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The decline of the roe deer (*Capreolus capreolus* L.) in the New Forest, Hampshire

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To my parents,

Sohan Lal and Kamla Sharma

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ABSTRACT

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THE DECLINE OF THE ROE DEER (*CAPREOLUS CAPREOLUS* L.) IN THE NEW FOREST, HAMPSHIRE

by Surender Kumar Sharma

The New Forest is an area of some 375 km^2 in Hampshire, southern England. Of the 267 km^2 administered by the Forestry Commission, some two-thirds (the 'Open Forest') consists of open heathland with varying expanses of bog, grassland, woodland and scrub. Domestic cattle and ponies range freely across this area. The remaining third is enclosed for commercial timber production. Five species of deer occur within the Forest: fallow, roe, red, sika and muntjac.

The Commission carries out an annual census count of each deer species except muntjac; the census counts for roe suggested a steady decline in the population in each of the Forest's beats over 1972-88. This purpose of this study has been to investigate this decline, both to determine its cause and as a study of the biology of a declining ungulate population. An initial assessment of the census data suggested the decline was real, and not merely an artifact of the data collection, and was associated with the areas of enclosed woodland rather than the Open Forest.

Both the annual changes in roe numbers over the period of decline, and variation in the present density of roe across the Forest were found to be strongly associated with the vegetation of the enclosed commercial woodlands. Changes in roe numbers over 1976-86 were consistently correlated with the decline in prethicket stage conifer stands. Roe density across 12 study sites in the Forest was also correlated positively with the local abundance of bramble, holly and ivy, and negatively with that of bracken and *Molinia*, relationships reflected in associations between roe density and the mature woodland stands at those sites which tend to bear such vegetation. Associations were also found between yearly changes in roe numbers over 1972-88 and several climatic factors, but the association with vegetation was dominant.

Field studies over 12 months at 6 sites of different roe densities corroborated the positive associations between roe numbers and the enclosed woodland vegetation. Overall, roe at sites 'poorer' in known food species selected the fewer food-bearing habitats more strongly than did roe at 'better' sites, but, except for autumnal use of broadleaf woods, were unable to restore usage levels through compensatory selection. Dietary studies based on faecal material also suggested both that the roe at poorer sites had a diet of lower nutritional quality than roe at better sites, with a higher intake of fibrous / cellulose material, and that the overall diet of New Forest roe today, compared with that of 1970-73 (Jackson 1980), showed a similar drop in dietary quality, especially in the lower current use of bramble and forbs. The most likely explanation is that the decreasing availability of ground vegetation, particularly bramble, in the Forest's enclosed woodlands from a maturing age-structure, has limited the roe population.

Changes in roe numbers over 1972-88 were also found to correlate significantly negatively with censussed numbers of red, sika and fallow deer for the same period. However, assessments of both differences in ranging patterns, and (using published accounts) of the likelihood of resource competition between roe and these species, and between roe and the Forest's domestic stock, suggested only a limited potential for competition. Moreover, for fallow, the Forest's most widespread and numerous deer species, the change in numbers over the period of decline in the roe could be at least partially explained as an independent response to the changing habitat conditions within the Forest over the study period.

In comparison with roe from two neighbouring forests, New Forest roe were found to have lower body weights and depressed reproductive performance, notably a lower proportion of does becoming pregnant. They also carry a slightly higher parasite burden, most likely the result of poorer body condition. These results are discussed in the context of current knowledge of the population regulation of the roe, and in relation to other declining ungulate populations, and fluctuations in roe numbers in commercial woodlands.

CONTENTS

Page

CHAPTERS

3. PRESENT DISTRIBUTION OF ROE DEER IN RELATION TO VEGETATION 56

4. THE USE OF HABITATS BY ROE IN THE NEW FOREST INCLOSURES. 78

5. DIETARY PATTERNS OF NEW FOREST ROE DEER 131

6. ROE AND OTHER LARGE HERBIVORES: ECOLOGICAL SEPARATION OR CONFLICT?. 151

APPENDICES

LIST OF FIGURES AND TABLES

List of Figures

List of Tables

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1. INTRODUCTION

1.1 BACKGROUND TO THE STUDY

This thesis presents the results of an investigation into a perceived decline of the roe deer *Capreolus capreolus* population in the New Forest, southern England. Of the 375 km^2 encompassed by the New Forest's juridical perimeter (the 'Perambulation'), just over two-thirds - some 267 km^2 - is Crown land administered by the Forestry Commission; of this about a third is given over to commercial timber plantations. The Forest supports a mixed economy and has a long tradition of common agriculture. In recent years, it has also become a popular recreational resort, and, at the same time, has been increasingly recognised as an area of outstanding conservation importance. Among its larger wildlife, five species of deer range within the Forest boundaries: as well as the roe, there are populations of red *Cervus elaphus*, fallow *Dama dama*, sika *Cervus nippon* and muntjac *Muntiacus reevesi*.

As part of its management responsibilities, the Forestry Commission monitors and regulates the number of deer on the Forest in order to limit both economic damage caused to the commercial timber stands, and damage to the Forest's ground flora which might impair its conservation value. At present, the deer management takes the form of a yearly cull, the size of which is based upon an annual census of each deer species taken in the spring. It should be noted that this census is intended to be a systematic count of all the deer within the Forest and not merely an index count. After an apparent steep increase in the roe population over the 1960s, the census figures for the 1970s and early 1980s suggested a steady decline in numbers (Table 1.1). This latter trend was in marked contrast to both the increasing numbers of the other deer in the New Forest, such as fallow (Table 1.1), and the trend for roe overall in southern England, where the species has for some years been increasing both in numbers and in distribution (Ratcliffe and Pepper 1987).

Against the background of this apparent decrease in roe numbers within the New Forest, the present study was initiated in 1984 to assess the level of decline and to identify the potential causal factors.

Table 1.1 *Census data for New Forest deer populations 1960 - 1988*

Year	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969
Roe	211	302	328	383	434	465	490	527	539	572
Fallow	788	857	931	933	994	1147	1036	968	855	893
Red	-	-	7	23	20	23	24	29	33	18
Sika	35	44	34	42	64	84	97	67	38	38

Year	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979
Roe	620	444	428	435	356	375	344	363	332	354
Fallow	1022	866	1017	904	909	834	973	908	927	950
Red	23	26	28	29	37	49	43	49	79	34
Sika	37	71	73	75	78	88	94	80	79	80

Year	1980	1981	1982	1983	1984	1985	1986	1987	1988
Roe	334	309	336	281	264	260	265	249	265
Fallow	1016	996	1049	1020	1033	1006	1086	1227	1152
Red	58	73	64	72	57	66	70	77	77
Sika	74	95	76	97	115	99	103	103	79

Source: Forestry Commission census data

1.2 STUDY AIMS AND OBJECTIVES

While the principal aim of the project is, as stated, to identify the cause, or causes, of the decline of the roe deer in the New Forest, an ancillary aim is to determine any intermediary mechanism through which the factor(s) identified may have operated. The project is not intended to be a management study, to suggest if and how the roe population should be managed.

As a starting point, a range of ecological factors may be identified as potentially contributing to the decline in the roe population, and these are listed below.

(i) Changes in the availability of suitable food
(ii) Changes in the availability of adequate shelter
(iii) Competition from other herbivores
(iv) Natural predation

(v) Disease / Parasites

(vi) Human interference, including the effects of the annual cull, road traffic accidents, poaching and disturbance

(vii) Abiotic factors such as climatic change.

It is recognized that these factors may combine or interact in their effects - for instance, competition may lead to the reduced availability of suitable food. It is likely that some factors have been more important than others, and it is certainly true that more information is available on some of these factors than on others: as far as possible, the project will examine the likely relative importance of each.

Beyond the immediate question of identifying the factors responsible for the decline in the roe deer population, the study has wider biological interest within the context of the population dynamics of the roe and other ungulates. Although the roe deer has, over the past 30 years, been the subject of many ecological studies, both in the United Kingdom and on continental Europe, almost all of these studies have involved animals which may be considered healthy (in expanding or stable populations), or individuals in captivity. The present study makes a particular contribution to our knowledge of roe by looking, unusually, at a population in decline and at very low density. There are several reasons why this is of particular interest. Recent work has contributed greatly to our understanding of population regulation in roe (e.g. Maizeret *et al.* 1989, Gaillard *et al.* 1992, 1993b, Hewison 1993), and suggested how different density-dependent and density-independent factors may act to affect overall population performance. As a declining population - but depending upon the reasons for the decline - the New Forest roe may present one of individuals close to their physio-ecological limits, and thus provide a singular case for comparison of population parameters (body condition, reproductive status etc.) with those reported from some of these other studies. We may also learn, through measurement of appropriate individual and population parameters, more about where those physio-ecological limits may lie.

In addition to adding generally to our knowledge of the ecology of the roe deer, this study can also be seen as one of a long series of ecological studies on the large herbivores of the New Forest carried out since the early 1970s (on fallow deer: Jackson 1974, 1975, 1977b, Parfitt (unpublished report cited in Putman 1986a), Thirgood 1990, Putman *et al.* 1993;

on sika deer: Mann 1983, Mann and Putman 1989a, b; on cattle and ponies: Edwards and Hollis 1982, Edwards 1985, Putman 1986a, b, Pratt *et al.* 1986, Putman *et al.* 1987, Gill 1987, and Burton 1992; and on roe deer: Jackson 1980).

1.3 THE STRUCTURE OF THE PROJECT

Following an assessment of whether the decline in the New Forest roe population appeared to be real, and not merely an artifact of data collection (Section 1.6), the study investigated potential causes of the roe population change. Initially this was done by seeking correlations between the changing population over the years of the decline and other environmental variables over the same period (or parts of it) for which there were available data. These variables included

(i) habitat factors i.e. measures of the vegetative environment
(ii) the numbers of the other large herbivores
(iii) use of the Forest for recreation, as a measure of 'human disturbance'
(iv) measures of a range of climatic factors.

Notwithstanding that both the quality and quantity of data available were limited, it was possible to investigate not only which factors may be important, but also to assess what might be their *relative* importance.

Next, the present day distribution and relative abundance of the roe population was examined in relation to geographical differences in vegetational characteristics over the Forest. Correlations were again sought between the level of the roe population of defined areas and the corresponding abundance of a range of plant species, embracing both the ground vegetation within the inclosures and the vegetation of the Open Forest.

Having established at least some of the vegetational factors associated with high and low roe populations in the Forest, field studies were undertaken to see which of these associations could be substantiated. Patterns of habitat use by roe were compared between relatively 'good' and 'poor' roe areas, in relation to both the relative availabilities of different types of habitat and the degree of selection of those habitats expressed by the roe: i.e. did availability or selection determine the observed patterns of habitat use, and were these patterns of use / selection in accord with the results of the earlier correlation-based investigations? These studies were supplemented by examining differences in diet between the same areas, and also comparing the present day diet with the published diet of roe from the Forest twenty years ago: were there differences in diet between roe with access to habitats of different quality, and has the overall diet of the New Forest roe changed from that reported by Jackson (1980) for the period 1970 - 1973?

Based upon both habitat use data collected in this study and published accounts of the ecology of the Forest's other large herbivore species, the possibility of resource conflict and competition between roe and these other species was assessed.

Whatever factors have been causal in the decline of the New Forest roe, coincident changes in the body condition and reproductive performance of the population may serve both to confirm those factors and to reveal how they have been effective. Available data from culled New Forest animals permitted comparison with those of healthier roe populations from neighbouring forests, enabling both body condition and reproductive rate to be assessed for New Forest roe.

The findings of this study are discussed in the context of the dynamics of mammalian populations, and other workers' findings on the roe deer in particular. Given the range of potential causal factors (listed earlier) which may influence the population level of the roe in the New Forest, which appear to have played a part in initiating, maintaining and (possibly) limiting the decline in the roe, and what is their relative importance? As a study on a low density and declining population, we can also consider whether the population is simply being suppressed or limited, or whether there is evidence of regulation. Finally, the past and present situations of the New Forest roe are considered, examining the relationship between forestry practice and population change.

1.4 THE ROE DEER

Classification and distribution

Of the species in the sub-family Odocoilinae of the deer family, Cervidae, the roe deer (genus *Capreolus*) is the only one which occurs exclusively in the Old World.

The roe has a very wide distribution across Eurasia. It is found throughout central and southern Europe, extending northwards into southern Scandinavia, and in a wide band across central Asia to the Pacific coast of Siberia and southwards to Manchuria. Opinion differs over whether the roe deer east of the Urals (generally referred to as the Siberian roe) should be given specific rank as *C. pygargus* or regarded as conspecific (*C. c. pygargus*) with the European roe (*C .c. capreolus*). The Siberian roe stands higher than the European by 15 cms. (Putman 1988), and hybrid male offspring are infertile (Stubbe and Smirnov 1972). Sokolov and Danilkin (1981, cited in Harrington 1985) report that across the range of the Siberian-European roe there is east-west clinal variation in the number of microchromosomes. See Groves and Grubb (1987) and Sokolov and Gromov (1990) for further discussion.

The European roe is found throughout most of Europe south of the Arctic Circle, and has recently been reported as extending its range north into the Arctic region (Holand and Staaland 1992). It is absent only from Iceland and Ireland, and from certain Mediterranean lowland regions, including parts of Spain, Portugal, Italy and Greece (Corbet and Ovenden 1980, MacDonald and Barrett 1993).

Within the United Kingdom the roe currently enjoys a very widespread distribution. In the north, the species is found throughout Scotland and northern England on both sides of the Pennines, and also occurs over much of East Anglia. In the south, it occurs throughout the southern and south-western counties, and is continuing to expand its range into the midlands, being recently reported from Oxfordshire and the Welsh border areas. Arnold (1993) gives a detailed recent distribution map of the roe in Britain.

History

While regarded as an indigenous species (Lister 1984), the current stock of the British roe population actually has a cosmopolitan origin. As noted, roe in the south of Britain appear to have become virtually extinct during the Middle Ages (some pockets may have remained in Sussex and Wiltshire) (Prior 1968), and much of the present population in southern England is descended from the animals introduced at Milton Abbas in 1800. Similarly, roe in the east of England are descendants of German stock released at Thetford in 1884 (Chapman *et al.* 1985). Although roe in Scotland and the north of England are thought to be of indigenous origin (Rowe 1982), those in the Lake District also include some from Austria (Lowe 1979, cited in Staines and Ratcliffe 1991). At least two roe from the Lake District were introduced to the New Forest during the 1960s (keeper Mr. G. Barrell, pers. comm.). Hewison (1993) looked at 15 populations of roe across almost the whole of Britain but found only limited evidence of genetic variation, perhaps suggesting little influence from imported animals, or that there have been other unknown translocations.

Size and appearance

The roe is one of the smaller deer found in Britain, with both sexes similar in size: adult bucks in the south and east of England average 23.9 kg. 'live' weight and adult does around 22.3 kg. (Staines and Ratcliffe 1991). Adults of both sexes stand around 63-67 cms. at the shoulder (Prior 1968).

The winter coat of the adult varies from brown-grey through dark brown to near black over dorsal areas and flanks, with a paler undersurface (Staines and Ratcliffe 1991). This is moulted between mid-March and late May to the bright reddish-brown summer coat, which lasts until September-October. Fawns - also termed kids - bear white spots on a light red-brown coat, losing these traits at their first winter moult for a more adult-like pelage. One of the most characteristic marks, in both sexes, is the distinctive black nose set against a white rim which extends around the chin. The roe bears a white or cream target, larger in the doe and more pronounced in both sexes in the winter. Although a tail-less species, females sport an anal tush of hair, which may give the illusion of a small tail.

The adult buck carries a pair of small antlers, seldom over 30 cms. in length, each of which usually bears three points or 'tines' in mature animals. Antlers are cast in November-December of each year, with more mature bucks shedding earlier (Prior 1968); a new and usually larger set is then grown in the following year. Growth is complete by March and the antlers are cleaned of the protective skin, or 'velvet', by April. The underlying endocrine cycles and associated sexual changes of the roebuck are further described by Short and Mann (1966) and Marchlewska-Koj and Kruczek (1988); their relationship with changes in photoperiod is examined in Sempéré *et al.* (1992).

Reproduction

The roe is unique amongst Artiodactyls in exhibiting embryonic diapause, first reported by Ziegler (1843). After fertilization of the egg - at about the end of July - the blastocyst remains in the uterus but develops very little, and does not implant in the uterine endometrium until sometime in late-December or early January. Shortly before that time the normal rate of embryonic growth and development recommences and thereafter continues as normal. This subject is reviewed by Short and Hay (1966) and the mechanism explained further by Aitken (1974).

Birth normally takes place in the south of England between mid-May and mid-June, with multiple births being the rule. Births are highly synchronised: 80% of births in a population from France occurred within a 30 day period (Gaillard *et al.* 1993a). Hewison's (1993) extensive data from across Britain revealed median values of 82% of adult does pregnant (range 67% - 94%) and 71% of yearlings (range 35% - 96% for sites with data for 10 or more individuals). At Chizé, France, Gaillard *et al.* (1992) reported even higher values, with 87% and 98% of yearlings and adult does respectively being pregnant. The median value for foetuses per pregnant doe (adults and yearlings combined) in Britain was 1.75 (Hewison 1993).

Well-nourished does tend to give birth to a higher proportion of female young (Ellenberg 1978, Hewison 1993). This is consistent with the local resource competition theory (Clark 1978), which suggests that the costs of rearing doe fawns, which are more philopatric than buck fawns (Strandgaard 1972a), may be considerably higher, as they are more likely to share resources with the mother. Verme (1969), studying white-tailed deer *Odocoileus virginianus* (which are also multiparous) also reported an inverse relationship between range nutritional quality and the proportion of male embryos.

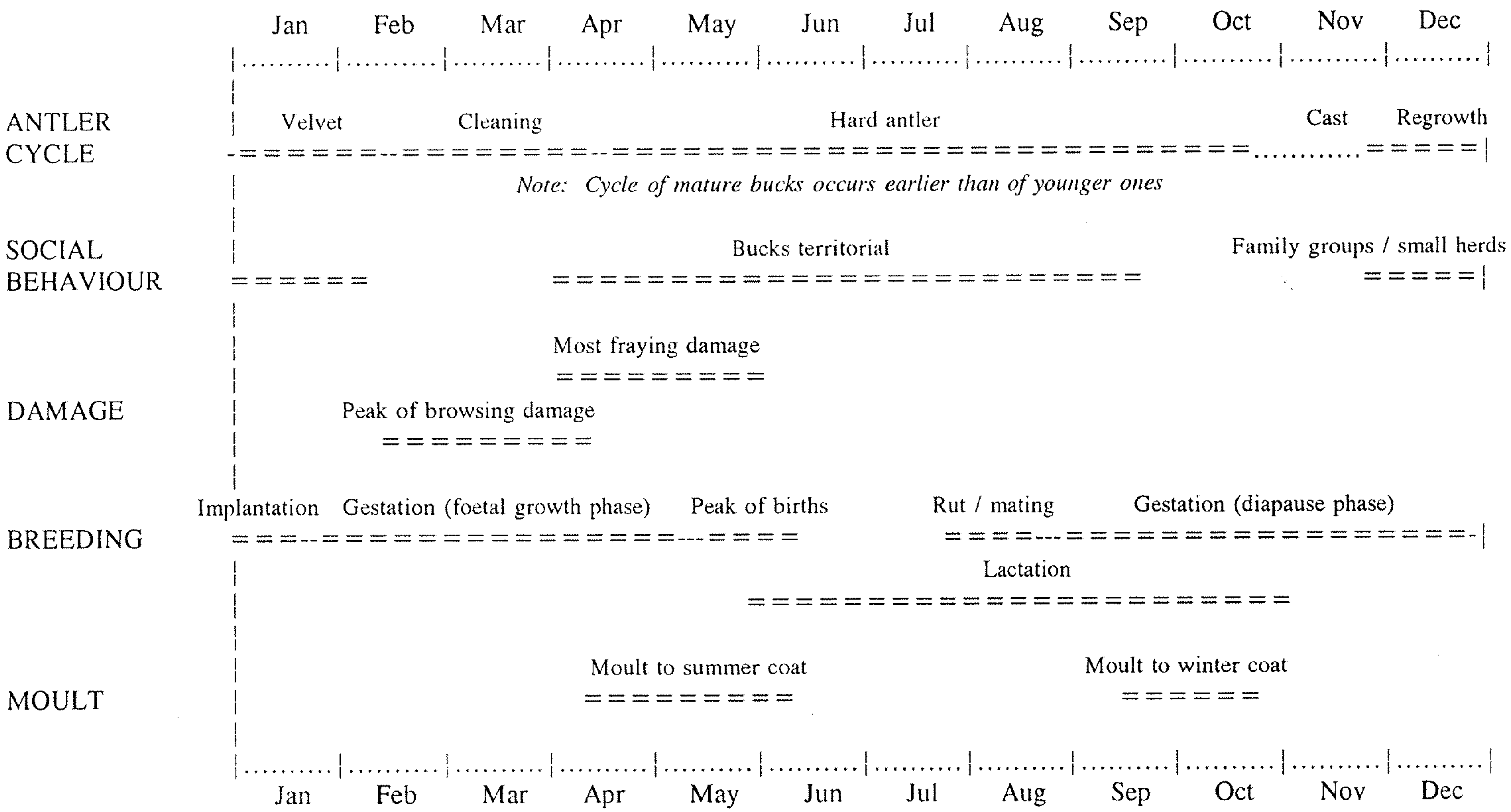
Survivorship

As does may begin breeding as yearlings and are likely to give birth every subsequent year throughout life, there is clearly a high potential rate of recruitment to the population. In practice, approximately 55-65% of fawns and 50-80% of yearlings are lost from populations due to mortality or emigration (Ratcliffe and Rowe 1985). Fawns generally stay with the doe until the spring, with buck fawns often driven away by April or May to outlying areas by the resident adult buck (Cumming 1966, Holmes 1973), and the doe fawns drift away (or are forced to leave) a little later (Bramley 1970a, Bideau *et al.* 1983), although they not infrequently establish themselves in ranges adjacent to, or overlapping with that of their mother (Bramley 1970a, Loudon 1979). The life cycle of the roe is shown in Fig. 1.1.

From a study at Kalø, Denmark, in which the entire roe deer population in an area was exterminated, Andersen (1953) reported a mean population age of 3.1 years (excluding fawns) and 2.0 years overall; at Kalø a 2 year old could expect to live another 2 years. Ashby and Henry (1979) concluded that an individual roe in their 2+ year old class at Hamsterly Forest, Co. Durham, had a life expectancy a little higher at 2.8 years, and they estimated that both sexes in their population suffered an annual static mortality of 30%.

Overall roe conform to the general pattern of mammalian age-class survival described by Caughley (1966). Gaillard *et al.* (1993b) found juveniles may be sensitive to density-independent factors such as climate, but mortality among prime adults was much lower and remained fairly constant until the age of about 7, the onset of a senescent phase. Although roe in the wild may occasionally reach the age of 10 years (Andersen 1953, Holmes 1973, Ashby and Henry 1979), and Mattioli *et al.* (1992) reported one animal from their study area of 11 years, survival beyond 8 is rare (Staines and Ratcliffe 1991), perhaps because of tooth wear (Gaillard *et al.* 1993b). Females suffer a less steep decline in survival upon senescence and generally have longer life spans than males (Johnson 1982, Gaillard *et al.* 1993b). Rowe (1982) presents a concise review of the many mortality factors which may act on roe in Britain, although as Staines and Ratcliffe (1991) point out, man is the species' principal predator with over 15,000 animals culled annually.

Fig. 1.1 Simplified annual cycle of the roe deer in southern England



Habitat, range and activity

While roe in Britain may be observed on open moorland and heathland as well as arable areas and pasture, they are most often associated with woodland. They tend to remain in or close to available cover during the day, but venture further onto the more exposed open areas during the hours of darkness (Prior 1968, Hinge 1986, Thirgood 1984).

Range size varies considerably, depending upon the resource base (Loudon 1979, Johnson 1984). In conifer plantations in southern Britain, Bramley (1970b) reported a mean range size for non-territorial bucks of 16.2 ha., while Johnson (1984), studying roe on agricultural land at Porton Down, Wiltshire, found roe had mean ranges of some 22.3 ha. Workers in upland conifer forests have reported much larger ranges. Thus Cumming (1966) gave the mean range size for adult bucks as 35.2 ha. for woodland and moorland in northeast Scotland, and Hinge (1986) reported an annual range of 85 ha. for bucks in mixed-age conifer forest at Glenbranter, western Scotland, with ranges significantly larger in winter than in May-June. Does usually have slightly smaller and more overlapping home ranges than bucks (Johnson 1984) which vary less widely over the year than those of bucks (Hinge 1986); at high densities, however, does may have ranges larger than those of bucks (Bideau *et al.* 1992).

Roe deer are active over all 24 hours of the day, alternating periods of foraging with rest and digestion, but are most active at dawn and dusk with a peak of activity in the twilight period (e.g. Prior 1968, Hinge 1986, Vincent *et al.* 1979). Periods of activity and rest are likely to be related to rumen fill and rumination (Hinge 1986, Holand 1992), and vary seasonally as roe consume more bulky, less digestible feed in the winter (Cederlund 1981).

