collared animals were sought on each outing but, as signal strength varied, weak transmitters were not liways located. Thus the number of records per individual was weighted towards animals that The contribution of individuals to the data set was were easily located. further distorted because the collar of Male 2 was detached in August 1981, and in October 1981 Female 3 disappeared, probably having left the wood.

The activity states inferred from signal characteristics were not verified. Signals clearly varied and were placed in one of three categories: active, inactive and indeterminate. The first two of these correspond to categories in which observations were placed, but some actitivities may produce misleading signals. Head movements while lying grooming could for instance be classed as active from radio-tracking, whereas lying grooming would be classed as inactive if observed. Such uncertainties could be resolved with continuous chart recorders as used by Cederlund and Lemnell (1980) and Hirons and Owen (1982).

CHAPTER 4 DIEL ACTIVITY PATTERNS IN ROE DEER

4.1 INTRODUCTION

Several authors have described diel changes in the activity of roe deer. Prior (1968) noted peaks in activity around sunrise and sunset; such crepuscular peaks were documented by Turner (1980) and CederLund (1981). Several factors may contribute to these observed peaks:

- 1. Feeding may be limited to two cycles in any 24 hour period.
- 2. Longer feeding bouts or shorter lying bouts may occur at twilight.
- 3. Feeding intensity may vary with time of day.
- 4. More synchronised feeding cycles may occur at Cawn and dusk than at other times.
- 5. Deer may feed in more open habitats at dawn and dusk.

in isolation or interactively, these factors could result in peaks in distance to identify which factors are important?

Feeding cycles in free-ranging roe deer are unlikely to be limited to twilight hours, as captive roe deer have 8-12 feeding cycles per 24 hours (Bubenik 1960), and activity in wild roe deer was recorded during the day and night in an automated radio-telemetric study (Cederlund, 1981).

There is no firm evidence to corroborate the suggestion that either feeding bouts are longer or that lying bouts are shorter at dawn/dusk. Cederlund (1981) suggested that "long bouts" of activity (≥ 150 mins) tend to occur just after dusk in winter, and at both dusk and dawn in autumn, but he did not analyse bout length in relation to time of day (although using an automated radio-tracking system with continuous chart recorders is probably the only means of answering this question). Cederlund's study highlighted a further difficulty: individual variation in daily patterns of activity would obscure changes in bout length across the day, because of the limited sample sizes in radio-telemetric studies. Cederlund also found sex differences in daily activity patterns, which again suggest that sample sizes must be increased to resolve whether bout length, feeding intensity or feeding cycle synchrony are important factors in producing diel patterns of activity. Turner (1978) examined changes in bout length and feeding intensity between January and April, but did not consider changes over 24 hour periods (observations were limited to daylight and to females). He found that the proportion of time standing spent feeding (i.e. feeding intensity) was constant over the period studied while the proportion of daylight hours spent standing increased. Mean standing bout duration was also constant but there was a decrease in length of lying bouts. Turner studied roe deer living on farmland: direct observation of a focal animal was possible over protracted periods but he did not examine bout length, feeding intensity or synchrony of feeding cycles in relation to time of day.

Turner (1980) suggested that individual variation in digestion rates leads to unsychronised feeding cycles during the day and night. He proposed that crepuscular peaks in population activity occur because sunrise and sunset are cues which synchronise feeding cycles. A cue such as light intensity may be a proximate cause of activity peaks, but cycles could not be synchronised immediately by an external cue because of physiological constraints inherent in the ruminant digestive system.

Roe deer tend to use open habitats more during twilight and darkness (Chapter 3) and this would undoubtedly contribute to observed diel patterns of activity. Feeding cycles may be shorter in more open habitats, if food there is more digestible (see Chapter 5). More feeding cycles occur per day in agricultural areas than in woodland, and in both habitats more cycles occur in spring and summer, than in winter (Ellenberg 1978; Turner 1980). The rates of ingestion and digestion achieved by roe deer under different feeding regimes are therefore variable. Shorter feeding cycles, and an apparent increase in sychrony, because of habitat selection during twilight and darkness would accentuate activity peaks. However there is no literature relating diel activity petterns to the distribution or availability of food, or to habitat use.

In this chapter, three questions are considered:

- 1. Are there diel patterns of activity at Porton and Chedington?
- 2. Do activity patterns persist through the year or are they seasonal?
- 3. Are activity patterns related to habitat?

Two types of data are commonly used in field studies of activity Either a focal animal is observed for a period of time, or the patterns. behaviour of a sample of individuals is recorded at preset intervals. The focal animal method usually restricts sampling to a few individuals, but avolds the differential probability of sighting animals engaged in different activities (Clutton-Brock 1974). However, this is impractical for roe deer in most study areas, because their behaviour would dictate the start and duration of observation periods, weighting activities that occur in open in habitats except farmland, it would be difficult to observe a areas. focal animal continuously for a long enough period to optain meaningful Although automated radio-tracking systems (as used by Sempere data. (1980) and Cederlund (1981) on roe deer and by Hirons and Owen (1982) on woodcock (Scolopax rusticola)) have advantages, much biological information cannot be obtained from indirect monitoring.

At Porton behavioural records from a population sample were collected by 3 methods. Two methods involved direct observation: transects, and scans of fixed areas (carried out at preset intervals). The behaviour of a smaller sample of animals was obtained by radio-tracking. At Chedington, the only practical means of obtaining data was by radio-tracking. Techniques used for radio-tracking and details of transects were described earlier (Section 3.2), and so the following section deals only with scans of fixed areas at Porton.

Three sites were used: seed-grass (bounded by woodland), grassland, and woodland. At each site, an extensive area of the vegetation type could be scanned from an observation point selected to minimise disturbance. Observations were carried out over 2 dawns, 2 dusks and 1 daytime period per calendar month, (except October and December) between March 1979 and February 1980 inclusive. Watching at dawn began at first light and continued for 3 hours. Watching at dusk began 3 hours before darkness and ceased when it became too dark. The intervening daytime period was adjusted monthly to cover the hours of Night-time watching was abandonned: night-viewing devices daylight. were unavailable and regular illumination using a spotlamp caused disturbance. Scans were made at 5 minute intervals. For each deer, the variables described in the transect method (Section 3.2) were recorded

4.3.1 Diel patterns of activity of deer at Porton and Chedington

1. Porton.

The distribution of activities between time periods was tested first using transect data, covering the period March 1979 to February 1980 inclusive. Activities were grouped into four categories to obtain acceptable expected values: Feeding (grazing plus browsing); standing (inactive); moving (including social interactions) and lying activities. The distribution of deer between activities varied significantly with time period (χ^2 = 164.70, d.f. = 9, p < .001). The proportion of animals engaged in each activity is shown by time period in Fig. 4.1. The highest proportion of deer feeding (73%) occurred at dusk. in other periods the proportion feeding varied between 6I and 65%. The proportions standing (including moving), and lying showed greater At dawn, 31% of deer sighted were standing-up, but not variation. feeding, whereas at night this category accounted for only 10% of The reverse occurred with the proportion of animals seen lying sightings. down.

Data from scanning fixed areas coply to the same period and were tested for association between activity and period. Night-time observations were not collected, as they caused disturbance. However during daylight, there was a significant association between activity and period ($\chi^2 = 176.288$, d.f. = 6, p < .001). The proportion of deer engaged in standing, non-feeding activities was again highest (17%) at dawn, Figure 4.2. The proportion lying down was also highest (23%) at dawn, failing throughout the day, accompanied by an increase in the proportion feeding which reached a maximum of 78% at dusk.

Diel activity patterns occurred in radio-tracking data covering the period March to September 1981. Observations over this period were included because sightings were weighted towards active deer, whereas radio-locations were weighted towards inactivity. For observations, "active" was taken as all standing activities; for radio-locations, activity was determined by signal characteristics, the indeterminate category being excluded (Section 3.3.7). The activity of radio-tagged deer was





Porton study area, transects: March 1979 to February 1980 inclusive.

Key: Feeding (grazing and browsing) Standing (all non-feeding standing activities) Lying (ruminating and inactive lying)



Fig. 4.2. Proportion of deer engaged in feeding (clear), standing (light shading), and lying (dark shading) during daylight at Porton. Scans of fixed areas: March 1979 to February 1980 (excluding October & December).

significantly associated with time period (χ^2 = 83.409, *d.f.* = 3, *p* < .001). Distinct peaks in activity occurred at dawn and dusk (Fig. 4.3) when over 80% of records were of active deer. At night, the proportion active was still above 70%, whereas during the day it was only 42%.

The diel activity patterns determined from radio-tracking and from gransects were similar. From radio-tracking the level of activity was generally lower; crepuscular peaks were more pronounced, and the lowest level of activity occurred during the day, not during the night as it did in data from transects. However, transects covered twelve months, while radio-tracking covered seven.

Fig. 4.4 shows the proportion of deer active in each time period from transect data, over the seven months covered by radio-tracking, (but note: these data sets apply to different <u>years</u>). Although the association between activity and period is still significant ($\chi^2 = 115.745$, d.f. = 6, p < .001), the proportions in Figs. 4.3 and 4.4 remain distinctly different: excluding October to February had little effect on the diel patterns shown in Fig. 4.1.

2. Chedington

Diel activity patterns of all radio-tagged deer were examined over the period April 1981 to March 1982 inclusive. Activity of radio-tagged deer changed significantly with time period ($\chi^2 = 61.143$, d.f. = 3, p < .001). Activity of deer at Chedington was highest (71%) at night (Fig. 4.5) and lowest (34%) during the day. Deer were more active at dawn (65%) than at dusk (59%).

Diel patterns of activity of three individuals were examined. All three (one buck, two does) showed a significant association between activity and time period (Male 1, $\chi^2 = 11.592$, d.f. = 3, p < .001; Female 1, $\chi^2 = 22.126$, d.f. = 3, p < .001; Female 2, $\chi^2 = 27.706$, d.f. = 3, p < .001). Diel patterns of activity differed between individuals: the distribution of radio-locations between activity and inactivity varied with individual at dawn ($\chi^2 = 5.338$, d.f. = 2, p < .05), during daytime (χ^2 = 10.337, d.f. = 2, p < .01), and at night ($\chi^2 = 9.092$, d.f. = 2, p < .05), but not at dusk ($\chi^2 = 2.085$, d.f. = 2, ns). Female 1 was consistently more active than Female 2 or Male 1 in all time periods.



Figure 4.3 - Proportion of radio-collared deer active by time period.

Porton study area, observations plus radio-locations: March to September 1981.



Fig. 4.4. Proportion of deer active (shaded), by time period. Porton, transects: March -September 1979.



Fig. 4.5. Proportion of radio-collared deer active (shaded) by time period. Chedington: April 1981 to March 1982.

4.3.2 Seasonal changes in diel activity patterns at Porton and Chedington

1. Porton

The association between activity and time period was tested on paired adjacent months of transect data. The categories "standing" and "moving" were combined to increase sample size. In all six pairs of months the distribution of deer between activities was significantly related to time period:

Months	x ²	P(6d.f.)
March + April	37.054	< .001
May + June	41.799	< .001
July + August	17.986	< .01
Sept + October	84.537	< .001
Nov + December	21.679	< .01
Jan + February	30,257	< .001

Within time periods, the distribution of deer between activities was influenced by month at dawn ($\chi^2 = 54.376$, d. f. = 10, p < .001), and at dusk ($\chi^2 = 98.899$, d. f. = 10, p < .001), but not during the day ($\chi^2 = 2.572$, d. f. = 2, ns), or night ($\chi^2 = 16.443$, d. f. = 10, ns).

Changes in the proportion of deer engaged in each activity at dawn and dusk are shown in Fig. 4.6. Seasonal changes were similar in the two time periods: the proportion of deer feeding decreased from March/April to a minimum in July/August, accompanied by an increase in the proportion standing.

Data from scanning fixed areas were analysed similarly. Months were paired and tested for an association between activity and time period across daylight hours. The association was significant in each of the five pairs of months (no sampling was done in October or December):



Fig. 4.6. Seasonal changes in the proportion of deer engaged in feeding (clear), standing (light shading), and lyin_o (dark shading) at (a) dawn and (b) dusk. Porton, transects: March 1979 to February 1980.

Months	x ²	p(4 d.f.)
March + April	82.377	< .001
May + June	33.631	< .001
July + August	16.222	< .01
Sept + November	142.704	< .001
Jan + February	198.537	< .001

The proportion of deer engaged in each activity within two-month blocks is shown by time period in Fig. 4.7. The diel patterns of activity were different in all five pairs of months.

There was a significant change in the distribution of deer engaged in different activities within time periods across the year (dawn $\chi^2 = 145.167$, d.f. = 8, p < .001; day, $\chi^2 = 467.642$, d.f. = 8, p < .001; dusk, $\chi^2 = 261.296$, d.f. = 8, p < .001). Trends were similar to those in daylight transect data. In all three time periods, the proportion feeding decreased from March/April to July/August, when the peak in proportion standing occurred. However, in scanning data the proportion lying was higher overall, and was more variable, especially within the daytime period.

Radio-tracking data also showed changes in diel activity pattern with time of year. There was a significant association between activity and period between March and June (March/April: $\chi^2 = 43.687$, d. f. = 3, p < .001; May/June: $\chi^2 = 34.598$, d. f. = 3, p < .001) but not in July/August ($\chi^2 = 0.618$, d. f. = 3, ns). The proportions active and inactive are shown in Fig. 4.8 ("active" includes all non-lying activities and is equivale at to all feeding and standing activities in the other analyses). In March/April and May/June, the diel activity patterns were similar, with crepuscular peaks in activity, and the lowest level of activity occurring during the day.



Fig. 4.7. Seasonal changes in the proportion of deer engaged in feeding (clear), standing (light shading), and lying (dark shading), at (a) dawn (b) day, (c) dusk. Porton; scans of fixed areas: March 1979 to February 1980 (excluding October and December).



Fig. 4.8. Proportions of radio-tagged deer at Porton active (shaded) by time period in (a) March + April, (b) May + June 1981, determined by radio-tracking and observation.

2. Chedington

The association between activity and time period was tested using radio-tracking data in two-month blocks. In all pairings except May/June, the distribution of deer between the categories 'active' and 'inactive' varied significantly with time period.

Months	x ²	p(3 d.f.)
March + April	17.752	< .001
May + June	1.724	ns
July + August	13.399	< .01
Sept + October	19.920	< .001
Nov + December	21.535	< .001
Jan + February	11.391	< .01

The proportion of deer active in each pair of months is shown by time period in Fig. 4.9. The diel patterns of activity were similar in several pairs of months: In Nov/Dec, Jan/Feb, and March/April peaks in activity occurred during the night, and at dawn or dusk, with the least activity during the day. In July/August and September/October the level of activity was higher but deer were still least active during the day.

The only time period when the distribution of deer between activities changed during the year was dusk ($\chi^2 = 17.168$, d.f. = 4, p < .01). In other periods, this association was not significant, (dawn, $\chi^2 = 3.54$, d.f. = 3, ns). Changes in activity at dusk are shown in Figure 4.10. The level of activity increased between May/June and July/August, and remained high in September/October, before diminshing consistently until the following spring.

4.3.3 The influence of habitat on diel activity patterns

Habitat use at both Porton and Chedington varied with time of day. Individual deer did not use all habitats, nor were they confined to a single habitat. In this section, the activity distribution of those deer using a given habitat is considered across time periods, but this does not imply that deer composing the sample in different time periods were necessarily the same individuals.



Fig. 4.9. Proportion of radio-tagged deer at Chedington active (shaded) by time period in two-month blocks.



Fig. 4.10. Seasonal changes in the proportion of radiotagged deer at Chedington that were active (shaded) at dusk.

1. Porton

(a) Transects

In all habitats except pasture, there was a significant association between activity and time period across the whole year (Sample size precludes the possibility of testing this association within seasons).

Habitats	x ²	P
grassland	7.857	< .05
woodland	13.506	< .01
cereals	88.394	< .001
seed-grass	87.654	< .001
pasture	0.508	ns

Fig. 4.11 shows diel activity patterns for each vegetation type. Although there were differences between habitats, certain features were common: in all four habitats, feeding peaked at dusk, and the proportion of deer lying was highest at night. The proportion of deer feeding was lowest at night, except on cereals where it was lowest at dawn. The proportion of deer lying was lowest at dawn or during the day in all four habitats.

(b) Scanning fixed areas

In grassland, woodland and seed-grass, there were significant associations between activity and time period within daylight hours (grassland: $\chi^2 = 74.126$, d.f. = 4, p < .001; seed-grass: $\chi^2 = 77.340$, d.f. = 4, p < .001; woodland: $\chi^2 = 10.172$, d.f. = 4, p < .05).

The activity patterns of deer during daylight at each site are shown in Fig. 4.12. Diel patterns were similar, but not identical. The proportion feeding in grassland and seed-grass was highest at dusk, but this proportion was highest in woodland during the day. The proportion lying on seed-grass decreased throughout the day, but was almost constant in woodland and peaked during the day on grassland.



Fig. 4.11. Proportions of deer feeding (clear), standing (light shading), and lying (dark shading) by time period in (a) seed-grass, (b) cereals, (c) woodland (d) grassland at Porton. Transects: March 1979 to February 1980.



Fig. 4.12. Proportion of deer feeding (clear), standing (light shading) and lying (dark shading) during daylight on (a) grassland, (b) woodland, (c) seed-grass at Porton. Scans of fixed areas: March 1979 to February 1980 (excluding October and December).

(c) Radio-tracking

There was a significant association between activity and time period on grassland ($\chi^2 = 34.143$, d.f. = 3, p < .001) and woodland ($\chi^2 = 10.587$, d.f. = 3, p < .05), but not farmland ($\chi^2 = 1.855$, d.f. = 2, ns). As in previous analyses in this chapter, both radio-locations and observations of radio-tagged deer were included. Although the level of activity was lower in woodland than grassland (Fig. 4.13), the patterns of activity were similar. Activity was lowest during the day in both habitats. However in woodland, activity was highest at night, whereas on grassland, deer were least active at night.

2. ChedIngton

Across 12 months, the distribution of deer between activities changed significantly with time period for pre-thicket ($\chi^2 = 29.989$, d.f. = 3, p < .001), thicket ($\chi^2 = 9.399$, d.f. = 3, p < .05), and pole-stage conifer ($\chi^2 = 10.509$, d.f. = 3, p < .05), but not for thinned conifer ($\chi^2 = 6.906$, d.f. = 3, ns), or scrub/mature hardwood ($\chi^2 = 3.881$, d.f. = 3, ns). Sample size in other habitats at Chedington (rides, pasture and mature softwood) were too small to test in this way. The patterns of activity in pre-thicket, thicket and pole-stage conifer were similar (Fig. 4.14): activity was lowest during the day in all three habitats, a-highest at night (pre-thicket and thicket) or at dusk (pole-stage).

4.4 DISCUSSION

Deer in both study areas showed diel patterns of activity, but peak activity at Porton occurred at dusk, whereas at Chedington it occurred at night. Diel patterns of activity were found within two-month intervals: in both study areas, patterns changed with season, as non-feeding activities increased during the summer. Changes in activity distribution with time period were found in most habitats at Porton, but less than half the habitats at Chedington. At Chedington patterns within habitats were the same, whereas at Porton diel patterns differed between habitats.



Fig. 4.13. Proportion of radio-tagged deer at Porton active (shaded) by time period in (a) grassland and (b) woodland. March to September 1981, determined by radio-tracking and observation.



Fig. 4.14. Proportion of radio-tagged deer at Chedington that were active (shaded) by time period in (a) pre-thicket, (b) thicket and (c) pole-stage conifers, determined by radio-tracking
4.4.1 Diel patterns of activity over the year

Peak activity at Porton occurred at dusk, whether feeding is considered using transect or scan data, or activity using radio-tracking Non-feeding standing activities were most common at dawn: data. these activites were mainly moving from night-time feeding sites to areas used during daylight (see habitat use: Chapter 3). Transect data suggested that lying activities were most common at night. These were subject to observational bias and probably indicate that deer lay down in more open areas at night, since radio-tracking data showed peak inactivity during the By the scanning method, deer appeared to spend more time lying day. feeding bouts during the night ended at dawn and so at dawn: continuous presence for scanning enhanced the probability of identifying At Chedington, peak activity occurred at night, rather lying-up sites. than at dusk, although deer at Chedington were also least active during the day.

4.4.2 Diel patterns of activity within seasons

Patterns of activity occurred within two-month periods in both study areas. At Porton, the proportion of deer engaged in non-feeeding standing activities increased in summer at dawn and dusk, reaching a peak during the rut in July/August. This occurred at the expense of feeding (not lying) and so is unlikely to be an artefact caused by increased cover. Deer may spend less time feeding, as food quality and availability are higher in summer (Chapter 5), and so they devote more time to social activities, associated with kidding and rutting. After the rut, trends reversed and deer spent more time feeding at dawn and dusk throughout the winter.

There were differences in diel patterns of activity within two-month blocks: at ChedIngton, there were no diel patterns in May/June; and the distribution between activities across the year at Chedington changed only at dusk, whereas at Porton, it also changed at dawn. Age of the sampled deer, habitats, differences in study areas, methodology, and the categories used in radio-tracking and observations (Section 3.4.4) may all have contributed to these differences.

4.4.3 Diel patterns of activity in different habitats

Deer used habitats for particular activities (Section 3.3), and there were diel patterns of habitat use in both study sites. There were also diel changes in activity within habitats. At Porton, changes in activity with time of day were found in all habitats except pasture, where deer were predominatly feeding.

Transects showed that in all habitats deer fed most at dusk, and spent most time lying down at night; radio-tracking showed that deer were most active at dusk or night and least active during the day. These results suggest that diel activity patterns were the same, regardless of habitat.

Results from scans at Porton were different, and suggested that feeding continued throughout the day in woodland, but not in other habitats. Most feeding occurred at dusk on seed-grass and grassland, but most feeding was actually observed during the day in woodland. Methodological differences may again be important, but results from scans are probably more realistic, because of continuous observation.

At Chedington, diel patterns of activity were significant in only three of the habitats (pre-thicket, thicket and pole-stage conifer). In these habitats diel patterns were similar.

Diel changes in activity were more pronounced at Porton than at Chedington. In all Chedington habitats where significant diel patterns occurred, they were similar, whereas at Porton, there were important differences between activity patterns in woodland and the other habitats.

4.5 OVERALL DISCUSSION OF HABITAT USE AND ACTIVITY PATTERNS

Deer at Porton and Chedington showed seasonal changes in habitat use. These changes were the most obvious feature of habitat use, and were particularly pronounced at Porton. Several factors may shape changes in habitat selection through the year. Food supply will change cyclically and at Porton cycles may be out of phase because of agricultural practices. Deer may therefore maximise food intake (whether in quantity or net energy) by selecting the vegetation type in which they forage. But other factors will also influence this selection. Foraging in woodland increased in very cold weather at Porton, although food supply would not have improved until spring. Behavioural changes, associated

with kidding and rutting may also be important and changes in habitat selection coincided with events in the breeding cycle. Seasonal changes at Chedington were probably less pronounced because habitats were less varied in food supply and most offered sufficient cover to escape predators and gain shelter.

At both sites, habitats used during daylight offered more cover and were subject to less disturbance than those frequented during twilight and darkness. But diel patterns were more pronounced at Porton than Chedington, supporting the hypothesis that individuals compromise between the benefit of foraging on better food supplies, and the costs of disturbance and exposure. Since the probability of disturbance varies over 24 hours in a predictable manner, deer would be expected to select habitats accordingly, and deer used more open habitats for intensive feeding (e.g. pasture at Porton), but retired to cover when inactive.

Differences between habitats in the two study sites may also influence diel patterns of activity. Peak activity occurred during dusk at Porton but at night in Chedington, although in both areas deer were least active during the daytime. Several explanations of this are possible. Differences in sampling may be important, but the most plausible explanation lies in fundamental differences between habitats in the degree, timing and effects of disturbance.

At Porton, disturbance occurred almost exclusively during the day, and affected a large proportion of the study area. Feeding at Porton was suppressed during the day, and only resumed at dusk. At Chedington, this did not occur, as there was less disturbance and habitats offered more cover. The coordinated onset of activity at dusk at Porton did not therefore occur at Chedington.

Activity patterns changed with season, as the proportion of active time spent in non-feeding activities increased during the summer, to a peak in the rut. Habitat-type had little effect on activity patterns, except in Porton woodland, where most feeding occurred during the day, but this effect was probably influenced by diel patterns of habitat use.

CHAPTER 5 FORAGE AVAILABILITY AND QUALITY

5.1 INTRODUCTION

The availability of forage and its effects on the behaviour of roe deer was investigated by Hosey (1974) and Loudon (1979). Both authors noted that abundance of food varied between territories in summer, but neither showed clear relationships between food abundance and territory size. Their measures of food availability took no account of seasonal changes or food quality, and were made by categorising visual surveys of vegetation.

The aim of this chapter is to determine more precisely seasonal food availability in each habitat, and to establish how food quality varies with habitat and season. The visual estimates used by Hosey and Loudon were substituted by direct measures of standing crop of forage types (as 9 dry wt m^{-2} in each habitat).