Social organisation and behaviour

By habit adult roe in Britain are generally solitary, the small groups sometimes seen usually comprising buck and doe or, more usually, doe and fawn(s). Larger assemblages, usually seen in open pasture or arable land, tend to be gatherings of individuals rather than social groups. On continental Europe however, a ‘field ecotype’ roe has been extensively reported, from Poland (Kaluzinski 1974, 1982, Bresinski 1982, and others), Czechoslovakia (Zejda 1978), Switzerland (Turner 1987), and France (Maublanc, Bideau and Vincent 1985). These roe form large aggregations, sometimes approaching 100 individuals, which last from late autumn to mid-spring, and which exhibit a degree of internal organisation (Bresinski 1982). Fruzinski *et al.* (1982) compared weight and body measurements of forest and field ecotype roe, and found significant differences in growth rates in fawns, with the greater weights of field type fawns probably due to the greater availability of high-quality and easily digested food. Roe are also frequently seen in rural gardens, and in recent years have been reported from urban areas, even in major cities (Harris 1984).

Roebucks are generally held to be territorial over the period of April through mid-August (Kurt 1968a), the time leading up to and over the annual rut (approximately mid-July to mid-August) (Prior 1968, Bramley 1970a, Johnson 1984). A buck may hold a territory for 3 years (Staines and Ratcliffe 1991). Territory size, like that of home range, may vary greatly, also being related to the resource base (Johnson 1984), and may be around half the size of the range of a non-territorial buck (Bramley 1970b). In Chedington Wood, Dorset, several workers have reported territory sizes e.g. 7.4 ha. (Bramley 1970b), 8.2 ha. (Cumming 1966), 5.1 - 8.1 ha. (Hosey 1974), and 7.7 ha. (Johnson 1984). Loudon (1978) suggested that the minimum size of territory a buck requires is 4 - 5 ha. in good habitat, while the maximum size a buck may be able to defend is 50 - 60 ha. (Sempéré 1979). At high densities bucks may become more polygynous (e.g. Bideau *et al.* 1992).

Does are generally thought not to hold territories except, according to some authors, for a brief period around parturition (Espmark 1969, Kurt 1968a, Loudon 1978).

Diet

Many studies on roe diet have been carried out, both in Britain (Hosey 1974, Henry 1978, Jackson 1980, Nakhasathien 1980, Diakite 1983, Hearney and Jennings 1983) and on the Continent (Siuda, Zurowski and Siuda 1969, Szmidt 1975, Borowski and Kossak 1975, Gebczynska 1980, Helle 1980). These support the assertion made by Hofmann *et al.* (1976) from examination of the rumino-reticulum anatomy, that the roe is essentially a 'concentrate' selector, requiring a diet of high quality material rather than one of bulk, low-quality forage. The same dietary studies show a great range and diversity in the plant species which compose the diet of the roe across its European range, and a great variation in the seasonal choice of diet (eg. Siuda *et al.* 1969), suggesting the precise diet in a given site or season reflects opportunistic use of local resources. Overall, the roe can be described as a highly selective but adaptable feeder, and in feeding trials has been shown to be able to identify dietary quality of potential foods with respect to their protein and energy content (Rusterholz and Turner 1978) and can select both browse and herbs as required to balance its seasonal metabolic requirements (Perzanowski 1978, Oslage and Strothmann 1988).

The dietary composition of roe specifically within the New Forest was reported by Jackson (1980), based on the examination of the contents of 105 rumina. He showed that the major part of the plant matter ingested was browse, with bramble *Rubus fructicosus* agg. and rose *Rosa* spp. dominating over most of the year. Coniferous browse was used heavily in mid-winter, and broadleaved trees and shrubs and herbs formed an important group of items over the summer. Some dwarf shrubs, particularly ling, were found in moderate quantities at all times except summer, while a number of others appeared to be restricted to particular seasons, such as bilberry *Vaccinium myrtillus* in spring. Grasses were taken in moderate amount from spring to early winter, and a variety of other species were taken at specific times of year, e.g. ivy *Hedera helix* over winter, holly in June (when its leaves are at their softest), and fruits and nuts when available from autumn into winter, with acorns dominating within this category. Very similar overall dietary composition has been reported from the other studies carried out in the south of England (Hosey 1981, Nakhasathien 1980, and Diakite 1983).

There are two periods in the year when roe may be unable (or less able) to secure their nutritional requirements from available vegetation. In late winter roe may sustain an energy deficit through having to forage on a higher proportion of woody and / or cellulose rich diet (Weiner 1977, Holand 1992). Additionally, does during lactation may be temporarily unable to meet the extremely high demands for metabolizable energy (Weiner 1977), which may be as much as 2 or 2.5 times the normal level (Loudon 1985).

Roe and forestry

Throughout Europe the roe is recognised as a potential cause of damage to young forestry plantations (Rowe 1982). Gibson and MacArthur (1965) highlighted the problem in

Britain, where all commercial species are at risk (Ratcliffe and Pepper 1987). Most serious are the effects of winter / spring browsing on leading and lateral shoots, such damage peaking over January / February (Hosey 1974) as the new spring foliage emerges. In part the taking of leaders may also be related to the relative absence of alternative feed (over early summer in Welch *et al.'s* (1991) study). Local damage occurs through fraying of stock over spring and summer by roebucks when cleaning antlers and marking territories (Loudon 1978). Browsing damage on newly planted trees may continue for several years, until the trees achieve a height which places their leaders beyond the 1.2 m. browsing height of roe (Rowe 1982). Roe rarely strip bark for forage, perhaps as they have insufficient strength (Gill 1992a).

As forestry practices vary greatly across Britain, it is difficult to generalise about damage levels. In lowland areas, plantations may be more broadleaf based, or mixed, contain different species and species mixtures, and may also be in proximity to any of a wide range of different agricultural land usage. All of these factors may influence the damage sustained by trees, as different tree species not only differ in their liability to browsing damage, but the extent to which each may be browsed depends on the other species available and the foraging behaviour of the roe themselves (Crawley 1983). Prior (1987) notes that roe with access to agricultural crops containing small woodlands may 'concentrate' fraying / browsing damage in the latter. In general, broadleaves are damaged more in summer, and their slower growth may make them vulnerable for longer (Gill 1992a). Many other factors appear to influence the choice of tree for browse by roe, including the presence of secondary compounds, which in turn may vary according to soil and other factors, even for the same tree species (Bernays *et al.* 1989). For fraying, roe seem to select trees on the basis of their physical characteristics and spacing (Gill 1992a), while Thompson (1969) notes that roe prefer springy, unbranched sapling-sized stems.

Further details of damage to trees caused by roe and other deer are given in recent reviews by Gill (1992a, b), and the particular problem with regard to Sitka spruce in Scottish uplands, including the impact on the trees, is discussed by Welch *et al.* (1988, 1991, 1992). An historical perspective of the Forestry Commission's view of roe as a pest species is given by Teasdale (1982), while measures to control roe and limit the damage they cause are discussed by Loudon (1978), Rowe (1982), Teasdale (1982), Ratcliffe and Pepper (1987), Welch *et al.* (1991) and Ratcliffe and Mayle (1992).

Population regulation in roe deer

As the roe is a generally solitary, seasonally territorial species, several early studies examined the effect of social behaviour on population numbers. These studies suggested that aggressive territorial behaviour of bucks over April - August appeared to be an important, perhaps even the primary factor limiting the breeding population (Cumming 1966, Prior 1968, Bramley 1970a). The evicted juvenile (2 and 3 year old) males were indeed found to suffer higher mortality (Strandgaard 1972a, Loudon 1979).

That this action may effect population regulation was supported by the fact that these juvenile bucks are capable of breeding (Bramley 1970b) and territories which become vacant before the mid-summer rut are rapidly occupied by these surplus animals (Cumming 1966, Loudon 1978). This appeared to satisfy Watson's (1967) criteria for territorial behaviour to limit breeding: (i) there must be a surplus of non-breeding animals, (ii) these animals are prevented from holding territories and breeding by the established territory holders, and (iii) they are capable of taking territories and breeding if given the chance. Juvenile does are also expelled by adult females (Kurt 1968a), although less aggressively (Bramley 1970b), and may be forced onto poorer quality habitat and consequently suffer heavier juvenile mortality (Kurt 1968b).

Bobek (1977) considered that the availability of summer food, which in turn determines territory size, may act as the ultimate limiter of density, and that reproductive rates in roe may be density independent rather than density dependent. However, both territory and range size are themselves not independent of either the resource base (Loudon 1979, Johnson 1984) or the population density (Vincent and Bideau 1992), and it has now been shown that body weight and fecundity, as well as survivorship, are determined by an interaction of both density-dependent and density-independent factors (Maizeret *et al.* 1989, Hewison 1993, Gaillard *et al.* 1993b).

As noted, the roe is unique among artiodactyls in exhibiting embryonic diapause. In contrast to the reproductive processes in other deer, therefore, when fertilization and implantation are very close in time, in roe these events are separated by some 5 months. This has profound consequences for control of the reproductive cycle in roe, as quite distinct environmental conditions may exert influence on each stage.

As in mammals generally (Frisch 1984), age of first reproduction in roe is determined strongly by achievement of a crucial threshold body weight (Loudon 1987). Thus, while resource availability plays a primary role in determining whether juvenile roe achieve the required weight for ovulation - adults maintain high ovulation rates in nearly all populations (Gaillard *et al.* 1992, Hewison 1993) - other factors such as climate may at that stage also influence eventual reproduction success (in yearlings) to some degree through the number of ova released (Hewison 1993). Implantation in mid-winter is also affected by both resource availability (through body weight) and by winter climatic conditions. Hewison (1993) found the proportion of does implanting successfully to be strongly influenced by body weight and subject to density-dependence, and also subject to climatic influence, most notably the mean winter temperature; in yearlings, the influence of climate actually supplanted that of body weight.

Just as it is the reproductive success in juveniles which is most strongly subject to regulatory and limiting factors, patterns of survivorship in roe, recently studied by Gaillard *et al.* (1993b) also show that juveniles are more susceptible to the effects of density and climate. Gaillard *et al.* (1993b) were unable to measure survivorship in fawns under 8 months, but comparison of mortality patterns by sex and age-classes (juveniles, prime adults and senescent adults) at two areas in France differing in population density and winter climate severity, showed that prime adults of both sexes at both sites suffered only low annual mortality. Senescent adults showed higher mortality than prime adults (and males more so than females). Juveniles suffered a disproportionately higher mortality than adults at the study site with higher population density (but milder winter climate). Survival of both adults and juveniles was not significantly different at the other site, but juveniles suffered proportionately higher losses in more severe winters.

It is important to study population processes at a range of densities. As some authors have pointed out, the regulatory effect of population reduction at high densities may not necessarily be accompanied by enhanced increase at low densities, when populations may have more unstable dynamics (Rees and Crawley 1989, Lawton 1991). Low density populations can be more liable to the actions of density independent factors, and may suffer additional problems which act to prevent recovery, such as severe tooth wear resulting from an enforced change of diet (Skogland 1988). Further studies on population dynamics at low densities are clearly needed.

1.5 THE NEW FOREST

Location and geology

The New Forest is situated within the county of Hampshire in the south of England, between latitudes 50° 45′ N and 50° 58′ N, and longitudes 1° 22′ W and 1° 46′ W. It stands upon a bed of Tertiary clay rocks and sands, capped by more recent gravel and brickearth, set above the chalk syncline of the Hampshire Basin. The result is a region of diverse but generally poor acidic and neutral soils, although marine deposits of loams and clays in the south do provide some more fertile areas. The land slopes gently from the north - where the highest point lies at some 418 feet above sea-level - to the south in a series of eroded terraces; most drainage occurs southeast into the Solent via the Lymington and Beaulieu rivers, but there is also run-off to both the Avon in the west and the Test in the east. More detailed accounts of the geology may be found in Melville and Freshney (1982) and of the local geography in Tubbs (1986).

Climate

Overall the regional climate is mild and oceanic. The prevailing winds are south-westerly. Meteorological Office data for nearby Hurn, Bournemouth, over the period 1968 - 1985 showed mean minimum and maximum daily temperatures of 1.2 °C and 7.9 °C respectively in January, and 11.4 °C and 21.6 °C in July, and an average annual precipitation of 785 mm (range 510 to 980 mm), with 102 days per year of ground frost.

History and land use

Though the original, native forest of the area was probably cleared gradually from the later part of the Bronze Age (c. 1200 - 500 B.C. in Britain), the appearance of the New Forest today owes much to its having been declared a Royal hunting preserve by William the Conqueror, sometime between the Norman Conquest (1066) and the Domesday survey (1086). By this action, the Crown effectively took possession of all the Forest deer and, at the same time, placed severe restrictions on land-use by the local people (under 'Forest Law'). Over the succeeding years, some concessions were made, foremost of which was the right of local people to graze domestic animals over the area. Subsequently the locals' demands were given an increased, although still limited, measure of recognition, most notably by the Charter of the Forest of 1217. This charter recognised the Forest as having its own special administrative needs, and specially appointed individuals, termed 'Verderers', presided over one of the courts (The Court of Swainmote) for the purpose. This administration, and its associated judiciary, have evolved through the centuries, with the Court of Verderers given a statutory position by the New Forest Act of 1877. The Verderers' principal function at the present time is to protect and administer the 'ancient rights of common' tied to land ownership. The principal rights of common are of:

Pasture:	Commoners may still graze animals on the unenclosed lands of the Forest (as distinct from the enclosed areas set aside for timber production).
Mast:	the right to turn out pigs for a limited period in autumn for mast (pannage)
Turbary:	to take turf for fuel
Estovers:	to take wood for fuel
Marl:	to take marl (calcareous marine clay) from a number of designated pits, e.g. for soil improvement or buildings.

Today, these rights are administered in balance with the needs of other demands on the Forest's lands, recognizing the importance of conservation and recreation as well as of commercial forestry.

The region has been of importance for timber production from at least as far back as the 14th century. In 1698 an Act of Parliament formally allocated 6000 acres (2428 ha.) for silviculture. However, the ensuing land enclosure, gradually implemented over the eighteenth century, was greatly resented by locals as it restricted access to common land for their domestic stock. The passing of the Deer Removal Act (1851) only served to increase the conflict between Crown and the local population: this legislation was intended to clear the way for far more extensive forestry planting (allowing 6475 ha. for timber) and, at the same time, to reduce damage inflicted on plantations by eliminating the Forest deer. Strong local protest followed at the proposed enclosures, forcing the Government to change its policy. The New Forest Act of 1877 recognized the Forest as an area of national heritage, and limited the extent of land which could be enclosed for silviculture.

Since World War II, legislation has allowed some additional, poorer quality land to be used for forestry purposes (subject to commoners' consent), but has also been increasingly concerned with the need for conservation and recreational use of the Forest. Many of the Forest's vegetation communities are unique: in addition to containing the largest tract of lowland heathland in Britain, its extensive ancient woodlands and valley mires are among the finest in Europe. Much of the New Forest (essentially the Crown land, see below) was designated an SSSI (Site of Special Scientific Interest) in 1971, a status re-notified in 1986 under the Wildlife and Countryside Acts (1981 and 1985). More recently, the area's conservation importance has been further recognized by its designation as a Special Protection Area under the European Commission Directive on Bird Conservation, a Wetland of International Importance under the International Wetland Convention, and its proposal as a World Heritage Site (Tubbs 1994). In a statement issued in September 1992, the Government announced that the New Forest was to be accorded status equivalent to a National Park, but with its own unique constitution, and would be extended to afford better protection to the landscape and grazing rights (*The Times*, 25 September 1992). The full implementation of these proposals is, however, currently uncertain. The Department of the Environment (DoE) issued a news release on 14 July 1994, in which it stated that it was intended to apply the same planning policies to the New Forest Heritage Area (which presently covers some 54,000 ha.) as to national parks, and to extend the scope of development controls, but that the definition of the Heritage Area was still under discussion. There also remain concerns about the best management structure for the area: while the DoE decided against a new statutory co-ordinating body for the Heritage Area, others (e.g. Tubbs 1994) have expressed the view that new management expertise is essential for the effective conservation management of the area.

Currently, of the total New Forest area of some 37500 ha. within the Perambulation, about 9400 ha., or about a quarter, is either privately owned as estates or agricultural land, or has been developed for urban habitation. Another 1400 ha. is termed 'manorial waste land' and is owned either privately or by the National Trust. The remaining 26700 ha. is Crown land that, since 1923, has been managed by the Forestry Commission.

It is on this Commission land that the present study has been carried out and to which, unless stated otherwise, the term 'New Forest' or 'Forest' will hereafter refer.

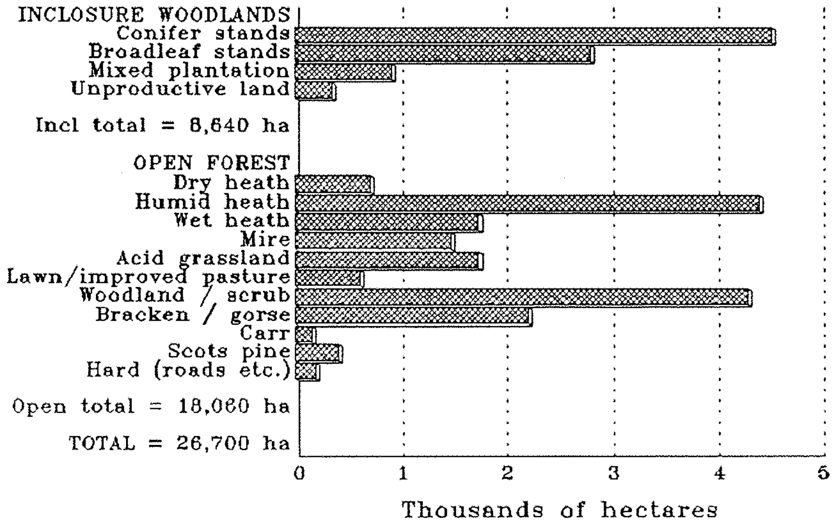
Reference has already been made to the distinction between enclosed and unenclosed (or 'Open') land within the Forest, the former being fenced areas ('inclosures') set aside for the production of timber. Across the open lands, however, a wide range of different habitats may be recognized, from open dry heathland to mire, and from pasture to rich Ancient & Ornamental woodlands; many of these habitats are of unique conservation value. Much of the well-drained open land is dry heath, dominated by ling *Calluna vulgaris* and purple moor-grass *Molinia caerulea*, with some bell heather *Erica cinerea* and bristle bent *Agrostis curtisii*, and varying amounts of gorse *Ulex* spp. and bracken *Pteridium aquilinum*. Wetter areas of heath are characterised by the presence of cross-leaved heath *Erica tetralix*. In valleys where mires and bogs have formed, *Sphagnum* mosses and other wetland plants such as bog myrtle *Myrica gale*, cottongrass *Eriophorum angustifolium*, and rushes *Juncus* spp. may be found. Carr woodland has formed in mires where some water flow permits, typically containing common sallow *Salix atrocinerea*, alder *Alnus glutinosa* and alder buckthorn *Frangula alnus*. On the Forest's more fertile clays and loams, there are open broadleaf woodlands, dominated by oak *Quercus* spp. and beech *Fagus sylvatica*, and often bearing an understorey of holly *Ilex aquifolium*. Areas of acid grasslands have developed on more exposed, fertile areas, dominated by bristle bent, with greater or lesser amounts of gorse and bracken. Grass lawns may be found adjacent to steams, made fertile by the nutrients deposited during flooding, and rich in grasses such as brown bent-grass *Agrostis canina*. Further details of the typical plant communities of the Open Forest habitats are given in Putman (1986a) and Tubbs (1986). The vegetation of the Forest inclosures will be considered in more detail in Chapters 2 and 3 of this report.

The overall habitat composition of the New Forest Crown lands is shown in Fig. 1.2.

Administration

Since the passing of the Forestry (Transfer of Woods) Act of 1923, and the New Forest Transfer Order of the following year, the Forestry Commission has been responsible for the overall administration of the New Forest. However, the Commission is obliged to comply with legislation (such as the Acts of Parliament of 1949, 1964, 1968 and 1970) which, among other things, limits the land area which may be enclosed for timber and assigns particular management responsibilities to the Commission. These include the maintenance of bridges and drainage, and the provision of recreational facilities for the

Fig. 1.2 Habitat composition of New Forest Crown lands



Compiled from English Nature Open Forest survey and Forestry Commission stockmaps (1984)

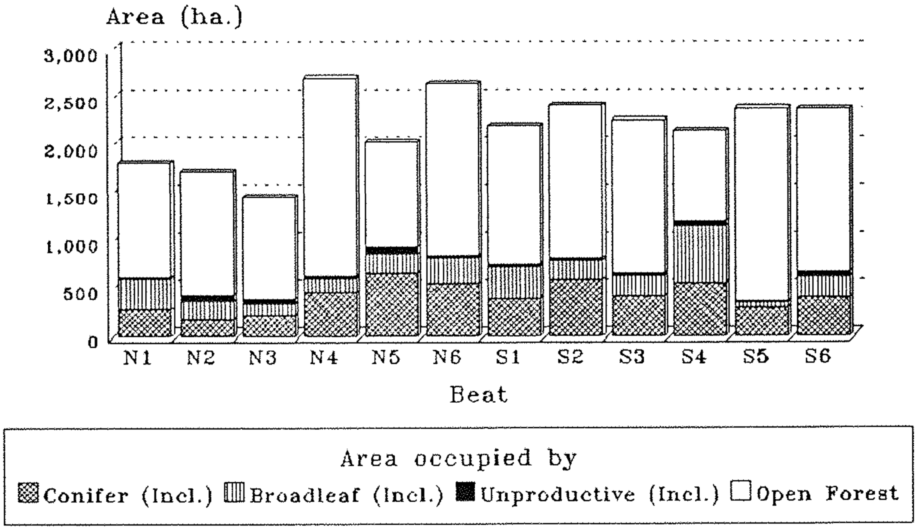
eight million day-visits per year (Perry 1990). The Commission works alongside and is constrained by other organizations, such as the Court of Verderers, which administers the rights of common, and English Nature, which exercises rights over planning issues within the Forest as an SSSI. A fuller view of the complexity of the management of the (entire) New Forest may be found in the report of the New Forest Review Group (1988).

The present study relies heavily on data collected by the Commission for its own management purposes; for this reason, it is necessary to describe in more detail certain aspects of the Commission's administration. In addition to the production of timber in the inclosures, the Commission manages the Open Forest lands, mainly through assisting heathland rejuvenation and the limitation of shrub and pine encroachment by cutting and selective burning; essentially, the aim of this is to preserve the character of the Open Forest. For range (including wildlife) management purposes, the New Forest is divided into 12 beats, each under the jurisdiction of a Forestry Commission keeper. It is the keeper who annually carries out the deer censuses and the requisite control of the deer within his beat. The 12 beats vary greatly in size. All contain both enclosed and open land, but differ considerably in the relative proportions of the two; they also differ in the relative mix of broadleaf and conifer plantations within the enclosed woodlands. Fig. 1.3 presents an overview of the composition of the individual beats, while Fig. 1.4 shows the beat locations and the distribution of enclosed and Open Forest land in the Forest.

The large herbivores of the Forest

There are currently eight major species of large herbivores in the New Forest: the five species of deer, and the domestic cattle, ponies and pigs which are permitted to feed under the rights of common. In addition, a few donkeys are grazed by some commoners, and sheep are kept locally on private land, some of which may occasionally intrude upon the Crown lands.

Fig. 1.3 Overall composition of the New Forest beats



Source: Forestry Commission stockmaps (1984)
Note: Mixed woodlands separated into conifer / broadleaf components

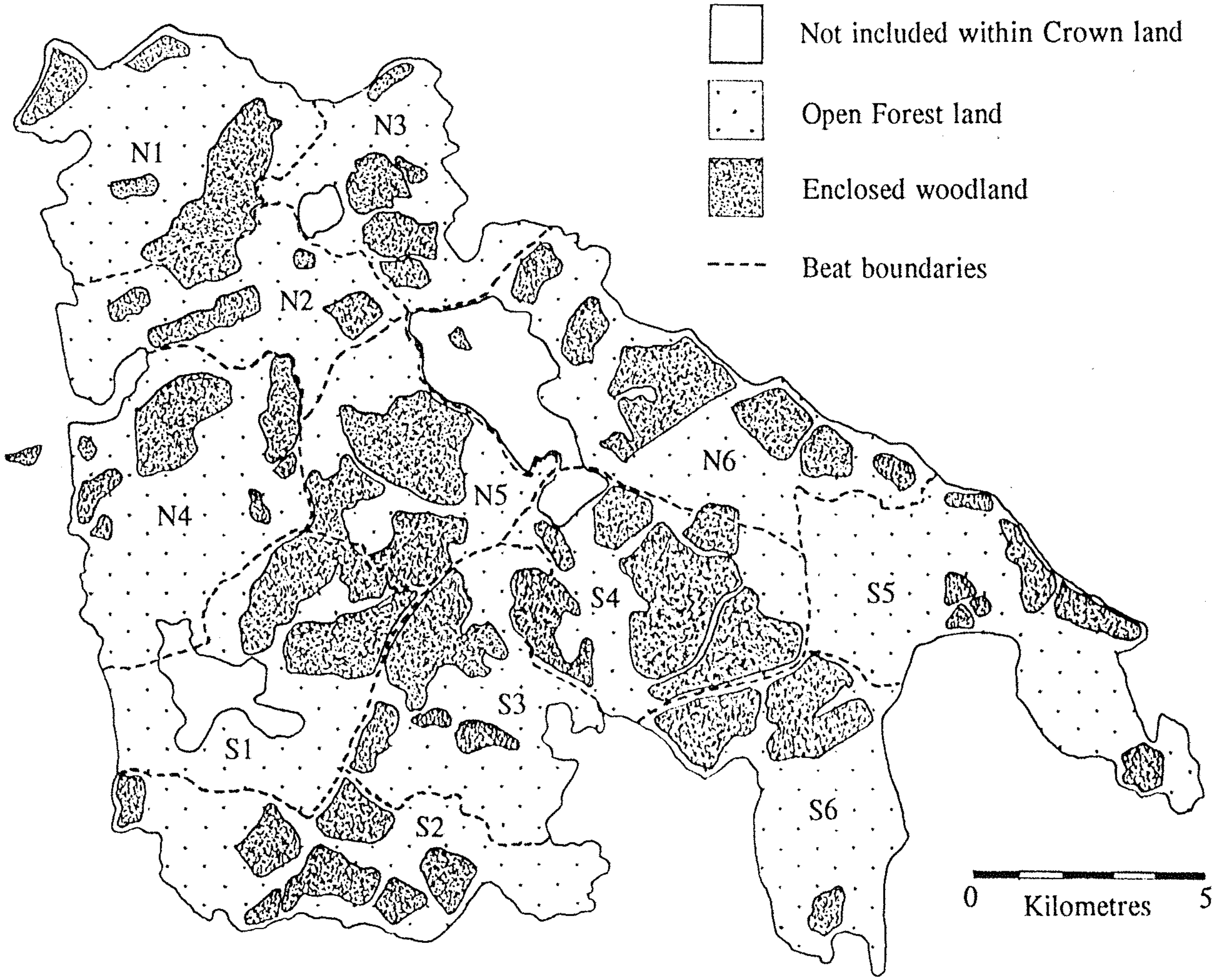
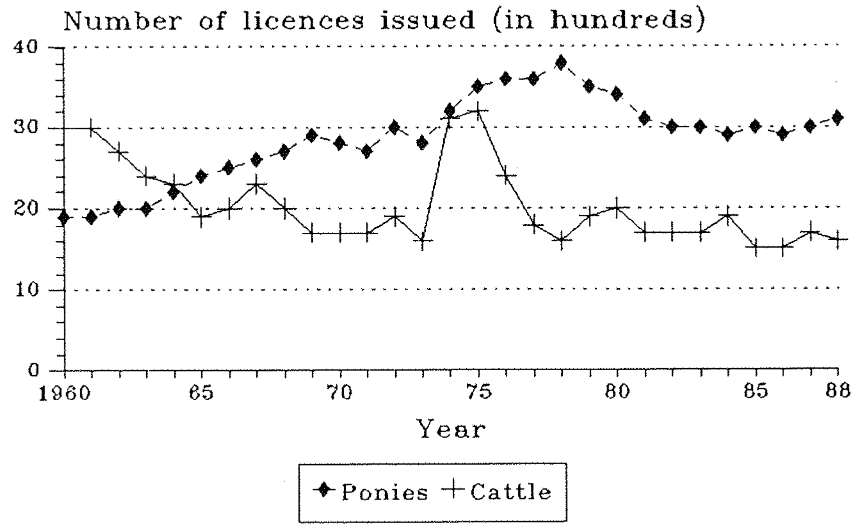


Fig. 1.4 *New Forest Crown lands, showing distribution of enclosed woodland and Open Forest within 12 keepers' beats (designated N1 - N6 and S1 - S6)*

The numbers of domestic stock are recorded and administered by the Court of Verderers each year by a licensing system (Fig. 1.5). Average figures from licences issued for 1989 - 1991 suggest there are at present approximately 3400 ponies and 1900 cattle turned out onto the Open Forest annually (in practice there will be slightly fewer). Many of these, in particular the ponies, remain out over much or all of the year. In addition some commoners are permitted under 'rights of mast' to turn out pigs over the pannage season, a 60 day period during autumn and early winter. The number of pigs turned out fluctuates greatly, according to the mast and acorn crop, but is generally low (under 200).

Fig. 1.5 Number of licences issued for cattle and ponies by New Forest Verderers Office 1960 – 1988



Source: Office of the New Forest Verderers

Of the deer species, the most numerous by far is the fallow, which is widespread throughout the Forest, and which was censussed in 1988 at around 1150 animals, a figure generally accepted as a significant underestimate of the true number present (Strange 1976). As indicated in Table 1.1, the trend as revealed by the censuses since 1971 is of a steadily rising population, and, indeed, the species is reported increasingly from private lands bordering the Forest.

Both red and sika deer occur only locally within the Forest. An indigenous species, red deer appear to have become locally extinct (or nearly so) in the New Forest area by the late 18th Century (Putman 1986a). The population level appears to have been low throughout the 19th and into the 20th Century - although there may have been occasional introductions made over that time (Insley and Clarke 1975). In 1908 three animals were released into Hartford Wood at Beaulieu, and established a resident Forest population, which was subsequently reinforced by three further animals released at Denny, and escapes from a Burley estate in 1962. The current census stands at around 80 animals, although this too is likely to be an underestimate. A species introduced into Britain in the 1860s (Ratcliffe 1987a), the New Forest sika deer population dates from the early 1900s, when individuals escaped from the neighbouring Beaulieu Estate (Insley and Clarke 1975). The number of sika in the Forest is currently estimated at around 100 animals, almost all of which are restricted to a single locality, Frame Inclosure.

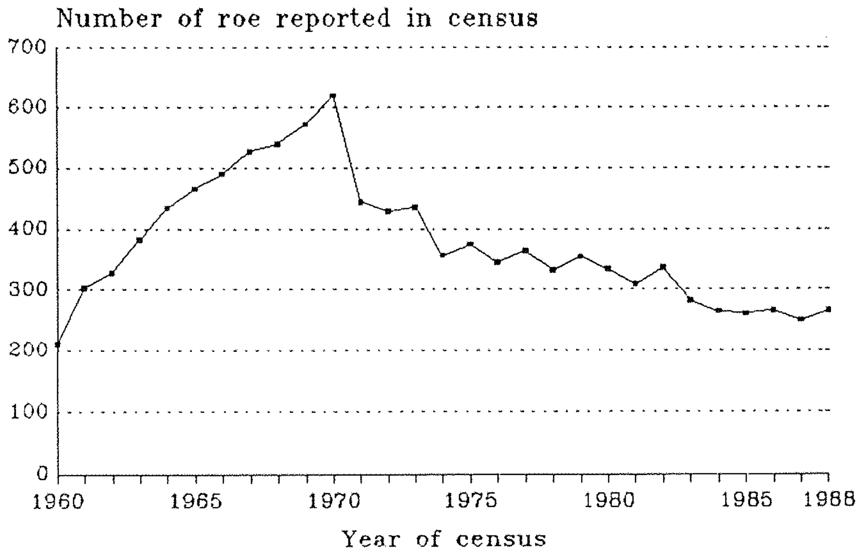
Another introduced species, the muntjac from South East Asia, has been reliably reported from the Forest since the mid-1960s (Jackson 1977a) and continues to be seen regularly in the Forest and nearby areas. No estimate of the population is available, and no census is carried out for this species by the Forestry Commission. So far, it is not known if there is an established breeding population within the Forest.

The roe deer, like the fallow, is widespread over the Forest, but the steady decline of the population as evidenced by the census counts (Table 1.1), has resulted in large areas, particularly in the central inclosures of the Forest, where they are now rarely if ever seen. Recent censuses (1993/4) suggest a total in the Forest of around 300 - 350 individuals. Historically, roe are thought to have become near-extinct over much of southern England during the Middle Ages, following the loss of protection for the species under Forest Law in 1338 (Prior 1968). At the start of the 19th Century however, the species was reintroduced into Milton Abbas in Dorset, with stock from Perthshire (Tegner 1951) and perhaps from France (Chard 1974). The roe subsequently reestablished and spread, probably re-entering the New Forest around 1870 (Jackson 1980).

1.6 AN ASSESSMENT OF THE POPULATION DECLINE

As previously noted, the annual census of the four principal deer species of the New Forest forms the basis of the deer management carried out by the Forestry Commission each year. From its records, the Commission was able to supply overall census data for roe deer for the period 1960 onwards, as presented earlier in Table 1.1. For convenience, these data are also shown graphically below (Fig. 1.6). As they form the basis for the present project, it is essential to examine these data carefully and ask whether they may be an artifact of the census method itself, rather than a reflection of a real decline in the New Forest roe population. In the latter case, we must further ask whether that decline may form part of a regular population cycle in the roe, as the answer to this may give some insight to the underlying cause of the population change.

Fig. 1.6 Census data for New Forest roe deer 1960 – 1988



Source: Forestry Commission census data (Table 1.1)

(i) The roe population until 1960

No systematic counts of the deer was carried out by the Forestry Commission until 1960, when Mr. W. A. Cadman, the Deputy Surveyor of the New Forest from 1959 to 1969, introduced the first censuses. Up until 1960, and for some years afterwards, the roe had been subject to control by teams of keepers with shotguns driving through areas where damage to plantations was considered high. There was no attempt to maintain a specific population level of deer in relation to repeated censuses. Anecdotal accounts suggest that the pre-war level of roe in the New Forest was higher than that recorded in the 1970s and 1980s: retired Head Keeper Jack Humby, for instance, recalls one occasion when 24 roe were shot in Parkhill Inclosure, an area in which no roe were censussed during the 1980s. Similar anecdotal accounts for other areas suggests that the pre-War roe population was high over the entire Forest. Vesey-FitzGerald (1946), writing around the end of the War, also describes the New Forest roe as being 'very common'.

The years following the War were of great significance for the Forest, as the late 1940s saw the extensive re-planting of the inclosures for timber. However, nearly all the new stock was conifer, whereas before the War around three-quarters of the enclosed Forest comprised hardwood trees (the current split of conifer to broadleaf hectarage is about 60:40 (Perry 1990)). Retired Head Keeper Bert Smith, who had been working in the Forest since before the time of the Commission's administration, considers that the 1950s saw a peak in the roe population level (pers. comm.), a view shared by a number of other keepers and ex-keepers: Mr. G. Barrell, for example, considers the population at that time to have been higher than at any time subsequently.

As noted, it was in 1960 that the first formal censuses were begun of roe and the other forest deer, at the instigation of Mr. Cadman. It is appropriate to consider the census figures for the periods 1960 - 1970 and post-1970 separately, as a number of changes in census methodology occurred following the departure of Mr. Cadman in 1969.

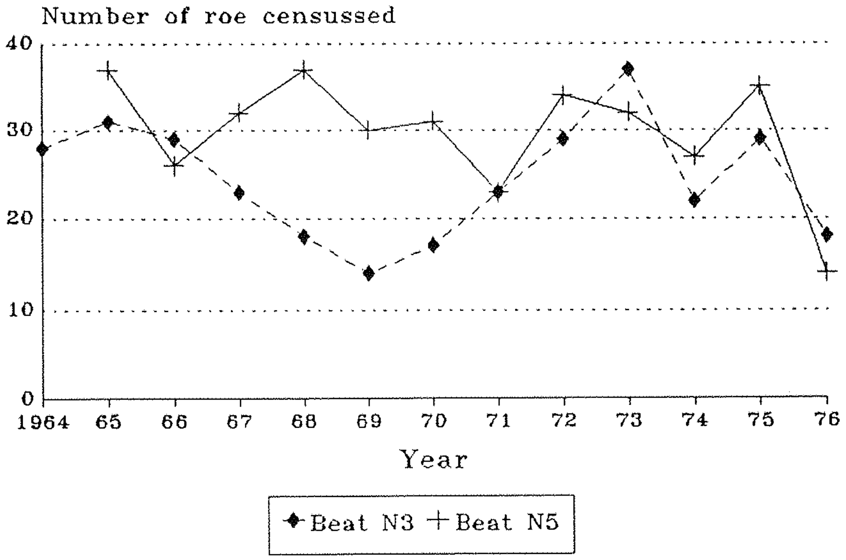
(ii) Period 1960 - 1970

During this period the census data suggest a rapid and sustained rise in the New Forest roe population. In order to try and verify this change in the population, we may consider the census method itself, other data from the period, and anecdotal accounts of the time.

It is not clear what precise method was used for the census when it was introduced in 1960. What <u>is</u> clear is that the census was not applied consistently over the whole Forest, and that as a new and developing technique, it may not have been applied consistently from one year to the next. For instance, retired keeper Wilf Cooke (pers. comm.), though a keeper over the whole of the 1960s, claims not to have done any censuses over that period, a fact confirmed by former Head Keeper Jack Ealing. Similarly, retired keeper Sam Gulliver began his census counts on his beat in 1964, while keeper Derek Thomson started his in 1965 (personal records). Overall, the picture seems to be that the census was introduced in 1960 but concentrated to begin with on selected areas only, and was gradually expanded in scope. The populations of deer in other localities for some of the time may have been assessed by extrapolation or ignored (keeper Graham Wilson, pers. comm.). In addition, it must be remembered that the keepers themselves were new to the technique at the time, and that Mr. Cadman himself 'almost certainly' augmented their returned figures by 30% on the basis that deer numbers would be underestimated (Arthur Cadman, pers. comm. 1990).

Two keepers (S. Gulliver and D. Thomson) were able to supply me with their beat census data for that period of the 1960s for which they carried out censuses; these are shown in Fig. 1.7 (up to 1976 when the decline had become a discernable trend).

Fig. 1.7 Census data for roe in beats N3 and N5 (1964 - 1976)



Source: Forestry Commission keepers for two beats concerned

In neither case do the data show the expected rise in line with that suggested by the overall figures (Fig. 1.6). In the case of beat N5 (D. Thomson) the data actually suggest a slight decline in the population. The picture for beat N3 is less clear, as there actually seems to be an increase at the end of the 1960s, as was suggested by the whole Forest data. For now, however, we cannot take the numbers as they stand as some of the census counts were 'augmented' and some were not.

One remaining line of evidence which suggests that the census figures for the time 1960 to 1969 should be viewed with caution derives from personal impressions of keepers from that period. When retired and serving keepers and head keepers were asked about their recollections of the roe population in the 1960s, not one agreed with the picture presented by the overall census data. Most thought that the population had been steady, and a minority that there had been a decline which continued through the 1970s. All agreed that the actual population level was far higher in the 1960s than it was in the 1970s, and records of the number of roe culled in specific localities support this: Jack Ealing recalls 36 roebuck being shot on one occasion in 1966 at Holmsley, while keeper John Gulliver quoted a figure of 45 roe shot in Set Thorns Inclosure over 1970/71 (although this year, which followed major changes in range management [see below], saw an exceptionally high cull, according to Mr. Cadman).

Overall, it seems that the roe population over the 1960s was fairly steady, or in slight decline after the peak level reached during the 1950s, and that the suggested rise of the census data for the period should be rejected as an artifact. No evidence has emerged of a population cycle in the roe.

(iii) Period 1970 - 1988

At the end of the 1960s, a number of changes were made to aspects of the Commission's range administration. New head keepers were appointed, and the census was applied consistently to all areas of the Forest, with all keepers carrying out counts in the spring using similar methods. In addition, the head keepers resolved cases of deer 'shared' between adjacent beats, and attempted to apply a quality control check to the figures returned, with no augmentation being made for possible underestimation.

It is generally accepted that estimates of deer population returned by any census method relying on direct observation give an underestimate of the true population levels (e.g. see Andersen 1953, Strange 1976, Loudon 1978, Staines and Ratcliffe 1987). However, for the New Forest over the period 1972 to 1986 (or with only one keeper change, to 1988) the same individual keepers conducted the census each year using consistent censussing methods. Each keeper visits all parts of his beat several times over March and early April and builds up an inventory of individual animals, noting any individual characteristics, and recording the number of adult bucks, does and fawns separately. Animals are noted as associated with particular woodland blocks, and keepers discuss boundary areas to avoid double-counting. The head keepers also ensure that such error is minimised by separate checks, and that the numbers returned over their beats are consistent with their own assessments. With this method of checks, the census data for the period 1972 - 1988 therefore may be taken as a fairly accurate *index* of the population change, if not of the absolute numbers of roe within the New Forest. Only the data for the period 1972 - 1988 are used for the present study.

One further feature of the decline in the roe population is indicated by the census data. Keepers return counts of the deer within their beats as split up into localities. Most localities encompass an inclosure, or group of inclosures, and part of the adjacent Open Forest, and it is not possible to ascertain numbers in each portion separately. There are, however, a few localities which consist only of Open Forest areas, and we can examine the census data from these areas to see if, during the period of the decline, there is evidence of a decline on the Open Forest specifically. Specific localities which may be used for this purpose are Mallard Wood, Matley wood, Shave Wood, Busketts Wood, Rushpole Wood and Hazel Hills (all in beat N6), and Whitley Wood (in beat S4); although all are woodlands, the censussed areas also include parts of the heathland and bogs of the Open Forest. These data, combined for all the named areas, are presented in Fig. 1.8.

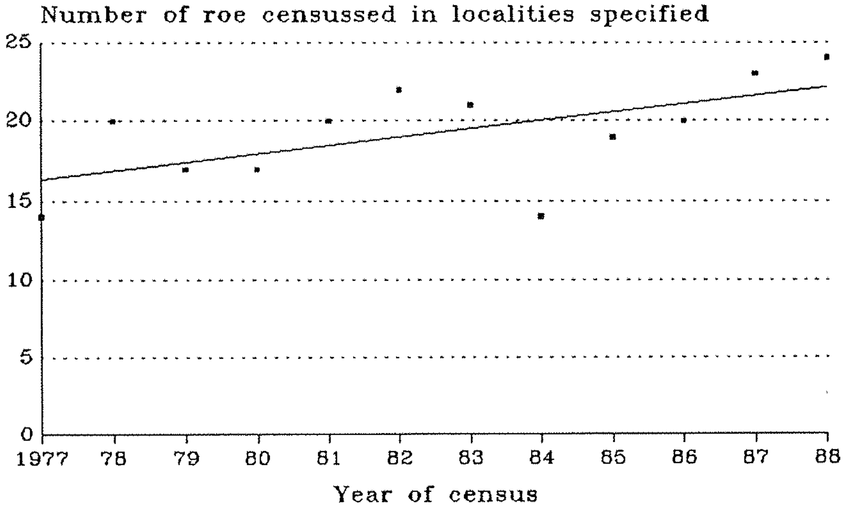


Fig. 1.8 Roe deer census data for Open Forest areas (specified in text) 1977 – 1988

Source: Forestry Commission beat census data

A slight, but significantly positive trend is apparent from the data (regression slope=0.52, SE=0.23, p=0.047), suggesting that roe numbers associated with Open Forest areas may either have changed little, or actually have increased, against the overall trend of the Forest as a whole. Thus, the enclosed woodlands may be the areas where most, if not all, of the population decline has occurred.

2. THE DECLINE OF THE ROE DEER POPULATION IN THE NEW FOREST AND CONTEMPORARY ENVIRONMENTAL CHANGES

Chapter summary

These initial investigations sought to identify local environmental factors which might be associated with the decline in the New Forest's roe population over the period 1972-1988. Inevitably, factors which could be considered were limited to those environmental variables for which data were available, or which could be estimated. These variables included the numbers of other large herbivores on the Forest, descriptors of the gross vegetational structure of the enclosed woodland (by tree species-type and height-class), visitor numbers, and of seasonal climate. Where possible, analytical consistency was sought using the Forest beats as replicates.

Roe numbers over 1972-1988 correlated significantly negatively with numbers of other deer species (red, sika and fallow) for the whole Forest, but did not correlate significantly with whole Forest numbers of cattle and ponies, or consistently with fallow at the beat level.

Significant and consistent correlations were obtained between roe numbers and changing woodland characters over the period 1976-1986: positively with prethicket stage conifers (several types) and with thicket stage Scots pine, and negatively with thicket conifer (excluding pine), establishment broadleaf (excluding oak), establishment Scots pine, mature spruces and mature broadleaves (excluding oak).

A separate, unreplicated correlation examined spatial variation in roe numbers across beats in relation to the same woodland characters and others (e.g. length of rides and of woodland edge). Roe numbers did not correlate significantly with any of the additional characters, and those significant correlations with woodland stages (mature spruces, mature Scots pine and establishment 'other pines') were not consistent with the more comprehensive temporal correlation results.

No significant correlation emerged between roe numbers and visitor numbers over the period 1972-1988.

Several climatic variables correlated consistently with changes in roe numbers over 1972-1988: positive correlations were obtained with February precipitation and mean March daily temperature, and negative correlations with mean daily winter (Nov.-Feb.) temperature, mean daily temperature over May and June, and the number of days in May-June with > 1 mm. precipitation. These climatic conditions applied to the 12 month period March - February prior to the April census; an additional significant negative correlation was obtained between roe numbers and the number of days in the 12 month period in the year previous to that with > 1 mm. precipitation. No significant trend in any of these climatic variables was detected for the period 1972-1988.

Using multiple regression analysis, variable descriptors of the woodland vegetation, notably the amount of prethicket stage 'other pines', accounted for by far the larger part of the variance in roe numbers over time, but climatic factors also contributed significantly.

2.1 INTRODUCTION

Evaluation of the Forestry Commission's census data for the period 1960 - 1988 suggests that roe deer numbers in the New Forest overall have been consistently declining since 1972 (Chapter 1). In order to identify possible causal factors for this decline, the change in roe numbers over that period may be explored in relation to changes in other environmental factors for which records exist or for which values may be determined. These factors include descriptions of the gross structure of the enclosed woodlands, the numbers of other large herbivores within the Forest, the degree of human (visitor) disturbance, and measures of local weather conditions. While any significant associations thus revealed cannot in themselves establish a causal relationship, much less indicate specific mechanisms, they serve to supply a list of 'candidate variables' whose effects on roe numbers can subsequently be examined in more detail.

All the factors to be considered may be expected, on theoretical grounds, as potential influences upon roe population levels, and indeed, most have been shown by other workers to have affected performance in roe or other deer species. Thus, for example, the specific physical structure of the woodland (expressed as age or height class) may have a direct impact on roe in terms of the food or cover offered, or offer species in the ground or shrub layers which are consumed by roe (Ratcliffe and Petty 1986).

Sympatric species with overlapping dietary requirements may conflict when resources are limiting (e.g. Challies 1985, Jenkins and Wright 1988, Chapman *et al.* 1993). As noted, populations of at least two species of deer (red and fallow: Table 1.1) have been increasing in the Forest over the period of the decline in the roe, and the area is also subject to heavy grazing by domestic stock. Jackson (1980) suggested that roe and fallow in the New Forest may compete for food during winter. While the evidence for conflict between the roe and these other species will be the subject of a later detailed assessment (Chapter 6), available data on population levels for the period 1972 - 1988 permit an initial 'historical' exploration.

Climate may have an effect on condition and performance either directly, for instance by affecting neonatal survival (e.g. Albon and Clutton-Brock 1988, Gaillard *et al.* 1993c) or over-winter mortality rates (Klein and Olson 1960, Mitchell 1984, Clutton-Brock, Albon and Guinness 1987, Gaillard *et al.* 1993b), or indirectly via vegetation availability (Moen 1978, Albon 1983, Teer 1984, Putman and Langbein 1992). While the climatic conditions in the New Forest are themselves mild, and the primary effects of climate may be expected to be mediated through vegetation quality and quantity, there could also be direct effects if the population is already stressed by other factors e.g. food-limitation (Sinclair 1989).

Work described in the present chapter seeks associations between the changing roe population and environmental factors of the New Forest. While emphasis here is placed upon temporal associations between the New Forest roe population change and environment, some measure of support for any revealed temporal associations may be obtained from investigating similar spatial associations over the Forest beats. A supplementary analysis is also described therefore, using data from the same period, which seeks correlations between the simultaneous census figures for roe deer numbers in the 12 different Forest beats and a range of vegetational and woodland structural characteristics for those beats. These characteristics include the woodland descriptors (as above), the amount of Open Forest, the length of rides, and also the length of woodland edge, which Andersen (1961) suggested might influence roe numbers.

These analyses rely on data collected by two of the New Forest's statutory bodies - the Forestry Commission and the New Forest Verderers - for their own management purposes rather than ecological study. This necessarily imposes some limitations both on the quality of the data (within the present context) and in the range of environmental variables which can be considered. Specific limitations of the 'quality' of the data are described further within the appropriate parts of the following sections. Data most obviously absent include details on the ground vegetation within the enclosed woodlands and on the vegetation of the Open Forest. Subsequent work within this project will address both of these limitations.