To assess forage quality appropriately requires knowledge of the animal's nutritional requirements, so that levels of important nutrients can be monitored. There is considerable literature on domestic ruminant nutrition, but none specifically on roe deer. The following parameters were chosen as indicators of food quality:

- 1) digestibility: which controls the proportion of ingested material accessible after digestion
- 2) calorific value: indicates the energy content of different foods
- 3) the levels of five elements:
 - (i) nitrogen (structural in proteins and enzymes, and essential for protein synthesis)
 - (ii) phosphorus (important in bones, and central to energy transfer mechanism)
 - (iii) potassium, (essential in membrane structure and protein synthesis)
 - (iv) calcium, (particularly important in lactation and antier growth)
 - (v) magnesium, (activates enzyme systems in animals).

All five elements are found at lower concentrations in plant tissue than in animal tissue. Other nutritional factors that were not assayed may be equally important.

5.2 METHODS

5.2.1 Field sampling: measuring standing crop and production, estimating offfake and obtaining vegetation samples for subsequent laboratory analysis

(a) Graze-types

The standing crop (i.e. availability) of each community was assessed by clipping samples of the complete sward (not individual species) at bi-monthly intervals. Measurements of production and offtake were made using temporary grazing exclosures. Samples of the sward were clipped from inside and outside the exclosure at the beginning and end of the two-month exclosure period. The exclosure was then moved at least 2 m from its previous position, in a set direction to avoid locating it in the same position later. Two exclosures were used at each site, so that periods of exclosure could be staggered giving overlap in the two-monthly data. This exclosure period was chosen to allow time for growth to occur, without the rate of production declining because of changes in standing crop.

For each sample, five replicate areas (250 cm²) were marked using a circular turf-corer, and all above-ground vegetation removed by clipping. Estimates of production were obtained from these initial measurements by subtracting the initial standing crop *outside* from the final standing crop *inside* the exclosure. Similarly, offtake was estimated by subtracting the final standing crop outside from the final standing crop inside.

At Porton, three replicate sites were assessed using this technique in both grassland and woodland. At Chedington two replicate sites were monitored in each of the following habitats: rides, grazing communities within softwood plantation (one site within pre-thicket and one within thinned conifers), and ground vegetation beneath scrub/mature hardwood.

Vegetation assessments on farmland at Porton were made differently, as there were too many fields to assess separately. Five samples per field were clipped monthly, and combined for each crop to obtain mean standing crop. Graze-types were assessed between February 1979 and April 1980. Samples were treated by the laboratory methods described in Section 5.2.2.

(b) Browse communities

Availability, production and offtake of browse materials were assessed at Porton in October 1979 and March 1980. Relative abundance of each browse species was assessed on transect lines, and the most abundant species sampled by the following techniques.

In scrub, all first year growth was clipped from below the browse line on three freestanding individuals of each species. Woodland edge was treated as a flat surface for browsing and first year growth was clipped from the area defined by a 1 m² quadrat. Browsed and unbrowsed shoots from each sample were sorted into size classes, measured and dry weighed to determined mean shoot weight and length of browse and unbrowsed categories.

Bramble was the only species assessed at Chedington, because it was widespread, abundant and constituted a major proportion of the diet in most months (Hosey 1974). In addition, structure, complexity and density of vegetation at Chedington would have made assessing more species extremely time-consuming. The availability, producting and offtake of bramble at Chedington was assessed during October 1979 on 10 I m² quadrats in pre-thicket and thinned conifers. All shoots within the quadrat below the browse line were clipped, and sorted into browsed and unbrowsed categories. The mean number of shoots m⁻² and the mean dry weight of unbrowsed shoots were calculated.

Browse assessments at Chedington were not repeated in the following spring,

Additional samples of first-year growth of browse species were clipped monthly between March 1979 and Feb ary 1980 in both study areas, to provide material for the chemical analyses described in the following section.

5.2.2 Laboratory methods: analyses of digestibility, calorific value and nutrient levels

Vegetation samples from the field techniques described were dried to constant weight in an oven at 80°C, and then weighed. A Gien Creston microhammer mill fitted with a I mm mesh was used to grind a subsample of each for the analyses below.

(a) Digestibility

The method used was taken from Jones and Hayward (1975), who found a close correlation (r = 0.96) between results from this meaned and *in vivo* digestibilities for sheep. Samples were incubated *in vitro* firstly in pepsin solution and then in fungal cellulase to determine dry matter digestibility. These reagents are standardised and hence results can be readily reproduced.

Two hundred mg sample was incubated with 20 ml of 0.2% pepsin in 0.1 N HCi for 24 hours at 40°C in a screw cap bottle. The supernatant was removed using a sinter stick (porosity 2). The stick was washed back into the sample, using part of the 20 ml aliquot of celic lase solution (125 mg cellulase in 20 ml phosphate-citrate buffer pH 4.6) the remainder of which was then added before incubating for a further 48 hours at 40°C. Bottles were shaken by inversion twice per 24 hours. The indigestible residue was isolated by filtering through a tared glassfibre paper (No. 1) which was then dried and reweighed. The amount of original material digested was calculated as a percentage of the original weight.

Samples from all main habitat categories were analysed at two-monthly intervals. Additional samples were assayed from intervening months when digestibility changed rapidly. Samples used from Porton were of grassland, woodland, pasture, cereals and seed-grass, and three browse species (bramble, privet and hawthorn). Samples used for Chedington were from rides, coniferous under-storey, deciduous under-storey and three browse species (bramble, hawthorn and Norway Spruce).

(b) Calorific value

Calorific values were determined using a Gallenkamp Ballistic Bomb calorimeter. Samples of approximately 0.5 g of oven-dried material

were compressed into a pellet incorporating a standard length (5 cm) of firing cotton. Pellets were ignited at 25 atm of oxygen, and heat output measured by a theromcouple connected to a potentiometer was displayed on a pen-chart recorder. The calorimeter was calibrated using dried benzoic acid of known calorific value, at two-hourly intervals. Organic weight was obtained by subtracting residual (inorganic) weight from the sample weight. Calorific values were expressed at J g⁻¹ organic matter. Four replicates were analysed for each vegetation type sample assayed and a mean obtained.

The vegetation types assessed were the same as those for which digestibility was determined; samples were used from April, July, October and January.

(c) Chemical analyses

Samples were digested using the modification of the Kjeldahl digest given by Allen (1974). This technique has advantages: several nutrients can be determined in one digestion; it is a relatively quick process; adaptable for replication and unlike dry-ashing procedures, there is no loss of volatile elements such as phosphorous. Elements were assayed using aliquots from the acid digested samples.

A Techalcon autoanalyser was used to determine nitrogen and phosphorous calorimetrically. Ammonium ions from the oxidation of organic nitrogen react with alkaline phenate and hypochlorite producing the indophenol colouration which is read at 650 nm. Phosphorous was the indophenol colouration which is read at 650 nm. Phosphorous was the molybdenum blue method using ammonium molybdate and ammonium metavanadate reagents, producing a colouration that is read at 420 nm. Both calcium and magnesium were determined by atomic absorption spectrophotometry using lanthanum chloride to suppress interference from aluminium (which depressed atomic absorption even when present at very low levels). Potassium was determined by flame photometry. A full description of reagents, procedures and precautions for the above techniques can be found in Allen (1974).

Acid digestions and chemical analyses were performed on monthly samples from outside exclosures in both study areas, on samples from fields at Porton, and on monthly samples of browse material. Readings in ppm were converted to mg g^{-1} before statistical analysis.

5.3 RESULTS

5.3.1 Standing crop, production and offtake

1. Graze-types

The mean monthly standing crop of vegetation per unit area was calculated from the dry weight of all samples (outside exclosures) for each community. In communities where exclosures were used, production and offtake were calculated as described in Section 5.2.1 (a). The significance of estimates of production and offtake was determined by an analysis of variance, since dry weights of replicates from inside and outside exclosures were variable, and differences between the means could therefore be misic ding. For instance, apparent production of ground vegetation under hardwood at Chedington was highest in June-July (7.0 g 250 cm⁻²), but the dry weights inside the exclosures at the end of the enclosure period were not significantly different from the dry weights from outside at the beginning ($F_{1,8} = 1.636$, ns).

For farmland at Porton, the mean standing coop was calculated from the dry weights of samples from all fields under each regime of cultivation. Net production for each month was calculated as the change in standing crop during the month.

Peak standing crop occurred in July in most communities (Figs. 5.1 - 5.9). Exceptions were standing crop of conifer under-storey and of rides at Chedington, which peaked in August (Figs. 5.8 and 5.9). Standing crop was lowest in January and February, except on cereals and seed-grass at Porton where standing crop was zero after cultivation in October - November.

Peak production occurred in June and/or July in all graze types at Porton, (Figs. 5.1 – 5.6), whereas at Chedington, it occurred in -diy/August in conifer under-storey and rides (Figs. 5.8 and 5.9), Estimates of production in broadleaved ground vegetation at Chedington were anomalous (Fig. 5.7): significant production occurred in October/November, but significant negative production occurred in November/December. These results arise because of patchiness in the occurrence of ground cover in this habitat outside the growing season. Elsewhere, production was lowest (i.e. significant negative values, implying a loss in biomass through senescence/decomposition) in winter,



Fig. 5.1. Seasonal changes in standing crop (mean \pm SE), production (light histograms indicate significant changes), digestibility, and nutrient levels of chalk grassland at Porton



Fig. 5.2. Seasonal changes in standing crop (mean \pm SE), production (light histograms indicate significant changes), % digestibility and nutrient levels of woodland ground vegetation at Porton.



Fig. 5.3. Seasonal changes in standing crop, growth rate, digestibility, and nutrient levels for pasture at Porton



Fig. 5.4. Seasonal changes in standing crop, rate of growth (bars), digestibility and nutrient levels of seed-grass fields at Porton. H = harvest, R = resown.



Fig. 5.5. Seasonal changes in standing crop, growth rate (bars), digestibility and nutrient levels of winter wheat at Porton



Fig 5.6. Seasonal changes in standing crop, growth rate, % digestibility and nutrient levels of spring barley at Porton



Fig. 5.7. Seasonal changes in standing crop (mean ± SE), production (light histograms indicate significant changes), digestibility and nutrient levels of ground vegetation beneath scrub/mature hardwood at Chedington



Fig. 5.8. Seasonal changes in standing crop (mean \pm SE), production (light bars indicate significant changes), digestibility and nutrient levels in grass communities beneath pre-thicket and thinned conifers at Chedington



Fig. 5.9. Seasonal changes in standing crop (mean \pm SE), production (light bars indicate significant changes),%digestibility and nutrient levels of rides at Chedington

with the exception of annual crops at Porton, where lowest values occurred in late summer after harvesting.

The exclosure technique can provide measures of offtake: estimates were calculated by subtracting mean weight outside the exclosure at the end of the exclosure period from the mean weight inside, and were therefore sensitive to sward variability (as described above for estimates of production). Sward variability was high, offtake per unit area was low, and there was no significant differences (F-test) between dry weights of samples from grazed and enclosed swards in any of the communities assessed by this technique at any time of year.

2. Browse species

(a) Scrub at Porton

The most abundant species in scrub at Porton were hawthorn, privet and buckthorn, and these were assessed by the technique described in Section 5.2.1(b). Results are shown in Table 5.1.

Production by privet was the highest over the growing season. Although clumps of privet were less numerous than hawthorn bushes, the number of shoots available for browsing was higher. A higher proportion of hawthorn hoots were browsed, but the estimated dry voight of privet consumed by deer during this period was higher. The recorded percentage of browsed hawthorn shoots actually fell outside the growing season (between autumn and spring), probably because sample size was inadequate. However, the level of browsed shoots on privet increased from 5 to 17%. Buckthorn production was the lowest of the three species assessed and the level of browsing was also low

(b) Woodland edge at Porton

The two blocks of woodland at Porton were assessed separately because their edges were dominated by different species.

The four most abundant browse species in the edge of Thorny Wood were hazel, gorse, hawthorn and bramble. Results of the assessment of these species are given in Table 5.2. No browsed shoots were found on gorse, and as roe were never observed browsing gorse further analysis was not performed. Only 3% of hazel shoots were browsed, although it was most abundant, producing 11.9 kg dry wt 100 m⁻¹ woodland edge. As with hawthorn in scrub, the percentage of shoots browsed was lower

TABLE 5.1

RESULTS OF BROWSE ASSESSMENT IN SCRUB AT PORTON

			Species	
		HAWTHORN	PRIVET	BUCKTHORN
Density (bushes ha ⁻¹)	46	25	16
Mean dry ±1	wt unbrowsed shoots (g) .S.E.	0.38 ± .05	0.54 ± .02	0.42 ± .02
Mean numł	oer shoots/bush	85	2764	162
Productic	on (kg dry wt ha ⁻¹)			
:	April - October	1.62	38.90	1.12
Offtake	(kg dry wt ha^{-1})			
5	April - October	0.14	1.65	0.01
1	November - March	-0.07	4.67	0.01

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RESULTS OF BROWSE ASSESSMENT OF THORNYWOOD EDGE AT PORTON

		Species	
	HAZEL	HAWTHORN	BRAMBLE
Z Wood and edge	26	15	14
Mean dry wt unbrowsed shoots (g) ± SE	0.98 ± 09	0.50 ± .05	2.89 ± .29
Mean number shoot m ⁻²	118	154	34
Production: April-Oct. (kg dry wt m ⁻ 2)	. 20	60 .	.12
Offtake (kg dry wt m ⁻²)			
" April - October	.04	.01	.02
" November - March	0	I	.01

after the winter (again probably reflecting sample size). Hawthorn in this woodland edge was less productive but more heavily browsed than hazel. Bramble was the most productive species (12.6 kg dry wt 100 m⁻¹) and was also the most heavily browsed (22%).

The four most abundant species within the edge of Winterslow Firs at Porton were privet, hawthorn, beech and dogwood. Table 5.3 shows results of the browse assessment. Dogwood and privet were the most productive, both yielding about 8 kg 100 m⁻¹. The largest proportions browsed were hawthorn during, and privet, outside, the growing season. Estimates of offtake during the year suggested that privet was consumed more than any other species.

(c) Assessments of browse at Chedington

The mean dry weight of unbrowsed shoots of bramble at Chedington was 2.06 \pm 0.15 g, and there was a mean of 38 shoots m⁻² (of which on average 29% were browsed). Production was 0.11 kg m⁻² over the growing season, and offtake over the same period was 0.03 kg m⁻².

5.3.2 Digestibility

Some authors have transformed *in vitro* values for digestibility from rumen liquor or enzymic digests to the equivalent *in vivo* value, using regression equations (e.g. Jones and Hayward 1975). The range of values used by Jones and Hayward for this regression did not include the full range of digestibilities obtained for samples from Porton and Chedington. There is no *a priori* justification for extrapolating their regression, nor for assuming any other relationship, and so direct enzymic results are presented as digestible percentages of dry weight of vegetation samples.

Peak digestibility of graze-types occurred between April and June. On seed-grass and pasture, the peak occurred in April (Figs. 5.3 and 5.4); In broadleaved ground vegetation at Porton and ChedIngton, and in cereals at Porton, it occurred in May (Figs. 5.2, 5.5, 5.6, and 5.7), but in grassland, peak digestibility occurred in June (Fig. 5.1). The lowest digestibilities of graze-types occurred usually in mid/late winter. Digestibility of browse species varied less than digestibility of graze-types. Peak digestibility occurred in September at Porton (mean of 3 species assessed, Fig. 5.10) but at Chedington the peak occurred in

TABLE 5.3

RESULTS OF BROWSE ASSESSMENT OF WINTERSLOW FIRS EDGE AT PORTON

		Jens	30.	
	PRIVET	HAWTHORN	BEECH	DOGWOOD
% Woodland edge	67	11	10	7
Mean dry wt unbrowsed shoots (g) ±SE	0.27 ± 0.01	0.37 ± 0.02	0.49 ± 0.06	0.35 ± 0.0
Mean number shoots m ⁻²	262	74	40	215
Production: April-October (kg dry wt m ⁻² . 10 ⁻²)	7.85	3.24	1.95	8,08
Offtake: (kg dry wt m ⁻² , 10^{-2})				
April - October	0.64	0.41	0	0.48
November - March	0.55	-0.32	0.17	0.08



Fig. 5.10. Seasonal changes in level of nutrients of deciduous browse species at Porton (mean \pm SE).

May, in all three species assessed (Figs. 5.11 and 5.12).

5.3.3 Calorific value

Calorific values varied little between communities (range was 20.3) Jg^{-1} for grassland to 22.44 Jg^{-1} for Norway spruce). There was little seasonal variation within communities (Table 5.4). *F*-tests showed two significant seasonal changes at Porton and at Chedington. These were in cereals ($F_{2,8} = 14.276$, p < .01) and privet ($F_{3,8} = 28.029$, p < .05) at Porton, and for rides ($F_{3,8} = 5,416$, p < .05) and bramble ($F_{3,8} = 8.162$, p < .01) at Chedington. In all four, the highest calorific values occurred in April.

5.3.4 Nutrient analyses

Acid digests and nutrient analyses were carried out on 650 samples. One sample was analysed per month for each browse species, for each set of five replicates clipped outside exclosures in grazing communities, and for each field at Porton.

After assaying nutrients, the mean nutrient level was calculated for each habitat type and month. Repults are presented graphically (Figs. 5.1 to 5.12). Standard errors (given where possible) indicate variation in nutrient levels between samples taken in the field. No attempt was made to assess the variation in the digestion techniques or the performance of the auto-analyser, because both are typically reliable to $\pm 2\%$ (Allen 1974).

5.3.5 Nutrient levels

1. Nitrogen

Peak nitrogen content occurred sually between March and May (e.g. Cereals, seed-grass and woodland ground vegetation, Figs. 5.2, 5.4, and 5.5), and declined to October (grassland, Fig. 5.1), or mid-winter (browse srp, Fig. 5.10). A different seasonal pattern occurred on Pasture (Fig. 5.3): the highest nitrogen level occurred in February-March and the lowest in June before mowing. Similarly, on Cereals (Figs. 5.5 and 5.6) nitrogen level was lowest in August before

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TABLE

CALORIFIC V JES OF GRAZE TYPES AND BROWSE SPECIES AT PORTON AND CHEDINGTON

		Mean Jg ⁻¹	r ratio	d.f.	d
PORTON:	Hawthorn	20.629	1.2626	3.9	ns
	Bramble	20,710	0.285	3 . 8	su
	Privet	21.999	28,029	3.8	< 0.01
	Grassland	20.308	1.1685	3.10	ns
	Woodland ground veg.	20.613	0.7673	3.10	ns
	Seed-grass	21.426	0.731	3.6	ns
	Cereals	21.815	14.276	2.6	< 0.01
	Pasture	20.428	1.1638	3.12	su
CHEDING	- NOT:				
	Hawthorn	21.007	1.7975	3.6	SU
	Bramble	20.759	8.1623	3.8	< 0.01
	Norway Spruce	22.444	2.240	3.8	su
	Ride	21.206	5.416	3.8	< 0.05
	Broadleaved under-storey	20.461	0.2602	3.8	su
	Softwood under-storey	20.873	1.664	3.8	ns



Fig. 5.11. Seconal changes in nutrient levels and digestibility of (a) bramble and (b) other deciduous browse spectes at Chedington



Fig. 5.12. Seasonal changes in nutrient levels and digestibility of Norway spruce at Chedington

harvesting, but a second peak was recorded for the under-storey after harvesting.

2. Phosphorous

Phosphorous usually peaked one month after nitrogen. In cereals and seed-grass for instance (Figs. 5.4 - 5.6), phosphorous peaked in April – June. The minimum values occurred in October for grassland (Fig. 5.1), and browse spp (Fig. 5.10). Phosphorous level showed less seasonal variation in other habitats, and generally varied less than nitrogen level.

3. Potassium

Peak potassium was synchronised with nitrogen in cereals at Porton (Fig. 5.5), and in softwood under-storey, rides and deciduous browse species at Chedington (Figs. 5,8, 5.9 and 5.11). In grassland, pasture, seed-grass and woodland ground vegetation at Porton potassium peaked one month after nitrogen (Figs. 5.1 - 5.6). Lowest levels of potassium occurred mainly in winter.

4. Calcium

Calciem peaked later in the growing season than other nutrients. Seed-grass was exceptional as calcium peaked in February (Fig. 5.4). In other communities the peak occurred between May (woodland ground vegetation at Porton, Fig. 5.2) and October (rides and deciduous browse species at Chedington, Figs. 5.9 and 5.11). Two calcium peaks occurred in pasture and cereals: In April/May and October/November (Figs. 5.3 and 5.5). Calcium levels were lowest mainly in late winter, apart from pasture and cereals, where the level was lowest before harvest.

5. Magnesium

Levels of magnesium were generally low and there were no pronounced seasonal changes in any of the communities.

5.4 DISCUSSION

There were two aims in this chapter: firstly to assess seasonal food availability in each habitat, and secondly to establish how food quality varied between habitats during the year.

5.4.1 Grazing systems

Standing crop varied between habitats and changed during the year. The highest standing crop overall occurred on grassland at Porton, where there was little seasonal variation. On farmland, growth occurred rapidly in spring, and standing crop fell sharply when harvesting occurred. Standing crops were higher in coniferous under-storey and rides at Chedington than beneath broadleaved species, but were lower in these habitats than in grassland at Porton.

Production was higher in grassland than in woodland. Significant production occurred in spring/early summer and significant loss in autumn/winter. Estimates of production at Chedington were more variable because there were fewer replicates per habitat. Net production on farmland is not directly comparable as the exclosure technique was not used. Changes in net production on farmland at Porton were more distinct than changes in production in unmanaged communities. Peak growth occurred between May and July, and the greatest loss in biomass in late summer when harvesting occurred.

Two possible sources of variation affect measurements of swards in unmanaged vegetation types: sampling errors (from clipping, handling and weighing), and sward heterogeneity. Sample errors were probably unimportant and low standard errors suggest that there was sufficient replication to accommodate the variability in swards.

Patterns of growth and senescence of swards would also affect measurements of standing crop, and estimates of production and offtake. In heavily grazed communities, most production is removed maintaining a low standing crop. Low grazing pressure at Porton and Chedington results in high standing crops in unmanaged habitats. Part of the plant biomass is continually senescing and is eventually lost to the litter zone by decomposition. Growth and sensecence occur at different rates throughout the year: a change in the balance between them will cause a change in standing crop. Clearer peaks in production might have shown if new growth and senescent blomass had been assessed separately.

Production would be lower in unmanaged communities, as growth rates decrease with increasing blomass in grazing systems. Low production would have been obscured by sward heterogeneity, since estimates depended on differences between mean weights of grazed and enclosed swards.

"stimates of offtake were not significant because of low grazing pressure. A "guesstimate" of offtake would be 36 kg ha⁻¹ 2-months⁻¹ (based on 1 deer ha⁻¹, assuming 0.6 kg dry matter day⁻¹ animal⁻¹ (Weiner 1975)). In grassland, peak production was 2,000 kg ha⁻¹ in June-July and hence offtake would be 1% of production, when 95% confidence limits for standing crop of grassland were ±26% of the mean: a level of variability against which 1% offtake would be undetectable. At Chedington, there were less replicates so estimates of offtake were not calculated because no confidence could be placed in any signiciant values that might have been obtained.

5.4.2 Browse assessments

Browse species were more difficult to assess than grazing areas because of several factors. Many browse species have different growth forms, e.g. hazel and bramble, and so each species must be assessed separately. Food items are discrete, but items of different species are frequently interspersed in a complex manner. However, browse assessments are simplified because shoots can be aged and it is obvious if they have been browsed.

Standing crop and production of browse at Porton were minor in comparison with grazing areas. Yield of privet (the most productive browse species in scrub) was 38 kg ha⁻¹ over the entire grazing season, whereas chalk grassland vielded 2000 kg ha⁻¹ in the 2 peak months of productivity. However, these measures of biomass may not be immediately important to deer.

Offtake of browse was measurable but generally low, agreeing with transect results (browsing accounted for only 3.7% of feeding observations but these are biased because browsing occurs in habitats

with cover). Annual offtake from privet was 6.3 kg ha⁻¹: using estimates from Weiner (1975), this would account for approximately 2% of the dry weight of food for one adult deer.

Browsing may have been under-estimated. Deer may preferentially browse either long or short shoots, but the estimates assume the same size-class distribution of browsed and unbrowsed shoots. Concentrate selectors like roe deer (Hofmann 1973) could remove single leaves of broadleaved species, but this would be impossible to assess since leaves may be lost from shoots for other reasons. Selection by deer could mean therefore that browse was a more important food source than is suggested by estimates of offtake.

Three factors may have caused the decrease in the proportion of browsed shoots of hawthorn and bramble at Porton over the winter. The twig-count method (Shafer 1963) used in spring may have been less occurate than harvesting all shoots. Old twigs and browsed shoots may have been confused more easily after the winter, or sample sizes may have been too small to accommodate variation.

5.4.3 Digestibility

There were marked seasonal changes in digestibility. Apart from bramble, digestibility was highest when plant material was young. In winter-sown crops peak digestibility occurred in winter, but in other communities, such as grassland, the peak occurred in spring.

Results from this technique should be reliable, since reagents are purified to a high standard, and the laboratory methods can be closely controlled. However, expensive materials precluded the possibility of replicating samples. In addition, no attempt was made to evaluate variation in digestibility within swards (only one sample was analysed per sward at a given time of year), and no attempt was made to assess the maximum digestibility that could be obtained by selection of particularly young growth from swards. Overall values obtained for swards may not be realistic for selective grazers.