2.2 METHODS

Data available for analysis

(i) The deer censuses

As described in Chapter 1, each New Forest keeper makes an annual return of the number of each deer species in his beat. This census is officially taken on a specified date in April each year, although in practice the keeper returns a figure at that time based upon his knowledge of his beat built up from a number of recent visits. All deer on the beat except muntjac are included, with returns broken down into smaller areas within the beat (typically by inclosure or another specified woodland block). As noted in Chapter 1, it is generally recognized that although the census figures underestimate the true population levels, they may be taken as reliably indicating the population trend since 1972. This is most likely to be true over 1972 - 1986, during which period the same individual keepers were involved and the figures were subject to consistency checking by the Commission head-keepers. From 1986 to 1988 there was a change of keeper on one beat, but examination of the census data for that period suggests close agreement between the two individuals' assessments; since 1989 there have been further staff changes, and the consistency of the data is less assured. Only the data for the period 1972 to 1988 are used in the present analysis.

For the period 1972 - 1988, the Forestry Commission supplied annual census data for roe and also figures for fallow, red and sika deer. Of these species, only fallow deer have occurred across all (or nearly all) beats during the study period. Red deer for most years were recorded in the census as present only in two beats (appearing regularly in a third only since 1985) while sika have been found almost exclusively within a single beat for the entire period.

(ii) Populations of other large herbivores: ponies, cattle and pigs

The Court of Verderers made available their records of the numbers of domestic stock (ponies, cattle, donkeys and pigs) for which marking fees had been paid, for each year since 1971. Of these species, only cattle and ponies are considered further, as donkeys are very few in the New Forest (some 80 individuals per year), and the occurrence of pigs is very patchy, generally low and restricted to a short period in autumn. As with the deer censuses, the Verderers' data should actually be taken as indices of the true population levels of cattle and ponies. A few animals may be commoned without payment of fees, and some licensed animals will not be present on the Forest for the whole year: cattle in particular are usually taken off the Forest for the winter (Pratt *et al.* 1986). All figures for domestic stock apply to the whole Forest.

The numbers of deer and domestic stock species were used as measures of overall pressure imposed on the Forest by other herbivores; numbers of cattle and ponies were also combined (within each year and as a rolling estimate for the '3 previous years' aggregated) as measures of recent grazing pressure. All the herbivore variables defined are shown in Table 2.1.

Table 2.1 *Descriptors of 'other large herbivore pressure' used in correlations against roe deer numbers (whole Forest)*

1. Numbers of fallow, red and sika deer of same census year
2. Number of ponies licensed to pasture (previous year)
3. Number of cattle licensed to pasture (previous year)
4. Number of ponies and cattle licensed in total (previous year)
5. Mean total number of ponies and cattle licensed (past 3 years)

As noted, the roe deer census in each year is actually taken over March - April. Numbers of all the 'other herbivore' variables listed in Table 2.1 have been chosen to represent the population levels most likely to have been influential on the censussed number of roe. Deer numbers are those for the same census year as the roe (i.e. already present), while the numbers of domestic stock are those for the previous year, as marking fees for any year reflect the number of animals which may be turned out later in that year, and thus actually apply to the time following that calendar year's deer census.

(iii) Vegetation and other characters of the Forest inclosures

Surveys of the Forest's timber stocks are undertaken on a regular basis. The Forestry Commission periodically carries out detailed inventories of all blocks within the enclosed woodlands, recording for each block the tree species present, their dates of planting and their estimated growth rate (yield class). These blocks are of known area, recorded accurately to within 0.5 ha. This information is held on a computer database and used to provide stock maps and timber production forecasts, and is updated at intervals as trees are felled or thinned and areas are replanted. The overall composition by tree species of the New Forest enclosed woodlands (using 1981 data) is shown in Table 2.2 below.

Table 2.2 *Tree species occurring within the New Forest inclosures in 1981 at approximately 1% or more of the total area enclosed*

Species		Area (ha.)	Percentage of enclosed area
Oaks	*Quercus* spp.	1990	23
Scots pine	*Pinus sylvestris*	1700	20
Corsican pine	*Pinus nigra*	1100	13
Douglas fir	*Pseudotsuga menziesii*	975	11
Beech	*Fagus sylvatica*	725	8
Norway spruce	*Picea abies*	445	5
Western hemlock	*Tsuga heterophylla*	240	3
European larch	*Larix decidua*	90	1
Japanese larch	*Larix kaempferi*	90	1
Sitka spruce	*Picea sitchensis*	84	1

Figures based on Forestry Commission subcompartment database (1981)

From these survey records information can be extracted on a number of vegetational parameters which might directly or indirectly affect the forest deer. However, such stock surveys are undertaken only every five to seven years and thus data are not directly available for all years. An estimate of the woodlands' structure for any year other than those for which data are available may, however, be obtained by extrapolation, since records show, for each planting, both age and yield class: these allow the rate of growth of each species represented to be accurately estimated (Rollinson 1985). A computer model which performs forward projections of forest structure from any start year for which records exist has been developed by the Forestry Commission (Ratcliffe, Hall and Allen 1986). The computer program permits tree species to be projected individually or in combinations of species, and the forest structure to be described in terms of any required height-classes. Thus, for instance, Forestry Commission management may be supplied with the expected hectarage of fir trees of between 5 and 10 metres in height in, say, three years time. The model can be also used to 'project' backwards in time as well as forwards, on the basis of standard forestry practices (Hibberd 1986), to recreate the Forest profile a given number of years ago. Any area for which stock records exist on the database may be specified, making it possible to carry out the projections separately for each of the New Forest beats, as well as for the Forest as a whole.

For the present study the computer model was used to 're-create' the structure of the enclosed woodlands of each beat over the period 1975 to 1985, based upon the survey data for the year 1981. For convenience, trees were categorized into seven 'species-groups' based as far as possible upon the clear predominance of certain species, as shown below in Table 2.3. It can be seen that every category except for one ('other conifers') is clearly dominated by a particular species of tree, suggesting each category will be fairly homogeneous across the different beats.

All species-group categories were further divided into five height-classes, broadly representing recognizable woodland growth stages:

Height-class (m.)	Growth stage
0 - 2	Establishment
2 - 5	Prethicket
5 - 15	Thicket
15 - 20	Pole stage
> 20	Mature

In all 35 categories which were used as descriptors of the woodland structure, each representing the extent of enclosed Forest carrying a particular height-class of a particular species-group (items listed under (a) in Table 2.4). As the generated forest profile is built

Table 2.3 *Composition of defined 'species groups' used in correlation analyses, by component species and percentage areas, over all Forest inclosures (1981)*

Species Group	Tree species included		Species composition (by area) of group
I. 'Scots pine'	Scots pine	*Pinus sylvestris*	100.0
II. 'Other pines'	Corsican pine	*Pinus nigra*	93.9
	Lodgepole pine	*Pinus contorta*	4.9
	Other pine	*Pinus* spp.	1.2
III. 'Firs'	Douglas fir	*Pseudotsuga menziesii*	97.0
	Grand fir	*Abies grandis*	2.3
	Other fir	*Abies* spp.	0.7
IV. 'Spruces'	Norway spruce	*Picea abies*	84.1
	Sitka spruce	*Picea sitchensis*	15.7
	Other spruce	*Picea* spp.	0.2
V. 'Other conifers'	Western hemlock	*Tsuga heterophylla*	43.3
	European larch	*Larix decidua*	16.4
	Japanese larch	*Larix kaempferi*	16.3
	Hybrid larch	*Larix eurolepis*	8.5
	Other conifer	Various	7.9
	Western red cedar	*Thuja plicata*	4.5
	Lawson's cypress	*Chamaecyparis lawsoniana*	2.8
	Mixed conifer	Various	0.3
VI. 'Oaks'	Oak	*Quercus* spp.	100.0
VII. 'Other broadleaves'	Beech	*Fagus sylvatica*	80.1
	Other broadleaf	Various	6.5
	Sweet chestnut	*Castanea sativa*	4.3
	Mixed broadleaf	Various	4.2
	Birch	*Betula* spp.	3.2
	Alder	*Alnus* spp.	1.0
	Ash	*Fraxinus excelsior*	0.4
	Poplar	*Populus* spp.	0.3

Source: Forestry Commission subcompartment database (1981) and tree species codings as defined in Forestry Commission Research Information Note 94/84/FS

up from individual planting records, both the 'species mix' and differences in expected growth rates between particular stands are taken into account in producing the forecasted forest profiles.

Such generated data are only considered reliable for some five or six years either side of the base year, owing to the inevitable accumulation of error resulting from discrepancies between the model projection and the true Forest; the model incorporates a number of assumptions, which are discussed later in this chapter.

Table 2.4 *Vegetation variables included in the temporal and spatial correlations against roe deer numbers*

(a) Temporal analysis (for each beat, 1975 - 1985)

1. Area of Scots pine of heights 0-2, 2-5, 5-15, 15-20, > 20 m.
2. Area of other pines of heights 0-2, 2-5, 5-15, 15-20, > 20 m.
3. Area of firs of heights 0-2, 2-5, 5-15, 15-20, > 20 m.
4. Area of spruces of heights 0-2, 2-5, 5-15, 15-20, > 20 m.
5. Area of other conifers of heights 0-2, 2-5, 5-15, 15-20, > 20 m.
6. Area of oaks of heights 0-2, 2-5, 5-15, 15-20, > 20 m.
7. Area of other broadleaves of heights 0-2, 2-5, 5-15, 15-20, > 20 m.

(b) Spatial analysis (across Forest beats, 1981 data)

Items 1-7 above, plus

8. Total extent of rides
9. Total area of open Forest
10. Total area of enclosed woodlands
11. Length of woodland edge
12. Total area of conifers of heights 0-2, 2-5, 5-15, 15-20, > 20 m.
13. Total area of broadleaves of heights 0-2, 2-5, 5-15, 15-20, > 20 m.
14. Area of mixed species woodland

In addition to these descriptors of the profile of the enclosed woodlands, a number of additional parameters were identified which, while they varied markedly between beats, did not vary significantly over time. These comprised the length of woodland margin, the length of woodland rides, and the amounts of open and enclosed Forest in each beat (items under (b) in Table 2.4). Data for these were obtained by direct measurement from large scale (1:10000) Forestry Commission maps. These were then included, in addition to the woodland descriptors, in that correlation analysis undertaken to relate roe deer numbers in the different Forest beats in a single year to vegetational characters of those beats (as described above). The year used for this analysis was 1982, which, following the year of the Forestry Commission's survey, allowed use of the most accurate woodland data.

With the exception of the area of Open Forest in each beat, the data used in all of the vegetation analyses relate to the enclosed woodlands only; these are, however the areas where roe are primarily concentrated, and are also considered to be the areas of greatest vegetational change over the period of the observed roe deer decline.

(iv) Disturbance by human visitors

Among its responsibilities, the Forestry Commission provides and manages facilities for visitors to the New Forest, including car parking sites, suggested walking routes and camp sites. The number of visitors to the Forest each year is monitored by sampling the number of vehicles at selected car parks and by the number of camping permits ("camper nights") issued. These data for the period 1971 - 1988 were made available by the Commission, and are taken once again as an index of the degree of disturbance caused by visitors over the Forest as a whole. No private cars have been allowed within the inclosures since 1971, except for a small number authorised by the Commission.

While these visitors may appear numerically to be the cause of most disturbance to the wildlife of the Forest, there are, in addition, many specialist recreational demands made on the forest, including orienteering, horse-riding and fox-hunting. Data on the degree of disturbance which may be caused by these activities have not been available, and would be far from simple to analyze as they are occasional and (as with fox-hunting) may be difficult to localize accurately. However, an attempt to assess their likely impact is made from personal observations and other work.

(v) Climatic factors

The climate of the New Forest is mild and oceanic, being in a temperate region and moderated by the proximity of the English Channel (Chapter 1). Overall, the period of the present study has included some of the warmest years on record, particularly during the 1980s, and prolonged severe winter conditions such as those of 1962/3 have been absent. Data on the regional climate were taken from the Monthly Weather Reports of the Meteorological Office (published by Her Majesty's Stationery Office, London). As there is no weather station in the Forest, data were taken for the nearest recording site, at Mayflower Park, Southampton, some 12 km. from the central New Forest village of Lyndhurst.

From these published data, variables on a wide range of climatic factors were derived, including a range of measures of both average and extreme seasonal and annual conditions. Variables were chosen to include those which had been found in other studies to be influential on deer populations (e.g. Picton 1984, Clutton-Brock and Albon 1989, Putman and Langbein 1992). Levels of precipitation were included in all seasons: winter (overall precipitation over November through February and for the coldest months, January and February); for spring (March and April, separately and combined); for summer (May and June combined); and autumn (September). Mean temperatures for the same periods were also used, but in the case of the coldest period (January / February) the colder of the two months was taken as a measure of winter temperature severity, and the mean minimum winter temperature was included as well as the mean winter temperature (November through February). In addition, the total number of days with over 1 mm. of rainfall, and the total number of days with recorded ground frost (at 0900 hrs.) for the entire year were also included. Table 2.5 presents a complete list of climatic variables used.

All the listed climatic variables were considered for the 12 month period to the end of February immediately before the census (termed the 'previous 12 months'), and for the year before that (referred to as 'two years ago'). These two years were also taken in aggregation to see if there was any evidence of an accumulated effect.

Analytical method

Where data were available as they applied at the beat level, as in the cases of the fallow deer census numbers, woodland vegetation and climatic factors, the correlations were carried out at that level using the 12 beats as replicates (this could only be applied from 1975 however, as roe census data were only available for all beats from that year). For the other categories, i.e. the other large herbivores and visitor disturbance, only whole Forest data were available (which may not reflect the situation at the individual beat level) and these correlations were carried out only for the Forest as a whole. These latter correlations were carried out using data over the whole period 1972 - 1988.

It is recognized that the repeated use of a statistical test such as correlation analysis carries with it the problem that some significant results may occur by chance, even if there is no

Table 2.5 *Climate variables used in correlation analyses against roe deer numbers*

(a) Measures of winter temperature and precipitation

Mean minimum temperature in January / February (whichever the lower)
Mean minimum temperature over November through February
Mean daily temperature over November through February
Total precipitation in January
Total precipitation in February
Total precipitation in January and February
Total precipitation over November through February

(b) Measures of early spring temperature and precipitation

Mean daily temperature March
Mean daily temperature April
Total precipitation March
Total precipitation April

(c) Measures of late spring / summer temperature and precipitation

Mean daily temperature over May - June
Mean daily temperature July
Total precipitation over May - June
Number of days over May - June with > 1 mm. precipitation
Total precipitation July

(d) Measures of late summer / autumn temperature and precipitation

Mean daily temperature August
Mean daily temperature September
Total precipitation August
Total precipitation September

(e) Measures of annual climate

Number of days over year with precipitation > 1 mm.
Number of days over year with ground frost at 0900 hours
Number of hours of bright sunshine over May through October

real association between the variables concerned, just as some 'real' relationships will fail to give significant correlations (the statistician's 'type 1' and 'type 2' errors). While it is impossible to identify these spurious correlations individually, in the present study, interpretation was based upon the emergent pattern of correlations, particularly in the consistency between beat replicates. Acceptance of results errs on the side of caution and, for the replicated correlations, the criterion was used that for any correlating variable to be accepted it should satisfy one of the two following conditions.

(a) From the 12 replicates at beat level the variable should be significantly correlated in two or more beats 'in agreement' (i.e. both or all either positive *or* negative), and no significant correlation should occur 'in disagreement'.

(b) When only a single significant beat correlation emerged, the pattern of positive and negative correlations across all 12 beats was inspected and the result deemed meaningful only if at least 9 of the 12 replicates (in total) showed a correlation in agreement with the sign of the significant correlation. This criterion is based upon the binomial distribution of outcomes for a number of events for which, by chance, a positive or negative outcome is equally likely (probability of 0.5). The chance of a split of one-tailed 9:3 outcome from 12 events (replicates) is $p = 0.054$, judged sufficiently close to the conventionally accepted level of 0.05 for the present purpose.

In summary, the following correlations were carried out against roe deer numbers:

(a) numbers of other species of large herbivores (red, sika and fallow deer, cattle and ponies), for the whole Forest over 1972 - 1988; for fallow deer, a more detailed analysis was also carried out by beats over 1976 - 1988

(b) enclosed woodland vegetational variables, specifying areas of 7 major tree species each by 5 height-classes, by beat for census years 1976 - 1986

(c) enclosed woodland vegetational characters as in (b), also length of woodland edge and rides, and area of Open Forest, across beats for 1982

(d) estimated numbers of visitors (as visitor-days) over the previous year for the whole Forest over 1972 - 1988

(e) a range of climatic factors describing seasonal weather conditions, principally of precipitation levels and average temperatures, by beat over 1976 - 1988.

2.3 RESULTS

Roe numbers and other herbivore populations

From the correlation of whole Forest herbivore populations, roe numbers were found to give significant negative correlations with all of the other deer species in the same year: with fallow ($r = -0.6816$), red ($r = -0.8177$) and sika ($r = -0.7210$) (all $p<0.01$). Only for fallow could correlation analyses be examined at the level of individual beats, but at this level no significant and consistent correlations between roe and fallow numbers emerged.

There were no significant correlations between (whole Forest) numbers of roe and of domestic stock, either when using numbers of cattle and ponies separately, or when aggregated as measures of present (previous year) or recent grazing pressure (past three years numbers combined).

Roe numbers and vegetational change

Table 2.6 shows those vegetational characteristics which correlated with roe numbers both significantly ($p<0.05$) and consistently over the study period (i.e. appeared in more than one replicate and did not occur as both positively and negatively correlated in different replicates).

It can be seen that of the eleven variables in Table 2.6 which showed significant and consistent correlation with roe numbers, five were correlated positively. These were firs (mainly Douglas fir), pines other than Scots pine (primarily Corsican pine), and 'other conifers' (mainly western hemlock), and larches, all in the 2 - 5 m. height-class or 'pre-thicket' stage, broadleaf species other than oak (ie. mostly beech), again of height-class 2 - 5 m., and Scots pine of 5 - 15 m. Roe also showed significant and consistent negative correlation with both 'other pines' and 'other conifers' of 5 - 15 m height, with both Scots pine and 'other broadleaves' of < 2 m., and mature (> 20 m.) spruces and 'other broadleaves'.

Table 2.6 *Variables from the beat level temporal analysis which emerged as significantly and consistently correlated with roe numbers*

	Variable (Species group and height class)		Number of beats correlated	
			$p<0.01$	$0.01<p<0.05$
(a)	Positively correlated			
	Other conifers	2-5 m.	2	
	Other pines	2-5 m.	1	1
	Firs	2-5 m.	1	1
	Other broadleaves	2-5 m.		2
	Scots pine	5-15 m.		2
(b)	Negatively correlated			
	Other conifers	5-15 m.	2	
	Other pines	5-15 m.	1	1
	Spruces	>20 m.	1	1
	Other broadleaves	>20 m.	1	1
	Other broadleaves	0-2 m.		2
	Scots pine	0-2 m.		2

The separate spatial correlation analysis considering variation in roe numbers across beats in relation to vegetational structure showed significant positive correlation between roe population level and mature woodland stages (> 20 m. height) of both Scots pine ($r=0.708$, $p=0.01$) and spruces ($r=0.628$, $p<0.05$), and 0 - 2 m. 'other conifers' ($r=0.648$, $p<0.05$).

From these results, the most striking pattern is seen in the consistency of positive temporal correlation between roe deer numbers and the prethicket stage of woodland development. The negative correlations do not reveal such a strong consistency of pattern. There was no correspondence between the spatial and temporal correlation results for any variable in <u>both</u> tree species and height- class, and a notable absence of the prethicket height-class for <u>any</u> species-group in the spatial analysis.

Roe numbers and visitor disturbance

No significant correlation emerged in the correlation between the roe population and the number of visitors.

Roe numbers and climatic factors

Climatic variables which were found to correlate significantly and consistently with roe numbers at the beat level are shown below in Table 2.7.

Table 2.7 *Climate variables which correlated significantly and consistently with roe deer numbers across 12 beat replicates*

	Variable	Number of beats correlating at $p < 0.05$ (and sign)		Split of 12 beats as agree : disagree (with sign)
(a)	Climate conditions over 12 months before roe census			
	Total precipt. February	3	+	8 : 4
	Mean daily temp. March	1	+	9 : 3
	Mean daily temp. May-June	4	-	10 : 2
	No. days May-June precipt. > 1 mm	3	-	8 : 4
	Mean daily temp. Nov-Feb	1	-	10 : 2
(b)	Climate conditions for 13 - 24 months before roe census			
	Mean daily temp. May-June	1	-	9 : 3
	No. days May-June precipt. > 1 mm	2	-	10 : 2
	No. days over year precipt. > 1 mm	1	-	9 : 3
(c)	Climate conditions combining past 2 years values			
	Total precipt. February	3	+	8 : 4
	Mean daily temp. March	2	+	9 : 3
	No. days May-June precipt. > 1 mm	3	-	9 : 3
	Mean daily temp. Nov-Feb	1	-	10 : 2

Roe deer numbers were found to be correlated significantly positively and consistently with both February rainfall and mean March daily temperature for the previous 12 months, and for the past two years combined. The marginally stronger result in the case of March temperature for the two years combined may suggest a weak cumulative effect; this is not seen for February rainfall. Other climatic variables were found to give significant and consistent negative correlations with roe numbers: the mean temperature over May - June, the number of days in May - June with over 1 mm. of rainfall (both of these for the past year and two years ago), and the number of days of the whole year with over 1 mm.

precipitation two years ago (although this may not, of course, be independent of the period over May - June). Finally, the previous winter mean daily temperature over November through February also correlated consistently and significantly negatively with roe numbers, a finding reflected in the result for the same measure over the past two years combined.

In general, it seems that many of the same climatic variables correlating significantly with roe numbers do so for the previous year, two years ago, and for the past two years combined (the last category being presumably in large part because of one or other of the other two). The strongest associations overall, however, are between roe numbers and climatic conditions of the previous year, and any cumulative effect appears to be subsidiary to this.

Relative importance of vegetation, climatic factors and fallow deer numbers

The results from these correlation analyses, even when viewed with a degree of caution, show clear consistent association between roe numbers and various individual characteristics of the biotic and abiotic environments. Most obviously, roe numbers appear to be related to changes in the vegetational structure of the New Forest enclosed woodlands (especially the prethicket stages), and to measures of climate in both late winter / early spring and early summer. Population levels of other species of large herbivores (in particular fallow deer) also show some association with roe numbers, but the influence of human visitor numbers appears insignificant. However, the relationships suggested have so far been considered only in isolation; in order, therefore, to assess the relative importance of these correlated factors in explaining the changes in roe numbers, the results from the correlation analyses were further examined together using multiple regression analysis.

From the variables shown as being significantly correlated with roe numbers, those for vegetation descriptors, climatic conditions and fallow deer numbers were considered for the regression. Red and sika deer were excluded from further consideration as both species have, as noted, only local distributions over the Forest. As relatively few years' data were available, it was necessary to restrict the number of variables entered in each regression analysis. Vegetation descriptors were examined with respect to the actual forecast areas of their respective vegetation types present over the period of the study. Several woodland types were found to occur only in very small extent, and the resulting correlations were thus more likely to be subject to small changes by chance and the insensitivity of the forecasting model (accurate to 0.5 ha.). Those vegetation types in which the change in area had been less than 1% of the enclosed woodland area (80 ha.) during the entire period of study were excluded, as they were unlikely individually to have contributed importantly to the overall and widespread decline in the roe. (They may have played a part, but only a local or minor one.) On this basis the following variables were excluded: establishment Scots pine (0-2 m.), mature spruce (>20m.), and establishment, 'prethicket' and mature other broadleaf (0-2m., 2-5m. and >20m.).

In addition, some variables were clearly 'related' and autocorrelated, e.g. prethicket and thicket changes of the same species of tree, or the number of days with over 1 mm. precipitation over May-June and all year. Only one variable from any group of 'related' variables was included in any one regression analysis.

A number of separate multiple regression analyses were carried out, using different combinations of input variables. Results given below (Table 2.8) are those for the regression model that gave the best fit in explaining the variance in roe numbers. All regression analyses were carried out at the whole Forest level, and a stepwise selection of variables was used.

Table 2.8 *Variables selected in 'best fit' multiple regression to explain variance in roe numbers over 1976 - 1988*

Step	Variable selected	Adjusted R^2	F-significance
1	Other pines 2-5 m.	0.929	0.000
2	Mean daily temp. March	0.957	0.298
3	Mean daily temp. May-June	0.974	0.042

Other variables not significant in explaining residual variance

The most important single variable accounting for variation in roe numbers was the area of prethicket (2-5 m.) other (Corsican) pine. Inspection of the areas of this woodland type over the period of study reveals a net decline from 412 ha. to only 97 ha. between 1975 and 1985 (according to the forecast model). There was a corresponding increase in Corsican pine thicket stage from 255 ha. to 778 ha. (Similarly, prethicket stage firs declined from 224 ha. to only 21 ha. over the 11 years studied.) Both of the climatic variables for late winter / early spring were selected by the regression as next most important explanatory variables, with the mean March temperature of the previous year chosen before February precipitation of the current year. In no regression analysis was the number of fallow deer selected as a significant contributory variable.

2.4 DISCUSSION

In an earlier study Putman and Sharma (1987) reported correlations between numbers of the Forest's large herbivore populations for the period 1962 to 1985. They found significant negative correlations between numbers of roe and those of the mean number of cattle and ponies (combined) over the previous three years, but no significant correlations between roe numbers and those of other deer. However, those analyses were carried out prior to the full assessment of the consistency and reliability of the census data (Chapter 1), from which it was concluded that the census data before 1972 should be regarded as suspect. Consequently, the results presented in this chapter supersede those of the earlier work.

In this study, no significant correlations were found between roe populations and the numbers of domestic herbivores. Both cattle and ponies occur largely on the Open Forest, particularly on the improved pastures (Putman 1986b), although ponies (and occasionally cattle) also occur in small numbers in many inclosures. Both species are predominantly grazers, and have limited dietary overlap with roe (Putman 1986b, and see Chapter 6 of this report).

With all three of the other species of deer, by contrast, roe did show strong negative correlations. In the cases of both red and sika deer, there is again a limited dietary overlap with roe (Putman 1986b) but, as noted in Chapter 1, both these species have relatively restricted local distributions in the New Forest, and are unlikely to be significant factors in the decline of the roe deer, which has occurred throughout the New Forest. Fallow deer, in contrast, have a higher dietary overlap with roe (Jackson 1977b, 1980; Putman

1986b) and, like roe, are found throughout the Forest. Although Jackson (1980) thought the two species may compete for food during the winter, based upon his dietary studies on both species, the issue of possible resource conflict between roe and fallow in the New Forest is complex, and is the subject of more detailed consideration in Chapter 6.

Of the range of environmental factors considered, the most striking correlations with roe numbers emerged from the (woodland) vegetational characters derived from the Forestry Commission's forecasting model. Vegetational descriptors employed in the analysis were dictated in part by the structural categories recognized by the forecasting model: it provided data on forest structure only by tree species planted and height-classes, and many potentially important factors could not be directly assessed. These factors include the presence of saplings by natural regeneration, and the quality and quantity of ground vegetation - notably species known to be important to roe, such as bramble, rose, bilberry, herbs and certain grasses (Jackson 1980). Similarly, it was not possible to consider the effects of changes in forestry practices, such as in planting and harvesting strategies (where these differ from the model's assumptions), ride management, the use of different stocking densities, and the leaving or removal of brash.

This lack of detailed vegetational data is unfortunate, as it may be just such characteristics of the ground vegetation which are the most important factors affecting the distribution and abundance of deer (e.g. Chapman *et al.* 1985, Ballon *et al.* 1992). Ground vegetation may be expected, however, to correlate to some extent with canopy cover, and the height-classes used for forest descriptors in this study were selected in an attempt to correspond with clear woodland growth stages (plantation, prethicket, thicket, pole and mature), which could be related, at least subjectively, to quality of shelter or forage (e.g. Ratcliffe and Petty 1986).

In addition, it should be noted that all vegetational data rely heavily on extrapolation from a single survey in 1981. The Forestry Commission's forecasting model works on the basis of supplied standard woodland thinning cycles. When an area is 'felled' by the model during a forward projection, the model then assumes the area will be replanted with the same species unless told otherwise. In this study the current New Forest practice was followed of replacing Scots pine and western hemlock by Corsican pine. When working retrospectively, the model leaves areas prior to their known planting date as unplanted. By examination of a randomly selected set of 30 sites within the Forest woodlands (based upon comparison with manual records retained by the Commission), the models assumptions were found to give an error of approximately 1.4 % of the area per extrapolated year, an error judged acceptable given a maximum projection of six years from the base date.

The results of this study show a consistent positive correlation between roe deer and a variety of coniferous plantings, most obviously with those at the prethicket stage of growth. Such areas will in general be relatively dense and provide good lateral cover, but have a sufficiently open canopy that they will be able to support a ground flora which had developed during the preceding plantation phase. This type of habitat thus provides both ready cover and food, and has long been recognized as one favoured by roe (Gibson and MacArthur 1965, Prior 1968, Staines and Welch 1984). The positive correlation between roe and the thicket stage of Scots pine may also be the result of food availability, as Scots pine retains a more open canopy than other conifers into this stage.

Results from the correlations and multiple regression analyses suggest the decline in the availability of conifer prethicket - most obviously Corsican pine and Douglas fir as the most widespread species - may have been an important factor in the decline in the roe population. Neither Corsican pine nor Douglas fir itself appears to form an important forage species for roe in the New Forest (Jackson 1980), suggesting an importance for cover or the ground vegetation associated with the stands. The absence of a significant correlation between roe numbers and prethicket stage Scots pine is at first surprising, as this tree species is itself an important source of food for the roe in the New Forest (Jackson 1980). However, inspection of the forecast model's output reveals that the actual area of this woodland type available over the period investigated was always less than 1% of the total enclosed woodland area, and thus has probably not been of importance in the decline of the roe over the period investigated. Gill (1992a) indicated that Scots pine was not always a strongly preferred forage species over other conifers, but from his presented information (his Table 1) there are wide differences between populations.

Roe deer numbers were also found to be negatively correlated with a number of Forest structural vegetational characteristics, although with a less clear pattern than was evident for the positive correlation results. The negative associations with 'other conifers' and Corsican pine thicket stages (5 - 15 m.), suggest that within a forest growth stage, the species of planting may be significant; however, this may be the result of some characteristic of the trees themselves (such as needle fall), or simply as different trees tend to be planted in different soil types or planting conditions, and these conditions are not favourable to the occurrence of the roe's preferred food plants. Further distinction cannot be made on the basis of this study, but a later analysis (described in Chapter 3) does consider the ground vegetation in more detail. It may be said, however, that the positive correlations which were found between roe deer numbers and area of prethicket stage woodlands, taken in conjunction with the lack of correlation with 'general' woodland measures such as the total area of woodland, or grazing areas (rides), are in agreement with the view of roe as a species selective in its choice of habitats.

There was no suggestion from this study that the increasing number of visitors to the Forest was associated with the decline in the roe population from 1972 to 1988. Although the impact of tourism and recreation on wildlife is a matter of increasing concern, relatively few studies until recently have attempted to measure that impact (e.g. Freddy *et al.* 1986, Tyler 1991).

In a recent study, Langbein and Putman (1992a) investigated the possible impact of visitors on performance of fallow and red deer in two London parks, following suggestions that heavy, continuous disturbance may affect the animals' social behaviour and activity (Humphries *et al.* 1989, Bullock *et al.* 1990, 1993). Langbein and Putman (1992a) found that, while visitor disturbance did result in short-term changes in behaviour (e.g. degree of alertness), there were no significant long-term effects in terms of time budgets or patterns of habitat use, or any deleterious effects on body weight or over-winter mortality. Similarly, studies on the effects of orienteering on deer suggest that while the animals will move away from the disturbed area into cover, they usually return within a day, usually at nightfall (Jeppesen 1987, Douglas 1991). Distances moved by roe under such circumstances may be as much as 1 km. [females] and 1.8 km. [males] (for roe in Sweden: Swedish Orienteering Federation [no date], cited in Langbein and Putman 1992a), although Jeppesen (1987) recorded mean distances of 432 metres (median 262 m.) at Kalø, Denmark. Jeppesen noted, however, that frequent (more than weekly) serious disturbance of areas e.g. by larger orienteering events, may cause the roe to leave areas permanently, and suggested that such events should not be carried out over the period March - June, to minimise disturbance to the roe over late pregnancy and fawning (Jeppesen 1987).

Personal observations on deer in the vicinity of large scale recreational use of the New Forest, including orienteering, fox-hunting and military exercises - in the latter case of several days' duration - support the notion of a minimal effect on deer beyond the duration and location of the activity itself. In addition, although the New Forest is a major recreational area (Perry 1990), in practice, the majority of visitors to the Forest remain close to the car parks, use only the Forest rides and tracks, and mostly visit a number of designated tourist sites. Moreover, in the New Forest, care is taken to ensure that particular areas are not used frequently for events that cause widespread or persistent disturbance (Head Keeper Martin Noble, pers. comm.). The specific potential problem posed to roe by dogs of visitors is examined in Appendix 2.

The effects of climatic influence on population performance of deer can be complex. Clutton-Brock and Albon (1989) pointed out that, as well as increasing energy demands and sometimes restricting access to food (Borg 1970), the influence of climate is also mediated through changes in the available quality and quantity of food. Further, climatic factors may interact with each other and with other environmental factors in their effects on vegetation productivity (see Riley and Skjelvåg 1984). Although interpretation of the possible action of specific climatic features is thus often necessarily speculative, the effects are most clearly evident when the population is also under stress from high density (Picton 1984) or (at lower density) from nutritional limitation (Klein and Strandgaard 1972). This may lead to a reduction in body condition and consequently in survival and / or reproductive success, often in specific age categories (e.g. Albon, Clutton-Brock and Guinness 1987, Hewison 1993, Gaillard *et al.* 1993b).

In this study significant positive correlations emerged between roe numbers (censussed in April) and both the mean March temperature of the previous year and the amount of February rainfall in the same year. Studies in Scotland and elsewhere show that April rainfall is linked to grass productivity (Albon, Clutton-Brock and Langvatn 1992, Roberts and Dunbar 1991) and subsequent calf birth weights in red deer (Albon, Guinness and Clutton-Brock 1983), and may also affect rates of development in roe fawns (Gaillard *et al.* 1993c). Such effects may not, however, be reflected in the whole population level for roe (as used in this study) as they may be masked by subsequent regulation on juveniles or adult mortality e.g. Bramley 1970a, Gaillard *et al.* 1993b. A similar encouragement of browse foliage growth in the New Forest may be promoted by higher March temperatures and February rainfall, allowing roe to recover body condition prior to fawning. (As may be expected, numbers of the New Forest fallow, which are primarily grazers, show a significant positive correlation with April rainfall levels; this study, Chapter 6).

Roe are well adapted to much harsher climatic regions elsewhere in Europe (Holand and Staaland 1992), which suggests that the negative significant correlations with mean daily temperatures over November - February in the New Forest may be acting upon a population under stress from other causes, most likely to be related to vegetation availability. The negative association between roe numbers and mean daily temperature over May - June is unclear: one possible mechanism is through the action of higher temperatures reducing the organic matter digestibility and increasing the cellulose / lignin content in stems and leaves (Bennett and Mathias 1984, Deinum 1984, Wilson, Deinum and Engels 1991). However, it seems equally likely that this might be offset by the warmer temperature reducing heat loss in fawns.

Further speculation is not justified on the basis of the limited analyses carried out. Overall, the action of recent climate over the period of the decline appears to have been secondary to effects from changes in the vegetational environment and effective only on a year by year basis. None of the climatic factors correlating significantly with roe numbers showed a strong (significant) trend over the study period (linear regressions, all $p > 0.05$), and roe populations in adjacent estates have not shown the same decline as roe in the Forest (Commission keepers, pers. comm.).

All the conclusions from the analyses described in this Chapter must for the present remain speculative, for they are all based only upon observed correlations and assessments, with no proof of any causal relationship. However, the evidence does suggest that the decline of the roe is primarily associated with changes in the vegetation of the New Forest; this association is examined further in the next part of the study.

3. PRESENT DISTRIBUTION OF ROE DEER IN RELATION TO VEGETATION

Chapter summary

As available data used for the 'historical' analyses described in Chapter 2 were inevitably limited, additional investigations, described in this chapter, were undertaken to identify present day factors which may determine roe distribution in the New Forest. As such, this work serves both to confirm and complement those earlier analyses.

Correlation techniques were again used, to seek associations between an estimate of roe density at 12 selected enclosed woodland sites based upon recent census returns, and the vegetation available at those sites based on detailed surveys. Vegetation characteristics of sites were expressed variously as
(i) woodland structure alone (as in Chapter 2)
(ii) ground vegetation alone (herb and shrub layer)
(iii) both woodland and ground vegetation combined as distinct 'habitat types'.

In addition, a correlation analysis is described which sought associations between censussed roe numbers and Open Forest habitats across the Forest beats.

When sites were characterised as the same woodland structural variables used in Chapter 2 (species group by height class), site density of roe correlated significantly positively with conifer (excluding Scots pine) thicket, and negatively with pole-stage Scots pine.

Characters of the ground layer which correlated significantly positively with roe number across sites included the local amounts of bramble, holly, ivy and shrub, while two other species, bracken and *Molinia*, correlated significantly negatively with roe number.

Using defined habitat types which combined woodland stage and ground vegetation features, roe numbers correlated significantly positively with areas of both food-bearing mature conifer and food-bearing mature broadleaf, and negatively with (food-depleted) mature conifer with bracken (and close to significantly negative with food-depleted mature conifer without bracken). Overall, there was a consistent pattern of more positive correlation of roe number with food-bearing woodland than with equivalent food-depleted woodland, across all woodland growth stages.

From the Open Forest habitats (defined by a recent English Nature survey) roe numbers correlated significantly positively with the availability of partially improved grassland, across beats; however, upon evaluation this result was considered to be spurious.

Overall, the strongest associations between roe density and vegetation in the present day Forest was obtained with the availability of the species' known food plants, whether expressed simply, or as contributing to woodland habitat types. There was some evidence that the woodland growth stage also influenced roe density, and that areas with bracken or *Molinia* may be avoided by roe. As with the previous analyses (Chapter 2), all findings are provisional, pending field studies of actual habitat use and selection by roe.

3.1 INTRODUCTION

Changes in roe deer numbers over much of the period of decline in the New Forest are, as we have seen, closely associated with changes in the gross vegetational characteristics of the enclosed woodlands. However, the available data did not permit resolution of anything more than a somewhat superficial relationship between the two. Whether roe abundance over the period in question actually depended upon the availability of prethicket woodland or was more directly linked to other associated factors remains to be seen. In the absence of detailed historical data, investigations of spatial patterns in present day occurrence of roe in the New Forest can help identify determinants of roe distribution, and thereby suggest more precisely the nature of the association between roe population density and habitat character. Underlying this approach is the assumption that, in an equilibrium situation, the relative abundance of habitat factors beneficial to roe is greater in areas of higher roe density, i.e. that more roe are found in 'better' quality areas than in 'poorer' quality areas.

Such a pattern of distribution is most simply described by the "ideal free" model of Fretwell and Lucas (1970). These authors suggested that, in the absence of competition, and assuming no or minimal costs of searching and moving between habitats, individuals would attempt to maximise their own fitness with respect to resource availability. Animals are taken as "ideal" in the sense that are able to evaluate habitat patches fully, and are "free" to move between them. Better quality habitat patches would become progressively more crowded until, through density-dependent effects (acting through intraspecific competition), the greatest net return to any individual would accrue from selection of a less crowded patch, albeit of poorer quality.

Though widely accepted (see e.g. Flood *et al.* 1977), the validity of such a distribution was examined critically by Van Horne (1983). She pointed out that the assumptions may not hold under a number of conditions, such as when habitats are subject to strong seasonal variation in vegetation quality and quantity, or when used fairly briefly during a migratory phase, or where social interactions (e.g. territoriality) may lead to some animals being excluded from high quality habitats. Van Horne (1983) suggested that the relationship between population density and habitat quality may even appear 'inverted' in such cases. In response, Fagen (1988) argued that, when animal distributions do meet the assumptions of Fretwell and Lucas' (1970) model, habitat carrying capacities would be directly reflected by use / availability indices. Subsequent modelling studies by Hobbs and Hanley (1990), and empirical work (Hobbs and Swift 1985), do support Van Horne's (1983) call for caution. While not entirely refuting Fagen's comments, this later work indicates that the relationships between carrying capacity and population density are dependent primarily upon the interaction between vegetation quality and quantity.

For the case of the roe deer in the New Forest, it seems likely that the population density of roe in a locality may be taken as at least an approximate guide to habitat quality. Aggregation of juveniles in poorer sites is unlikely as the surrounding estates and farmland offer high quality areas to which deer may disperse (and where deer are controlled). Adult roe also tend to be resident in their chosen localities and, if the entire annual range is considered when assessing habitat quality and if population density (or occupance) is also taken over the yearly cycle, then population density is indeed more likely to relate to that quality. These considerations are incorporated in the approach taken in work described in this chapter and the next.

The purpose of this part of the study is both to extend and to refine the earlier correlation-based investigations. As noted, the data available for that investigation were severely limited by the 'historical' nature of the study, the most serious omissions being the lack of information on both the ground vegetation of the Forest's enclosed woodlands and the Open Forest vegetation. These omissions were of concern as the ground vegetation may well be the conduit through which roe performance is affected by the influence of all the factors found to associate significantly with roe numbers (stand type, climate and other deer numbers). The present work addresses these limitations, using data collected specifically for the purpose, in an independent investigation of spatial associations between roe deer numbers and vegetational characters of the environment. As with the earlier analyses, of course, these correlation analyses cannot establish causal relationships, but again serve as a filter to identify a shortlist of environmental variables from the many potential factors which may influence roe numbers.

Specifically, levels of roe populations at a number of selected inclosure sites from the Forest are examined in relation to both the local stand type and ground vegetation availability, to address the questions: (i) can variation in roe deer density be best explained in terms of either level of vegetation alone - and if so which? - or (ii) is it better accounted for by expressing the vegetational characteristics of localities as specific 'habitat types' formulated using both? A third enquiry examines variation in roe numbers across the Forest at the beat level in relation to the vegetational characteristics of the Open Forest.

3.2 METHODS

The principal correlation analyses to be described were performed by relating roe deer numbers estimated during routine Forestry Commission censuses at 12 enclosed woodland sites in different geographical regions of the Forest to vegetational characteristics of those sites. All measurements and correlations were carried out between November 1987 and April 1988. These analyses are supplemented by correlations carried out in parallel, for six of the same sites, based upon the same vegetation data but using an estimate of roe occupance at each site subsequently derived from my own field work (Chapter 4), giving an alternative measure of population density. An additional analysis is also described which correlates Open Forest vegetation variables (derived from data collected by English Nature over 1984 - 1986) with 1986 roe census data at the beat level.

Inclosure vegetation characters and roe deer numbers

(i) Selection of study sites

Twelve study sites were chosen on the basis of information supplied by the Forestry Commission. Several criteria were applied for site selection: between them, the sites should encompass the range of habitat types found within the enclosed woodlands of the New Forest (i.e. both broadleaf and conifer woodlands at all growth stages); they should span the range of actual roe deer population densities; they should not be subject to excessive or continuous human disturbance; finally, sites should be geographically separated such that they have independent roe populations.

A list of the sites chosen is given in Table 3.1, and the sites' locations are shown in Fig. 3.1.

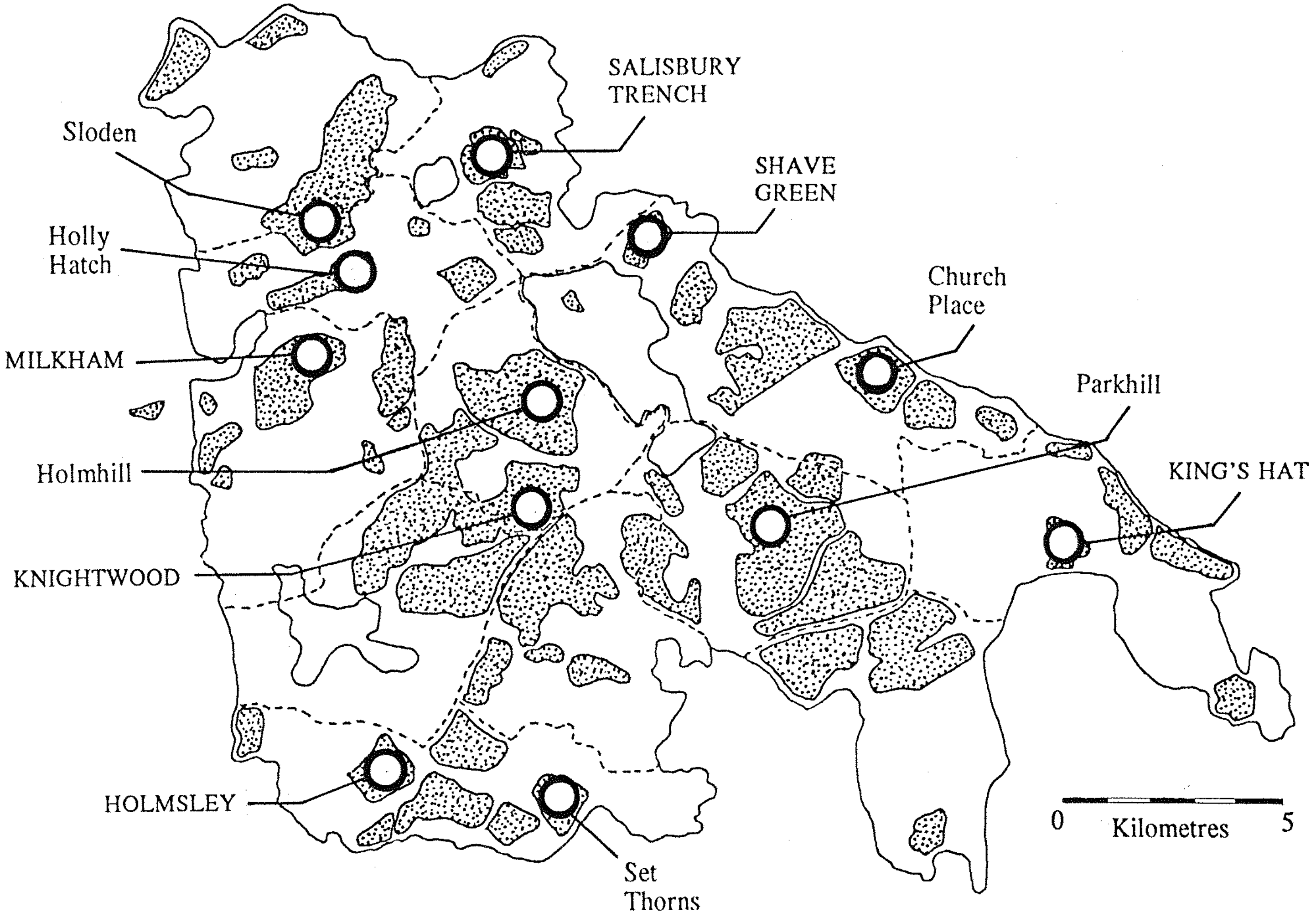


Fig. 3.1 *New Forest Crown lands, showing locations of 12 enclosed woodland study sites used for vegetation surveys (this chapter). The six sites used for subsequent studies of habitat use and selection by roe (Chapter 4) are named in capitals.*

Table 3.1 *New Forest sites selected for vegetation surveys*

Site	Survey area (ha.)	No. of sub-compartments
Church Place	139.0	47
Holly Hatch	94.5	37
Holmhill	141.0	63
Holmsley	95.0	62
King's Hat	65.5	24
Knightwood	103.5	61
Milkham	127.0	49
Parkhill	135.0	26
Salisbury Trench	130.0	62
Shave Green	102.0	33
Sloden	115.0	24
Set Thorns	106.0	61

(ii) Vegetation surveys of the enclosed woodlands

For silvicultural purposes, an inclosure, or area of enclosed woodland, is made up of a number of 'compartments', each of which is a continuous area of (typically) between 5 and 10 ha. Each compartment in turn consists of a variable number of 'sub-compartments', usually three or four, although there may be any number from one to ten. The sub-compartment is the basis of forestry operations, and in nearly all cases the result of a single planting ('component') which has been subject to the same management history, and thus forms an area of fairly uniform habitat. Adjacent sub-compartments may be similar, or they may contain different species at different growth stages. An inclosure also contains a network of gravelled tracks and grassy rides, on average some seven metres in width, for access and to act as firebreaks.

To determine the area to be surveyed at each site, Forestry Commission stockmaps were used. A point was chosen close to the centre of each site. A circle of radius 0.7 km. was drawn around this point, and all sub-compartments falling wholly or largely within the circle were included for survey. A circular frame was chosen as the actual home ranges of the roe were not known. The size of the sampling frame size chosen was based upon the need to include a sufficiently large area to represent the composition of the habitats available within the home range of the roe, but not so large as to overlap adjacent ranges and populations. In coniferous woodland annual roe home range size varies considerably, but may be as much as 85 ha. (Hinge 1986); as the Forest is clearly a poor quality habitat and larger range sizes may be expected, such a figure may be taken as approximating a minimum working value. The minimum sampling frame radius was thus set at 0.6 km., enclosing some 113 ha. (although not all of this would necessarily be enclosed woodland). While the Forest's central inclosures are largely contiguous, many of the inclosures within the outer beats occur as woodland 'islands' set within the Forest's open vegetation. Both central and isolated inclosures were necessarily included as study sites to span the range of population densities required. Sampling frames of radius size of between 0.6 km. and 1 km. (increasing in 0.1 km. steps) were superimposed on the Commission stockmaps and compared on the basis of the enclosed woodland included: a frame size of radius 0.7 km. was found most efficient at enclosing the 'island' sites, enclosing a minimum of 65.5 ha. of inclosure - judged to be adequate - with minimal risk of overlap; a frame of 0.9 km. radius gave some risk of overlap between populations at close sites.