5, 4, 4 Calorific value

Samples tested showed little variation in calorific value with season and there was no marked differences between habitats. Digestible energy

might vary more and would perhaps have been a more appropriate variable to relate to diet and feeding behaviour. Digestible energy is often calculated from digestibility and calorific value (Holmes 1980), assuming that energy is distributed evenly between the digestible and undigestible fractions. Since this relationship was untested and may vary between communities or seasons, digestible energy was not calculated.

5.4.5 Nutrient assessments

The techniqces used are well tested and results should be reliable. Results from Porton can be compared with published data on agricultural crops. Holmes (1980) quotes mean crude protein for under-stocked pasture as 175 g kg⁻¹: equivalent figures were 83 g kg⁻¹ for grassland and 124 g kg⁻¹ for pasture at Porton. Soil-type would affect nitrogen levels in vegetation, but pasture quoted by Holmes was probably treated with nitrogen-rich fertilisers. Crude protein was higher overall in winter wheat (172 g kg⁻¹) and seed-grass (188 g kg⁻¹) at Porton, where fertilisers were applied.

Seasonal changes in nutrients were related to the growing season and followed similar trends between communities. However, seasonal changes in availability and quality were not closely correlated in most vegetation types. Winter wheat was an exception where all nutrients and digestibility showed similar seasonal changes. Availability (i.e. standing crop) showed similar seasonal changes between communities, particularly agricultural crops, but seasonal changes in nutrients were most similar in woodland and grassland; nutrients in agricultural crops did not follow similar seasonal trends.

CHAPTER 6 FEEDING BEHAVIOUR AND DIET AT PORTON

6.1 INTRODUCTION

The diet of roe deer has received wide attention in several countries. In Britain, studies were undertaken by Hosey (1974), Henry (1975), Loudon (1979) and Jackson (1980); in France by Cannac (1978); in Switzerland by Voser-Huber and Nievergelt (1975); in Poland by Sluda *et al.* (1969), Borowski and Kossak (1975), Szmidt (1975), Pielowski and Pucek (1976), Perzanowski (1978) and Gebczynska (1980); in Sweden by Cederlund and Nystrom (1981) and in Finland by Helle (1980).

Roe deer have been regarded traditionally as browsers (Prior 1968), preferring to feed on the shrub layer rather than on herbs or grasses. Prior suggested that grasses are only important in early spring when little other food is available. However, studies of roe deer have shown that the proportions of herbs and grasses in the diet can vary considerably. For instance, Siuda *et al.* (1969) found that leaves and twigs of broadleaved species were the major component of diet, but Gebczynska (1980) found that herbs accounted for over 65% of the winter diet, and 80% of the diet in summer.

Since both these studies analysed rumen contents, it is unlikely that their different findings result from methodology. The differences emphasise the variability of roe deer diets between different geographical This is further illustrated by differences in diet with latitude localities. over the range of roe deer. Sluda et al. recorded 178 species in the diet of roe in Poland, whereas Helle found only 17 species in the diet of roe deer in Finland, and interestingly, arboreal lichens accounted for over 20% of the diet in Finland whereas in most roe habitats such plants would be uncommon. Even within Britain, differences in diet were found between the north and south. In the New Forest (Hampshire: Jackson 1980) and at Chedington (Dorset: Hosey 1974), broadleaved species were the major food, bramble being particularly important. But in Hamsterley Forest (Durham: Henry 1978b) dwarf shrubs (Callun a sp. and Vaccinium sp) were more important.

Regarding roe deer as browsers clearly does not explain their feeding behaviour since diet is varied. Ruminants can be categorised by rumen morphology and size in relation to body volume (Hofmann 1973) and this provides a more useful interpretation of observed diets and feeding behaviour. Hofmann recognised three categories: unselective "bulk feeders" like buffalo; "Intermediate feeders" such as reindeer, in which the rumen mucosa can change to accommodate changes in dietary quality, and "concentrate selectors" like roe deer, dik-dik and giraffe. Concentrate selectors have small mouth-parts facilitating food selection and a low rumen capacity in relation to body size. Food has to be highly nutritive and digestible so that the rate of flow through the relatively small rumen is high enough to maintain metabolic requirements.

Roe deer are therefore, highly selective feeders, and diet in a locally reflects selection and not simple availability. Roe would be expected to prefer high quality food items, although the specific factors influencing preference have not been identified. Szmidt (1975) demonstrated preference by offering a choice of foods to captive roe To test whether roe select high energy foods, Perzanowski (1978) deer. examined the effect of dietary composition on energy balance in winter, basing energy requirements on data from Weiner (1977). The lower digestibility of food plants in winter (Bobek et al. 1974, see also chapter 5) has energetic consequences for small concentrate selectors, whose metabolic rate is high because it is proportional to body weight0.75 (Kleiber 1961). Perzanowski offered captive deer diets where herbs varied from 0-100%, and measured digestible energy intake, concluding that herbs must constitute at least 55% of dry matter intake for roe to be in energy balance. There are obvious limitations in this research: captive deer were used; costs of foraging were artifically equal for different food plants; and food offered may not have been typical. But the results are interesting, because they suggest that deer in many populations studied would be in negative energy balance throughout the This is supported because mortality occurs predominantly in late winter. winter and is highest in severe winters when snow restricts access to herbs and grasses.

Maximising digestible energy intake is an inherently attractive explanation for food preferences, but requirements for other nutrients may also influence food selection, as shown in other ungulates by Westoby (1974).

Diet has evidently received more attention than other aspects of roe deer ecology, but there is no literature relating diet of free-ranging roe deer to forage status, nor any studies of habitat use for feeding in relation to forage quality or availability. Two aims were therefore identified for this chapter:

- 1. To establish the major components of diet at Porton and to relate these to forage availability and nutritive value.
- To relate patterns of feeding use of habitats at Porton (Chapter 3) to food quality and abundance.

Diet at Porton was determined by vo methods: analysis of plant fragments in rumon samples (from deer culled over the ranges) and in faecal samples (collected from the study area). Direct observation was not used because of the difficulty in distinguishing exactly which plant species are being taken from a community (Prior 1968).

6.2 METHODS: Dietary analysis of faecal and ruminal samples

6.2.1 Reference material

Dried plant specimens from Porton and an illustrated flora (Keble-Martin 1965) were used in rumen analysis.

For faecal analysis, a collection of cuticular fragments was prepared from fresh leaves of 60 species. Leaves were ground in water using a pestle and mortar, and cuticular fragments were isolated under a low power binocular microscope (Kyowa 7-45X). Cuticle is recognisable by its regularity and single cell thickness. Fragments were mounted in glycerine gel and photomicrographs (X200) were made for easy reference.

6.2.2 Level of identification

The reference collection and the key prepared by Hosey (1974) showed that identifying fragments from faecal samples would be time consuming and would involve an unacceptable level of subjectivity. Broad categories were selected with distinct cuticular characteristics and biological relevance:
- a) browse species (conifers and broadleaves species) characteristic cell-type: epidermal cells and stomata in straight rows, small cells, thick walls. Or, epidermal cells not in straight rows, walls straight or curved, cells small with irregular stomata.
- b) grass species
 epidermal cells and stomata in straight rows but cells large with thin walls and small guard cells
- c) forbs and ferns
 epidermal cells (and stomata, if present) not in straight rows,
 walls either straight or involuted, cells very large.

In rumen analysis, conifers and broadleaved species were separated. In both methods, presence of individual species was recorded If particles were unequivocally identifiable.

6.2.3 Rumen analysis

Rumen samples were obtained from 66 deer (19 female, 47 maca) culled over the Porton Ranges between 1978 and 1980.

Rumina were agitated to homogenise their contents before sampling as settling may occur during the 48 hour storage period. The sample (250 cm^3) was stored in 10% formalin. In the laboratory, samples were again homogenised before sub-sampling and washing through a 2 mm sieve, to remove smaller particles that cannot be identified. Dirschi (1962) and Owaga (1968) showed that this did not significantly affect the Poportion of different items in the diet. A 10 ml sample of the washed residue was spread on a white tray ruled with a 2 cm grid. Frequency of Occurrence of different forage categories was scored by identifying each particle in contact with the grid.

The probability of scoring hits on the grid depends on particle size, which may vary between species if plants fragment differently. To correct for this, particles from each plant group were removed and stored during analysis, so that the number of hits/unit volume of each plant group could be determined. Further details of this volumetric correction are given in Staines and Crisp (1978).

6.2.4 Faecal analysis

Collection of faecal samples from quadrats was described in 3.2.3. Pellets were also collected each month from farmland at Porton. For dietary analysis, 5 pellet groups were used each month, representing all habitats in the study area.

Five pellets from each group sampled were ground in a pestle and mortar with 0.1 N NaOH and left to stand for 24 hours, so that fragments cleared and separated. Samples were then agitated and allowed to settle and the smallest particles (remaining in suspension) were decanted. This procedure was repeated five times for each sample using water to replace the supernatant. Remaining fragments were transferred to a 9 cm petri dish, scored with a 1 cm² grid. Particles in contact with the grid were identified using a Kyowa zoom (7 – 45X) binocular microscope, and allocated to categories in Section 6.2.2. Non-epidermal fragments and those that could not be allocated with certainty to a category were not scored. Three replicates were analysed for each pellet group. Results are presented as means.

6.3 RESULTS AND ANALYSES

6.3.1 Diet of roe deer at Porton

a) Rumen analysis

Rumen samples were obtained from deer culled in 1978-1980 from the entire area of the Porton Ranges. Samples from does were collected between November and February 1978/79 and 1979/80 samples from bucks between May and June in 1979 and 1980. Doe rumen samples interefore represent winter diet, buck samples diet in early summer.

The composition of analysed rumen samples is shown in Tables 6.1 (females) and 6.2 (males). There was a strong tendency for individual rumina to be dominated by a single species and so the correction for particle size was not used. In all 66 rumen samples examined, one food category accounted for >50% of particles and in over half the samples, one category accounted for >90% fragments. These tendencies were more pronounced in rumen samples from females than those from males.

TABLE 6,1

RESULTS FROM ANALYSIS OF RUMEN SAMPLES FROM CULLED

FEMALES AT PORTON DOWN

November-February 1978/79 and 1979/80

Location	Date	Pe	rcentag	e compositi	on	Dominant
	} = same } group	Grasses	Forbs	Deciduous	Conifers	species
	.				• • • • • • • • • • • • • • • • • • •	<u></u>
Bl a kes Firs	28,1,79	-	-		100	Yew
	и	-	_	4	96	?
	24.2.79	-	2	7	91	Scot's pine
	10.2.80	-		1	99	Scot's pine
40 acre pl.	3,2,79	-	-	16	84	Scot's pine
	24.2.79	3	-	1	96	Juniper/Yew
Boscombe Dn	13.1.79	15	-	60	26	?
Porton Down	27.1.80	-		1	99	Juniper
		_	_	3	97	Juniper
]	2	-	-	98	Juniper
	л	100	-	-	-	Lolium
Roche Court	20.1.79	100	_	-	-	Lolium
	24.2.79	33	-	9	58	?
	13,1,80	100	-	-		Lolium
	26.1.80)	100	-		-	Lolium
	н (100	-	-	-	Lolium
	, 20.1.79	82	1	1	17	?
	28.1.79	-	_	_	100	Yew
	1)	1	1	1	97	Yew+Scot's pine
	27.1.80	-	-	-	100	Yew+Scot's pine+juniper
	n	-	-	5	95	Yew+Scot's pine
	2 2 80	8		58	33	?
IOW HILL	2,2,00	39	-	52	9	?
	42.4.13	78	-	6	16	?
	11 14	19	-	15	66	Scot's pine + Yew
		1	-	-	99	Yew
	H 11	100	-	-	-	Lolium

TABLE 6.1 (continued)

RESULTS FROM ANALYSIS OF RUMEN SAMPLES FROM CULLED

FEMALES AT PORTON DOWN

November-February 1978/79 and 1979/80

Location	Date	l Pe	ercentag	on	Dominant		
	} = same group	Grasses	Forbs	Deciduous	Conifers	species	
	19.11.79	41	_	59	-	?	
		16	4	34	47	Scot's pine +Yew+Sycamore	
	11	14	-	53	33	?	
	13,1,80	95	-	5	_	Lolium	
	n	89	-	-	-	Lolium	
New							
Plantation	20.1.79	5	1	7	87	?	
	28,1,79	-	-	3	95	Yew	
	13.1.80	100	_	-	-	Lolium	
Winkerslow							
Firs	13,1,80	2	-	30	68	?	
	13,1,80)	27	-	1	72	Juniper+Yew	
	13.1.80	40	-	3	57	Juniper+Yew +Wheat	
	10.2,80	97	-	3	-	Wheat	
	1€ 2,80)	98	-	1	1	Wheat	
	16.2.80)	99	1	-	-	Wheat	
Battery							
Hill	20.1.79)	100	-	-	-	Lolium	
	20.1.79	95	-	5	-	Lolium	
	20,1,79	100	-	-	-	Lolium	
	3.2.79	99	-	1	-	Lolium + Agrosti s	
Unknown	3 19 78	7	-	51	41	?	
	9.12.78	82	-	17	1	Wheat	

TABLE 6.2

RESULTS FROM ANALYSIS OF RUMEN SAMPLES FROM CULLED MALES AT PORTON DOWN May-June 1979 and 1980

Location	Date	Pe	rcentag	e compositi	on	Dominant	
	·····	Grasses	Forbs	Deciduous	Conifers	species	
Blakes-							
Fire	21 4 79	8	92	-	-	?	
+/	21,4.75	82	18	_	1	· ?	
14	21.5.15	24	65	1	_	ว	
ta .	2.0.79	54	24	-		r -	
	28.6.79	76	40	-	-	?	
	25.5.80	54	40	7	-	?	
Roche -						••	
Court	27.4.79	98	2	-	-	Wheat	
11	12.5.79	46	54	-	-	?	
IOW Hill	12.5.79	25	53	22	-	?	
u	18.5.79	5	76	19	-	?	
41	18.5.79	6	94	-	-	?	
*1	19.5,79	45	54	-	1	?	
н	10.6.79	17	83	-	-	?	
n	15,6. 7 9	56	44	-		?	
11	30,6,79	7	93	-	-	?	
New-							
Plantation	26.5.79	87	13	-	-	Barley	
14	27.5.79	38	59	3	-	Wheat	
Winterslow.	-						
Firs	9.6.79	7	93	-	-	?	
Tower Hill	30,6.79	17	83	-	-	?	
Unknown	?	33	67	-	-	?	

Diet varied between individuals. Animals shot in the same locality on the Ranges tended to have similar diets. It is clear that conifers were the major food source of females in areas like Blake's Firs, Forty Acre plantation and Isle of Wight Hill (Table 6.1). Grazing on farmland occurred in several areas and agricultural crops were identified in 31% of rumen samples.

Rumen samples of males and females were different: Male diet was less variable and showed no clear differences between areas. The mean proportion in each food class for both males and females, is shown in Fig. 6.1. There are clear differences in diet between summer (males only) and winter (females only). Although the proportion of grass in the summer and winter samples was not significantly different (Mann-Whitney U Test, U = 433.5, $n_1 = 19$, $n_2 = 47$, ns), the proportion of both browse categories was lower in summer (decidous, U = 257, $n_1 = 19$, $n_2 = 47$, p < .01; coniferous U = 170, p < .001) and the proportion of herbs was clearly much higher in summer (U = 25, $n_1 = 19$, $n_2 = 47$, p < .001).

Rumen contents of individuals culled from the same feeding group were similar. There were six occasions when more than one female in a group was culled (Table 6.1). In four cases, we females shot together were of different ages (mature and subadult) and rumen contents were identical. Both members of the other groups were mature, and diets were similar.

b) Faecal analysis

There was little variation between the replicates of each pellet group, but diet of individuals was varied within most months (Table 6 3). Variation between months was however significant for all three food classes (Kruskal-Wallis one-way Anova: grasses, H = 21.45, N = 12, $p \le .02$; herbs H = 27.18, N = 12, $p \le .01$; browse, H = 25.41, N = 12, $p \le .01$).

There were no significant changes between adjacent months in the grass or browse categories. However the proportion of herbs increased significantly in April/May (U = 2, $n_1 = 5$, $n_2 = 5$, p < .05) and decreased significantly in June/July (U = 0, $n_1 = 3$, $n_2 = 5$, p < .05), and September/October (U = 1, $n_1 = 5$, $n_2 = 5$, p < .05). Fig. 6.2



Fig. 6.1. Percentage diet of roe deer at Porton determined by analysis of rumen contents. (a) Males (summer); (b) Females (winter)

TABLE 6.3

FAECAL	ANALYSIS	RESULTS	FROM	PORTON

Month	N	Browse	Grasses	Herbs
М	5	39.9 ± 13.1	50.0 ± 14.8	9.4 ± 6.0
A	5	50.7 ± 11.0	46.2 ± 9.5	0.9 ± 0.9
М	5	28.1 ± 10.5	61.4 ± 10.4	8.4 ± 3.4
J	3	1.3 ± 0.4	3.3 ± 1.9	95.4 ± 1.2
J	5	8.5 ± 2.2	55.2 ± 18.8	35.8 ± 19.5
A	4	5.4 ± 2.0	92.0 ± 2.8	2.7 ± 1.1
S	5	22.0 ± 10.7	58.8 ± 17.8	18.2 ± 9.1
0	5	35.8 ± 12.1	62.6 ± 12.0	1.1 ± 0.7
N	5	32.6 ± 7.0	65.0 ± 7.5	1.9 ± 1.7
D	5	37.1 ± 8.5	46.8 ± 8.7	16.0 ± 12.8
J	5	27.3 ± 4.7	60.0 ± 6.6	11.9 ± 6.0
F	5	17.1 ± 7.2	81.0 ± 7.3	1.1 ± 0.2
MEANS				
ot-Mar	ch:	31.6 ± 3.7	60.8 ± 4.2	6.9 ± 2.6
pri1-Se	ept:	21.3 ± 4.5	52.1 ± 6.8	25,9 ± 7.2

Mean % fragments \pm 1 S.E.

shows seasonal changes in diet by faecal analysis.

The most pronounced seasonal changes occurred between April and August, when the proportion of herbs increased. During the rest of the year, herbs constituted less than 20% of the diet. The proportion of grass varied less peaking in August at 74.3%. Browse peaked in April at 50.7%.

The species identifiable within each category changed with In winter, only ferns and mosses were identified in the season, herb component, but they were absent in summer when trichomes (unicellular structures with a characteristically spiked shape) The species from which trichomes originated were not predominated. determined but they are characteristic of broadleaved forbs. The only graminid species identified was wheat, which was the main component of the grass category in winter and spring, but was absent in summer Between August and October grass particles were increasingly months. fibrous but were not identifiable to species level. Browse species wer not positively identified in any months but there were no clear seasonal changes in composition of the browse category.

(c) Comparison of diet determined by faecal and ruminal analyses

The mean proportion of each food category in faecal samples from summer and winter are shown in Fig. 6.3. The six-month groupings are comparable to the seasons used in rumen analysis (Fig. 6.1). The relative proportion of food types differed between the two methods. Grasses were a larger proportion of the diet in the results for faecal analysis than from rumen analysis in both summer and winter. There were also differences between the results for the two methods for browse and herbs. Faecal analysis showed more herbs and less browse in the diet in winter than rumen analysis.

However, the two techniques showed similar changes in diet between Summer and winter. Changes in rumen samples were described above. For faecal samples the proportion of grass was not significantly different between summer and winter (U = 361.5, $n_1 = 27$, $n_2 = 30$, ns), but the proportion of browse was higher in winter (U = 247, $n_1 = 27$, $n_2 = 30$, p < .02) and the proportion of herbs was higher in summer (U = 277, $n_1 = 27$, $n_2 = 30$, p < .05).



Fig. 6.2. Annual diet of roe deer at Porton determined by faecal analysis (mean \pm SE).



Fig 6.3. Percentage diet of roe deer at Porton determined by face 1 analysis

6.3.2 Relation of seasonal diet to seasonal quality and availability of food.

The first aim of this chapter was to determine seasonal diet and relate it to seasonal quality and availability of food. Faecal analysis results will be used for three reasons: They cover the entire year, whereas rumen samples cover parts of the year; both sexes were represented, and faecal samples were collected from the study area (to which vegetation data apply) whereas rumen samples came from the whole range.

Dietary and vegetation data do not correspond directly, because different categories were used. Data on browse species were compatible, but other vegetation data applied to communities (such as grassland, woodland ground flora) and not to food types to which plant fragments were assigned in faecal analysis. Presence/absence of key species

was used in conjunction with data on habitat use (Chapter 3) to deternine the most appropriate vegetation data to correlate with the grass and herb categories in faecal analysis. The vegetation data appropriate to dietary categories are shown in Table 6.4.

Spearman rank correlation coefficients were calculated for each food type between the monthly proportion of diet and food availability/nutrient data. Values of r_s are given in Table 6.5. There were no significant correlations and very few coefficients approached significance.

6.3.3 Relation of habitat use to seasonal food availability and quality within habitats

The second aim of this chapter was to investigate relations between seasonal changes in habitat use and forage status within habitats. In this section, this relationship will be examined within habitats, considering seasonal changes.

Three indices of use are applied to each habitat:

D Number of deer feeding as a proportion of the total occupying the habitat. This is used to show whether the tendency for deer with a habitat to feed is correlated with food availability/quality.

TABLE 6.4

PORTON VEGETATION DATA USED TO CORRELATE WITH DIET

Month	Veg. data corresponding	Veg.data corresponding
	to "grass" category	to "herb" category
М	winter wheat	woodland
A	winter wheat	woodland
М	winter wheat	grassland
J	grassland	grassland
J	grassland	grassland
A	winter wheat	wheat under-storey
S	winter wheat	stubble
0	grassland	stubble
N	grassland	stubble
D	winter wheat	woodland
J	winter wheat	woodland
F	winter wheat	woodland

$\frac{\text{CORRELATION COEFFICIENTS (}r_{_{S}}\text{)} \text{ Between the proportion of food}}{\text{CATEGORIES IN THE DIET (DETERMINED BY FAECAL ANALYSIS)}}$

AND NUTRIENT CHARACTERISTICS

(Sample size in parenthesis); * p < .05

					Dietary Ca	ategory		
Proportion	in di	et	Grass	ses	Herl	bs	Browse	
correlated	with:							
standing	crop		. 235	(12)	.310	(12)		
productiv	vity		231	(12)	.092	(12)	_	
nitrogen			312	(12)	635*	(12)	.082	(11)
phosphoru	15		252	(12)	-,516	(12)	.160	(11)
potassium	n		112	(12)	343	(12)	.059	(11)
calcium			294	(12)	123	(11)	364	(11)
magnesium	ı		.060	(12)	552	(10)	083	(11)
% digesti	.bilit3	,	382	(10)	126	(9)	600	(4)
dig x N			467	(10)	533	(9)	. 200	(4)
" P			406	(10)	400	(9)	.400	(4)
o K			249	(10)	317	(9)	800	(4)
" Ca			455	(10)	167	(9)	- , 800	(4)
" Mg			152	(10)	217	(9)	600	(4)
"st.	crop		.365	(10)	017	(9)		
st.crop X	N		. 217	(12)	088	(12)		
**	Р		.161	(12)	035	(12)		
	К		. 217	(12)	028	(12)		
4	Ca		.189	(12)	.091	(12)		
11	Mg		. 280	(12)	.146	(11)		
st.∈ op x	dig. x	N	.127	(10)	150	(9)		
		Р	030	(10)	017	(9)		
11	ц	к	030	(10)	083	(9)		
	4	Ca	.164	(10)	150	(9)		
11	11	Mg	.382	(10)	- ,083	(9)		

ii) Number of deer feeding in a habitat as a proportion of all deer feeding in the month (equivalent to Hunter's index, used in Chapter 3 to determine feeding preference). This is used to show whether feeding preference for a habitat varies with its forage status.

 iii) Number of deer occupying a habitat as a proportion of deer occupying all habitats. This is again equivalent to Hunter's index, but uses total number rather than number feeding. Correlations with this index show whether preference for occupying habitats is influenced by forage status.

Correlation coefficients were calculated between monthly values of these indices and monthly values of vegetation parameters (Table 6.6). There were no consistently significant relationships between any of the indices and any of the vegetation parameters tested.

6.3.4 Relation of preference for feeding within months to the relative levels of nutrients and availability of forage in habitats

The relationship between habitat use and forage status is examined within months, to see whether feeding preference within a month was related to the value of forage within habitats. Feeding preference was used because it incorporates relative areas of habitats sampled.

Correlations were calculated between preference and vegetation parameters as in the preceeding section. There were again no consistent patterns of correlation and most coefficients did not approach significance (Table 6.7).