All enclosed woodland within the sampling frame at each site was surveyed in detail as described below. Areas of Open Forest caught within the frame were not surveyed but were assigned to broad habitat categories that were identifiable from the stock maps:

(a) Agricultural / Estate land
(b) Open heathland / pasture
(c) Urban area
(d) Unenclosed conifer woodland
(e) Unenclosed broadleaf wood
(f) Inaccessible (e.g. beyond a major fenced road or railway).

The extent of each of these habitat categories was estimated by superimposing a 1 ha. squared grid on the sampling frame and counting the number of squares in which each category was the dominant vegetation type. (The vegetation types of the Open Forest are considered in more detail in a subsequent analysis, described later in this chapter).

At all sites surveys of the enclosed woodlands within the 0.7 km. sampling radius were carried out by a standard procedure. Within the designated area, each sub-compartment was located using the Commission stockmaps, and traversed to check for consistency of the vegetational composition. The two principal tree species in the sub-compartment were noted, and for each the height in metres estimated (estimation had been practised on trees of known height and found accurate to within 10% in nearly all cases). Very few sub-compartments had more than two planted species; where this was the case the third species was simply noted as present. Mean spacing between trees was paced out, and recorded to the nearest metre. Glades of any size were not present at any of the study sites. Ground vegetation in the sub-compartment was defined as that below 1.2 m. height, the maximum foraging height for roe (Prior 1968), and estimated as percentage cover; species-count sampling (e.g. Braun-Blanquet 1921, 1932) was not practical given the scale of the task. The percentage cover of bramble, holly (below the specified foraging height), ivy, heathers, bilberry, purple moor grass, other grasses (not separated to species) and bracken were noted in this way. In addition the percentage cover of brash and litter were also recorded, and are included in the term 'ground vegetation' for convenience. Shrub cover - including vegetation above 1.2 m. - was also recorded as percentage cover, with no regard to species; in practice, except for holly within some of the broadleaf woodlands, shrub cover is uncommon within most of the Forest inclosures sampled, comprising some gorse but little else. The area for each sub-compartment was obtained from the Forestry Commission's sub-compartment database. All items recorded in the survey are listed in Table 3.2.

In the New Forest inclosures, the boundaries between sub-compartments are generally without special vegetational characteristics, and were therefore not recorded separately.

Rides were surveyed separately and recorded as a separate woodland vegetation category. Twenty points were selected randomly (from stockmaps) on rides at each site. At each point in the field the ride width was measured and the ride vegetation over ten metres either side was assessed for the percentage cover of the species of vegetation (as above). These data were averaged for the area of rides at the site as a whole, the total length being measured from the 1:10000 scale stockmaps using a Silva map-measurer.

Table 3.2 *Survey data collected for each subcompartment at each site*

Item	Survey character	Recorded as: [See Notes]
(a)	Characters of woodland / shrub structure (> 1.2 m.)	
1.	Principal tree	Species
2.	Height of (")	Metres
3.	Secondary tree	Species
4.	Height of (")	Metres
5.	Spacing	Metres
6.	Canopy	% closure
7.	Other trees [1]	Present / absent
8.	Open spaces [2]	Present / absent
9.	Shrubs (all spp.) [3]	% cover
(b)	Characters at ground level (< 1.2 m.)	
10.	Brash	% cover
11.	Litter	"
12.	Bramble	"
13.	Holly	"
14.	Ivy	"
15.	Heathers	"
16.	Bilberry	"
17.	Purple moorgrass	"
18.	Other grasses [4]	"
19.	Bracken	"

Notes: [1] E.g. self-sown beech from nearby sub-compartment
[2] If discernible variation in vegetation from surroundings
[3] Mostly holly, occasionally gorse
[4] Not identified to species

For consistency of recording between sites, all surveys were conducted between November 1987 and January 1988, as there was little vegetation growth over the winter period. Data recording was preceded by a period of practice, and consistency of recording was checked after completion of all sites by resurveying 20 subcompartments from each of the first two sites surveyed: fewer than 1% of quantifiable measurements were recorded differently between the first and second surveys at the two sites. (For those measurements which did disagree, the difference (e.g. in tree height, percentage ground cover) was generally of the order of 10% - 20%.)

(iii) Estimation of roe deer population levels at the sites

The only direct estimates of numbers of roe deer in the New Forest are the annual census counts carried out by the Forestry Commission keepers. Although these counts were used in the earlier analysis (Chapter 2) for whole beats, the census is actually recorded at a finer level - termed here the sub-beat - which typically relates to an area of enclosed woodland and a defined area of the surrounding Open Forest, or to a group of contiguous inclosures. Areas of unenclosed woodland, such as the Forest's Ancient & Ornamental woods, are generally also recorded separately.

The roe deer population level at each of the 12 sites in the present analysis was derived from the appropriate sub-beat census count from the 1986 census. The roe population applying to the area of woodland surveyed was calculated as the proportion of the sub-beat census value represented by the proportion of the total sub-beat enclosed woodland within the 0.7 km. sampling frame.

In addition, a second estimate of roe presence in six of the study sites was available from other studies carried out as part of this project. Details are given in Chapter 4 of studies on habitat use and selection by roe at 6 sites: Holmsley, King's Hat, Knightwood, Milkham, Salisbury Trench and Shave Green. At each site, a transect through the site was used to assess habitat occupance by roe in all habitat types (see below) occurring at that site; transects were of equal length and sampled the habitat types in proportion to their occurrence at the sites. The transect at each site was walked 108 times over a 12 month period, and the number of observations of roe made over the year thus formed an estimate of roe usage at those sites; this estimate was used in correlation analyses with those sites' vegetational characteristics.

Inclosure vegetation and roe deer: analytical method

Numbers of local roe populations at the 12 study sites based upon sub-beat census counts, and from observation data at the 6 sites subsequently used for habitat use studies, were used in correlation analyses against site vegetational variables. These variables were derived from the survey data and expressed in three different ways, as: (a) tree stand type defined by species groupings and height classes as in the original Forestry Commission records; (b) the abundance of each species of ground vegetation at each site; and (c) habitat types defined in terms of both the growth stage of specified tree categories and the relative availability of ground vegetation. It is stressed that these three analyses are not, of course, to be regarded as independent, rather as focusing on particular aspects of the same data.

(a) Stands expressed as tree species-groups and height-classes

In order to facilitate direct comparison between results obtained in the present analyses and those from the historical analyses of Chapter 2, the vegetational structure of the 12 sites was first expressed at the same level of resolution - or as close as possible - as that used in the earlier analysis.

The survey data were used to divide the enclosed woodland at each site into the same seven species groups used in the previous analysis: Scots pine, other pines, firs, spruces, other conifers, oaks, and other broadleaves. Each of these was then divided into five height-classes as before, for trees of 0 - 2, 2 - 5, 5 - 15, 15 - 20 and > 20 metres. The area of each category for each site was then calculated, using the sub-compartment areas from the Commission's sub-compartment database records (on which, for mixed plantings, the area assigned to each species is recorded separately).

(b) Abundance of ground vegetation species

In a separate analysis, roe deer numbers were correlated with measures of the availability and abundance of ground vegetation only, without reference to the tree species or growth stages. This permitted investigation of which features of the composition or structure of the ground flora may relate to roe performance. By definition, however, this analysis ignores any contribution to roe performance made by the trees' provision of food or cover.

The total availability of each species or category of ground vegetation (listed in Table 3.2) at each site was calculated as the sum or weighted average, as appropriate, of the individual sub-compartments' values of percentage-cover and area. Estimates in this way were made for bramble, ground holly, ivy, heathers, bilberry, purple moor-grass, other grasses, and bracken. Amounts of shrub (including holly above approximately 1.2 m. from the ground) and brash were calculated in the same manner.

(c) Stands and ground vegetation combined as 'habitat types'

Finally, roe deer population estimates were considered in relation to the abundance of different 'habitat types' at the 12 sites, derived as complex combinations of tree species type and growth stage and the ground flora.

Clearly formulating such a scheme of habitat categories may be done in a variety of ways and, in many wildlife studies, habitat types may be recognized by natural species assemblages, with some subjective assignment of intermediate areas and boundaries. In the New Forest inclosures, however, the vegetation is determined, or at least heavily influenced, by management practice; natural assemblages are absent or unclear. Accordingly, a more objective method of determining habitat categories was sought and the use of multivariate methods for classification of vegetation survey data was explored in attempts to provide a suitable set of habitat categories. Full details are given in Appendix 1 of this report, but results from these investigations failed to produce simple categories that were recognizable in the field, and the discrimination of such categories also proved very sensitive to changes in vegetational parameters included in the site description and to the inclusion / omission of single data variables (Appendix 1).

For this part of the study, therefore, a scheme of habitat classification was devised based upon simple criteria to define field-recognizable habitat types to which individual woodland blocks could be assigned. The number of categories, or types, appropriate for studies such as this should be determined, ideally, as that which maximises information gained relative to effort expended (Moore *et al.* 1970), or which maximises between-group variance compared to within-group variance (Pielou 1977). For practical purposes, Dale (cited in Popma *et al.* 1983) suggested a simple rule that the number of clusters would be approximately the square root of the number of observations (the number of surveyed sub-compartments in this case). From the 549 subcompartments surveyed, it was thus decided to define between 18 and 24 categories, the final number to be determined by the number of sub-compartments allocated to the smaller categories.

The following criteria were used to define habitat categories from the survey data:

(a) whether or not the area was open (i.e. bare or establishment)
(b) whether the trees were conifer / broadleaf (or whichever was dominant)
(c) the growth stage of the trees: prethicket, thicket, pole or mature
(d) if thicket or older, then the degree of closure of the canopy
(e) whether the ground was bare (or almost so), or bore only purple moor-grass
(f) whether bracken was present to afford some degree of cover (defined as 20% presence or above)
(g) if known food species were present to a significant degree (> 5 % ground cover in total).

Not all possible combinations of characteristics occurred within the sites, and some were rare. Thus, after assigning habitat categories to all sub-compartments, it was apparent that some rationalization was required to generate realistic and useable categories. If a given category of a woodland type (conifer or broadleaf) and growth stage with either bare ground or bracken only, occurred 4 times or fewer (across all sites), it was combined with that of the same woodland type and growth stage with bracken only. Rides were considered a separate habitat type. The final scheme of habitat classification comprised 20 habitat types and is given below (Table 3.3).

Vegetation characteristics of the Open Forest

Using a combination of aerial photography and ground fieldwork, over the period 1984 - 1986 English Nature (then the Nature Conservancy Council) compiled a detailed survey of the Open Forest vegetation. For this survey English Nature recognized a number of broad habitat types occurring in the Open Forest, including acid grasslands, improved and reseeded grasslands, dry, humid and wet heathlands, valley mires, carr, lawns, woodland / shrub and closed canopy Scots pine; some of these categories were further divided according to the dominance of bracken or gorse. The area of each type of habitat was recorded or estimated to within 0.01 ha. for each defined area (compartment) of the Open Forest (Table 3.4). From these data, variables describing the total availability of each habitat type within each beat, and of a number of aggregate habitat types, were calculated and were correlated against the beat census figure for roe returned in the 1986 census.

Table 3.3 *Habitat classification scheme defined using woodland and ground vegetation characters (shown grouped by woodland character)*

Habitat Type	Description
1	Open or establishment, ground: bare, or bracken / *Molinia* only
2	Open or establishment, food species present
3	Prethicket conifer, ground bare, or bracken / *Molinia* only
4	Prethicket conifer, food species present
5	Thicket conifer, ground bare, or bracken / *Molinia* only
6	Thicket conifer, food species present
7	Pole-stage conifer, ground bare, or *Molinia* only
8	Pole-stage conifer, food absent, bracken cover present
9	Pole-stage conifer, food present, with or without bracken
10	Mature conifer, ground bare, or *Molinia* only
11	Mature conifer, food absent, bracken cover present
12	Mature conifer, food present, with or without bracken
13	Close conifer thicket or older, dense, with bare ground
14	Small to pole-stage broadleaf, ground bare or *Molinia* only
15	Small to pole-stage broadleaf, food absent, bracken cover present
16	Small to pole-stage broadleaf, food present, with or without bracken
17	Mature broadleaf, ground bare or *Molinia* only
18	Mature broadleaf, food absent, bracken cover present
19	Mature broadleaf, food present, with or without bracken
20	Rides, may be predominantly gravel or grass covered

Table 3.4 *Variables used as descriptors of Open Forest habitats in correlation against roe deer numbers across 12 beats*

(a) Habitats identified by English Nature Open Forest survey

1. Acid grassland (non-calcareous)
2. " " with bracken
3. " " with bracken and gorse
4. " " with gorse
5. Dry heath (*Erica tetralix* absent)
6. " " with bracken
7. " " with bracken and gorse
8. " " with gorse
9. Humid heath (contains *E. tetralix*)
10. " " with bracken
11. " " with bracken and gorse
12. " " with gorse
13. Wet heath (as item 9, typically with *Sphagnum venellum, Juncus* spp.)
14. " " with gorse
15. Carr (willow thicket on bog or alder carr proper)
16. Lawn (typically floodplain, flushed areas)
17. Partially improved grassland
18. Reseeded grassland
19. Bracken covered
20. Bracken with gorse
21. Gorse (i.e. high gorse with closed canopy)
22. Scots pine (closed canopy)
23. Valley mire
24. Woodland / scrub (oak / beech broadleaf woodland)
25. Roads and other 'hard' areas

(b) Aggregate habitat types derived from above

26. All acid grasslands (total of items 1 - 4)
27. All dry / humid heaths (total of items 5 - 12)
28. All wet heaths (total of items 13 + 14)
29. All improved grasslands (total of items 16 - 18)
30. All bracken covered areas (total of items 19 + 20)

As no replication was possible for any of the correlations described in this part of the study, the same criteria for consistency of results used previously (Chapter 2) could not be applied. Instead, all significant correlations were plotted as 'scatterplots' and inspected: where no trend was apparent and the correlation's significance appeared to be based on a single, exceptional point, then that correlation was rejected as 'spurious'.

3.3 RESULTS

Enclosed woodlands

(i) Correlation between roe deer numbers and stand structure

This set of correlations used categories of woodland habitats in species-groups and height-classes as close as possible to those used in the earlier analysis (Chapter 2). Across the 12 sites only two of the 35 variables considered were found to be significantly correlated with the roe deer distribution:

(a) Other conifers of 5 - 15 m. height $r = +0.6741$ $p < 0.05$
(b) Scots pine of 15 - 20 m. height $r = -0.6048$ $p < 0.05$

Both species-groups involved, 'other conifers' and Scots pine, for different height-classes also showed a mix of both positive and negative correlations, and the same was true for other species-groups within both 5 - 15 and 15 - 20 m. height-classes, and there was thus no 'internal' consistent pattern of correlation results.

Neither was a clear pattern of correlations found from the analysis using 6 sites and the observed usage by roe of those sites. Three significant positive correlations emerged with roe usage: firs 2-5 m. ($r = 0.8144$), 'other conifers' > 20 m. ($r = 0.8886$), and 'other broadleaves' 5-15 m. ($r = 0.8883$) (all $p < 0.05$).

(ii) Correlations between roe deer numbers and characteristics of the ground vegetation of the enclosed woodlands

The overall availability of ten characteristic species of ground vegetation in the enclosed woodland sites was calculated from their percentage cover (Table 3.2). Of these six were found to be significantly correlated with roe deer numbers at $p < 0.05$ (three at $p < 0.01$), as listed in Table 3.5.

Table 3.5 *Inclosure ground vegetational variables correlating significantly with roe deer numbers across sites*

	Variable	Correlation Coefficient	
(a)	Positively correlated		
	Abundance of bramble	0.629	*
	Abundance of holly	0.812	**
	Abundance of ivy	0.872	**
	Abundance of shrub	0.581	*
(b)	Negatively correlated		
	Abundance of *Molinia*	- 0.644	*
	Abundance of bracken	- 0.715	**

From inspection of the scatterplots, the correlation between roe numbers and 'shrubs' was considered as spurious, and rejected. Three species of ground flora correlated positively and significantly with roe: bramble, holly and ivy; two species, purple moor-grass and bracken, correlated significantly negatively with roe deer numbers.

Only the availability of holly ($r = 0.8897$, $p < 0.05$) emerged as a significant correlate with roe usage across the 6 sites, in agreement with the previous result from 12 sites. However, the correlations of all other species did agree in their signs with the results from the 12 site analysis.

(iii) Correlations between roe deer numbers and woodland habitat types combining characteristics of both tree stands and ground flora

Results for the correlations of roe deer numbers with availability of the subjective habitat categories (defined on the basis of stand type, growth stage and the ground vegetation) are given in Table 3.6.

Table 3.6 *Coefficients of correlation between estimates of local roe population (based on 1986 census) and habitat types, across sites*

<table>
<tr><th>Woodland type</th><th>With food</th><th>Bare ground /</th><th>With bracken</th></tr>
<tr><td>Open / Establishment</td><td>-0.116</td><td colspan="2">-0.430</td></tr>
<tr><td>Prethicket conifer</td><td>0.179</td><td colspan="2">-0.572</td></tr>
<tr><td>Thicket conifer (excl. dense)</td><td>0.415</td><td colspan="2">0.140</td></tr>
<tr><td>Dense thicket conifer</td><td>n/a</td><td colspan="2">0.149</td></tr>
<tr><td>Pole-stage conifer</td><td>0.389</td><td>0.274</td><td>-0.446</td></tr>
<tr><td>Mature conifer</td><td>0.773 **</td><td>-0.555</td><td>-0.735 **</td></tr>
<tr><td>Pole-stage broadleaf</td><td>0.362</td><td>0.234</td><td>-0.379</td></tr>
<tr><td>Mature broadleaf</td><td>0.591 *</td><td>-0.192</td><td>-0.296</td></tr>
<tr><td>Rides (all)</td><td>-0.494</td><td></td><td></td></tr>
</table>

Notes: * denotes $0.01 < p < 0.05$, ** denotes $p < 0.01$

As can be seen, there are two significant positive correlations, mature conifer with food ($r = 0.7734$, $p < 0.01$) and mature broadleaf with food ($r = 0.5908$, $p < 0.05$), and one negative, mature conifer with bracken ($r = -0.7349$, $p < 0.01$). Inspection of the scatterplots suggested none to be obviously spurious.

In addition to these, the availability of one other habitat may be considered of interest, as it did show an apparent trend from the scatterplot ($r = -0.5552$) and only just failed to reach significance at $p < 0.05$. This was the habitat type defined as mature conifer with little or no understorey, and is worthy of note here as it is the third remaining mature conifer habitat type. There is a clear difference between the strong positive association between roe numbers and those woodland habitats which are associated with a food-rich understorey, and the negative (or less strongly positive) relationship observed with the same type of woodland which has a bracken understorey or bare ground. Further, the negative correlation between roe numbers and woodland stands with bracken understorey is consistently stronger than the negative relationship observed with those without any significant understorey at all. The pattern of correlations across all habitat types is itself significant (sign test, $p < 0.01$), against the null hypothesis of an even chance of greater or lesser correlation coefficients for woodland types with or without food species (irrespective of bracken). If the only difference between the mature conifer stands with bracken and those with nothing *is* the presence of bracken, then it is possible that roe actually have an aversion to that species: this will be investigated in Chapter 4.

The availability of one of these habitat types also correlated significantly in the 6 site analysis, mature conifer with food ($r = 0.8486$, $p < 0.05$); in addition, another type emerged as significant which was not so before, dense thicket ($r = 0.9086$, $p < 0.05$).

Open Forest

Only one variable correlated significantly with the roe population across the Forest beats using the English Nature Open Forest data, the partially improved grassland ($r = 0.5995$, $p < 0.05$). Examination of the scatterplot for this correlation does not suggest a clear relationship between roe and this habitat type, and the result may be spurious. Moreover, no significant correlations were found between roe and other similar habitats of the Open Forest, the acid and reseeded grasslands.

3.4 DISCUSSION

The current pattern of distribution of roe deer in the New Forest clearly reflects the patterns of abundance of a number of vegetational characteristics. Several species of ground vegetation in particular appear to be associated, either positively or negatively, with the local abundance of roe. Three recognized food species, bramble, ground holly and ivy, all correlated positively and significantly with roe, while two other species, purple moor-grass and bracken, correlated significantly negatively. Jackson (1980) found bramble (and rose) to be the dominant item in New Forest roe diet over much of the year, with holly and ivy of seasonal importance. In the New Forest, holly and ivy are mainly associated with the mature woodlands, broadleaved stands in particular, and the significant correlation of roe numbers with that habitat type probably reflected this. Bilberry, a species taken in any measure only in spring (Jackson 1980), was not found to be significantly correlated with roe abundance, but this species now occurs somewhat patchily over the Forest, and only four of the 12 study sites contained over 0.1 ha. equivalent.

Similarly, Jackson (1980) found that heathers were taken by New Forest roe in small amounts over the greater part of the year. As a major constituent of the Open Forest vegetation, however, it is not certain that the relatively limited quantities within the enclosed woodlands are of much importance overall. The negative correlations between roe numbers and both *Molinia* and bracken may indicate that both species are of little or no interest to roe (and that their presence correlates negatively with that of preferred food species), or that they are actually positively avoided by roe. The latter suggestion is supported by the fact that correlations between roe numbers and stands of mature conifer were more strongly negative when they contained a bracken understorey than when they merely had bare ground beneath the canopy. Neither *Molinia* nor bracken is a recognised food species (Jackson 1980), and where either occurs it is often as the dominant, if not only, species of ground vegetation.

The revealed associations do not, of course, give any indication of the value of the vegetation species, which may be utilised for food or cover. Hofmann (1985) noted that one of the characteristics of smaller, concentrate selectors such as roe, is that the species of vegetation they use for food and cover tend to be the same. The extremely low levels of ground vegetation in the New Forest, however, would appear to be unsuitable for cover which, presumably, is provided more by woodland such as prethicket and thicket stands. It is more likely that the associations found in this study reflect the food requirements of the roe rather than cover.

Results presented in this chapter may be compared with those of the earlier spatial and temporal analyses (Chapter 2). With the earlier spatial analysis there is poor overall consistency. No one species-group / height-class variable occurred in <u>either</u> of the present correlation analyses (six or 12 sites) which used the same woodland structural categories <u>and</u> the earlier one using the same categories. A more general, if weak, similarity may be seen in the positive associations of roe numbers with food-bearing conifer (both six and 12 site analyses in this chapter) and with Scots pine and spruces (both >20 m.) in the previous analysis. Against this, however, the majority of the mature coniferous woodlands are food-depleted, and no >20 m. species-group variable emerged as significantly negatively correlated with roe numbers in the earlier analysis in agreement with the negative correlations with food-depleted mature conifer of the present (12 site) analysis.

As pointed out in Chapter 2, the results from the earlier <u>spatial</u> correlation analysis showed no agreement with those of the <u>temporal</u> analyses. In comparison against the results of those temporal analyses, we also find a limited consistency with the present results. Again no one variable using the woodland structural categories occurred consistently in both analyses, and, perhaps most notably, the strong pattern of prethicket associations with roe numbers in the temporal study was not reflected by significant correlations with the equivalent prethicket habitat types here. However, when the results are looked at as complementary, and are taken in conjunction with other studies, a consistent picture emerges. Other workers (Prior 1968, Loudon 1978, 1982, Ratcliffe and Petty 1986) have described the association between roe deer density and particular stages of commercial conifer woodland successional stages, i.e. those stages in which light levels permit the development of ground vegetation (early and prethicket stage, and to an extent in the mature, thinned areas). As noted in Chapter 2, the amount of prethicket in the New Forest has fallen drastically over the period of the decline, and now (from the survey data) covers only some 2% - 3% of the enclosed woodland area; indeed, it was not found at all the sites surveyed. It may be this low and patchy distribution which accounts for the lack of any significant correlation with roe numbers in the present study, which has also indicated that the woodland habitat types which play a more important role in influencing the <u>current</u> distribution of roe are in fact the more widespread, food-bearing mature stands (both coniferous and broadleaved). These latter habitat types are in fact, the areas within the inclosures where most of the food species taken by roe now occur.

Other studies have also reported that the distribution of deer can be described strongly in terms of the availability of its food resources. Ballon *et al.* (1992) found bramble to be a precise predictor of roe density in the oak forests of Dourdan, France, while Chapman *et al.* (1985) reported in their study in the King's Forest, Suffolk, that muntjac distribution could be best explained with respect to that of certain species of ground vegetation, particularly bramble and raspberry, and the percentage of nut-producing broadleaf trees. Similarly, Hanley (1984), looking at habitat selection in the Cascade Range, Washington, by two species of deer, wapiti (*Cervus elaphus nelsoni*) and Columbian black-tailed deer (*Odocoileus hemionus*), also found that each species preferred those habitats where its own food availability was greater. In the New Forest, the vegetation surveys data shows that of the total 591 ha. of mature conifer woodlands within the 12 study sites, only 167 ha. (28%) consisted of the food-bearing type. The correlation between roe numbers and the area of this latter habitat type thus seems to reflect the importance to roe of areas with even comparatively low amounts of forage.

The same association with roe numbers was seen with the food-bearing broadleaf stands. In this respect it may seem surprising that no significant correlation was found between roe numbers and the extent of the Forest's unenclosed broadleaf woodlands; many of these are established, often Ancient & Ornamental woods which are known to harbour roe (Chapter 1, Fig. 1.8 data). The reasons for this may be twofold. Firstly, the English Nature survey does not distinguish between the different types of broadleaf woodland found on the Open Forest, and includes in a single category not only the Ancient & Ornamental woods, but areas of broadleaf scrub, and this may mask any association that might exist between roe abundance and the presence of older, 'true' broadleaf woodland. In this respect, it should be remembered that correlations between roe numbers and overall woodland categories in many of the spatial analyses of this chapter and the previous one were poor or non-existent; the correlations only emerged when the woodland was subdivided into height classes or on the basis of ground vegetation. Secondly, there are no reasons to suppose that the ground vegetation of even the older Open Forest woodlands are of equal value to roe across the Forest, as the flora may be expected to change with soil quality.

That roe also make some use of the Open Forest habitats is certain. The animals may occasionally be encountered on the Forest's open heathland, and some may be largely resident in such areas. This type of habitat is occupied by roe in northern parts of Britain, and can provide the major part of the species' diet (Robertson (1967), Hosey (1974), working in Scotland, and Henry (1975, 1978) in Hamsterley Forest, Co. Durham). The only significant correlation obtained between roe and the Open Forest habitats was a positive association with the amount of partially improved grassland. These grasslands are areas of the Open Forest which, after the War and up to the 1960s were treated e.g. using lime, to provide better grazing for domestic stock; subsequently they have been reverting to species-rich acid / neutral grassland (Tubbs 1986). The total area of partially improved grassland in the whole of the New Forest is approximately 77 ha., making it a fairly minor habitat type overall. Moreover, in a study of habitat use of the Forest's grasslands Edwards and Hollis (1982) reported evidence of fallow deer presence, but not of roe deer. Overall, the expressed view (Chapter 2) that roe performance in the New Forest is more closely related to enclosed woodlands than to the Open Forest habitats is supported.

So far, all conclusions are based on correlations only. They may, however, be substantiated if the habitats which were found to be correlated significantly positively with roe distribution can actually be shown to be used preferentially by roe. This investigation is described in the following chapter.

4. THE USE OF HABITATS BY ROE DEER IN THE NEW FOREST INCLOSURES

Chapter summary

Field studies were carried out at 6 enclosed woodland sites to determine patterns of habitat use and selection by roe in the New Forest. The objectives were to corroborate the findings of earlier analyses (Chapters 2 and 3) by identifying which habitat types roe preferred and which they avoided, and to see how patterns of use and selection differed between sites of better and poorer quality (as reflected by roe density). Specifically, it was asked whether roe at poorer sites attempted to achieve the same level of use of the available good habitat types by selecting them more strongly than did roe at better sites, and if so, did they succeed?

The study sites were chosen to represent the range of roe densities currently found in the New Forest. Visual transects at the sites over a 12 month period allowed all habitat types at each site to be surveyed in proportion to their availabilities, and any roe observed were recorded. These patterns of habitat use were examined in relation to habitat availability, and comparisons of seasonal habitat usage were made within and between sites. These comparisons necessarily used a higher level system of habitat classification than that used previously; it was, however, possible to compare results from the two systems.

Patterns of habitat use by roe were found to be determined by both habitat availability and habitat selection. Usage generally differed significantly between sites in a season and between seasons at a site, and was more similar at sites of more similar habitat composition. Patterns of faecal deposition observed in all habitat types at the six sites over a six month period, after correction for differential decay / disappearance rates, supported the patterns of habitat occupance from visual transects, suggesting 24 hour patterns of usage did not differ greatly from those observed during daylight hours.

Food-bearing open/prethicket was the most strongly selected woodland habitat class, especially at poorer sites; with comparable ground vegetation, prethicket appeared to be more strongly selected than open ground. Food-depleted (older) conifer areas were avoided to some extent at all sites in all seasons, but roe at poorer sites were forced to make relatively greater use of them. In contrast, food-bearing conifer was used and selected at all sites, especially in winter, but, as in the case of food-bearing open/prethicket areas, roe at poorer sites were unable to compensate for low availability of those habitat types through stronger selection. Broadleaf woodlands were used all year in those sites when food-bearing, but at all sites over autumn and winter (whether food-bearing or food-depleted), when levels of use by roe at poor sites were comparable with levels of use made by roe at better sites. Rides overall were neither selected nor avoided, but did appear to be selected at some sites, mainly during summer.

Results from these studies strongly supported the positive associations found between roe numbers and the abundance of certain species of ground vegetation in earlier chapters. In contrast with previous results, however, analyses of habitat selection within sites suggested that bracken was not a significant factor in habitat use by roe. Roe at poorer quality sites in the New Forest do not appear to achieve usage levels of food-bearing habitats as high as those achieved by roe in better sites.

4.1 HABITAT USE AND SELECTION BY LARGE HERBIVORES

For large herbivores, as for other animals, any investigation into population abundance and distribution must be founded upon understanding the relationship between the animals and their resources. In accessing these resources large herbivores seldom if ever use all parts of their range in a random or uniform manner (Duncan 1983, Collins and Urness 1983); rather, they show preferential use of some localities (habitats) and a degree of avoidance of others.

In studying the use of space by any animal, it can be extremely difficult to relate geographic pattern of distribution directly to specific resource distribution. Levels of food and cover, for instance, often vary greatly over short distances and may change seasonally in the quality and quantity of resource offered. Furthermore, other factors of potential importance, such as in the chemical composition of the food material, may not be apparent to an investigator or may be impracticable to obtain. To get round these problems, Duncan (1983) proposed that habitats could be classified *a priori* into a number of 'habitat types' based upon average values of the local abundance of resources; the time spent by the study animals in each defined habitat type could then be measured. (An attempt to derive a more 'objective' scheme of habitat classification for this project is described in Appendix 1.) Such an approach is both efficient and adequate for most management purposes. However, it is important to acknowledge, after Johnson (1980), that a complete understanding of the animal's ecology would not be achieved from a single such study alone: the resource composition of the defined habitat types must be determined, and the conclusions should be subject to confirmation that the resources used for the habitat classification were indeed those being selected in the habitats by the animals under study.

Within their home range - or the chosen study area - deer may select different habitat types for different purposes, such as for food, water, shelter from weather and predators, rest and rumination (Beier and McCullough 1990). Further seasonal changes in habitat use may reflect either a change in resources offered by different habitats, or a change in the animals' requirements for different resources. When viewed together, the use of all habitat types within a range reveal a *pattern* of habitat use for the population under study, showing some areas, or types of areas, to be used proportionally more than others. In most studies this observed pattern is compared to the corresponding pattern of habitat availability in order to identify those habitats - and by implication the resources - of most importance to the species. It should be remembered, however, that while the fundamental needs of any free-ranging animal (for food, water, etc.) may determine the animals 'preferred' patterns of habitat use, the actual (observed) patterns of habitat use may be strongly influenced by factors other than resource availability; examples include social behaviour (in primates: see Struhsaker 1975), wind strength (in sheep: Rawes and Welch 1964), and biting insects (in cervids: Skogland 1975, Peek *et al.* 1976, Espmark and Langvatn 1979).

Although the terms 'preference' and 'selection' when applied to animals' choice of resources (or habitats) have often been used synonymously, Johnson (1980) suggested that the term 'preference' should be used only to indicate the likelihood of a resource being chosen only when offered on an equal basis with another. In practice, this would largely restrict the term to those studies of resource usage carried out under controlled conditions (e.g. Werner and Hall 1974, O'Brien *et al.* 1976). 'Selection' would be applied more generally, being the process of choosing a resource component, and 'selective usage' would indicate that a resource was chosen disproportionately to its availability. Other investigators have applied different definitions of these terms, e.g. Peek (1986). This study is concerned with habitat selection *sensu* Johnson (1980). The term 'avoidance' is also used to specify negative selection i.e. when the use of a habitat is disproportionately less than its availability.

The differential use of habitats has further led a number of authors to define habitat 'selection indices' which express quantitatively the degree of use made of a habitat type in relation to its availability. Such indices have been proposed by, among others, Ivlev (1961, and see Jacobs 1974, Strauss 1979), Hunter (1962), Vanderploeg and Scavia (1979), and Johnson (1980). That of Hunter (1962) is one of the simplest, and is calculated by dividing the proportional use made of a habitat by the proportion of that habitat's availability within the range of the animal. The resulting index has a value of 1 for neutral selection, but suffers from having a highly skewed distribution and ranging between zero and infinity. Goodall (in Hirst 1975) proposed an offset arctan transformation of Hunter's index, which gives an evenly distributed index with a value of zero for neutral usage, and bounds of -1 (for zero use) and +1 (for infinitely high use). It is Goodall's index which is used in this study.

In the work described in the present chapter, patterns of habitat use for roe deer in the New Forest are examined in relation to habitat availability at chosen sites, and also compared between sites with different habitat availabilities. By such comparisons, it is possible to see if differences between the observed patterns of use at different sites result merely from differences in habitat availability, or whether the roe are showing differences in habitat selection in order to make optimum use of limited resources.

In order to ascertain whether or not differences in vegetational character might affect roe deer habitat choice on a day-to-day basis, field studies were undertaken to examine the present day patterns of habitat usage in different areas of the New Forest.

Specifically, investigations were carried out to see

(a) what general patterns of habitat use and selection are expressed by roe in the New Forest

(b) if habitat types shown to be selected or avoided by roe correspond to those which were found to be correlated significantly (positively or negatively respectively) with roe abundance in the earlier parts of this study (Chapters 2 and 3)

(c) whether patterns of habitat use differ between sites of different site quality (as discussed in Chapter 3)

(d) whether the differences observed in the patterns of habitat use displayed by roe at different sites are determined purely by different habitat availability at those sites, or whether there is evidence to suggest that the roe at 'poorer quality' sites try to compensate for deficiencies in habitat availability by a change in habitat selection (and thereby try to achieve patterns of habitat use similar to those at 'better' sites).

4.2 STUDY SITES

As described in Chapter 3, twelve sites were chosen as areas encompassing between them the range of roe population densities found in the New Forest. Six of those sites were now selected for the detailed investigations on habitat use described in the present Chapter.

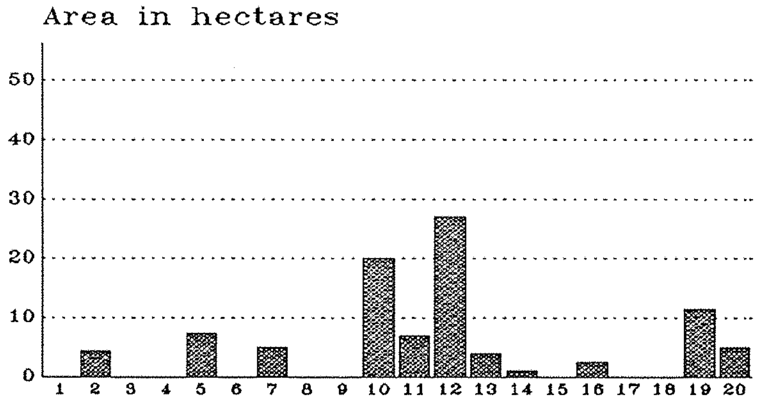
As before, sites were selected in order to include areas of both high and low roe density as far as could be estimated from the census (but excluding those sites from which roe were absent), with the additional requirement that observations of the occupance of habitats by roe should as far as possible be unbiased by visitor disturbance. The sites selected were Holmsley and Salisbury Trench (both of which appeared to have relatively high density roe populations), King's Hat and Shave Green (medium / high), and Knightwood and Milkham (poor). The terms 'better' and 'poorer' as site descriptors will be used synonymously with sites of high / medium density and sites of low density respectively. The locations of these sites were shown previously (Fig. 3.1), and their habitat compositions are presented below (Fig. 4.1).

It is useful to have some objective assessment of the sites' degree of similarity or difference in terms of their vegetational structure and composition. Whittaker (1972) proposed 'β-diversity' as a measure of change in species diversity, expressing either the rate and extent of change in species composition along a gradient, or the difference between the species composition of two communities. Such change may be investigated using either standard methods of classification - such as cluster analysis and ordination techniques (see e.g. Grieg-Smith 1983) - or by one of a range of specific indices which have been proposed, the best known of which are the indices of Jaccard (1908; see also Bray and Curtis 1957) and Sørenson (1948). The range of such indices of β-diversity in common use have been reviewed in Clifford and Stephenson (1975), Southwood (1978) and Magurran (1988). Of those considered, the Morisita-Horn index (Morisita 1959, Horn 1966) was regarded as being among the most satisfactory, as being least affected by sample size and species richness (Wolda 1981, Smith 1986 [cited in Magurran 1988]).

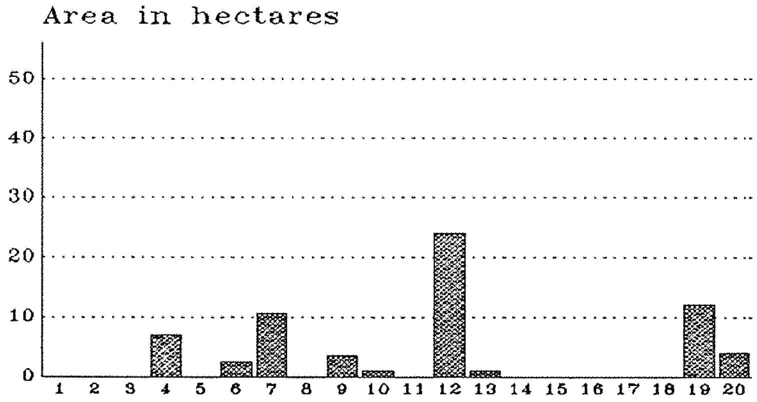
All six sites were compared using both the Morisita-Horn index and cluster analysis (using Ward's method) on the basis of percentage composition of habitat types. While the results qualitatively showed some degree of accord, the Morisita-Horn indices were difficult to interpret and even appeared potentially misleading, as high index values were obtained for pairs of sites which intuitively seemed dissimilar. The cluster analysis was regarded in this context as giving the more meaningful results, and these form the basis of site comparisons presented later in this chapter.

Fig. 4.1 *Habitat composition of six study sites by habitat types derived from vegetation survey (see Table 3.3 for full habitat type descriptions).*

(i) Holmsley



(ii) King's Hat



(iii) Salisbury Trench

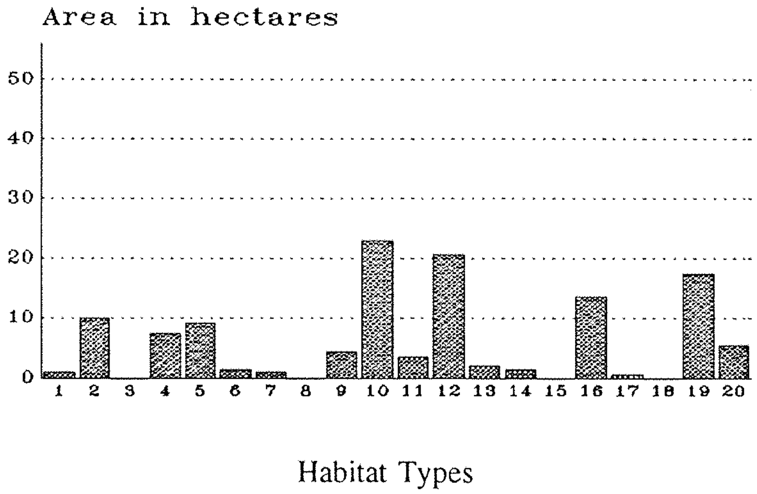
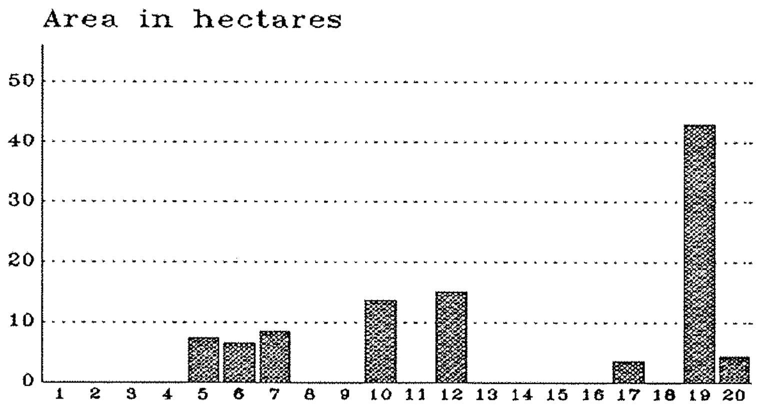
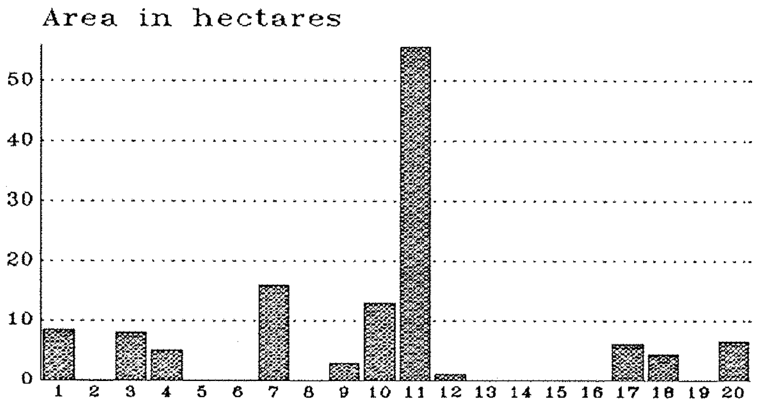


Fig. 4.1 *continued.*

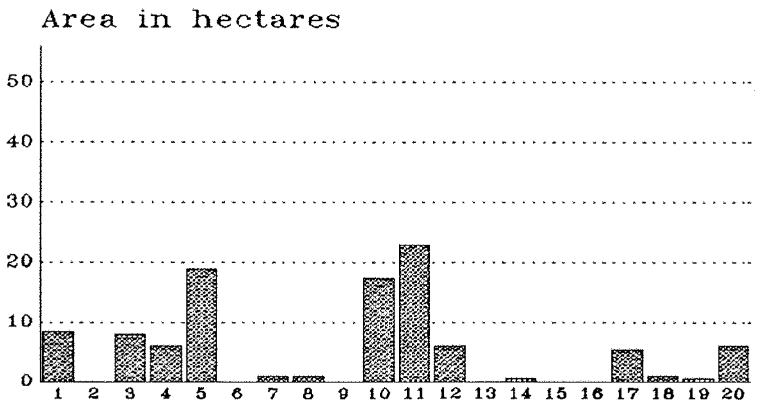
(iv) Shave Green



(v) Milkham



(vi) Knightwood



Habitat Types

4.3 ASSESSMENT OF HABITAT USE

4.3.1 Visual observations of roe from transects

Using the Commission's large-scale stockmaps, a transect route was carefully designed for each site which would allow effective sampling of all the habitat types occurring at that site. All the transects were of approximately equal length (about 2 kms.), and were designed to permit observation of each habitat type in close proportion to its availability at the site as a whole. For this reason, and in order to include areas free of visitor disturbance, transect routes were designed as a mixture of 'on' and 'away from' rides. Where possible, the route included more than one plot of each habitat type to allow for chance usage of different plots by deer. All transect routes were walked "on test" for a few weeks prior to use for recording, and minor modifications made as necessary. Once the final route was established, it was adhered to for the whole study period of one year. The proportion of the total area surveyed at each site by habitat type (as reflected by the length of transect route) in relation to the habitat type representation at the site are shown in Fig. 4.2.

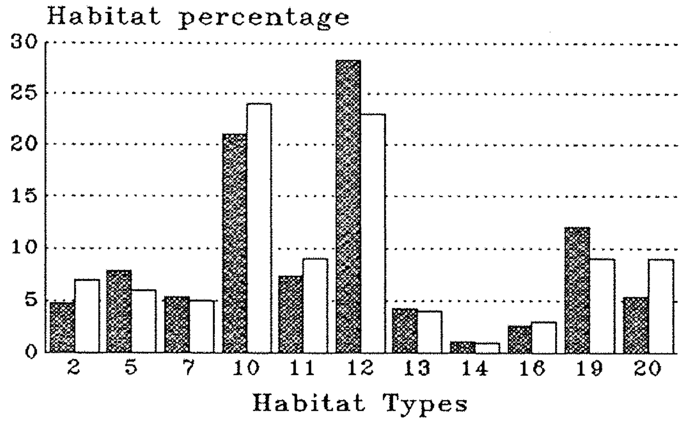
The close fit between proportion of habitat type availability and transect length does not suggest that the actual area of each habitat type visible, and therefore surveyed, was in the same proportion; different habitat types offer different degrees of visibility, and this potential problem with the method is discussed in detail later (Section 4.6.1).

Over 12 months (January through December 1989) visual observations were made from the transect routes at all six sites. Each site was visited 9 times per month, and the transects timed to spread evenly over the period of daylight available. In order to minimise disturbance to patterns of habitat use as a consequence of observer presence, no site was visited more than once a day where practicable; on the few occasions when this was unavoidable, visits were separated by a gap of at least three hours.

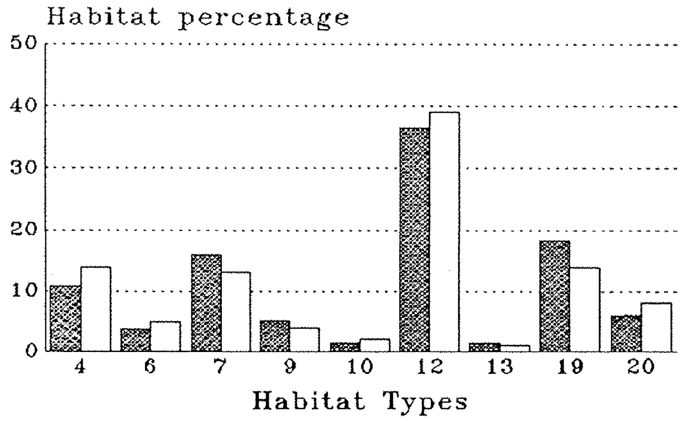
In the New Forest, as has been noted earlier, it is impossible to obtain 100% freedom from other users, but as far as possible the transect routes were designed and visits were timed with this in mind. Weekends, other than in the early morning, were avoided as they were periods of above-average visitor use. Prior consultation with the Forestry Commission

Fig. 4.2 *Site composition by percentage of each habitat type, and transect composition by percentage of its length passing adjacent to or through each habitat type.*

(i) Holmsley



(ii) King's Hat



(iii) Salisbury Trench

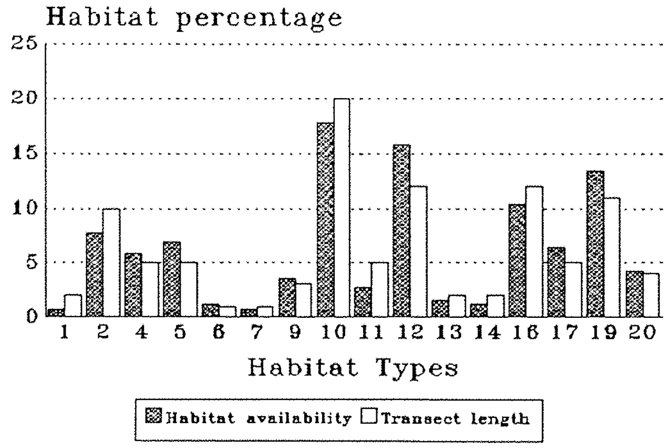
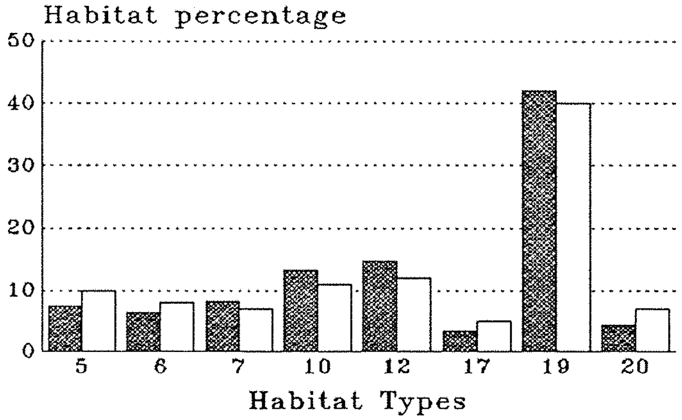
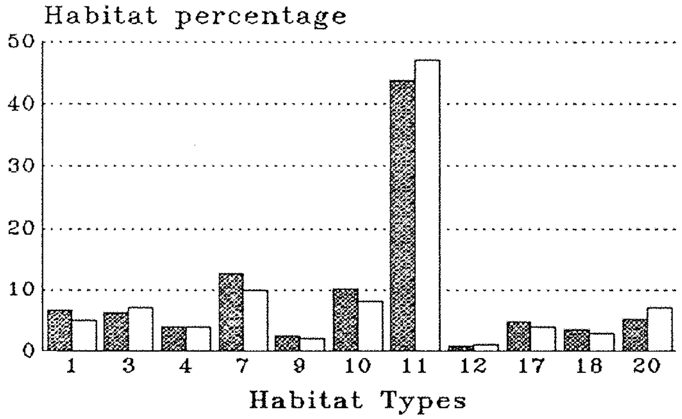


Fig. 4.2 *continued.*

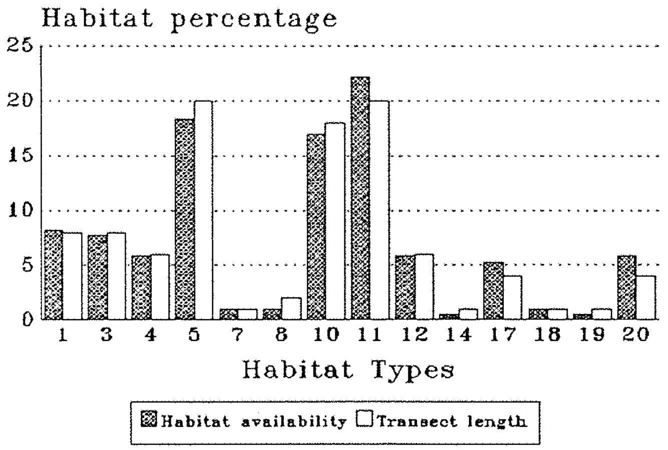
(iv) Shave Green



(v) Milkham



(vi) Knightwood



allowed the avoidance of days of heavy usage of a site by other Forest users (e.g. for orienteering, fox-hunts or military exercises).