6.3.5 Relation between the use of habitats for feeding and the levels of digestible and available nutrients within months

In the previous section, there were no consistently significant correlations between feeding preference and standing crop, digestibility or any single nutrient. Preference for habitats varied however with season (Chapter 3) and it is possible that preference changes in response to

TABLE 6.6

CORRELATION COEFFICIENTS (r_s) BETWEEN INDICES OF HABITAT

USE FOR FEEDING AND OCCUPANCE AND MONTHLY VALUES OF AVAILABILITY AND QUALITY OF FORAGE WITHIN HABITATS N = 12 unless stated otherwise, * P<.05; ** P<.01

Index ⁺	Forage Char.	Pasture	W.Wheat	Sp,Barley	Seedgrass	Grassland	Woodland
Feed/	st.crop	408	712*	252	600*	422	256
Total	prod	589*	197	158	197	864(11)	**~ 123(11)
**	N	.342	.175	.523(11)	.595*	.018	322
**	Р	.750**	.124	.382(10)	.483	230	. 411
**	К	. 369	015	.254(11)	, 329	459	385
**	Ca	157	.018	.397(11)	.364	168	.312
**	Mg	218	.126	.566(11)	. 403	199	. 229
**	%dig	081	.226	0 (5)	.196	238	. 252
11	%digxN	.388	.175	0 (5)	. 564	252	. 329
Feed/	st.crop	739**	. 572	195	353	.105	.175
Mfeed	prod	-,400	370	055	.135	.127(11)	.201(11)
**	N	.644*	.307	.495(11)	. 207	144	.210
"	Р	.458	. 272	,277(10)	.211	.113	. 295
11	К	058	. 466	.242(11)	067	.189	.259
**	Ca	392	.012	.317(11)	.242	284	.112
**	Mg	390	.178	.440(11)	-,181	.067	.095
**	%dig	385	.342	0 (5)	039	,245	.126
17	%digxN	.182	. 318	0 (5)	. 280	.035	, 224
Total/	st.crop	676*	.740**	. 332	049	.060	645*
Itotal	prod	336	190	. 530	.189	.109(11)	206(11)
.,	N	.636*	.169	.251(11)	056	. 039	042
11	Р	. 359	.138	.152(10)	.004	.174	214
**	ĸ	193	.381	.247(11)	217	.151	490
11	Ca	389	046	.002(11)	.042	336	291
**	Mer	383	.057	.009(11)	468	057	394
*1	~~∍ %diø	448	.176	.051(5)	133	.119	427
11	%digxN	.056	.169	.051(5)	.035	0	245

+ Feed = no. deer feeding habitat; Mfeed = deer feeding in month Total = all deer occupying habitat; Mtotal = all deer seen in month

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						FOR	HABITATS AN	VD RELATIVE	LEVELS OF	NUTRIENTS					
	Prefere	ence					AND AVA	AILABILIT	THIN MONTH	HS					
	correls	ated								1					
	with:		W		۷	W	Ŀ	ъ	A	S	0	z	-	•-	6
~	st.crop		.371	•	486	.086	143	203	.116	203	.771	. 377	435	725	101
	productivity		100((4)	429	.029	-,543	-,088	.493	464	- 114 -	. 203	- 103 -	412	464
9 # N	N		200	ŗ	543	771	600	.319	.551	638	.086	.029	464 -	100(5)	
unless	Ω.		200	ŕ	429	600	943**	900*(5)	029	-,174	.086	257	- 265 -	051(5)	506
stated	×		.314	ï	200	600	714	.029	.406	261	.086	. 257	- 319		202.
other-	C	_	.143	•	371	.257	600	279	-,667	.074	.314	. 543	522	(3) 0	058
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CORRELATION COEFFICIENTS (rs) BETWEEN FEEDING PREFERENCE

* p < .05, ** p < .01

interactive effects between nutrients and either digestibility and/or standing crop.

The density of a nutrient within a habitat may be indicated by the product of standing crop and nutrient level (units are mg nutrient per unit area), and this may be more biologically meaningful than nutrient level (mg g^{-1}). Similarly, the dry matter per unit area available to deer may be more accurately represented by the product of digestibility and standing crop.

There may not be a simple relation between digestibility and nutrient accessibility: nitrogen for instance is present in both cell walls and contents, but may not be distributed evenly between the digestible and non-digestible components. However the amount of a nutrient available will depend on the bulk of food that can be processed by the digestive system. Hence the product of nutrient level, standing crop and digestibility may be important to feeding preference, regardless of the distribution of nutrients in relation to digestible fibre.

This analysis considers the influence of 'obtainable nutrients' (as above) on habitat preference within months. Correlations were calculated within each month between feeding preference for habitats and nutrients per unit area (nutrient level x standing crop), dry matter digestible per unit area (% dry matter digestibility x standing crop), digestible nutrients (% digestibility x nutrient level) and available nutrients (% digestibility x nutrient level x standing crop). Table 6.7 shows the coefficients and significance values obtained. There were no consistently significant correlations and few values approached significance.

6.4 DISCUSSION

6.4.1 Diet

(a) Rumen analysis

Diet varied considerably between individuals but most samples were dominated by a single food plant. Winter diet was composed mainly of grass crops, like rye-grass, or conifers such as yew, Scot's pine and juniper. Broadleaved species formed a minor part of the winter diet.

Summer diet was composed mainly of either grasses or forbs. The proportion of grasses did not change significantly between the summer and winter samples, whereas the proportion of forbs was significantly higher and the proportion of both conifers and broadleaved species were significantly lower in the summer samples. However within the grass category, agricultural crops were less common in summer (17%) than in winter (31%).

There was a clear tendency (especially in winter) for diet to differ between localities. Females shot on isle of Wight Hill had fed mostly on conifers while those shot about i km away on Roche Court Down had fed mostly on farmland. This tendency was not apparent in summer, possibly because sample size was lower and fragments were less frequently identified to species level. Females shot in the same group had very similar diets, probably reflecting similarities in the availability of food, possibly enhanced by constraints on feeding within the same social group. This effect was not examined within the male samples because there was only one occasion when more than one male from a group was culled.

The composition of rumen samples is influenced by several factors. Sex difference in diet might be expected because roe are sexually dimorphic: as males were only shot in summer and females only in winter it was not possible to distinguish sex differences from seasonal changes. However, faecal analysis results and published literature (op. cit) show seasonal dietary changes, but in rumen samples from Porton these may have been either increased or decreased by sex differences.

The distribution of culling was highly skewed because stalkers surveyed the population and culled when weather was optimal. This had two effects on the sample. Firstly it reduced sample size within most months, so monthly dlet was not examined. Secondly, some viscera were discarded because too many deer had been culled to retain all Consequently samples were not obtained from all culled deer. viscera. in addition, most culling occurred at dawn and dusk, because at weekends the Ranges were used for recreation during the day. Since habitats are used at different times of day (Chapter 3), the diet determined by rumen analysis would favour food types occuring in open habitats such as farmland and young plantations. This tendency increased because stalkers concentrated on plantations and farmland in response to complaints of damage from foresters and farmers.

The predominance of single food species in most rumen samples suggests that they reflect the last feeding bout before death. It this is true, it would further bias diet towards food plants in open habitats because of the factors discussed above. However roe feed on more than one plant during a feeding bout (Prior 1968). Apart from deer culled while feeding on monocultures, the tendency for one species to predominate may therefore have been artificially increased by washing through a 2mm sieve. Dirschi (1962) and Owaga (1978) investigated the effects of washing through sieves of various sizes, but they considered only the bulk/roughage and intermediate feeders of Hofmann's ruminant categories. Since roe deer are concentrate selectors, the effects of sieve mesh size may differ.

(b) Faecal analysis

individual diets were varied within months, but the range of variation was lower than in rumen samples. Faecal samples probably represent a longer period of feeding than rumen samples, as they have spent longer in the digestive system. Individual variation within months might arise from sex or age differences. It seems unlikely that they are attributable to age, since rumen samples from females of different age within the same group were so similar. Pellets cannot be sexed reliably and so sex differences i diet cannot be evaluated by this method either. It remains probable that diets of individuals even from the same sex and age class may differ.

Variation in diet between months was greater than variation within The proportion of herbs varied more than the proportion of months. either grass or browse, reaching a peak of over 90% in mid-summer, but remaining below 20% throughout the rest of the year. The proportion of grasses was highest in August at over 90% and, apart from June, grasses formed the largest proportion of the diet, fluctuating around 50-60%. The proportion of browse peaked in April at 50% and was lowest during mld-summer, but remained around 30-40% through the winter. The species identified changed with seasons: wheat (the only identified grass species) was present in winter/spring, but was absent during the remaining months. The herb component contained ferns and moss during winter, and forbs (species unidentified) in summer. Although the species of browse particles was not clear, characteristic fragments were

recognisable that were present throughout the year.

Methodological problems are greater in faecal analysis than in rumen analysis. The small particle size hinders identification, and inaccuracies may arise if different cuticular patterns occur on adaxial and abaxial leaf surfaces (Stewart 1967). Stem fragments may also differ, but a comprehensive reference collection of all possible fragments was not feasible in this study.

Digestibility of different plants varies considerably (Chapter 5 and op. cit) and digestibility may also vary between parts of a single plant. Such variation would affect fragments in two ways: either smaller or fewer fragments might be produced from more digestible plants. Both possibilities would result in undercounting of more digestible species.

(c) Comparison of diet determined by the two methods

Rumen samples were drawn from the entire Ranges, so diet might vary more by this method, than from faecal analysis which was based on samples from the study area. The direction of changes between summer and winter was similar by both methods; the proportion of grasses did not change between summer and winter but the proportion of herbs increa ad in summer and the proportion of browse decreased. This suggests that seasonal changes in diet occur either in both sexes or that sex differences are small in comparison with seasonal changes.

The diets of roe deer at Porton appear quite distinct from diets described for other British populations of roe. In the New Forest and at Chedington, diet contained a larger proportion of broadleaved browse (bramble and rose), conifers were rarely consumed, and grasses were a minor dietary component (Hosey 1974, Jackson 1980). At Porton, the high proportion of grasses throughout the year reflects the dominance of grassland communities.

6.4.2 Relating diet to feed quality and availability

No significant correlations were found between the seasonal changes in the proportions of food categories in faecal analysis results and any of the measured aspects of food quality or availability. Several factors contribute to this.

The three categories used in faecal analysis were broad because

species are difficult to identify with certainty; the selection of food items by roe may however occur on a finer scale. Thus if deer response to changes in availability and/or quality by adjusting the proportion of a particular species in their diet, a corresponding change in the dietary proportion of a major food category may reploccur.

The nutrient categories were also broad and applied to communities. If deer select at species level or even for particular parts of plants, correlations with the nutrient data would be unlikely to yield significant values. An improvement would be to identify diet to species level by a more comprehensive faecal analysis and to assess nutrients for each food species separately.

Mean diet was used in the analysis, based on five samples per month. The variation in individual diet within months suggested that individuals select food differently either because they differ in their digestive physiology (as shown for Swedish roe deer by Cederlund and Nystrom 1981), or because availability of food plants varies between home ranges. Using means for food availability and quality, and for dietary composition may therefore obscure relationships.

A further error arises from the matching of nutrient and dietary data, because the categories were not directly comparable. The categories used in dietary analysis were plant types which were confined to particular communities. Matching data on the besis of species presence/absence and on habitat use assumes that a plant type is consumed in only one habitat, an assumption that is probably over simplistic in the present analysis.

6.4.3 Relating habitat use to seasonal changes in forage within communities

There were no obvious patterns of correlation found in this analysis and coefficients were generally low. This may be caused by factors other than responses to forage availability and quality affecting the number of deer occupying habitats. The index of preference would be affected by changes in population density caused by juvenile dispersal, natural mortality or culling, and by changes in visibility caused by behaviour or vegetation density.

Testing the hypothesis that seasonal changes in use will be related to food status assumes that food selection will occur on the same basis

throughout the year. This assumption may be false, because of changing nutritional requirements throughout the year in response to temperature, reproductive cycles and other factors.

The third inherent weakness in this analysis lies in not accounting for other influences on habitat selection. These might include cover for shelter and to avoid disturbance, the avoidance of biting flies and intra-specific competition for feeding, kidding and rutting sites. The relative importance of these factors would change seasonally and affect the number of deer feeding in, or occupying habitats confusing any relationship between the proportion feeding and forage status.

Relating preference for feeding within months to relative 6.4.4 levels of nutrients and availability of forage in habitats

There were again no consistent patterns of correlation between habitat preference within months and forage status. Examining feeding preference within months avoids the assumption that selection takes place on the same basis throughout the year, but the results are still subject to several sources of error. All habitats are not equally accessible to all deer because of the dispersion of home ranges and habitats. Apart from access, there is a differential cost in travelling to habitats that cannot be taken into account.

Nutrient measures may be too general, because they apply to communities. In addition, deer may not select habitats for feeding on the basis of single nutrients, standing crop or digestibility. This possibility was investigated by testing for correlations between feeding preference within months and products of nutrients, digestibility and standing crop. There were no consistently significant correlations and most coefficients would explain little of the variance in feeding preference. Once again, a probable explanation of these results is that the level of nutrient assessment was inappropriate for the level of food selection.

The preference index may be misleading, because it corrects for the relative areas of habitats sampled but takes no account of the heterogeneity of habitat use (Section 3.4.1). The index is therefore weighted towards small habitats that are not used patchily and consequently, rankings within a month may be biologically meaningless. The index may have confused relationships. The largest numbers of

feeding deer occurred in the habitat with the highest 'obtainable nutrients' in four months (March, April, August and January). In all these months there was a clear distinction between the most used habitat and other habitats: in March for instance, 62 deer were feeding on seed-grass compared with 29 on pasture and even less on other habitats. When the highest number feeding did not occur in the habitat with the highest 'obtainable nutrients' the differential between numbers feeding in different habitats was much lower, suggesting that selection was lower and that small errors in observations could completely alter the habitat rankings. This occurred in May, October, November and February, which were the months when the index of selection was lowest (Chapter 3). In June and July, grassland was used most for feeding and herbs formed the main Food selection by roe may therefore be more dietary component. pronounced at this time of year and so nutrient data on the grassland community may differ markedly from the actual nutrient value of food. There may also be strong selection pressures at this time of year associated with kidding and rutting that would influence the dispersion of deer between habitats.

Rankings may overlook important biological considerations. Standing crop for instance, varied from zero to over 60 g/250 cm² and within this range, the effect on foraging efficiency may be non-linear or fragmented. There is probably a threshold below which foraging efficiency is impeded and a value above which selective intake is profitable because of either species diversity (within communities such as grassland) or differences in the value of different parts of plants (within monocultures).

The correlations used in this chapter to examine forage characteristics that might be related to feeding ecology or diet may not be sensitive enough to show such relationships, given that only six to twelve points were used in non-parametric correlations. It would therefore be interesting to perform other analyses, such as modelling the foraging of a concentrate-selector, to find how closely individuals conform to Predictions. In some cases, deer were faced with a clear choice of food types with different values, for instance, how did deer with ranges centred on Thorny Wood and Winterslow Firs (Map 1) differ in their use of fields given that some but not all fields available were identical?

Factors influencing diet and feeding ecology are probably complex, and experimental manipulation would be an alternative appropach to

determine exact functional responses of roe deer to different feeding conditions.

CHAPTER 7

GROUPING BEHAVIOUR OF ROE DEER AT PORTON

7.1 INTRODUCTION

The social organisation of roe deer is interesting, and has been widely studied, because roe are territorial and more solitary than other British arvids. Prior (1968) regarded their social system as patriarchal, centred on adult males with most groups composed of a pair of adults with juveniles. However, this view does not explain variation in group size and composition.

Group size varies with season: roe at Gien Dye (Scotland) showed an annual cycle (Cumming 1966), varying from groups of up to 6 deer in winter, to smaller groups in spring and summer, and Bramley (1970a) described a similar cycle at Chedington (Dorset), with winter groups of up to 8 deer. Although seasonal changes in group size are evident in all populations studied, group size in winter appears to depend on habitat. Large winter groups on farmland in Czechoslovakia contained up to 89 deer, with a highest monthly mean group size of 16.3 in February (Zedja 1978). However the influence of habitat on grouping behaviour of roe deer has not been investigated. It is not known whether the same seasonal changes in group size occur in all habitats, or whether differences in winter group sizes between habitats also occur in summer. Groups are usually composed of a mixture of age and sex classes

Groups are usually composed of a strandgaard 1972), but adult males are (Cumming 1966; Bramley 1970a; Strandgaard 1972), but adult males are less frequently members of groups than other age/sex classes: they constituted 70% of solitary individuals on farmland in winter (Zedja 1978), and groups at Chedington never contained more than one adult male (Bramley 1970a). Interpreting group composition is difficult because few (Bramley 1970a). Interpreting group composition is difficult because few Individuals were marked in most of the populations studied (except Strandgaard 1972) and because relatedness between individuals is uncertain. These problems are unavoidable, as roe are difficult to mark Individually, and relatedness requires longterm observation, but it is practical to investigate how group size and composition varies with habitat and season. The main aims in this chapter are to investigate the influence of habitat, month and time of day on group size and composition. In addition, the spacing of individuals within groups will be examined and associations between marked individuals will be considered. The presentation is confined to the Porton study area, as too few observations were obtained from ChedIngton.

7.2 METHODS

Data presented in this chapter were collected on transects (3, 2, 1), by scans of fixed areas (4, 2, 1) and by observation while radio-tracking (3, 2, 2).

7.3 RESULTS AND ANALYSES

7.3.1 Defining groups

Previous research on roe deer has not defined "group", but used unspecified and probably subjective criteria to determine membership of groups. In this study, nearest-neighbour (NN) distances were recorded for all deer visible at each observation, and individuals were assigned to groups according to an arbitrary NN distance, derived by the method described in Clutton-Brock *et al.* (1982).

If individuals aggregate, they will be closer to members of their own group than to members of other groups. Hence, inter-animal distances will show an overall bimodal distribution, the lower mode corresponding to intra-group separation, the upper to inter-group distance. To save calculating all inter-animal distances, the NN distance of each animal can be measured in a fixed direction, since this also yields a bimodal frequency distribution (Slutton-Brock et al. 1982).

Fig. 7.1 shows the distribution of NN distances, measured in a northerly direction for all deer at Porton seen on each outing in March and April 1981. The lower mode (Intra-group distance) occurred at 10 m, and the bimodal division was between 45 and 55 m. The inter-group peak was less clear. Separating farmland and woodland/grassland had no effect on the distribution of NN distances, and so a separation of 50 m was used to determine group membership in all habitas.



Fig. 7.1. Distribution of nearest-neighbour distances measured in a northerly direction for deer seen at Porton in March/April 1981.

7.3.2 Variation of intra-group separation

For convenience, NN distances were assigned in the field to 3 categories: $\leq 10 \text{ m}$, $>10 \leq 20 \text{ m}$, $>20 \leq 50 \text{ m}$. Transect data were broken down by month, time period and habitat to examine changes in spacing within groups, using these categories.

1. Seasonal variation in spacing within groups

The distribution of individuals between the three NN categories changed significantly during the year ($\chi^2 = 140.327$, d.f. = 20, p < .001). Members of groups tended to be further apart in winter and spring (Fig. 7.2). In summer, both before and during the rut, NN distances diverged and members were either closer together or further apart, but seldom in the intermediate category. After the rut, the proportion of deer in category 3 (>20 < 50 m) decreased, and individuals maintained closer proximity to one another, but throughout the winter members of groups gradually separated, and the proportion in category 2 (>10 < 20 m) increased.

2. Diel variation in spacing within groups

The spacing of individuals within groups changed significantly with time period (χ^2 = 37.897, d.f. = 6, p < .001). Spacing varied little during daylight hours, but members of groups were more widely spaced at night.

3. The influence of habitat on intra-group spacing

There were signifiant differences over the year between habitats (χ^2 = 24.579, d.f. = 8, p < .01). Fig. 7.3 shows that members of groups were more widely spaced on seed-grass than in other habitats, and that groups were more compact in woodland.

Intra-group spacing was significantly associated with habitat in winter (December, January, February: $\chi^2 = 17.489$, d.f. = 8, p < .05), and in spring (March, April, May: $\chi^2 = 37.382$, d.f. = 8, p < .001), but not in summer (June, July, August: $\chi^2 = 3.439$, d.f. = 2, ns) or autumn (September, October, November: ($\chi^2 = 14.640$, d.f. = 8, ns).



Fig. 7.2. Seasonal changes in the spacing of individuals within groups at Porton: transects:March 1979 to February 1980 inclusive. Clear histograms indicate \leq 10 m; light shading > 10 \leq 20 m; dark shading > 20 \leq 50 m.



Fig. 7.3. Spacing of individuals within groups in different habitats at Porton: transects March 1979 to February 1980 inclusive. (P = pasture, C = cereals,

S = seed-grass, G = grassland, W = woodland).

4. The influence of group size on intra-group spacing

Spacing of members of groups was significantly related to group size $(\chi^2 = 80.655, d.f. = 14, p < .001)$. Fig. 7.4 shows the variation of intra-group spacing with changing group size at Porton. In groups of two, more individuals than expected were in the category >20 \leq 50 m. In groups of 3 to 7 deer, there was a tendency for an increasingly smaller proportion to be within 10 m of one another, but this tendency reversed in groups larger than seven.

7.3.3 Group size

Previous authors have used mean group size to describe the aggregative behaviour of roe deer (e.g. Bramley 1970a; Zejda 1978). However, mean group size is not a good measure, as small groups tend to be more common in a finite population than larger groups (Jarman 1982). A more appropriate measure is the size of group of the median individues, obtained by rankinggroup sizes for all individuals and taking the median value (Clutton-Brock *et al.* 1982).

1. Variation in group size between habitats

Table 7.1 shows group sizes for the median individual in each habitat by month. Observed group sizes varied significantly between habitats (Kruskal-Wallis one-way ANOVA: H = 55.012, N = 5, p < .001). In this ANOVA, observed groups of deer were assigned a rank from 1 - N(N = 857) and the mean rank calculated for each habitat. Mean ranks (Table 7.1) show that groups were smallest in woodland and largest on seed-grass. Differences in group size between habitats were more pronounced in winter and spring than in summer and autumn (Kruskal-Wallis one-way ANOVA) see p.76:



Fig. 7.4. Intra-group spacing of individuals against varying group size at Porton: transects March 1979 to February 1980 inclusive.

Month	Pasture	Cereals	Seed-Grass	Grassland	Woodlan
М	3	3	5	2.5	3
A	3	3	5	3	3
М	2	3	3	2	2
J	1	1	1	1	1
J	1	1	1	1	1
A	2	2	1,5	2	2
S	2	3	2	2	3
0	2	3	4	3	3
N	2.5	3	3	2	2
C	4	3	7	2	3
J	2	5	3	2	2
F	3	4	5	2	3
n	86	230	126	304	111
mean rank	371.94	460.61	544.67	371,94	368.40
1 I-way ANO	VA)				

GROUP	SIZE	OF	MEDIAN	INDIVIDUAL	IN	EACH	HABITAT	BY	MONTH

SEASON	MONTHS	<u> </u>	<u></u>	<u>Р</u>
Winter	Dec, Jan, Feb	33.751	5	<.001
Spring	Mar, Apr, May	40.086	5	<.001
Summer	Jun, Jul, Aug	5.23	5	πs
Autumn	Sep, Oct, Nov	10.04	5	<.05

Table 7.1 shows that the largest median group sizes occurred on seed-grass and cereals in winter (maximum 7 in December), and that median group size was one in all habitats in June and July.

2. Variation in group size between months

Group size varied significantly with month in all habitats except woodland (Kruskal-Wallis one-way ANOVA):

HABITAT	Ħ	N	P
Pasture	20.712	12	<.05
Cereals	58,618	12	<.001
Seed-grass	50.035	12	<.001
Grassland	56.144	12	<.001
Woodland	11.187	12	ns

Significant changes in group size between adjacent months occurred in the following cases (Mann-Whitney U test on adjacent months in habitats except woodland):

HABITAT	PAIRED MONTHS	<u> </u>	<u>n</u> ₁	<u>n2</u>	<i>p</i>	direction
Pasture	May-June	12.5	9	9	<.02	decrease
Cereals	May-June	147.0	18	26	<.04	**
	Aug-Sep	876.5	4 0	75	<.001	increase
Seedgrass	Apr-May	107.5	16	24	<.02	decrease
	May-June	15.0	6	16	<.02	**
	Dec-Jan	13.0	10	11	<.02	••
Grassland	Apr-May	457.0	33	44	<.01	"
	Oct-Nov	56.5	15	17	<.02	

Group size decreased between April and June: significant decreases occurred in April-May on grassland and seed-grass, and in May-June on all farmland. The only significant increase was on cereals in August-September.

3. Variation in group size with time period

Table 7.2 shows the group size of the median individual in each habitat by time period. Grassland was the only habitat where group size varied significantly between time periods (Kruskal-Wallis one-way ANOVA):

HABITAT	<u></u>	<u>N</u>	
Pasture	3,802	4	. 284
Cereals	1.827	4	.609
Seed-grass	1.646	4	.649
Grassland	8.545	4	.036
Woodland	1.548	4	.671

Groups on grassland were consistently smaller at night than during daylight.
TABLE 7.2

GROUP SIZE OF MEDIAN INDIVIDUAL IN EACH HABITAT BY TIME PERIOD

Dawn	Day	Dusk	Night
3	1.5	3	3
3	2	3	3
4	4	5	7
2	2	2	1
2	2	2	2
	Dawn 3 3 4 2 2	Dawn Day 3 1.5 3 2 4 4 2 2 2 2	DawnDayDusk31.53323445222222

7, 3, 4 Group composition

Composition of groups was examined using data from transects excluding groups in which any member was not sexed or aged. Groups were allocated to one of 7 categories:

- i) single adult male
- ii) single adult female
- iii) single juvenile of either sex
- iv) adult male and female without juveniles
- v) juveniles (>2, either or both sexes) without adults
- vi) adult female(s) with juvenlle(s) without adult male
- vii) adult female(s) with juvenlle(s) and adult male(s)

1. Seasonal changes in group composition

The monthly proportion of groups in each category is shown in Fig. 7.5. Group composition changed significantly with month ($\chi^2 = 192.803$, d.f. = 42, p < .001).

Adult males were members of only 17% of all groups recorded, and most bucks (73%) were solitary. Only two adult bucks were seen alone together (in September) but on three occasions two bucks were members of the same group including females and juveniles. Bucks were most solitary between June and August, and were seen in mixed sex/age groups most frequently in March.

Adult does were seen more than bucks, both singly and in groups. The percentage of solitary does increased from February to June, when 50% of sightings were of solitary does. Fewer solitary females were recorded in July, when single does were more frequently accompanied by an adult buck. Adult female(s) with juveniles were the most common grouping except between June and August.

Solitary juveniles were most common in May, most being subadult males, because they associated less than subadult females did with adult does. Groups of juveniles without adults were rare in summer and occurred more often in late winter and spring.



Fig. 7.5. Changes in the composition of groups of roe deer at Porton: transects March 1979 to February 1980 inclusive

2. Diel changes in group composition

There was no significant change in group composition with time period (χ^2 = 20.286, d.f. = 18, ns).

3. The influence of habitat on group composition

The proportion of groups in each category is shown by habitat in Fig. 7.6. Different group compositions occurred with significantly different frequencies in each habitat ($\chi^2 = 59.590$, d.f. = 29, p < .001). The percentage of solitary bucks was highest on grassland and lowest in cereals. Solitary bucks were common on seed-grass, although seed-grass was used little during mid-summer when most males were seen. A similar percentage of solitary does were seen in all habitats except seed-grass where less were seen. Soliltary juveniles, and groups of juveniles without adults occurred infrequently on farmland, and both were more common in woodland. Pairs of adults (male with female) were seen mainly in cereals but rarely on other farmland. The larger groups composed of adult female (s) with juveniles and adult male(s) were seen mostly on farmland, and rarely in woodland.

4. Associations between marked deer

Group composition was analysed, but marked animals are needed to examine which individuals associate and why associations occur. Two problems arise: relatedness between individuals was unknown, and because there were unmarked deer, some changes in association were inevitably undetectable.

Table 7.3 shows how many combinations of collared animals could occur each year at Porton, and how many were observed (frequencies are considered below). Few combinations were recorded and there were no obvious tendencies for particular age/sex classes to associate.

Association matrices are cumbersome and so are not presented. Frequencies of association between individuals were low: >60% of associations were observed only once or twice. Others usually accounted for most of the associations for an individual. For instance, 80% of sightings (n = 10) of doe 2 (subadult) in the first field season were with



Fig. 7.6. Group composition in habitats at Porton, transects March 1979 to February 1980 inclusive. (P = pasture, C = Cereals, S = Seed-grass, G = Grassland, W = Woodland)

	March 79 - Feb 80	March 80 - Feb 81	March 81 - Sept 81
Association:		·	
AM x AM	-	0/3	4/15
AM x AF	-	2/27	8/48
$AM \times SM$	-	0/11	4/15
AM x SF		0/3	4/24
AF x AF	4/21	3/28	0/36
$AF \times SM$	16/98	16/88	7/24
AF x SF	4/77	1/24	4/32
SF x SF	1/55	0/3	1/10
SF x SM	8/154	5/33	3/12
$SM \times SM$	4/14	7/55	3/3

SUMMARY OF ASSOCIATION BETWEEN MARKED DEER AT PORTON

DATES

Key:	numerator	=	no.	different	combinations	observed
	denominator	r =	no.	different	combinations	possible

A = adult

S = subadult

M = male

F = female

doe 6 (adult). These associations represented only 31% of sightings of doe 6, because after doe 2 dispersed, doe 6 associated with unmarked individuals. Certain individuals associated more than others: in 1979/80 adult doe 5 was seen on occasions in winter and spring with four other marked does, none of which were ever observed with any doe other than doe 5. Most associations occurred while deer were feeding, but only one association between adult males occurred while feeding; others involved aggressive encounters between territory holders.

7.4 DISCUSSION

7.4.1 Defining groups

The distribution of NN distances was bimodal, the trough occurring at 50 m, which was therefore used to determine membership of groups. This distance was also the critical separation for group membership of red deer on Rhum (Clutton-Brock *et al.* 1982), despite differences in body size, social organisation and habitat.

Peak intra-group NN distance was 10 m and NN distances extended above 400 m producing a less pronounced peak for inter-group separation. The tail of this distribution is extended by entire groups being hidden in areas of cover, but lower values in the distribution were not affected because visibility was good in grassland and farmland in spring when the data were collected.

The distribution was less clearly defined when farmland and woodland/grassland were separated, but the bimodal split was unchanged, suggesting that the NN distance critical to membership of groups does not depend on habitat. The distinct bimodal split when habitats were combined supports this. If the bimodal split occurred at different distances between habitats, it would be obscured when habitats were combined. The critical distance for group membership may change seasonally but was not examined because the influence of changes in vegetation density could not be controlled.

7.4.2 Spacing within groups

Within groups, nearest-neighbour distances were related to season, time-period, habitat and group size. The separation of members of

groups was larger in winter/spring than in autumn. In summer, individuals showed two tendencies, to associate closely (≤ 10 m,) or to be much further apart (>20 ≤ 50 m). Individuals may have changed groups more frequently in summer (and so have been recorded more often approaching the critical distance for group membership), or the function of individuals associating may have been different. Groups in summer were mainly adult (male with female) rather than female plus subadults, and were associated with mating behaviour rather than feeding.

Separation within groups across time periods varied significantly because individuals were more widely spaced at night. Deer were probably less alert at night and reduced wariness would lead to larger intra-group separation. In addition, most groups at night were on farmland where individuals tended to be more widely spaced.

Intra-group separation varied between habitats. Members of groups were most widely spaced on seed-grass and closest together in woodland. Intra-group distance in woodlind was subject to bias, because of dense cover concealing animals. However groups may be more compact in woodland for several reasons. Food distribution may affect separation and foraging patterns of individuals, and deer may respond to higher densities by aggregating more closely.

7.4.3 Group size

Group size varied significantly between habitats. Differences were most pronounce in winter and spring, and were not caused either by seasonal changes in habitat use, or by differences in visibility in habitats: significant monthly variation occurred in all habitats except woodland (where groups were small throughout the year).

Monthly variation in group size was similar in all habitats. Larger groups were more common in winter on farmland, but the median individual in all habitats was solitary in June and July. Group size decreased significantly between April and June, mainly on farmland, and increased significantly only between August and September. Although adults everywhere were accompanied by kids at this time of year, this increase was confined to cereals, because they were used heavily, and sample sizes elsewhere were too small to show significant changes. The effect was accentuated on cereals as visibility increased after harvesting.

In grassiand, diel variation in group size was consistent between

months, but in the other habitats, seasonal inconsistencies may have masked diel changes. Group size in grassland was lower at night than in other time periods.

Comparisons of group size between different studies are limited. Group size varies with habitat and month, but most authors (e.g. Cumming 1966; Bramley 1970a; Zejda 1978) quote mean group size which would be affected by the months and proportions of different habitats sampled. Reichholf (1980) also found similar group sizes between habitats in summer, which diverged sharply in autumn as group size increased on farmland.

7.4.4 Group composition

The most common grouping was an adult female with juveniles: usually a single adult female, but pairs of adult females with juveniles were observed. Adult does were more common (alone and in groups than adult bucks. Adult bucks were members of less than 20% of all groups (including single animals), and most adult males seen (73%) were solitary. Low male activity outside the rut may have contributed to the small number seen, or they may have been seen less if they prefer habitats with more cover than females. However, there was no evidence of segregation of the sexes between habitats, and since it is unlikely that adult males with antiers were misidentified, the reason why less bucks were seen than does was either lower activity, or an uneven sex ratio caused by lower male survivorship (Andersen 1953).

Grouping tendencies of juvenile males and females were different. Solitary subadult males were more common than solitary subadult females. This may reflect how easily subadult males and females could be identified: adult and subadult female body sizes were similar and so they may have been confused when there were no other age/sex classes for comparison. However, adult females were seen less frequently with subadult males than with subadult females.

Composition of groups changed significantly with month. The major differences were between June/August and other months. Throughout autumn and winter, groups were mainly composed of adult female(s) with juvenile (s). Solitary does became more common in March, as more juveniles were in groups without adults. By May, groups of juveniles had fragmented and single juveniles were common before dispersal. The

percentage of solitary does increased from March until June, and throughout the rut adult females were most frequently accompanied by an adult male (juveniles had dispersed and kids were relatively immobile until after the rut). Solitary bucks were more common immediately before and during the rut, than in other months. After the rut, group sizes increased once again as kids accompanied adults.

Group composition did not vary with time period, but was related to habitat. Solitary adult females were seen in all habitats, and they represented a similar proportion of groups in all habitats. Groups comprising adult female with juveniles also occurred in all habitats, but this category represented a larger proportion of groups on farmland than in wood ad. In contrast, solitary juveniles and juveniles without adults were rare on farmland, but were seen frequently in woodland, suggesting that their ranges were restricted to habitats with cover, unless accompanied by adults. Solitary adult males were seen mostly on grassland, although pairs of adults during the rut occurred mainly in cereals.

Associations between marked deer suggested that individuals did not associate widely with other members of the population. Individuals comprising groups changed at Porton, but unlike the Kalo population (Strandgaard 1972), most associations occurred infrequently. Capture locations and the different proportions of the Kalo and Porton populations marked would affect the number of associations that occurred. Functional explanations of those associations at Porton that did occur with higher frequency could only be speculative, as relatedness was uncertain and samples were too small to examine differences in association between habitats, seasons or time periods.

CHAPTER 8 THE INFLUENCE OF HABITAT ON THE SIZE AND DISPERSION OF HOME RANGES AT PORTON AND CHEDINGTON

8.1 INTRODUCTION

"Territory" is defined here as a fixed area, defended by a resident against intruding rivals. Territories are exclusive. The term will be applied only to adult males during spring and summer, when territorial behaviour occurs (Cumming 1966). The areas used by adult males outside this period, and used by other age/sex classes throughout the year will be referred to as "ranges", defined as the area an individual uses for normal activities such as feeding, maxing and rearing offspring (Brown and Orians 1970). Ranges are not exclusive. Other conspecifics are tolerated and so ranges may overlap. Ranges are annual unless described in a time-frame such as summer range.

Several studies provide information on territory and range size of roe deer. Their results are summarised in Figure 8.1. Most of the authors quoted in this section calculated areas using the minimum polygon (Stickel 1954), which is the convex shape enclosing the outermost loci where an individual has been recorded.

Both male territory and female range size differ between studies. The smallest were found at Chedington in data collected by Francis (Loudon 1979). The upper limit for female range size is undocumented because female ranges were not measured in the areas such as Gien Dye (Cumming 1966) and the Chizé forest in France (Sempéré 1980) where territories were largest. In most other studies, male territory size was slightly larger than female range size.

Different studies have produced conflicting conclusions about seasonal changes in male range size and position. Bramley (1970a) and Loudon (1979) found that winter ranges of males were almost identical to their territories, suggesting that seasonal changes in size and position do not occur in males. Their results differ from those of Strandgaard (1972), who found that males defended areas of farmland during the rut, but utilised areas of woodland at other times of the year, suggesting that territories and winter ranges are in different positions. Sempéré (1980) described a similar change for two radio-tagged males in the Chizé forest. Winter ranges were mapped by continuous, automated



radio-telemetry and both ranges increased in size in early spring. The failure of some studies to detect seasonal changes in range size of males may reflect inadequate sample sizes or methodology. The reasons for seasonal differences in the range size of males have not been investigated.

Most attention has been directed at male territory size because territorial behaviour is interesting and easily observed, but less is known about female range size. There are no clear indications of whether female ranges change with season. The absence of this information has not deterred some authors (e.g. Cumming 1966; Loudon 1979) from attempting to relate the configuration of male territories to the annual ranges of females. No firm conclusions about the breeding system of roe deer can be drawn from these comparisons, because territories and annual ranges of females may not correspond to one another if either or both change seasonally. However Cumming (1966) concluded that male territories are formed independently of female dispersion and this idea has since persisted in research on the spacing behaviour of roe deer (see Loudon 1979), although direct comparisons have not been made between the sexes at particular times of year.

The main aim of this chapter is to relate annual and seasonal range sizes to habitat and food resources. To achieve this, methods of determining range size will be explored and the effects on dispersion of age, sex, season, year, food resources and study area will be investigated.

8.2 METHODS

The methods of collecting data for home range analysis were described in Chapter 3. The data presented from Porton in the following section include both observations and radio-locations, while data from Chedington are almost entirely radio-locations because few marked deer were sighted.

8.2.1. Methods of determining range sizes

Previous studies of range size of roe deer (op. cit) have used the minimum polygon method of Stickel (1954), to determine range areas. This is a conceptually simple method enclosing an area within a convex hull drawn around the outermost loci. The estimate is oversensitive to movements at the boundary: and does not necessarily represent a minimum (Voigt and Tinline 1980), and is also sensitive to sample size. Other disadvantages of the minimum polygon are that it provides no estimate of activity centres, nor of intensity of use across an individual's home range, and as pointed out by Sanderson (1966), and by Don and Rennolis (1983), knowledge of the size, shape and position of an animal's range is of limited ecological value. Ranges or domains were originally defined by clear boundaries (Tanaka 1963), but recently they have been considered in terms of probability contours, enclosing a certain proportion of the locations (or sightings) of an individual.

Several models have been developed to describe the intensity of use of areas within the range (termed the "utilisation distribution". Van Winkle 1975). Parametric models assume a particular distribution of loci (e.g. the bivariate normal model of Jennrich and Turner 1969), but since real data seldom conform to these idealised distributions (MacDonald, Ball and Hough 1980), estimates of range size can be misleading. The non-parar tric method developed by Ford and Krumme (1979) makes no a priori assumptions about the utilisation distribution, but their ranges cannot be related to the real plane or habitat types.

Current non-parametric alternatives to the Ford and Krumme method use kernel estimators, e.g. Dixon and Chapman (1980). A more recent model-based approach by Don and Rennols (1983) is inappropriate to this project because it requires knowledge of "biological centres" such as nest sites. The following analyses of range size and activity centres are therefore based on the Dixon and Chapman (1980) method.

This method estimates the density of the distribution of data points and finds the position where the density is highest. Its advantage is that the centre of activity (the harmonic centre, Dixon and Chapman 1980) always lies in an area of high density, whereas the arithmetic mean (Hayne 1949) can lie in a completely unused area with certain distribution of loci.

The main inaccuracies in estimating activity centres and range area

by this method arise because of the computation grid which is necessary to plot contours (Spencer and Barrett in press). The original Fortran computer program ("Dixon") calculated function values at the intersection points of the computation grid. Function values were the first inverse moment, based on the sum of the reciprocal distances of data points from a particular point on the computation grid. Undue weight was given to points on the matrix if this distance was small, because large reciprocals are generated. Dixon and Chapman compensated by the addition of 1 to the distance (r) if r < 1.0, but because the relationship between the matrix and the data is unique to a given scaling value of the computation grid, large shifts in harmonic mean centre and the shape of contours occur when the scaling variable is altered. Spencer and Barrett found that errors depended on grid density, scale and the number and dispersion of animal loci, and that errors were largest if the centre of activity was not strongly dominant.

Such inaccuracies can be avoided by calculating the function values at the animal loci, so that the value and position of the harmonic centre is independent of the computation grid (values are then comparable between individuals and in time series analysis). However, computer contouring requires discrete gridded data and so the matrix must still be used. To reduce the disproportionate weighting of data points lying on or near grid intersections, Spencer and Barrett recommend translocating all data points to the centres of the computation grid cells in which they lie, before calculating function values. All data points are then equidistant from the nearest grid cell intersection and consequently none are disproportionately weighted.

The program "Dixon" was therefore modified in two major ways:

To calculate function values and centre of activity at the data points.
To translocate all data points to the centres of the grid cells in which they lie before plotting contours.

Further improvements were made as follows:

3. Plot the location of the harmonic mean centre of activity and the arithmetic centre.

A. Select the function values for contours based on the inclusion of specified proportions of the data points, rather than the trial-and-error

methods that were necessary with the original version.

5. Calculate the area (hectares) enclosed within contours drawn on the basis of (2) above.

6. To provide an option for plotting an isometric projection of the function values on the computation grid.

All programming modifications were written in Fortran. The program was run on an ICL 2970 mainframe at Southampton University computing centre and plots were produced on a Calcomp 1051 plotter.

8.2.2. Use of probability contours to define range area

Individual animals usually have characteristic home ranges, over which intensity of use varies. Occasional sallies may be made away from the normal range. Including all locations of an individual leads to over-estimates of range size and overlap between individuals. To avoid this, a proportion of the locations of an individual are used to define the typical range. As the proportion of peripheral locations excluded is increased, the area enclosed will decrease. If individuals use peripheral areas at a low intensity, a plot of area against the proportion of loci excluded will show a change in gradient when excluding further points starts to exclude areas used at a higher intensity (Clutton-Brock *et al.* 1982).

Fig. 8.2 shows the results of performing this analysis for individuals at Porton and Chedington on which most loci were obtained. The curves for the two study areas are similar, showing a sharp initial decrease as large, infrequently used areas were excluded. The gradient changed when 25% of loci were excluded suggesting that a contour enclosing 75% of the locations of an individual will exclude areas used infrequently. A second change in gradient appears when 50% of the loci are excluded, suggesting that this level is appropriate to define the core of an individual's range.

Throughout the following analyses, the home range area is defined by the contour enclosing 75% of the locations for an individual, and the core is defined by the contour enclosing 50% of locations.

A sample of the output from the range plotting program is shown in Fig. 8.3. This plot is of the loci obtained by radio-tracking Female 4 at Chedington in 1982 from August to November inclusive. It shows the range and core areas, the position of the activity centre, and the



Fig. 8.2. Change in the proportion of the total range that is included within concours as the percentage of outlying loci is increased.



Fig. 8.3. Home range map of Female 4 (adult, radio-tagged) at Chedington from August to November inclusive 1982. H1(X) = centre of activity, S (o) =arithmetic mean. Crosses indicate loci (note loci represented more than once are not distinguished). Outer contour encloses 75% of the loci (range); inner contour encloses 50% of loci (core). Axes are grid co-ordinates corresponding to Map 2. distribution of loci, although it is not possible to distinguish loci represented more than once.

8, 2.3. Correction factors for the influence of sample size on range area

Estimates of range area increase with sample size to an asymptote, when further sightings of an individual lie within the area already defined. It is important to assess the minimum number of locations which will accurately depict an individuals range since this value is probably unique to any study, depending on the ranging behaviour of the study animal, the sampling procedure and the characteristics of the plotting method. It is possible to estimate true range area when n is below the minimum (Village 1982).

To do this, individuals with a large number of observations were selected from both study areas. Data used from Porton covered spring/summer 1981 on 3 radio-tagged males and females; data from Chedington covered April 1981 to March 1982 inclusive divided into three 4-monthly blocks for one male and one female. For each individual varying percentages were subsampled from the data using the "SAMPLE" procedure in SPSS. Each subsample was run on the range plotting program to obtain an estimate of range area and core size for that number of observations. Range area and core size were plotted against sample size for each individual.

Fig. 8.4 shows range and core size against increasing number of loci for one female at Porton: areas increased to asymptotes at about 30 loci for the core and 50 loci for the range.

Village (1982) estimated the range area of individuals with small sample sizes, using a regression of the rate of increase to 15 observations against final range area for those individuals with adequate numbers of loci. By finding the rate of increase to 15 observations for individuals with small numbers of loci, Village used the regression line to estimate true range area. However, it was not necessary to use the rate of increase, since a regression of range size at 15 observations against final range size would produce the same results (all values on the x axis were divided by 15).

To estimate true range sizes at Porton and Chedington, Village's method was modified by fitting quadratic regression lines to the data on individuals with more than 40 loci (see Fig. 8.4). Range size for each



No. observations sampled

Fig. 8.4. The effect of increasing number of loci on range and core areas for F male 63 (subadult, radio-tagged at Porotn, March-June inclusi = 1981) showing fitted quadratic regression lines.

number of observations was plotted against the asymptote value, and a linear regression was fitted. Hence a series of linear regression were obtained, and these were used to estimate true range for individuals with 10-40 loci (Fig. 8.5).

8.3 RESULTS AND ANALYSES

8.3.1 Range size

Areas were estimated using the modified Dixon and Chapman program. Individuals were excluded from the analysis if they had less than 10 loci. Range and core areas were corrected by the method described above, if $10 \le n \le 40$. For n > 40, areas were not corrected as regression line slopes were close to one. Annual ranges (and March - September 1981, Porton) are given in Tables 8.1 - 8.4; seasonal ranges are given in Appendix 4, Tables 1-6.

Correlation coefficients were calculated between both uncorrected and corrected areas, and the number of loci (Table 8.5). Uncorrected range size was significantly positively correlated with the number of loci for females at Porton (adults + subadults) between March and September 1981. There were no other significant positive correlations and the correction method reduced all positive values. This suggests that the influence of sample size on ranges areas was not strong.

1. Annual range and core sizes

At Porton, annual range sizes were obtained for two years: April 1979 - February 1980 and March 1980 - February 1981. Range sizes are also presented compring the period March - September 1981.

In the first field season (March 1979 - February 1980), sufficient data were obtained to estimate range and core areas of five :dult females, four subadult females and three subadult males (Table 8.1). There were no marked adult males during this period. Mean corrected annual range size of adult females was 11.6 \pm 1.82 ha while that of subadult females was 12.2 \pm 3.7 ha and subadult males was 17.8 \pm 2.72 ha. Mean core areas (corrected) for this period were: adult females 3.3 \pm .53 ha; subadult females 5.4 \pm 2.7 ha; subadult males 4.5 \pm .63 ha.



Corrected range size (ha)

Fig. 8.5. Regression lines used to correct sizes of ranges (solid lines) and cores (dashed lines) for individuals having between 10 and 40 loci.

TABLE 8.1

RANGE SIZES OF COLLARED DEER AT PORTON

April 1979 - February 1980

				Areas	(ha)	
		No. of	Uncorr	ected	Corrected	l
Sex/Age	Deer	records	core	range	core	range
Adult	4	34	3.0	10.2	3.4	14.4
females	5	30	2.5	9.4	2.5	13.0
	6	39	4.2	11.1	4.4	12.7
	2 10	23	1.7	9.6	1.7	13.5
	16	23	2.9	4.3	4.4	4.4
Mean ± SE					3.3 ± .53	11.6 ± 1.82
Subadult	1	20	1.2	3.0	1.2	3.0
females	2	19	1.8	5.8	1.8	10.0
	9	20	5.3	10.9	13.0	15.8
	18	10	1.8	5.4	5.4	20.0
$\underline{\text{Mean}} \pm \text{SE}$					5.4 ± 2.7	12,2 ± 3.7
Subadult	1	26	2.8	8.3	4.1	13.0
males	3	13	2.0	6.7	3.6	18.0
} 	4	21	3.1	10.5	5.7	22.4
Mean ± SE					4.5 ± .63	17.8 ± 2.72

TABLE 8,2

RANGE SIZES OF COLLARED DEER AT PORTON

March 1980 - February 1981

				Areas	(ha)	
		No. of	Unce	orrected	Correct	ted
Sex/Age	Deer	records	core	range	core	range
4dul +	4	25	0.7	5 0	2.0	
Addit		20	4,1	5.9	3.8	7.8
females	6	12	2.3	3.1	3.6	8.0
	8	10	1.6	4,2	4.6	13.5
	10	17	3.3	5.3	9.8	12.4
	> 15	10	2.7	4.9	11.0	17.5
	16	13	1.3	4.8	2,6	17.0
	19	11	2.9	4.5	12.0	15.4
aan ± SE					6.8 ± 1.51	13.1 ± 1.50
١						
Adult	12	13	2.7	8,9	10.6	27.2
males	. 16	17	4.6	7.7	9.4	15.0
Mean					10.0	21.1

TUDUU 0.

RANGE	SIZES	OF	COLLARED	DEER	AT	PORTON
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March - September 1981 (* - radio tagged)

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				Are	as (ha)	
		No. of	Un	corrected	Correc	ted
Sex/Age	Deer	records	core	range	core	range
Adult	4	30	4.2	8.9	7.6	12.2
females	5	22	3.5	10.6	6,8	22.6
	6	15	3.5	8.1	10.8	24.0
	8	23	3.5	6.1	5,8	11.0
	10	14	2.2	5.3	4.4	12.4
	15*	62	7.7	13.7	7.7	13.7
	16	14	2.0	7.0	3.6	19.4
Mean ± SE					6.7 ± .58	16.4 ± 2.0
Adult	16*	74	8.9	21.9	8 .9	21.9
males	62*	81	3.8	11.2	3.8	11.2
ł	63*	61	4.5	13.2	4.5	13.2
Mean ± SE					5.7 ± 1.6	15.4 ± 3.2
Subadult)	61*	23	2.0	5.4	2.0	6.9
females	6 2*	56	5.3	12.9	5.3	12.9
ć	63*	40	5.7	13.3	5.7	13.3
	64*	21	5.6	10.5	14.0	22.2
<u>Mean</u> ± SE					6.8 ± 2.55	13.8 ± 3.1
Subadult	59	21	4.0	10.0	8.6	20.8
males	60	25	6.2	15.7	13.2	28,2
	61	26	5.0	10.8	9.8	18.0

Mean ± SE

 10.5 ± 1.38 22.3 ± 3.04

TABLE 8.4

ANNUAL RANGE SIZES OF RADIO-TAGGED DEER AT CHEDINGTON April 1981 - March 1983

Areas were not corrected as number of loci per individual was high. (All individuals were adult, M = male, F = female)

				Areas	(ha)
Deer	Da	te	No. loci	Core	Range
М1	April 81	- March 82	210	2.7	5.7
Fl	April 81	- M ar ch 82	213	5.9	12.1
F2	April 81	- March 82	222	1.5	4,6
F3	April 81	- Oct 81	54	2.5	5,9
		Mean (female)	± SE	3.3 ± 1.33	7.5 ± 2.31
		-			
M1	April 82	- March 33	228	3.3	9.7
МЗ	April 82	- March 83	305	3.3	7.6
Fl	April 82	- July 82	108	4.6	8.8
F2	April 82	- March 83	319	2,6	6.5
F4	April 82	- M ar ch 83	338	3.6	7.9
		Mean (female)	± SE	3.6 ± .58	7.7 ± .67

TABLE 8.5

CORRELATION COEFFICIENTS BETWEEN NUMBER OF LOCI AND RANGE SIZE

Study area	Age/sex class	Period covered	Range si	ze estimates	Corrected 1	range size
		Ν	H	<u>р</u>	54	
Porton	adult female		.70	3 ns	.512	, Ns
	juv. male+female	1979/80 7	.36	4 ns	356	2 8
	adult female	1980/81 7	. 69	2 ns	622	
	adult +juv. female	March-Sept 1981 10	.78	8 <.05	- 288	
	adult + juv. male	March-Sept 1981 6	65.	an o	- 590	
	adult females	summer/winter 79/80 6	. 58	on ns	.102	
	adult females	2-monthly 1981 10	. 33	ō ns	- 680	
	Juvenile females	2-monthly 1981 8	. 70	ns	.135	
	adult males	2-monthly 1981 11	. 22	a ns	152	
	juvenile males	2-monthly 1981 6	.75:	8u 18	. 499	80
Cheding ton	all individuals	annual range 81/83 9	.04	ងព		
	F1, F1, ¥2	2-monthly 1981/82 18	. 369	na		
	MI, M3	2-monthly 1982/83 11	450	ns		
	F2, F4	2-monthly 1982/83 12	, 096	ns		

In the second field season (March 1980 – February 1981) sufficient data were obtained to estimate range and core areas of seven adult females and two adult males (Table 8.2). Corrected mean range size of adult females was 13.1 \pm 1.50 ha; mean range size of adult males was 21.1 \pm 6.10 ha. Corrected core areas were 6.8 \pm 1.51 ha for adult females and 10.0 \pm 0.60 ha for adult males.

in the third field season (March - September 1981), all individuals for which ranges are presented were radio-tagged except six of the adult females (Table 8.3). Mean range size over this six month period was 15.4 ± 2.06 ha for adult females and 15.4 ± 3.28 ha for adult males. Mean subadult range sizes were 13.8 ± 3.15 ha for females and $22.3 \pm$ 3.04 ha for males. Mean core areas were $7.2 \pm .88$ ha for adult females and 5.7 ± 1.6 ha for adult males; 0.8 ± 2.55 ha for subadult females and 10.5 ± 1.38 ha for subadult males.

At Chedington, only adult deer were radio-tagged. Range and core areas are shown in Table 8.4. A larger number of loci were obtained per individual than at Porton and so corrections for sample size bias were unnecessary in estimating annual range sizes. Between April 1981 and March 1982, one adult male was successfully radio-tagged and found to have a range of 5.7 ha, with core of 2.7 ha. (The radio of the other male tagged in March 1981 was hard to locate and failed during the summer). Two adult females were tracked over the entire year producing range sizes from 4.6 to 12.1 ha. Two males and two females were radio-tracked throughout the following year producing a mean male range size of 8.7 ha (core 3.3 ha) and a mean female range size of 7.2 ha (core area 3.1 ha).

Mean uncorected male and female annual range sizes for both study areas are shown in Figure 8.1.

2. Seasonal range and core sizes

From the first field season at Porton, data on three adult does were divided to estimate for each individual the range and core areas in summer (April to September inclusive) and winter (October to March inclusive). Mean range sizes were 9.4 ± 3.41 ha in summer and 9.5 ± 1000

3.78 ha in winter. Mean core sizes were $2.7 \pm .47$ ha in summer and $3.3 \pm .96$ ha in winter (Appendix 4, Table 1). Sample sizes for other marked deer during this field season were too small to subdivide.

During the second field season all sample sizes were to small to carry out seasonal breakdowns.

Data from the third field season covered spring and summer (March – September 1981) but more data were obtained as most marked animals were radio-collared. Where sample size permitted, records on individuals were divided into two-month periods (Appendix 4, Tables 2 and 3). Since sample sizes were limited, months were paired with both the preceeding and following month. The effects of this are discussed in Section 8.4. Mean range size of adult females in March + April 1981 at Porton was 14.2 ± 2.34 ha with a mean core size of 3.3 ± 1.77 ha, and in April + May, mean range size of adult females was 14.0 ± 1.75 ha, with a mean core of 6.6 ± 1.32 ha. For subadult females, mean range size was 11.1 ± 2.33 ha in March + April and 13.5 ± 2.42 ha in April + May while the mean cores were 6.1 ± 1.88 ha and 6.2 ± 2.31 ha respectively.

In the third field season, two-monthly ranges and cores were determined in three adult males and two subadult males. For adult males, mean range sizes were 17.6 ± 4.74 ha in March + April, $8.7 \pm 2,69$ ha in April + May and 7.0 ± 2.15 ha in May + June, with core sizes of 8.4 ± 1.32 ha, 3.3 ± 0.79 ha and 3.2 ± 1.25 ha respectively. For the two subadult males, mean range sizes were 13.8 ha in March + April, 20.6 ha in April + May and 17.3 ha in May + June, and cores were 8.1 ha, 5.7 ha, and 11.5 ha respectively.

The larger sample sizes obtained for radio-tagged deer at ChedIngton were split into two-month periods between April 1981 and March 1983. Results for the first year of this period are presented in Appendix 4. Table 4, for the three individuals on which data were obtained throughout the year. Range size varied between 6.8 ha in June + July to 3.3 ha in February + March for male 1; between 12.2 in August + September and 5.0 ha in June + July for female 1; and for female 2 between 6.0 ha in April + May and 1.8 ha in December + January.

In the second year of radio-tracking at Chedington sufficient data were obtained on two males and two females. Results for males are presented in Appendix 4, Table 5, those for females in Appendix 4, Table 6. Over this year (April 1982 – March 1983), range size of males varied

from 9.8 ha in February + March, to 5.1 ha in October + November for male 1; and from 7.9 ha in April + May, to 2.3 ha in October + November for male 3. The largest range sizes of the tagged females were found in October + November (female 1: 5.7 ha) and August + September (female 4: 9.8 ha) while the smallest ranges occurred in April + May (female 1: 2.5 ha) and December + January (female 4: 3.1 ha).

3. The relation between annual and two-monthly ranges

This has examined using data from Chedington, because two-monthly ranges at Porton were determined for only part of an annual cycle. Table 8.6 shows the percentage of the annual ranges of radio-collared deer at Chedington that was used in each two-monthly period. The percentage of the two-monthly range that lay outside the annual range is also given. The annual range need not enclose the entire data set for a given two-month period becaute the probability contour defining the range excludes 25% of the loci.

The mean of the annual range used in any two-monthly period was 57%, and in three quarters of the comparisons drawn, the two-monthly range accounted for more than 40% of the annual range. There was only one instance where more than 50% of a two-monthly range lay outside the annual range (F4: 82/83, months 2+3) and in this case the number of loci was limited to ten because of transmitter problems.

8.3.2 Dispersion of ranges

Unmarked animals were present in both study areas. Males were recognisable under certain conditions (i.e. in good light and clear view) but too little data were collected to analyse. The presence of unmarked animals has implications in how results from marked deer are interpreted and these will be considered in Section 8.4.

1. Relative dispersion of adult buck ranges

a) Porton

The relative dispersion of adult male ranges at Porton was examined

TABLE 8.6

THE PROPORTION OF ANNUAL RANGES USED IN TWO-MONTHLY PERIODS BY RADIO-TAGGED DEER AT CHEDINGTON

(.a) Males

		Range area	% Annual	% Outside
		(h a)	range	annual range
Ml:	1981/82			
	Annual	5.7		
mon th	is 4+5	5.3	68.4	27
м	6+7	5.4	56,1	40
n	8+9	6.1	66.7	38
"	10+11	4.9	86.0	0
н	12+1	3.6	63.2	0
u	2+3	3.3	49.1	16
<u>M1:</u>	1982/83			
	Annual	9.7		
month	s 4+5	6.1	62.9	0
"	6+7	5,8	47.4	20
n	8+9	6.1	62.9	0
н	10+11	5.1	50,5	5
24	12+1	-	-	-
۳	2+3	6.7	41.2	40
M3:	1982/83			
	Annual	7.6		
months	s 4+5	7.9	77.6	20
	6+7	5.9	59.9	12
u	8+9	4.4	52.1	24
ч	10+11	2,3	30.3	17
"	12+1	2.9	38,2	Ş
4	2+3	4.6	49.6	41

TABLE 8,6 (continued)

THE PROPORTION OF ANNUAL RANGES USED IN TWO-MONTHLY

PERIODS BY RADIO-TAGGED DEER AT CHEDINGTON

(b) Females

		Range area	% Annu a l	% Outside
		(ha)	range	annual range
F1:	1981/82			
	Annual	12.1		
mont	h s 4+5	6.6	43.8	20
	6+7	3.5	25.6	12
н	8+9	6.6	41.3	24
"	10+11	7.2	49.6	17
11	12+1	10.4	76.0	9
н	2+3	6.4	31.4	41
F2:	1982/83			
·	Annual	6.5		
month	h s 4+5	2.5	38.5	0
'n	6+7	3.0	46.2	0
4	8+9	5.6	49.2	42
н	10+11	5.7	83.1	5
н	12+1	5.2	72.3	10
u	2+3	4.3	55.4	16
F4:	1982/83			
	Annual	7.9		
month	a s 4+5	4.6	58.2	0
ц	6+7	6.8	82.2	4
Ħ	8+9	6.9	77.2	11
11	10+11	4.9	62.0	0
ų	12+1	3.1	44.3	0
ч	2+3	2.5	4.8	84

between March and June 1981 when sufficient data were obtained on three adult males fitted with radio-collars. There was extensive overlap between the ranges of these three bucks (Table 8.7). Over this period, the mean overlap was 76.8%.

Overlap decreased between March and June. All three individuals showed a sharp and consistent increase in the proportion of their ranges that was exclusive of the other males considered (Table 8.7). The largest change occurred for Male 16. Only 17.4% of Male 16's March + April range was exclusive, whereas by May + June this had increased to 77.5%. Insufficient data were obtained to examine relative dispersion of adult males in winter.

b) Chedington

The loci collected on the two males radio-collared between April 1982 and March 1983 overlapped in geographical position. Figure 8.6 shows that the annual minimum polygons overlapped, but that the ranges def. 3d by 75% probability contours were exclusive.

The seasonal ranges plotted for these two males showed little overlap. In July/August there was an overlap of less than 2% of the range size of either male, but all other seasonal ranges were exclusive of the other males in the comparison (Fig. 8.7).

2. Relative dispersion of adult female ranges

a) Porton

There was extensive overlap between annual ranges in all three years (Table 8.8). Mean overlap was 45.9% in 1979/80, 64.7% in 1980/81 and 70.8% between March and September 1981. The number and dispersion of seasonal ranges that were described in the previous chapter prevent comparisons of seasonal changes in relative dispersion of adult female ranges at Porton.

b) Chedington

There was no overlap between either annual or seasonal ranges of any radio-collared females at Chedington because none had neighbouring

TABLE 8.7

PERCENTAGE OVERLAP IN AREA OF ADULT MALE RANGES AT PORTON BETWEEN MARCH AND JUNE 1981

Adult m a le	Months	% range area				
		exclusive	shared with:			
			<u>м16</u>	M62	M63	both others
M16	March-June	20.1	_	38,7	38.9	2,1
M62	March-June	19.4	76.3	-	О	4.3
M63	March-June 1	30.1	66.2	0	-	0
M16	March-April	17.4	-	30.3	47.1	5.2
M62	March-April	35.3	55.3	-	0	9.4
M63	March-April	19.8	72.3	0	-	7.9
M16	April-May	3.4	-	19,1	27,5	0
M62	April-May	37.5	62.5	-	0	0
M63	April-May	40.0	60.0	0	· -	0
W1 C	Mary Tune	77 5	_	२२ ∕	11 0	0
MCO	May-June	75 4	24 6	44,4	TT • A	0
M62	M ay-June	10.4	44.0	-	U	U
M63	M ay-June	69.2	30.8	0	-	0

Overlay: minimum polygons for the data used in Fig. 8.6.



Fig. 8.6. Annual ranges and cores of two radio-collared adult males at Chedington: April 1982 to March 1983 inclusive. (X = centre of activity, (\bigcirc) = grid ref 540690).



Fig. 8.6. Annual ranges and cores of two radio-collared adult males at Chedington: April 1982 to March 1983 inclusive. (X = centre of activity, (\bigcirc) = grid ref 540690).


Fig. 8.7. Two-monthly ranges and cores of two radio-tagged males (M1 and M3) at Chedington between April 1982 and March 1983 inclusive. Insufficient data to plot ranges in Dec/Jan (X = centre of activity, \bigotimes = grid ref. 540690)

TABLE 8.8

PERCENTAGE OVERLAP BETWEEN RANGES

OF ADULT FEMALES AT PORTON

Individual	Year	Range area (ha)	% exclusive of other
			marked does
F04	79/80	10.3	
F05	19/80	10,2	47.9
r05		9.4	44.7
F06	u u	11.1	54.6
F10	*/	9.6	66.2
F16	11	4.3	16.1
			<u>Mean</u> = 45.9%
F04	80/81	5.9	52.7
F06	B	3.1	100
F08	भ	4.2	63.7
F10	n	5,3	81.7
F15	11	4.9	100
F16	n	4.8	26.2
F19	If	4.5	28.9
			$\underline{Mean} = 64.7\%$
FO4	March-Sept 81	8.9	87.6
F05	34	10.6	100
F06	k	8.1	90.1
F08	11	6.1	95.1
F10	*	5.3	32.0
F15	۹.	13.7	45.7
F16	4	7.0	45.4

 $\underline{Mean} = 70.8\%$

ranges.

3. Relative dispersion of male and female ranges

a) Porton

Between March and June 1981, there was no close correspondence between boundaries of adult male and female ranges or their cores (Figs. 8.8 and 8.9). However, activity centres seemed to be related, since distances between activity centres were lower between sexes than within either sex. Table 8.9 shows that all nearest-neighbour distances of activity centres between males and females were lower than those between individual males or females. Sample sizes were too low to test the significance of this troid, and insufficient data were obtained to compare relative dispersion of other seasonal ranges of males and females at Porton.

b) Chedington

Only one pair of radio-collared deer showed any extensive overlap of annual ranges. These were male 3 and female 2 between April 1982 and March 1983. Their annual ranges (Fig. 8.10) overlapped by a mean of 88%: 93% of the range of female 2 was shared with male 3, but only 83% of the male range coincided with that of female 2. Seasonal ranges (Fig. 8.11) also overlapped extensively. In all pairs of months, alm st the entire range of one individual was contained within that of the other. The shape of the two-monthly ranges changed considerably (c.f. August/September and December/January, Fig. 8.11)

Several differences were evident between these two individuals. The female's range contracted sharply in May/June spanning the period of kidding, whereas the male range contracted in the autumn after the rut. Thus in October/November the male range was considerably smaller than the female's. Throughout the winter, both individuals ranged less widely than in summer.

Core areas also coincided to a high degree, and in April/May centres of activity were the same for the two individuals. When radio-located, these two deer were frequently within 50m of one another and they were also sighted together.



Fig. 8.9. Relative dispersion of ranges and cores of radio-tagged adult females at Porton between March and September 1981. (X = centres of activity, \oplus = grid ref. 510440).

Fig. 8.8. Relative dispersion of the ranges and cores of three radio-tagged adult males at Porton between March and September 1981. (X = centre of activity, \oplus = grid ref. 510440).



Fig. 8.9. Relative dispersion of ranges and cores of radio-tagged adult females at Porton between March and September 1981. (X = centres of activity, \oplus = grid ref. 510440).

TABLE 8.9

NEAREST-NEIGHBOUR DISTANCES BETWEEN CENTRES OF A IVITY OF MARKED ADULT MALE AND FEMALE RANGES AT PORTON March-September 1980

	NN Individuals	Separation of CA (M)
Males vs Females		
	M16 - F05	45
	M62 - 04	100
	M63 - F16	81
Males vs Males		
	M16 - M62	179
	M62 - M16	179
	M63 - M16	369
Females vs Females		
	F04 - F10	206
	F05 - F16	410
	F16 - F15	297



100m

Fig. 8.10. Annual ranges and cores of Male 3 (thick line) and Female 2 (thin line) at Chedington between April 1982 and March 1983. (S indicates grid ref. 540690).



June/July



August/September



December/January

8



May/June (kidding)



July/August (rutting)



October/November





Fig. 8.11. Two-monthly ranges and cores of Male 3 (thick line) and Female 2 (thin line) at Chedington between April 1982 and March 1933. (\emptyset = grid ref. 540690; \eth and \wp indicate centres of activity.

N

8.4.3 Effects of age, sex, season and year on corrected range and core areas

1. Age

Range and core sizes were compared between adult and juvenile females at Porton in 1979/80 and between March and September 1981 (Table 8.10). Juveniles had significantly larger ranges and cores than adults in 1979/80 but there was no significant difference in size in either the 6-month areas in 1981 or in the two-monthly comparisons drawn (Table 8.10). Sample sizes for males were too small to show significant differences using two-tailed non-parametric tests, and so they were not tested.

2. Sex

Range and core sizes compared between adult males and females at Porton between March and September 1981, showed no significant differences (Table 8.10). Annual range and core sizes at Chedington (1981/82 and 1982/83 lumped) were also not significantly different between adult males and females (Table 8.10). Sample sizes of juveniles were too small to compare between sexes.

3. Season

Ranges and cores of eight females at Porton (four adult and four juvenile) showed no significant change in size between March/April and April/May (Table 8.11). Two-monthly adult male ranges and cores at Porton did change significantly between March and June 1981 (Table 8.11): the areas used by adult males became smaller after March/April. Juvenile males were excluded from this test because both individuals showed an increase of more than 40% between March/April and April/May (Appendix 4, Table 3).

At Chedington, neither males nor females showed significant variation In two-monthly range or core sizes between April 1981 and March 1983 (Table 8.11). MANN-WHITNEY U TESTS FOR SIGNIFICANT DIFFERENCES IN RANGE AND CORE SIZE WITH AGE/SEX-CLASS

P = Porton; C = Chedington

All range and cores used were corrected (see 8.2.3)

VARIABLE	COMPARISON	DATA SE	T RESULTS
female age	juvenile vs adu	lt	
	ranges	(P) 1979/80	U=1, n ₁ =4, n ₂ =5, p=.032
	cores	(P) 1979/80	$U=1, n_1=4, n_2=5, p=.032$
	ranges	(P) March-	± 2
		Sept 81	$U=10, n_1=4, n_2=6, ns$
	cores	(P) "	$U=8$, $n_1=4$, $n_2=6$, ns
	ranges ((P) March+ April 8:	$1 U=7, n_1=4, n_2=4, ns$
	ranges ((P) Ap ri l+ M ay 81	$U=6$, $n_1=4$, $n_2=4$, n_3
	cores ((P) March+ April 81	U=4.5, n ₁ =4, n ₂ =4, ns
	core s ((P) April+ May 81	$U=6.5, n_1=4, n_2=4, ns$
Sex	adult ma) vs fe	emale	
	ranges (P) March- Sept 81	U=8, n ₁ =3, n ₂ =6, ns
	cores (P) "	$U=6$, $n_1=3$, $n_2=6$, ns
	re ges (C) 1981/82 + 82/83	$U=9, n_1=3, n_2=6, n_8$
	cores (C) ''	U=9, n ₁ =3, n ₂ =6, ns

	Ranges and	OF SIGNIFICA cores used we	NT DIFFEREN ire correcte	CES IN d (8.2.	RANGE A 3) unle	ND CORE SIZE WITH ss stated otherwi	SEASON, YEAR A se, ν = Porton,	ND STUDY AREA C = Chedington.	
Variable	Con	parison				Data Set	S t 81	tistical Result*	
year	individuals	paired 2-mont	ылу	ranges	(C)	81/82 - 82/83	T = 15,	N = 11,	ns
•	=	-		cores	(C)		T = 21.5,	N = 11,	50
se on	all females	Mar/Apr Vs Ap	r/May	ranges	(C)	1981	T = 6,	N = 8,	SU
:	=	-	6	cores	(c)	=	T = 16,	N = 8,	ns
Ŧ	adult males:	variation in	2-month	ranges	(P)	M ar-Jun. 1981	H = 9.289,	2 d.f.	p < .004
:	=	:	1	cores	(P)		H = 8,867,	2 d.f.	<i>p</i> < .004
E		:	E	ranges	(c)	Apr. 81 - Mar. 83	H = 7.122,	5 d.f.	មា
:	:	-	-	cores	(c)	:	H = 7.646,	5 d.f.	su
Ŧ	adult female	es: variation	in 2-month	enges ((c)	1	H = 4.356,	5 d.f.	su
-	7	Ξ	=	cores ((c)	.	H = 3.970,	5 d.f.	su
study area	adult males:	Porton vs Ch	edington			all ranges > 6 m	th. $U = 0$,	$n_1 = 3, n_2 = 5,$	p < .04
	:	Ξ	=			all cores ≥6 m	th. $U = 0$,	$n_I = 3, n_S = 5,$	p < .04
=	" females	:	Ξ			all ranges > 6 m	th. $U = 12$,	$n_{I} = 6, n_{S} = 18,$	p < .02
5	:	:	=			all cores > 6 m	th. $U = 29$,	$n_I = 6, n_2 = 18,$	នជ
	" males	:	=			uncorrected rang	ев U = 2,	$n_{I} = 3, n_{S} = 5,$	Su
:	" females	=	=			" cor	ев U = 50.5,	$n_I = 6, n_2 = 19,$	នជ

= Mann-Whitney * T = Wilcoxon matched petrs; H = Kruskal-Wallis; U

4. Year

At Porton, too few individuals were common to consecutive years to test differences in areas used between years. At Chedington, paired comparisons of two-monthly range and core sizes of the same individuals in consecutive years showed no significant differences between the two years (Table 8.11)

8.3.4 Differences in range and core sizes between study areas

Sample sizes were increased for this analysis by combining data across years in each study area, as there were no significant differences between years where it was possible to test in the previous section.

1. Uncorrected areas

Estimated ranges for all individuals (including those with small numbers of loci) were compared between study areas using Mann-V.Sitney U tests. Neither male nor female ranges showed significant differences in size (Table 8.11).

2. Corrected areas

Adult males at Porton had eignificantly larger ranges and cores than males at Chedington (Table 8, 11). Female ranges were also significantly larger at Porton than at Chedington (Table 8, 11) but female core sizes were not significantly different between the study areas (Table 8, 11).

8.3.5 Influence of habitat and food resources on range size

Range size did not vary significantly with sex, season, (except males at Porton), or year in any of the comparisons tested in Section 8.3.3. Corrected range size was significantly larger at Porton, although uncorrected range sizes were not significantly different between the study areas (8.3.4). The following analysis examines the influence of habitat on range sizes at Porton (ranges at Chedington were not examined as the number of annual ranges was low), and then examines differences in food resources between ranges in the two study areas. Uncorrected ranges were used as corrected areas cannot be related to geographical locations. Juveniles were excluded, because none were radio-tagged at Chedington.

1. Areas of habitats contained within ranges

Areas of vegetation types were measured using a planimeter and a vegetation map, overlaying the ranges which were plotted by the modified Dixon and Chapman program. Areas are given in Tables 8.12 and 8.13.

None of the adults sampled in either study area used all available habitats, but at Porton, the ranges of some females contained only grassland. Range size was plotted against the area of each habitat at Porton (Fig. 8.12). These plots showed no trends. (Correlations were not calculated because the two variables are not entirely independent). The absence of trends suggests that ranges are not adjusted to include only a minimum area of a habitat, which would tend to restrict values to a line of zero slope, or produce a negative correlation. The plots suggest that as range size increases, the area of all habitats contained tends to increase, and this could be attributed either to the dependence of the two variables or to the disposition of habitats.

2. Food resources contained within ranges

Three aspects of food resources were assessed: total abundance of food (i.e. plant blomass), availability of food (i.e. digestible plant biomass) and available nitrogen (i.e. nitrogen in the available food). Abundance and availability were obvious choices to assess; nitrogen was chosen as it is probably the most important nutrient.

a) Calculations

Mean annual standing crop (tons ha⁻¹) was calculated for each vegetation type from monthly mean dry weight of standing crop (Chapter 5), so that months were equally weighted and standard errors in Appendix 4, Table 7 represent temporal, not spatial variability. Total production was not estimated, as no data were available for farmland.

For scrub and woodland edge at Porton, and for bramble at

TABLE 8.12

AREAS OF HABITATS CONTAINED WITHIN RANGES

OF ADULTS AT PORTON

		Area of 1	habitat (h	a)	Length of	Tot al
Sex / ar	Deer	wood1 and	grassland	farmland	woodl.edge (m)	area
Females]	4	0	10.2	0	0	10.2
1979-80	5	4.9	2.4	2,1	450	9.4
}	6	0	10.0	1,1	0	11.1
	10	4.3	3.9	1.5	950	9.7
J	16	3.4	0.4	0,5	300	4.3
Females	4	0	5,9	0	0	5,9
1980-81	6	0	3.1	0	0	3.1
	8	0	4.2	0	0	4.2
}	: .0	0.8	2.4	2.0	300	5.3
	15	2.7	2,2	0	310	4.9
	16	0	4.8	0	0	4.8
J	19	0	4.5	0	0	4.5
Females]	4	0	8,6	0.3	0	8.9
March-	5	3.1	4.4	2.1	500	10.6
Sept 81	6	0	7.7	0.4	0	8.1
}	8	0	5.0	1.1	0	6.1
	10	1.7	2.8	0.8	630	5.3
	15	5.3	2,9	4.3	970	12.5
	16	5.5	0	1.5	340	7.0
Males	12	5.0	2,5	1,3	750	8.9
1980-81	16	4.4	1,7	1.6	320	7.7
Males]	16	11.8	9.0	1.1	700	21.9
March-	62	2.2	9.0	0	330	11,2
Sept 81	63	10.9	0.4	1,9	450	13.2

TABLE 8.13

AREAS OF HABIT CONTAINED WITHIN RANGES OF RADIO-TAGGED DEER AT CHEDINGTON

• . £ . £ F ρ < Ξ F c ARFA

	CON	I F E R S				-
rides pre-thicket	thicke	t thinned	pole-stage	mature	scrub/mat	pasture
.3 3.5	1	I		1	narawood	
.6 5.7	1	ст.	ر م	1	9 (- -	1
.3 2.7	8.	1	2 1 1 1	I	• · ·	1
1.4	6.7	0.2		Į	0	0
. 6	3.7			1	I	2.0
.3 2.0	1) • • •	9 	I	1	3.2
.4 2.6	ł		2.0	t i	α Γ.	1
. 5	1.4	3.7	ı	I		ч с •
в	•			1	1	

7.9

2

сł

4.

I

2.6

3.6



Fig. 8,12. Annual range sizes of adults at Porton against areas of (a) Woodland, (b) Grassland and (c) Farmland

Chedington, data on autumn dry weights (per bush or m²) were combined with abundance (per ha) to produce density. Ground vegetation and browse densities were combined to estimate overail density in habitats where both food sources were available.

The total blomass of food within ranges (Tables 8.14 and 8.15) was calculated from the products of food density and the areas of component vegetation types.

Monthly digestible standing crop and the annual mean for each vegetation type were calculated, using percentage digestibility or interpolated values for months when digestibility was not analysed. Total digestible standing crops for ranges were calculated as above (Tables 8.14 and 8.15).

Annual digestible nitrogen contained within ranges was calculated as the mean of the products of monthly digestible dry weight and nitrogen level (Tables 8.14 and 8.15).

b) Analysis

Ranges at Porton contained a greater biomass of food than those at Chedington (both sexes, all ranges, Mann-Whitney U test, U = 45, $n_1 = 9$, $n_2 = 24$, z = 2.547, two-tailed p = .011), and a higher biomass of digestible food (U = 51.5, $n_1 = 9$, $n_2 = 24$, z = 2.284, two-tailed p = .023). However, there was no significant difference in the amount of digestible nitrogen within ranges between study areas (U = 84, $n_1 = 9$, $n_2 = 24$, z = 0.970, two-tailed p = .332).

8.4 DISCUSSION

Mean range size of adult males at Porton varied from 15.4 ± 3.28 ha (March - September 1981) to 21.1 ± 6.10 ha (1980/81). Adult female range sizes were similar, varying from 11.6 ± 1.82 ha (1979/80) to 15.4 ± 2.06 ha (March - September 1981)

Adult male range size at Chedington varied from 5.7 to 9.7 ha; mean adult female range size was 7.5 \pm 2.31 ha in 1981/82, and 7.7 \pm 0.67 ha in 1982/83. Neither range nor core size of adult males and females were significantly different from each other at either Porton or Cedington.

Mean subadult male range size at Porton was 17.8 ± 2.72 ha

TABLE 8.14

FOOD RESOURCES CONTAINED WITHIN RANGES

OF ADULT MARKED DEER AT PORTON

		Plant	Digestible	Digestible
		biomass	biomass	nitrogen
Sex/Year	Deer	(tons in range)	(tons in range)	(kg in range)
Females	4	54.2	12.8	171.8
1979/80	5	34.2	11.4	202.8
l	• 6	55.4	13.5	182.4
	10	37.7	11.4	192.8
J	16	11.7	3.8	75.4
Females	4	31.4	7.4	99.4
1980/81	6	16.5	3.9	52.2
	8	22.3	5.3	70.7
}	10	18.8	8.9	143.0
	15	17.1	4.4	73.4
	16	25.5	6.0	80,8
	19	23.9	5.6	75.8
Females	4	46.3	11.1	148.6
March-	5	37.9	11.1	183.7
Sept 81	6	41.7	10.0	134.8
ļ	8	30,9	8,3	119.7
	10	21.5	5.9	96.2
	15	43.2	14.4	259.1
j	16	17.0	5.9	122.3
Males	12	30.6	9.5	169.3
1980/81	16	26.8	9.0	161.2
Males	16	93.1	20.1	345.9
March-	25	52.3	12.6	181.3
Sept 81	63	80.6	11.9	240.5

TABLE 8.15

FOOD RESOURCES CONTAINED WITHIN RANGES

OF RADIO-TAGGED DEER AT CHEDINGTON

		Plant	Digestible	Digestible
Deer	D ate	biomass	plant	nitrogen
		(tons in range)	(tons in range)	(kg in range)
M1	<u>^1/82</u>	22.2	6.1	158.6
м1	82/83	33.4	9.2	205.0
МЗ	н	15.2	4.7	96.6
Fl	81/82	23.3	7.7	126.0
Fl	82/83	17,4	6.2	97.8
F2	81/82	12.3	3.3	79.9
F2	82/83	17.4	4.9	102.4
F3	81/82	19.5	5.6	94.6
F4	82/83	18.5	5.4	98.4

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(1979/80), and 22.3 ± 3.04 ha (March - September 1981); mean subadult female range size was 12.2 ± 3.70 ha (1979/80) an 13.8 ± 3.15 ha (March - September 1981). No juveniles were tagged at Chedington.

There was extensive overlap in both adult males and female ranges at Porton: male-male overlap was over 75% between March and June 1981, but decreased consistently during this period. Seasonal changes in overlap were not examined for females, as sample sizes were too small. Male and female range boundaries at Porton did not correspond, but centres of activity were closer between, than within sexes.

Male ranges at Chedington did not overlap, although males 1 and 3 were neighbours. No females tagged at Chedington were close neighbours and so no ranges overlapped. Home ranges of one male and female coincided: boundaries, centres of activity and seasonal changes in shape and area were similar.

No significant differences were found in range (or core) areas between juveniles and adult females, or between sexes (adults only) at Porton. Adult male range and core sizes at Porton dropped significantly between March/April and May/June 1981, as territories were established and overlap between males decreased. Female ranges and core areas (adults and juveniles combined) did not change significantly between March/April and April/May. Neither range nor core size varied significantly with season, for either sex at Chedington, although sample sizes allowed two-monthly comparisons across 24 months.

Ranges of both males and females were significantly larger at Porton than at Chedington. Cores of males were also larger at Porton. This applied only to corrected ranges: uncorrected areas were not significantly different between study sites.

None of the marked adults in either study area used all available habitats. However habitats like rides at Chedington were used by all individuals sampled. There were no clear relationships between range sizes and either area or proportion of any component vegetation types.

Estimates of food resources suggested that adult ranges at Porton contained a greater biomass, and digestible biomass of potential food, but that the digestible nitrogen contained within adult ranges in the two study areas was similar.

Estimates of home range size can be influenced by the number of loci per individual. Uncorrected ranges were significantly positively correlated with sample size in one year, but corrected ranges showed no correlation with sample size. However, correlations cannot prove that all ranges were unaffected by sample size: they show that across the sample for a year, there was no significant overall influence.

An advantage of the Village correction method is that is uses information on sample size and the density of points. The correction of a small range with 20 loci will be a smaller percentage than the correction to a larger range with 20 loci, as regression line slopes are less than one. However disadvantages are that the corrected range cannot be related to habitat, and a single correction factor may not be sensitive to idiosyncrases in ranging behaviour of marked deer, sampling regimes or the effect of terrain.

Hosey (1974) and Loudon (1979) used "adjusted" minimum polygons, which were related to real space. They corrected boundaries to correspond to topographic features so that territories were contiguous, as observed by Cumming (1966) and Bramley (1970a). By this subjective method, boundaries may not conform to those perceived by the study in addition Hosey and Loudon's estimates of range size were animals. influenced by sample size. Hosey obtained a mean of 30 observations in 1972, varying from 5 to 54 for 9 bucks. Territory size was not significantly correlated with sample size (r = .302, N = 9, ns; Table 7.1, p. 194; sample sizes extracted from Figs. 53, 54, 55), but this does not imply that the four territories estimated for small samples (T7. T10, T11, T12, with 13, 5, 10, 11 loci respectively) were accurate. Loudon did consider the influence of sample size on his estimates of range area. However two errors in his calculations produced nonsignificant correlations, which were really significant (minimum polygons; bucks 1974 (excluding "fringe" bucks), r = .699, n = 12, p < .02, Table 3, p.37, calculated by Loudon as r = .612, n = 12, quoted as ns; bucks 1975, r = .671, n = 11, p < .05, Table 3, p.37, calculated by Loudon as r = .465, n = 11, ns).

Rainge sizes found in this study at Porton lie between those at Kalo (Strandgaard 1972) and Gientress (Loudon 1979). Fig. 8.5 shows that the ranges of radio-tagged deer at ChedIngton are the largest ranges there since Cumming (1966). Loudon (1979) suggested that range size had consistently diminished throughout the seventies, but changes in

cover over this period have reduced visibility and have probably caused the observed decline in range size. The extensive use of radio-telemetry overcomes such problems and so should provide more accurate estimates of range size.

The analyses in this chapter were constrained by the number of individuals marked, which was beyond control (as it depended on which animals were caught, their survival and the field performance of radio-transmitters). Some marked individuals were discarded, as too little data were collected to justify plotting ranges. An arbitrary minimum of 10 loci was used (after Village 1982), as there is no straightforward method of determining the minimum below which ranges would be unrealistic.

Sample sizes in the comparisons of age, sex, season and year were just adequate to use two-tailed non-parametric statistics, and so only strong trends would show. Conclusions drawn about the effects of these variables on ranges size should be considered in this light: larger samples might show significant differences, because variation within categories would be less likely to mask differences between categories.

Seasonal comparisons of range size at Porton were limited by the data obtained. Pairing months with the preceeding and succeeding month to increase sample sizes may have obscured differences. More detailed data were obtained at Chedington, but there was no significant variation in seasonal range sizes. However, the number of individuals tagged at Chedington was low. In both study areas the refore, seasonal range sizes could be investigated more fully.

Corrected range sizes were significantly larger at Porton than at Chedington. However there were methodological differences. Deer were located regardless of activity at Chedington using radio-telemetry, but at Porton most records were observations of deer feeding in open areas, where boundaries would therefore be more accurate. (The effects of the two methods on range size at Porton were not assessed as sample sizes were too small). Ranges in the two study areas may not be directly comparable.

A further problem in comparing range sizes between study areas is that only Porton ranges were corrected, (as sample sizes at Chedington were large). Without correction, range sizes were similar between study sites. Porton ranges were probably larger, as indicated by the corrected areas, but only uncorrected areas could be used in estimating food resources.

Estimates of food resources to which individuals have access are obviously subject to errors if range sizes are inaccurate, but there are Using annual means of standing crop takes no other points to note. account of the seasonal importance of vegetation types (e.g. for feeping, see Chapter 3), nor of the heterogeneity of food within habitats, which was indicated by standard errors on monthly standing crops in Chapter Measures of standing crop may not reflect food availability as roe 5. feed selectively (Chapter 6), and differences in habitat structure could lead to food sources, like deciduous browse, being weighted differently between study areas. Percentage digestibility was determined on samples of swards but it was an overall measure, and food selected could have a considerably higher digestibility in heterogeneous vegetation types like grassland. The product of standing crop, digestibility and nitrogen content may not represent the amount of nitrogen available, because it assumes that nitrogen is distributed evenly between digestible and undigestible parts of the plant (see Section 5.4). Digestible nitrogen values should therefore be treated with caution.

The results suggested however that range size may increase in response to lower nitrogen availability in local vegetation types. The evidence was not conclusive, because of short-comings in the home range data, and because of the assumptions underlying the estimation of food resources. The food resources commanded by individuals would be influenced by the number of other individuals sharing access. Overlap between ranges was not compared between study areas, as samples were small, but differences could occur. Range size or food resources of females with singletons of twins could differ or there may be differences in breeding success of either males and/or females in relation to food resources contained within their ranges.

CHAPTER 9 GENERAL DISCUSSION

Roe deer exploit a variety of habitats, but certain basic characteristics seem essential to support breeding populations. This study and others (e.g. Strandgaard 1972; Loudon 1979) have identified cover as an important pre-requisite for roe deer: at both Porton and Chedington, populations were centred on blocks of woodland. At Porton however, grassland also supported deer and it would perhaps be more instructive to view the basic requirement as freedom from disturbance, since other studies have also noted that roe deer may colonise open spaces with little or no cover. Some roe deer in Czechoslovakia for instance are resident in large fields created by recent changes in agricultural practices (Zejda 1978; Zejda and Miloslav 1980).

Roe deer regularly used agricultural land at Porton, but unlike the Swiss population studied by Turner (1979), few deer remained in fields Some individuals in Turner's study used fields throughout during daylight. the year, while others moved between fields and woodland. Strando ⊴d. (1972) found similar behaviour at Kalo: small fields were used only at night, whereas some larger and less- frequently disturbed fields were used by deer for complete 24 hour periods. At Porton deer tended to use habitats that provided cover during daylight. Farmland was used mainly at night and small fields which were regularly disturbed (e.g. pasture) were used only between dusk and dawn. Those deer at Porton that did remain in large fields during the day, appeared to use local topography to minimise their exposure to disturbance and weather. Deer living entirely in Swiss farmland moved to ploughed fields to ruminate possibly because micro-climates were more favourable or because these fields offered better camouflage (Zejda 1978), but potential danger may also have been more readily seen. However Cumming (1966) suggested that the main function of habitat selection is not to maximise shelter, since his measures of wind speed and temperature showed that some habitats which were used very little offered more shelter than the areas of habitats that were used frequently.

The highest numbers of deer feeding at Porton were seen at dusk.

Other studies have in general found peak activity at either dusk (e.g. Cederlund and Lemnell 1980; Cederlund 1981) or at dawn (Turner 1980). At Porton feeding may be depressed during the day when deer select habitats primarily for cover, although food abundance and quality were lower for much of the year in such habitats (i.e. woodland and grassland) than on farmland. The higher level of nitrogen, higher digestibility and large available areas of agricultural crops would compensate for their low standing crops in winter. Fields contained a large amount of food that would have been inexhaustible for the resident roe deer. As long as food can be located easily at night, deer would probably benefit by feeding less during the day in sub-optimal habitats, and by concentrating their feeding between dusk and dawn in fields where they could maximise the rate at which they obtained nutrition.

Diel patterns of habitat use at Chedington were different from those at Deer at Chedington showed less pronounced diel changes in Porton. habitat use and they showed peak activity at night, instead of dusk. The two factors that probably account for these differences are food supply and disturbance. As already discussed the habitats at Porton varied in food quality and abundance, but food supply varied much less between habitats at Chedington, and further, nearly all habitats at Chedington offered cover. Hence feeding during daylight would not be depressed so much as it was at Porton: deer feeding would be less exposed and they could probably not compensate for time lost from feeding during daylight by feeding more intensively during darkness, because of the similarity in food supply in different habitats. Patterns of disturbance would contribute to the differences between the two study areas. Disturbance at Porton occurred mainly during office hours because it was associated with M.O.D. activity. At Chedington, people on recreational visits were the most regular cause of disturbance, and these tended to occur in late afternoon and early evening, or at weekends. Because of this, deer at Chedington would be expected to show lower activity at dusk than those at Porton, and it also explains why activity was depressed less during the day at Chedington. Weekend disturbance in the two study areas was similar and so it would be interesting to investigate whether diel activity patterns and habitat use differed between weekdays and weekends.

Habitat use and activity changed with season: for instance deer appeared to spend more time feeding in winter. Similarly Turner (1979) also found that roe deer spent more time feeding in winter, and

suggested that energy requirements were higher in winter because of the increased demands of thermoregulation (Moen 1973). Hence deer would spend more time feeding in winter to maintain their energy intake, and this would be further increased because food quality is lower in winter. This argument is logical and it is supported by the fact that Turner also found that bouts of rumination were longer in winter presumably because food was less digestible.

Seasonal changes in ruminant feeding are however more complex than the scheme above would suggest. Rumen size and morphology change in winter (Hofmann *et al.* 1976) to accommodate a more fibrous diet which takes longer to digest. In addition metabolic rate falls to conserve energy and hence appetite changes with seas a (Kay 1979; Kay and Suttie 1980). Increased digestion time and reduced energy requirements would both lead to less time being spent feeding in winter. So why did deer at Porton and in the population studied in Switzerland by Turner (1979) apparently spend more time feeding in winter?

Ellenberg (1974) found that in captive roe deer (fed ad libitum) in late summer and autumn feeding increased to accummulate fat reserves before winter, suggesting that seasonal changes in feeding of roe deer are unlikely to differ from those seen in other ruminants. Studies of free-ranging deer are subject to bias from changing visibility: increased feeding in winter could therefore be caused by deer feeding more in open However, roe deer living in agricultural areas are in an unusual bltats. position compared with other wild ruminants, because they still have access to relatively high quality food in winter: morphological changes in their digestive systems could therefore differ from those in other If differences do occur, then perhaps this would explain why ruminants. roe deer have recently started to colonise farmland more extensively

Distribution of food resources would be expected to influence behaviour (Jarman 1974). Deer on farmland tended to be in larger groups than those in woodland, which would agree with the predictions made by Jarman that group size should decrease as individuals feed more selectively on discrete, high quality food items. Since roe deer are concentrate selectors (Hofmann 1973), they would be expected to feed selectively in woodland in order to maximise the quality of food they consume. However, on farmland they may be less selective because food items are uniform, especially in winter. Feeding competition and interference would be higher in woodland and so smaller groups should

occur in woodland.

Exposure in different habitats may also influence group sizes. in more open or more disturbed habitats, individuals would benefit from increased vigilance and by spending less time alert. At Porton, members of groups were more widely spaced at night than at other times, which may suggest that they are less wary at night. However, wariness may depend on status: Cumming (1966) found that an adult doe lifted her head four times as frequently while feeding as her yearlings did. Wariness may vary between individuals of the same age and sex-classes: Strandgaard (1972) noted that groups were more readily frightened when particular individuals were nearest to the observer.

Seasonal changes in habitat use may be a response to several factors, including changes in cover, parasite density, disturbance and the distribution of food. Diet of roe deer at Porton changed with season, and this may be either a cause or an effect of changing habitat use. In summer, deer consumed more herbs, reaching a peak of over 90% of the fragments in faecal samples in June; grasses were consumed most in August and only fell below 40% of the diet when herbs were heavily consumed; consumption of browse peaked in spring. Diet of roe deer living in agricultural areas or using farmland extensively had not previously been analysed: most dietary stud: s are of roe deer living in woodland (e.g. Slurta et al. 1969; Jackson 1980), although some populations living in forest habitat have been shown to consume large quantities of herbs in summer (e.g. Gebczynska 1980)

Diet at ChedIngton was not analysed in this study, but previous work by Hosey (1974) showed that it also changed with season. Changes in diet were less marked at Chedington and this also corresponds to less marked seasonal change in habitat use. The variability of food items and differences in their distribution between vegetation communities in the two study areas may account for the differences in diet and probably contributes to differences in habitat use. However the clear seasonal changes in diet, feeding behaviour and habitat use at Porton were not correlated with measures that were made of food abundance and quality, although previous authors have suggested that changes in food supply would explain variations in diet and habitat use (e.g. Strandgaard 1972; Hosey 1974). The reasons why non-significant correlations were not meaningful were discussed in Section 6.4; the fact that seasonal changes in food supply explained little of the variance in diet, feeding behaviour or

habitat use does not prove that food supply has no influence. Several factors were not taken into account and measures of food supply need to be refined so that they apply to food items, not plant communities. Since this would be difficult to achieve, it might be more instructive to design experiments manipulating food supply by creating high and low quality areas and observing the effects on feeding behaviour.

At Porton, roe deer were always dispersed between available This applied also to large groups which formed on farmland in habitats. winter, and throughout the year individual deer had characteristic home No evidence was seen of territoriality in males outside the ranges. period April to August, and adult males were seen occasionally feeding in the same groups during winter and early spring. Similarly, there was no evidence of territorial behaviour between females, and the level of social interaction was in general very low. Loudon (1979) suggested that aggression of adult females causes dispersal of juvenile females but there were no observations that confirmed this at Porton. Most interactions that were observed involved adult males on their territories driving juvenile males away, which seems to be a feature common to all roe deer populations studied. Cumming (1966) viewed such behaviour as a mechanism of population regulation, but this involved group selection, and it is now viewed as a process by which individual males would be expected to maximise their reproductive success.

The ultimate factors which cause juveniles of either sex to disperse are unknown, as is their rate of success in establishing home ranges elsewhere. Loudon (1979) showed that non-dispersing juvenile females at Chedington tended to settle on or near their maternal range, which suggests that relatedness may be high between females with overlapping ranges, as in red deer (Clutton-Brock *et al.* 1982). Perhaps this is a reason why female roe deer are not territorial. It is impossible to speculate about the relatedness of territorial males, since settling patterns of juvenile males have not been documented.

Territories are defined as being exclusive of other conspecifics, and other studies have described territories of roe bucks as exclusive, and non-overlapping. Cumming (1966) and Bramley (1970a) suggested that males remain on their territories throughout the year, but only defend them actively in spring and summer. However, at Porton, male territories overlapped considerably. The proportion of territories shared declined as the rut approached, but overlap still persisted in May/June.

Only two males were radio-tagged at Chedington and their territories did not overlap, although using minimum polygons (as were used by previous authors) annual ranges overlapped, which again differs from the suggestions made by Cumming and Bramley. It was not possible to compare overlap between the study areas, but perhaps the extent of overlap may depend on the distribution of food resources, absolute size of ranges/territories, or on the dispersion of females. Since the distribution of food resources may influence territoriallity, a study of the effect of living entirely in farmland on territorial behaviour of roe deer would be extremely interesting.

Dispersion of males and females between habitats changed with season, as would be expected since seasonal ranges are composed of a series of day-ranges, which themselves change in response to habitat Other factors such as intra-specific competition, particularly use. territorial behaviour, would also influence seasonal changes in Seasonal range sizes at Chedington did not vary consistently dispersion. between two-month intervals, although range maps showed that deer were using slightly different areas on the ground. A recent study of radio-collared adult does at Chedington (Gent 1983) found that adult does used only 37.8% of summer and 22.0% of their winter range each day. However, day ranges varied in position, and so within a few days an individual may cover the entire area used in a season. Similar studies were not undertaken at Porton, but marked individuals behaved differently from deer at Chedington, many apparently using the same day range for several weeks before switching to either new feeding or lying-up These differences may again reflect habitat types. At Porton fields sites. provided abundant food, and particular crops may have been optimal for feeding over several weeks after which deer would switch to an alternative. Also at Porton there were fewer lying-up sites and so particular sites would probably be used more frequently. However at Chedington lying-up and feeding sites were intermingled, which would result in more variable day-ranges.

Range sizes did not differ significantly within the study areas between ages or sex-classes. Male roe deer have been traditionally regarded as having larger ranges than females, but statistical comparisons have not been made by other authors. Range size (minimum polygons) of males at Glentress were significantly larger than females in one year (1976) of Loudon's study (Loudon 1979, Tables 3 and 4, U = 4, $n_1 = 4$, $n_2 = 9$,

p < .05) but differences were not significant in either 1974 or 1975. The absence of significant differences at Porton and Chedington, and in Loudon's study, may reflect small samples sizes, but this is a research area that would benefit from further attention.

Ranges at Porton were significantly larger than those at Chedington. However only ranges at Porton were corrected to compensate for sample size, because adequate numbers of loci were obtained for individuals at Chedington. Although true ranges (i.e. corrected ones) were larger at Porton, the uncorrected estimates were not significantly different between the study areas, and uncorrected areas had to be used to estimate food resources. Nevertheless, these ranges at Porton contained more food than ranges at Chedington, in terms of both total biomass and digestible biomass. The amounts of total available nitrogen (the product of digestible nitrogen and standing crop) were however not significantly different between uncorrected ranges in the two study areas. This implies that range size is related to the quantity of digestible nitrogen that they contain.

Troe range sizes at Porton were larger than the uncorrected estimates and therefore available nitrogen would be higher, which might mean that Porton ranges contained more available nitrogen than those at Chedington, but this was not tested because corrected ranges could not be related to habitats. Food resources may therefore influence range size because of the availability of digestible nitrogen, which would partly explain why both Hosey and Loudon found that larger ranges contained more food. However, there is a further reason why Hosey andLoudon may incorpendently have reached the same conclusions about the relation of food abundance to range size.

The correlations they used have inherent problems that were avoided in this study by comparing range size and resources between two areas. Both Hosey and Loudon drew conclusions based on correlations calculated between variables that it now appears were not entirely independent. It is worth reconsidering their work in detail, to identify which of their conclusions remain valid.

Hosey calculated food value using three elements: abundance, importance and area. He assessed abundance of the main components of diet at Chedington in each plant community within ranges, and assigned an index of importance to each dietary component based on its rank in the annual diet. The product of these two was itself multiplied by

the area of each plant community within the animal's range. Hence total food value was the sum of a series of products:

total food value = $(fv_1 \times area_1) + (fv_2 \times area_2) + \dots (fv_n \times area_n)$.

where $fv_1 = food$ value of community one. The component areas were also summed to give the total area. The degree of variation in food values of communities would have affected how total food value could vary with respect to total area. Since food values varied very little (Hosey 1974; Appendix Table 3, pp.297-308, mean = 33.8 ± 2.2), close relations would be expected. When buck territory size and doe range size were correlated with total food value, significant positive coefficients occurred in Hosey's data on bucks: r = 0.903, n = 8, p < .01 (Table 7.1, p.195); and on does: r = 0.934, n = 13, p < .01 (Table 8.4, p.227). However correlations between territory or range size and food value per unit area are more meaningful, since they are no longer subject to dependence: the fact that neither was significant contradicts the conclusions drawn by Hosey (p.205), that larger territories tend to have less food per unit area than smaller ones.

Hosey's estimates of territory and ranges sizes had limitations (Section 8.4) and the food values which were based on mean <u>annual</u> diet were not strictly comparable with territories, since these were determined between April and August. Within these limitations the conclusion that can be drawn is that food value per unit area is no lower on larger territories or ranges than on smaller ones, and therefore that larger territories and ranges contain more food resources.

Loudon (1979) used exactly the same analytical approach, although he approached the problems of determining importance and abundance differently from Hosey. He identified ten key plant species from observations and then used faecal analysis to quantify the percentage of fragments of each species in the diet between October and March. This percentage was taken as a measure of dietary importance. He found the same rank order of importance by faecal analysis and observation, but this is less revealing than it would have been if all species had been examined in faecal analysis. Since Loudon used the same analysis as Hosey, his correlations of food score with territory size are subject to the same lack of independence described earlier. Significant positive correlation would therefore be expected between food score and

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territory/range size, and indeed Loudon found such correlations for most plant groups. Like Hosey, he found no significant correlations between food score per unit area and either territory or range size.

It is not surprising considering the methodological and analytical similarities between their work that the conclusions which can be drawn from Loudon are no different for those drawn earlier from Hosey.

Loudon also investigated the relation of visibility to the size of territory At each of 30 random points in each range, he estimated and ranges. the horizontally visible distance (1m above ground) for the four compass points, and obtained a mean for each range. There was a significant positive correlation between territory size of bucks and visibility. (See Section 8.4 for discussion of sample size bias for minimum polygons in 1975), but no significant correlation between doe range size and visibility. This lead him to suggest that visibility was important for bucks but not for does. His hypothesis was that bucks defended as large an areas as possible and that the limit to territory size was imposed by their ability to see intruders. Since does are not believed to be territorial (Cumming 1966), no significant correlation would be predicted between range size and visibility, and indeed the absence of this correction is an essential support of the hypothesis.

However if the correlation is tested using only breeding does (this excludes doe 12 (Table 38, p179, who did not breed during the 3 year study and was antiered (p. 33)) the correlation between range size and "open area" visibility (p. 176) is significant (r = 0.839, n = 8, p < .01). This correlation clearly does not support Loudon's hypothesis. It appears that for breeding adults of both sexes, lar(or territories/ranges are more open than smaller ones: if visibility was important in determining range sizes, topographic relief would also exert influence and yet this cannot readily be quantified. Food and cover may themselves be inter-related but their effects would be difficult to separate.

In conclusion, it is clear that habitat has a proximate effect on dispersion of roe deer via several pathways, including diet, ranging and social behaviour, and patterns of use of different communities. From this study it appears that food quality may influence range size. However, the ultimate factors influencing dispersion will be concerned with reproductive success, and this an area of roe deer biology that has received little direct attention. The function of territoriality in roe deer remains unclear, it is not known whether male roe deer are territorial in all

environments: this study suggests that territorialility may be less pronounced under certain conditions, which may be related to the distribution of food resources, but the mating system of roe deer living entirely in open habitats has not been examined. Territory size or position may affect reproductive success and some evidence has accrued from the long-term study at Chedington, which suggests that females move to particular territories or perhaps to the territories of particular males to mate (Loudon 1979), but the degree of polygyny in roe deer remains unclear. The quality of food in territories could also affect male reproductive success either indirectly through female choice of mate, or directly because better food may increase survival of offspring. There are clearly many interesting questions that remain to be answered about roe However future research requires careful planning so that clear deer. answers can be obtained, since studies of roe deer are beset with problems caused by visibility and the behaviour of the study animals.

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DEFINITIONS

Time periods:dawn:3 hour period extending from first
light which was normally approximately
30 minutes before sunrise.dusk:3 hour period preceding last light,
which was usually approximately
30 minutes after sunset.day:period between dawn and dusk.
night:

Age class...: kids: from birth to 6 months. juveniles/ subadults: from 6 months to 12 months (note kids were included with juveniles in most analyses) adults: from 18 months onwards

TABLE 1

NUMBER OF PELLET GROUPS FOUND ON 8 (50m²) QUADRATS AT PORTON, MARCH 1979 and FEBRUARY 1980 INCLUSIVE

Farmland was not assessed

MONTH	WOODLAND	GRASSLAND
M	20	_
	20	5
A	19	5
M	17	4
J	3	1
J	1	2
Α	2	1
S	4	1
0	5	9
N	4	6
D	9	9
J	13	5
F	4	2

TABLE 2

		(X =	Mis	sed	or incomplete		tri	transect)					
		M	A	м	J	J	A	s	0	N	D	J	F
	Replicate							· · · · · · · · · · · · · · · · · · ·		<u> </u>			
Dawn] 1	0	2	2	0	0	2	11	21	0	0	0	3
	2	0	2	0	4	0	9	16	8	0	0	0	о
	3	0	0	1	3	0	12	7	Х	х	1	2	0
	j 4	0	0	X	X	0	6	25	X	х	x	4	x
Day] 1	0	0	0	0	3	0	3	0	0	X	0	0
	2	0	0	0	1	0	0	0	X	0	X	0	0
	3	0	0	0	0	0	0	0	2	3	X	0	0
•] 4	0	2	3	1	0	0	0	X	0	X	0	0
Dusk] 1	0	6	7	4	0	6	21	1	0	0	2	1
	2	0	4	11	5	0	3	5	5	0	0	0	6
	3	2	6	3	7	0	4	10	20	х	0	0	2
	4	16	10	2	1	2	10	28	X	x	х	1	13
Night	1	0	8	8	2	1	15	6	X	0	0	5	7
	_ 2	1	12	0	3	0	3	27	x	0	0	х	1
] 3	х	X	x	X	X	х	30	X	х	X	x	x
	mean	1.4	/3.7	2.	8/2.4	1/0.4	(5.6	/12.6	/8.1	/o.3	/0.1	/1.1	/2.5/

NUMBER OF DEER OBSERVED ON CEFEALS AT PORTON ON TRANSECTS

TABLE 3

NUMBER OF DEER OBSERVED ON SEED-GRASS AT PORTON ON TRANSECTS (X = missed or incomplete transect)

		M	A	М	J	J	A	S	0	N	D	J	F
	Replicate					<u></u>		•					
Dawn	1	4	7	2	2	0	1	0	0	о	0	0	0
	2	4	8	0	1	0	0	2	0	0	0	0	0
ſ	3	11	7	Ö	0	0	4	0	X	х	0	0	0
J	4	1	7	Х	x	0	3	3	X	х	x	0	x
Day	1	0	0	0	0	0	0	0	0	о	x	0	0
	2	4	0	0	0	0	0	0	х	0	х	0	0
ſ	3	0	5	8	0	0	0	0	0	0	х	0	0
•	4	З	4	0	0	0	0	0	х	0	X	0	0
r sk	1	15	13	6	0	2	1	1	2	4	0	3	5
	2	5	18	14	1	0	0	0	0	12	7	0	3
ſ	3	15	11	0	1	1	1	1	8	х	10	0	<u>*:</u>
j	4	14	5	0	1	1	0	1	х	x	х	1	6
Night]	1	0	12	7	0	2	0	1	X	4	8	0	0
+	2	5	8	6	0	0	0	3	Х	0	7	x	0
J	3	x	X	X	x	х	X	0	х	х	x	x	x

mean

5.8/7.5/3.3/0.5/0.4/0.7/0.8/1.4/2.0/4.0/0.3/1.5/

TABLE 4

NUMBER OF DEER OBSERVED IN WOODLAND AT PORTON ON TRANSECTS (X = missed or incomplete transects)

		М	A	М	J	J	A	S	0	N	D	J	F
	Replicates												
Dawn	1	5	1	2	1	0	0	1	0	5	0	0	0
	2	1	3	7	0	2	0	8	0	2	2	1	1
	3	1	3	4	1	0	6	2	Х	x	0	0	3
	4	2	1	х	x	0	1	0	X	х	X	2	x
Day	1	0	4	1	0	0	1	0	0	0	х	0	0
	2	0	5	2	0	0	0	0	X	0	x	0	0
	3	0	1	2	0	0	0	0	0	0	x	0	2
J	4	0	0	2	1	0	0	0	Х	0	х	1	0
Dusk	1	1	4	1	1	0	2	1	4	2	4	6	7
	2	0	2	0	0	0	1	4	2	0	2	0	4
	3	0	0	2	0	0	1	0	1	х	0	2	9
J	4	2	2	2	0	0	0	0	Х	х	x	0	7
Night]	1	0	4	0	0	2	0	1	Х	0	0	0	0
-	2	5	0	1	0	0	0	0	Х	1	0	х	2
J	3	x	X	x	х	X	x	0	x	X	x	X	x
	MEAN	1.2	/2.1	/2.0	/0.3	/0.3	/o.9	/1.1	/1.0	/1.0	/1.0	/0.9	/2.7/

TABLE 5

				- 16 V L.	D IN	GNA	SSLAP	D AI	POL	RTON	ON	TRANS	SECTS
		(X =	mis	sed (or i	ncom	plete) tra	nsec	cts)			
		M	A	M	J	J	A	S	0	N	D	J	F
	Replicate												
Dawn] 1	3	2	3	9	0	0	3	4	-1	0	3	1
	2	2	5	8	8	3	2	10	12	6	6	10	3
	3	0	5	11	4	2	1	0	X	X	0	5	2
	4	6	1	х	х	5	0	7	X	х	х	3	х
Day	1	0	0	1	5	1	0	0	3	0	x	3	0
	2	0	1	0	1	1	0	0	X	3	х	1	0
	3	0	10	9	9	0	0	3	0	0	x	7	0
· ,	4	0	12	1	0	1	0	0	x	3	x	0	0
Dusk	1	4	10	8	14	2	2	7	8	2	6	3	8
	2	3	7	11	8	1	0	7	9	12	1	4	10
	3	0	8	3	3	1	1	6	3	X	4	6	6
	4	0	4	9	6	4	0	3	х	x	x	8	7
Night]	1	0	3	2	4	1	0	1	X	0	1	0	0
ŀ	2	0	0	3	2	0	0	0	х	0	0	x	0
ļ	3	х	x	x	Х	х	Х	3	x	x	x	x	X

NUMBER OF DEER OBSERVED IN CRASSIAND AT DODTON ON TRANSPORT

mean

1.3/4.9/5.5/5.6/1.6/0.4/3.3/5.6/3.0/2.3/4.1/2.8/

MILLIDIA 2

TABLE 6

		М	A	М	J	J	A	S	0	N	D	J	F
	Replicate												
Dawn]	1	7	1	2	0	0	0	2	0	3	4	2	0
	2	3	3	1	2	0	0	0	2	2	3	2	5
r	3	0	4	2	1	1	0	4	X	X	2	0	0
J	4	0	2	X	x	0	0	2	X	x	х	4	Х
Day]	1	0	0	0	0	0	0	0	2	0	X	0	0
	2	0	0	0	0	0	0	0	x	0	Х	0	0
ſ	3	0	0	0	0	0	0	0	0	1	X	2	0
.]	4	0	0	0	0	0	0	0	X	0	X	0	0
Dusk	1	1	0	5	0	1	0	0	0	0	0	0	0
	2	1	4	1	1	0	0	0	0	0	0	0	0
r	3	5	2	0	1	0	0	0	0	x	0	0	0
j	4	9	3	0	1	0	3	0	х	х	X	0	0
Night]	1	4	7	6	4	0	1	3	x	3	6	2	5
-	2	3	7	2	0	0	0	0	Х	2	0	x	9
J	3	х	х	X	x	x	x	0	x	x	x	x	x

$\frac{\text{NUMBER OF DEER OBSERVED ON PASTURE AT PORTON ON TRANSECTS}{(X = missed or incomplete transect)}$

Mean

2.4/2.4/1.5/0.8/0.1/0.3/0.7/0.6/1.1/1.9/0.8/1.5/

APPENDIX 2

				Q			<,001			su			ns		sampled
	AREA			×"			13.22			3.26			4.78		labitat vation.
AUTAS NOTS				Total	Ğ	0 0	00 148		101	41 142	2	71	23		area of h by obser
RVATION D				8×		ł	I		4	1	ç		11.0	n total	
ND OBSEI		ARMLAND	75.2	(Exp)		I I	I		1	I	(10 5)	(15.0)	(0.01)	x colum	nd tota
ACKING A	Lnc.	Ŀı		0bs	1				I	ł	α) v	22	v total	8 7 8
BLE 7 RADIO-TR/	st 1981 j otal			××	6,61	0.68		1 82	0 29) 1 	3.18	0.01		NO L	ł
TA INED BY	h - Augu n; T = t	NOODLAND	22.7	(Exp)	(37.3)	(13.0)		(37.7)	(5.7)		(5.7)	(01.)	.	lows:	, 2
N DETERM	Marc servatio	-		0bs	53	16	69	46	7	53	10	0	12	d as fol	1
AT OCCUPATIC	lata; 0 = ob	0		×	5.77	0.16		1.09	0.05		0.66	0.23		ns calculate	
OF HABIT.	racking (GRASSLANI	83.7	(Exp)	(42.7)	(55.0)		(63.3)	(35.3)		(4.8)	(5.9)		servatio	total
ARISON	radio-t		- 00	Obs	27	52	52	55	34	89	ო	2	10	for ob	. row
COMP	Ш С4		pled by ob	Data	R	0	Ŀ	щ	0	Ч	R	0	£4	ted values	exp, = X
			% Area sam]	Months	March +	April		May +	June		July +	August		Expec	

TABLE 1

SUMMER AND WINTER RANGE SIZES OF MARKED ADULT FEMALES AT PORTON April 1979-March 1980

⁺(Summer (S) = April-September 1979; Winter (W) = October 1979-March 1980)

			r	(h a)		
			unco	rrected	corre	cted
Deer	Season	No. obs.	Core	Range	Core	Range
4	S	24	2.6	7.5	3.6	11.2
	W	10	1.2	2.5	2.0	4.2
5	S	15	1,8	5,8	2.6	14.2
	W	15	3.2	6.4	5,8	16.8
6	S	17	2.0	2.8	2.0	2.8
	W	22	3.2	4.8	5,2	7.4

Mean ± SE

summer: 2.7 ± .479.4 ± 3.41winter: 3.3 ± .919.5 ± 3.78

TABLE 2

TWO-MONTHLY RANGE SIZES OF ADULT FEMALE ROE DEER

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AT PORTON, March-September 1981
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(* = radio-tagged)
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Area	(ha	()
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					Alea (Ink)					
				uncor	rected	correc	ted			
Sex/Age	Deer	Period	No obs.	Core	Range	Core	Range			
Adult] 4	Mar+Apr	16	2.1	4.7	3.9	10.0			
females		Apr+May	18	3.7	7.2	7.8	13.0			
	5	Mar+Apr	11	3.2	5,9	13.5	22 4			
	•	Apr+May	15	3.2	7.0	9.4	19.3			
	6	Mar+Apr	12	2.8	6.1	7.6	15.7			
	} ·	Apr+May	13	2.8	6.3	7.5	16.5			
	15*	Mar+Apr	19	3.1	5.7	5.4	9,6			
	•	Apr+May	29	1.6	7,3	1.6	10.8			
	•	May+Jun	17	3.5	5.5	11.0	13.3			
-	" 	Jul+Aug	21	3.4	5.7	6,6	9.9			
Subadult	61*	Mar+Apr	13	2.2	3,6	3.8	5.4			
females	•	Apr+May	21	1.6	4.8	1.6	7.4			
	62*	Mar+Apr	31	3.9	8.1	5.4	11.0			
	"	Apr+May	38	4.9	9.0	6.4	12,4			
	63*	Mar+Apr	18	2.6	6.2	3.6	11.0			
	•	Apr+May	30	3.4	10.7	4.4	15,5			
	64*	Mar+Apr	14	3.7	6.4	11.6	16.8			
J	٠	Apr+May	20	5.2	9 .2	12.5	18.8			

	correc	sted
	Core	Range
Mean adult (March+April) ± SE	6.1 ± 1.88	11.1 ± 2.33
(April+Mey) ± SE	6.2 ± 2.31	13.5 ± 2.42
Mean aubadult (Merch+April)± SE	8.3 ± 1.71	14.2 ± 2.34
(April+May) ± SE	6.6 ± 1.32	14.0 ± 1.75

TABLE 3

TWO-MONTHLY RANGE SIZES OF MALE ROE DEER AT PORTON, MARCH-SEPTEMBER 1981

(* = radio-tagged)

Area (ha) uncorrected corrected Deer Sex/Age Period No. obs. Core Range Core Range 16* adult Mar+Apr 31 5.7 16.6 9,6 25.6 males 11 Apr+May 51 5.5 13.9 5.5 13.9 May+Jun ti 31 3.9 7.0 5.6 10.2 а Jun+Sep 23 3.7 9.5 7.6 15.5 62* Mar+Apr 2,6 46 8.6 2.6 9.2 ` " Apr+May 54 2.5 4.9 2.5 4.9 н May+Jun 33 2.6 6.4 2.6 7.8 63* Mar+Apr 25 5.0 10.8 13.0 18.1 n Apr+May 2.0 32 6.1 2.0 7.3 ł. May+Jun 21 1.4 2.9 1.4 2,9 H Jul+Aug 15 2.2 4.9 3.9 10.8 60 subad.] Mar+Apr 13 3.2 7.7 9.2 14.8 18 males Apr+May 20 3.7 10.5 7.6 22.1 a May+Jun 12 3.1 6.0 12.2 22.5 61 Mar+Apr 16 2.7 5.4 6.9 12.8

3,4

2.7

н

h

Apr+May

May+Jun

19

8

			corrected				
			Core	Range			
Mean adult	(Mar+Apr)	± SE	8.4 ± 1.32	17.6 ± 4.74			
•	(Apr+May)	± SE	3.3 ± 0.79	8.7 ± 2.69			
t y	(May+Jun)	± SE	3.2 ± 1.25	7.0 ± 2.15			
Mean subadult	(Mar+Apr)		8.1	13.8			
и	(Apr+May)		5.7	20.6			
4	(May+Jun)	1	1.5	17.3			

7.0

3.9

3.8

10.8

19.0

12.0

TABLE 4

TWO-MONTHLY RANGE AND CORE AREAS OF RADIO-TAGGED DEER

AT CHEDINGTON, APRIL 1981 TO MARCH 1982 INCLUSIVE

Figures in parenthesis are uncorrected values where $n \leq 40$

Deer	Months	No. loci	Core	(ha)	Range	(ha)
•						
Ml	4+5	31	3.2	(2,8)	5.9	(5.3)
	6+7	26	3.4	(2.3)	6.8	(5,4)
	8+9	25	2.4	(2.2)	8.3	(6.1)
ſ	10+11	58	2.7		4.9	
	12+1	53	1.8		3.6	
J	2+3	50	2,0		3.3	
Fl	4+5	20	2.4	(2.2)	9.3	(6.6)
	6+7	16	1.2	(1.2)	5.0	(3.5)
	8+9	20	9,4	(4.2)	12.2	(6.6)
ſ	10+11	54	2.4		7.2	
	12+1	54	4.2		10.1	
	2+3	49	2.9		6.4	
F2	4+5	22	1.5	(1.5)	6.0	(4.2)
	6+7	17	3.2	(2.4)	3.8	(3,3)
	8+9	23	1.8	(1.8)	5.8	(4.9)
	10+11	56	1.1		3.0	
	12+1	54	0.8		1.8	
J	2+3	49	2.1		4.8	

TABLE 5

TWO-MONTHLY RANGE AND CORE AREAS OF MALES AT CHEDINGTON

APRIL 1982 - MARCH 1983 INCLUSIVE

Figures in parenthesis are uncorrected values

Deer	Months	No. loci	Core (ha)	Range (ha)
-				
Ml	4+5	58	2.3	6.1
	6+7	52	2.6	5,8
	8+9	64	2.2	6.1
٢	10+11	47	2.0	5.1
	12+1	0	-	-
J	2+3	26	3.9 (2.7)	9.8 (6.7)
мз	4+5	58	4.0	7.9
	6+7	46	3.1	5.9
Ļ	8+9	62	2.4	4.4
	10+11	53	1.1	2,3
	12+1	56	1.4	2.9
	2+3	42	1.6	4.6

TABLE 6

TWO-MONTHLY RANGE AND CORE AREAS OF RADIO-TAGGED FEMALES AT CHEDINGTON April 1982 to March 1983 inclusive

Figures in parenthesis are uncorrected values.

Deer	Months	No. loci	Core (ha)	Range (ha)
F2	4+5	58	1.0	0 5
	6+7	49	1.2	3.0
	8+9	59	2.8	5.6
}	10+11	52	1.7	5.7
	12+1	61	2.2	5.2
J	2+3	40	2.2	4.3
F4	4+5	62	2.2	4.6
	6+7	57	3.9	6.8
Į	8+9	49	4.0	6.9
	10+11	54	2,9	4.9
	° 2+1	39	1.6	3.5
ļ	2 +3	10	2.0 (1.2)	4.8 (2.5)

TABLE 7

VEGETATION DATA USED TO CALCULATE BIOMASS IN ANNUAL RANGES

Veg.	type	Mean annual	Mean annual	Mean annual
		standing crop	digestible	digestible N
		(tons ha ⁻¹)	standing crop (tons ha ⁻¹)	$(kg ha^{-1})$

PORTON

grassland	5.27 ± 0.249	1.23 ± 0.143	16.54 [±] 2.285
scrub	0.04	0.02	0.30
woodland	2.01 ± 0.225	0.58 ± 0.121	13,42 [±] 3,434
woodland edge	$8.23.10^{-3}$ tons 100	m^{-1} 3.73.10 ⁻³ tons100m ⁻¹	0.06 kg $3^{N} 100 m^{-1}$
pasture	2.05 ± 0.500	0.88 ± 0.266	12.74 \pm 1.554
cereals	5.53 ± 0.2830	2.68 \pm 1.486	45.97 ± 21.204
seed-grass	3.96 ± 1.687	1.80 ± 0.810	32,23 [±] 22,393

CHEDINGTON

ground veg

i)srub/mat.			
hardwood	2.30 ± 0.323	0.54 [±] 0.109	37.76 ± 27.009
ii)conifer	3.53 ± 0.449	0.83 [±] 0.162	14.39 [±] 2.429
rides	3.87 ± 0.200	0.92 ± 0.122	14.08 [±] 2.038
bramble	0.78	0.34	5,98

(Standard errors are variation between months, not replicates within months)