For each survey, the transect route was walked at a slow and steady rate and all sightings of roe and other deer were recorded: for each observation records were made of the site, date, observation time (GMT), species of deer, location when seen, location to which the deer fled (if any), the number of deer seen, and the distance from the observer when seen. When possible, additional records were made of the sex of the deer and behaviour, although most observations were inevitably fleeting. As roe are generally solitary, most observations were of single animals; young fawns (under about 7 months) were not considered independent of their mother and were counted within 'her' observation, but older fawns, or pairs of adults, which could use nearby habitats independently, were recorded separately.

In studying a declining population of herbivores in a changing environment, a number of special considerations apply. Rare animals produce few data. In the New Forest there are now extensive areas of enclosed woodland in which no roe have been recorded in the annual census for over 10 years. For the present study two sites (Milkham and Knightwood) were deliberately chosen because they each contained (by best estimate) only a single resident roe doe. However, even the most densely populated New Forest inclosures - such as Holmsley - have, by the standards of nearby estates and private woodland, quite low populations of roe. As this resulted in a relatively low number of observations of deer, especially at the low density sites, it was necessary to aggregate the observations seasonally, each season defined as an arbitrary three-month calendar block:

Winter: December - February
Spring: March - May
Summer: June - August
Autumn: September - November.

From the observation data collected, both the amount of use (occupance) and the proportional use of each habitat type at each site were calculated. From the site characteristics (Fig. 4.1) the availability of habitats at each site was known; together, these permitted the calculation of selection indices for habitats at each site.

4.3.2 Assessment of habitat use from faecal deposition

In order to provide an independent assessment of habitat use from that obtained by the visual transect surveys, a second method for investigating the habitat use by roe was employed, using the recorded distribution of faecal pellet groups deposited at each site.

This technique assumes the number of faecal pellet groups counted within a representative area of a given habitat type can give a measure of the relative occupance of that habitat type by the species in question. Two alternative methodologies are generally recognised, that of 'faecal standing crop' and that of 'accumulation on cleared plots' (see reviews by van Etten and Bennett 1965, Neff 1968, Putman 1984). The 'faecal standing crop' method in its simplest form requires counting the number of faecal pellet depositions in a known area of habitat. Before these counts can be related to habitat use, however, some correction has to be made for the rates of accumulation and loss of the material (which may differ between habitats and seasons); information on these rates is usually obtained from separate trials. The 'accumulation on cleared plots' method involves marking out areas of known extent which are cleared of 'old' faecal deposits, and then periodically counting the rate at which new deposits are made. This procedure is usually repeated with sufficient frequency that separate decay rate trials are unnecessary; new depositions are removed or marked at each visit, allowing the rate of accumulation to be related directly to the occupance of the habitat type concerned.

Both methods rely upon certain assumptions. Most notably, it is taken that the amount deposition of dung in a site is related directly to time spent there, and thus, implicitly, that animals dung regularly throughout the 24-hour period, and are not selective with regard to habitat used for defecation.

While the accumulation method requires no corrections from separate decay / disappearance studies, the results may be difficult to analyze statistically (especially in the case of rare animals) as actual pellet group density recorded will be very low, with many 'zeroes' in the data set. By comparison, the higher figures which may be expected from the standing crop method permit sampling intensity to be lower (Neff 1968, Putman 1990). Ratcliffe (1987b) concluded that the standing crop method, applied carefully, could give consistent results and could give a better return on information for the effort expended

(Ratcliffe 1987b, Staines and Ratcliffe 1987). For this study, the faecal standing crop method was selected as being the most appropriate.

Once a month, each site was visited and all the habitat types at that site were sampled for the presence of faecal pellet groups. 10 transect samples were carried out in each habitat type which, where possible, included more than one different sub-compartment of that type at the site. The method of survey chosen was that of belt transect walks.

A belt transect was defined as an area of 50 m^2, and was sampled by the observer pacing slowly for 25 metres, scanning the ground 1 m. either side of his position and recording any faecal pellet groups observed. For certain habitat types where canopy closure made ground sampling difficult a wide-beam torch was used. (The number of paces required for a 25 m. transect had been established for each habitat type by trials conducted prior to the start of sampling, using a tape measure, and checks were periodically carried out during the actual sampling: all were found to fall within 4% of 25 m. The observer's judgement of 2 m. for the transect width was similarly practised, and a tape measure was used during the sampling where necessary to eliminate doubt about the inclusion of any particular faecal pellet group.)

Not all faecal pellets are deposited in discrete groups, which could pose a further difficulty for using the counts of pellet groups as measures of habitat occupance. On occasion, roe defecate while walking (pers. obs.), and this may result in small clumps or strings of pellets. Mitchell *et al.* (1985) encountered the same problem and ignored groups with fewer than 15 pellets; the same procedure was followed here.

Pellet surveys were undertaken in all sites from August 1989 to January 1990 inclusive, but were discontinued following the severe storms in the south of England at the end of January 1990. During that event many of the study sites were rendered inaccessible and, in any case, had had their habitat structure so radically altered as to render further surveys meaningless.

4.3.3 Decay rates and detection of faecal pellets

A requirement for effective use of the faecal standing crop method is the need to know the period of time over which the faecal pellets recorded in any survey have been accumulating and the probability of detection. These may not be the same for all habitats or seasons. In effect, it is necessary to know the probability of persistence and subsequent detection of a given faecal sample with time, so that suitable correction factors may be devised to enable an accurate estimate to be made of the number of pellet groups actually deposited in the sampling area in any given period. For this study simple trials were carried out using freshly dropped faecal pellets in order to estimate such correction factors.

Over December 1989 - January 1990, freshly deposited faecal samples of roe were collected from a captive adult doe and placed out (within one hour) in representative areas of all habitats. For this work, similar habitat types were grouped on the basis of their woodland type as this rather than the abundance of resource species defined the characteristics of the forest floor; this gave 8 different habitat groups (Table 4.1), and it was assumed that the results would be applicable equally to each of the habitat types in a group.

Table 4.1 *Groupings of habitat types for trials to determine rates of disappearance of faecal pellet groups*

Group	Description	Habitat types included
1	Open / establishment	1, 2, 20
2	Prethicket conifer	3, 4
3	Thicket conifer (excl. dense)	5, 6
4	Pole-stage conifer	7, 8, 9
5	Mature conifer	10, 11, 12
6	Dense conifer thicket	13
7	Immature broadleaf	14, 15, 16
8	Mature broadleaf	17, 18, 19

Note: Full descriptions of habitat types are given in Table 3.3

The date and time of placement were recorded, and the locations marked for easy recognition. Each group consisted of at least 20 individual pellets, and three groups were places in each habitat category (the limited sample size was enforced by the supply and time available). The locations were visited every 2 or 3 days, and the number of groups still identifiable for each habitat category was noted. The criterion used for recording was whether the same group would have been recognized and recorded during a belt transect survey. If there was doubt about a group, it was scored as being half-present. Only one set of faecal pellet decay / disappearance trials was carried out as a result of the disruption of the study by the storms of January 1990, and since analyses of pellet group data were in any case restricted to the winter period, the same correction factors calculated for the different habitat categories were used throughout.

Resulting data were plotted as 'number of groups remaining' against time (days) for each habitat type and a formula derived which allowed the number of faecal pellet groups deposited in that habitat type over a specified period to be calculated from the actual counts obtained during the transect surveys. The formula allowed for both faecal pellet groups which may have persisted since before the previous count (in this study about 30 days before) and those which had been deposited and had disappeared in the same counting period.

The formula used was

$$N = n \sum p_i \quad \text{for } i = 1 \ldots \text{infinity.}$$

where N = the number of faecal pellet groups counted at the end of a period

n = the number of pellet groups deposited on one day of the period concerned

p_i = the probability of a pellet group persisting i days.

As N was known, estimating $\sum p_i$ would give a value for 'n', which could be directly related to habitat use after correction for the available area of the habitat type at the site. This estimation could be derived empirically from the pattern of disappearance of the faecal pellet groups (see Section 4.5.2).

Additionally, in the New Forest there is also the possibility of confusion between the faecal pellets of roe and those of other species. Confusion was likely only with those of fallow deer since droppings of other ungulate species' are very distinct from those of roe in size and shape. In order to assess the likelihood of error from misclassification, a series of blind tests were carried out in the laboratory using samples of known roe and fallow faeces: with practice the error rate was reduced to under 2%. In the field, there were very few ambiguous pellet groups encountered during the survey work, and these were ignored.

4.4 DATA ANALYSIS

4.4.1 Habitat classification for comparison of habitat use

Each of the study sites chosen for the investigation of patterns of use and selection of habitats contained a different combination from the 20 defined habitat types (shown previously in Fig. 4.1). This made direct comparison of habitat usage difficult as only rides and three of the 19 woodland habitat types occurred at all six sites.

As a solution, a second, higher-level scheme of habitat classification was adopted, combining specific habitat types into categories of like-structured type, which were represented in all (or nearly all) sites. Thus the defined habitat types were aggregated into six 'habitat classes' for the comparison between sites, as shown in Table 4.2.

(The terms 'habitat type' and 'habitat class' will hereafter be used to distinguish between references made to the two levels of habitat classification. 'Habitat type' refers to the original, more finely resolved scheme shown in Table 3.3, and is applied for comparisons within sites and for relating current results to those of earlier parts of the project. 'Habitat class' refers to the aggregated scheme, which is used for between sites comparisons.)

It can be seen that the overall basis of the new classification (habitat classes) is broadly consistent with that used for the original definition of habitat types, as the latter are clumped according to whether they contain pre-dominantly broadleaf or coniferous stands, are generally open or not, and are food-bearing or food-depleted. Under this scheme, nearly all sites contained all the new habitat classes in some measure, the actual habitat class areas at each site being given in Table 4.3.

Table 4.2 *Correspondence between two schemes of habitat classification*

Habitat Class	Description, and constituent habitat types	
I	FOOD-DEPLETED ESTABLISHMENT / PRETHICKET	
	1	Food-depleted open or establishment
	3	Food-depleted prethicket
II	FOOD-BEARING ESTABLISHMENT / PRETHICKET	
	2	Food-bearing open or establishment
	4	Food-bearing prethicket
III	FOOD-DEPLETED CONIFER	
	5	Food-depleted thicket
	7	Food-depleted pole-stage, bare ground
	8	Food-depleted pole-stage, bracken cover
	10	Food-depleted mature conifer, bare ground
	11	Food-depleted mature conifer, bracken cover
	13	Dense thicket, ground bare
IV	FOOD-BEARING CONIFER	
	6	Food-bearing thicket
	9	Food-bearing pole-stage
	12	Food-bearing mature conifer
V	BROADLEAF WOODLAND	
	14	Food-depleted immature broadleaf, ground bare or *Molinia*
	15	Food-depleted immature broadleaf, bracken cover
	16	Food-bearing immature broadleaf
	17	Food-depleted mature broadleaf, ground bare or *Molinia*
	18	Food-depleted mature broadleaf, bracken cover
	19	Food-bearing mature broadleaf
VI	RIDES	
	20	Rides (all)

Table 4.3 *Composition of six study sites by habitat class in hectares: terms 'good', 'medium' and 'poor' reflect roe densities at sites.*

Habitat	Good		Medium		Poor	
Class	HM	SA	SG	KH	ML	KN
I	0.0	1.0	0.0	0.0	16.5	16.5
II	4.5	17.5	0.0	7.0	5.0	6.0
III	43.5	38.5	29.5	12.5	84.5	61.5
IV	27.0	26.5	21.5	30.0	4.0	6.0
V	15.0	41.0	46.5	12.0	10.5	7.5
VI	5.0	5.5	4.5	4.0	6.5	6.0

Sites: HM - Holmsley, KH - King's Hat, SA - Salisbury Trench,
SG - Shave Green, ML - Milkham, KN - Knightwood.

In order to ensure that there was ecological consistency between the two methods of classification, a correlation analysis was carried out between the numbers of roe (derived for each site from the census data as described in Chapter 3) and the availabilities of habitat classes across sites. This analysis included all the 12 sites surveyed for the earlier work, and in essence repeated the one described in Chapter 3, but using habitat classes instead of habitat types.

4.4.2 Statistical analysis of patterns of habitat use

The data obtained from the monthly visual transect surveys at each site were aggregated into seasonal patterns of habitat use. Each pattern thus comprised the number of deer observed in each of the habitat types or habitat classes occurring at the site in a given season. The patterns were examined and compared to see if there were differences in the patterns of habitat use exhibited by roe, both between seasons at each site, and between sites for each season. For the latter case, the observed patterns of use were further compared to the patterns of habitat availability at the sites, to see if the use could be explained simply as being reflections of those availabilities or whether they suggested deliberate selection of particular habitats.

Many approaches to the statistical analysis of habitat choice by large mammals have been used and discussed in the ecological literature. A full review is not attempted here, but even a superficial scan of the methods employed by different authors shows the use of regression and ordination techniques (e.g. Hill 1981, Beardall *et al.* 1984, Hanley 1984), the *z* test for significance of a binomial proportion (Collins and Urness 1981), rank analyses (Johnson 1980), and, most commonly, goodness-of-fit tests such as the log-linear test (G-test) or chi-square (see for example Thomas and Taylor (1990) and references therein). Some of these methods are restricted in use to studies which involve marked individuals, such as those involving radio-tracking methods (Alldredge and Ratti 1986). All the methods have limitations, and many suggestions have been made on how these may be overcome. Neu *et al.* (1974) proposed the use of the Bonferroni statistic (Miller 1966) as a way of assigning confidence intervals to chi-square tests, and Johnson (1980) argued strongly for the use of rank tests as robust and less liable to being adversely affected by the investigator's decisions on which resources to include. In an examination of four different methods for comparing resource use and availability - those of Neu *et al.* (1974), Johnson (1980), Friedman (1937) and Quade (1979) - Alldredge and Ratti (1986, 1992) concluded that no single method was best in all circumstances, and drew attention to the implications for ecological interpretation which may result from the insensitivity to the degree of resource usage inherent in rank tests, such as that of Johnson (1980). They made the further, crucial observation that each of the methods of analysis is testing against a different null hypothesis, and that the investigator in any study of resource usage should choose the appropriate test for his / her work. In a review of 54 studies reported in the literature over 1985-1988 which used a range of different methods, Thomas and Taylor (1990) also expressed a number of concerns about the way these tests were applied: the assumptions of having observations which were independent, of having sufficiently large sample sizes, and of having known (or very precisely estimated) availabilities were often violated. Thomas and Taylor, like others before them (e.g. Ben-Shahar and Skinner 1988) recommended that where possible analyses should be repeated using a second method to overcome some of these problems (Thomas and Taylor 1990).

For the present study, the independence of observations was not considered a problem (see Section 4.3.1), and estimates of habitat availability were necessarily obtained from detailed Forestry Commission records; but the small number of observations of roe actually obtained at some sites were a potential source of bias, and posed problems for analysis. Where necessary therefore, categories were excluded or aggregated in order that the minimum expected values for chi-square tests were met (Siegel and Castellan 1988, Quenouille 1972). There were still, however, a few cases where the necessary minimum number of observations could not be met, and consequently the pattern of habitat use could not be tested statistically against the availability, i.e. the null hypothesis was retained; these cases are indicated. Within these constraints, the seasonal and annual habitat usage of habitat classes in relation to their availabilities at all sites were tested by chi-square tests.

The comparison of patterns of usage between seasons and between sites required the use of contingency table testing rather than goodness-of-fit tests; here too, small sample sizes posed a potential problem. One test (Fisher's Exact Test) specifically offers a means of comparing the frequency patterns in small samples. Until recently, this test was suitable only for contingency tables of size 2 x 2, but following Kendall and Stuart (1979), its use was extended to *r x c* contingency tables. Unfortunately, the method is at present computationally very demanding, and the analysis of patterns containing many classes becomes impracticable in terms of computer memory and time, even on mainframe computers; for this reason, analyses were restricted to patterns of habitat use in respect of habitat classes rather than habitat types. The analyses were carried out using the implementation of the technique in version 6.06 of SAS[1] (SAS Institute 1990), which uses Mehta and Patel's (1983) network algorithm.

Finally, it is necessary to consider the measure of habitat selection. All of the indices described in Section 4.1 (including Goodall's index chosen for the present study) suffer from the limitation that, as they are derived from ratios, they retain no record of the numerical basis of the observations on which they are based. Most workers use subjective criteria for their assessment and interpretation (Duncan 1983, Putman 1986c, Hinge 1986); this practice was also adopted for this study, with some allowance also made for the sometimes small number of observations on which the indices were calculated. Index values between 0 and ± 0.1 are considered as being neutral i.e. there is no real selection (positive index value) or avoidance (negative index value) of the habitat type; this corresponds to an arithmetic ratio of proportional habitat use to availability of between 1 and 1.2 for positive selection (inverse values apply for avoidance). Absolute index values of between 0.1 and 0.3 are taken as showing 'slight' selection or avoidance (ratio between 1.2 and 2), between 0.3 and 0.5 as being 'moderate' (ratio between 2 and 3), between 0.5 and 0.7 as 'strong' (ratio between 3 and 6), and above 0.7 as 'very strong' to 'extreme'

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[1] SAS is a registered trademark used to identify products or services of SAS Institute Inc.

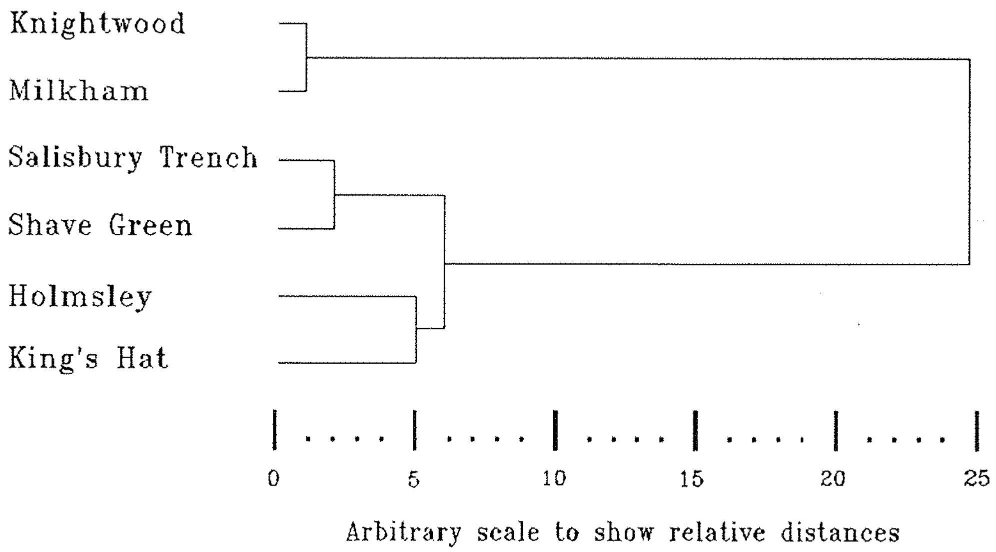
(ratio above 6). The relationships between the index values and the ratios are approximate but do give an idea of the arithmetic basis of the index values used. The overall pattern of selection may also be analyzed using non-parametric tests (e.g. Catt and Staines 1987); in the present study this pattern is analyzed using the sign test, which compares the observed outcomes against those expected from the binomial expansion given a null hypothesis of two equally likely events (Siegel and Castellan 1988). This permits analysis, for instance, of whether the direction or degree of selection of a particular habitat class at sites of low roe density differs significantly from that at other sites.

4.5 RESULTS

4.5.1 Similarities between sites

Similarities and differences between the sites in terms of vegetational composition and habitat availability were examined at the level of grouped habitat classes using cluster analysis: some clear similarities and differences between sites were revealed (Fig. 4.3).

Fig. 4.3 *Dendrogram (using Ward's method) showing rescaled distances between six study sites defined by percentage composition of habitat classes*



The similarities exhibited are in accord with those which might be expected by inspection of the sites' habitat profiles (Table 4.3). The two closest sites were Knightwood and Milkham, the sites with lowest roe densities. These sites have similar habitat structures in nearly all respects, particularly in having much food-depleted mature conifer woodland and a fair amount of food-depleted establishment / prethicket area. The next closest pair were Salisbury Trench and Shave Green; although these sites' compositions differ in the number of different habitat types present, they both have very large amounts of broadleaf woodland, and very similar proportions of mature conifer wood both with and without food species. The third cluster comprised the Holmsley and King's Hat sites; neither site contains any food-depleted open or prethicket areas, and both have substantial areas of food-bearing conifer stands.

In the case of each of the three pairs, there was also a significant ($p < 0.05$) positive rank correlation between the two sites' habitat compositions, supporting the result from the cluster analysis. No other pairs of sites were thus found to be significantly correlated.

4.5.2 Use of faecal pellet counts to verify visual transect data

All of the plots of pellet group persistence against time showed a similar form (Fig. 4.4). After an initial period of little change, there was a period over which the pellet groups disappeared at a fairly constant rate: the durations of both these periods varied between habitat types but, as noted, by 35 days all pellet groups had disappeared. In most habitat groups faecal pellet groups were judged to be half-gone (i.e. had an LD_{50} value) between 22.5 and 28 days of planting; in prethicket habitat types (which typically had a *Molinia* ground layer) the time was only 10.75 days. It can be seen that with reference to the formula given in Section 4.3.2 and the calculation of its term $\sum p_i$:

- for the initial period of persistence (D1 days) $p_i = 1$
- as the period over which the pellets disappeared is well described by a linear function, the mean value of p_i for the period (D2 minus D1 days) is 0.5
- clearly, for the period above D2, $p_i = 0$.

i.e. $\sum p_i = D1 + 0.5 * (D2 - D1)$

which therefore gives the number of faecal pellet groups deposited per day, as a measure of habitat occupance.

A possible explanation for this pattern may be suggested. The initial period reflects the period when the faecal pellets behave as a group, in close contact and associated with a degree of mucus covering. In time, the pellets lose the mucus and dry out, becoming disassociated and thereafter behaving as individual pellets. As such, they are more easily 'lost' in the vegetation or decomposed.

The number of faecal pellet groups recorded at each site, by habitat type for each month from August 1989 to January 1990, are presented below in Table 4.5. These data are based on an equal area (500 m^2) surveyed of each habitat type.

These counts of faecal pellet groups were then corrected for the availability of each habitat type at each site and for the life-expectancy using the correction factor, to give an estimate of the number of faecal pellet groups estimated to have been deposited each month in each habitat type for each site: this is termed the 'adjusted count'.

The adjusted count of the number of faecal pellet groups deposited thus gave a measure of the usage of that habitat type by roe for the previous 30 days (i.e. since the previous survey) and was used in a Spearman rank correlation against the number of roe observed over the same period in the same habitat type at each site from the visual transects (for the two three-month blocks where data were available from both methods). The correlation results are shown in Table 4.4.

Fig. 4.4 *Disappearance of faecal pellet group samples (in 8 habitat groups defined in Table 4.1). Vertical axis: pellet groups remaining; horizontal axis: time in days since placement of pellet groups. Trend line between last visit when all pellet groups present and when none remained.*

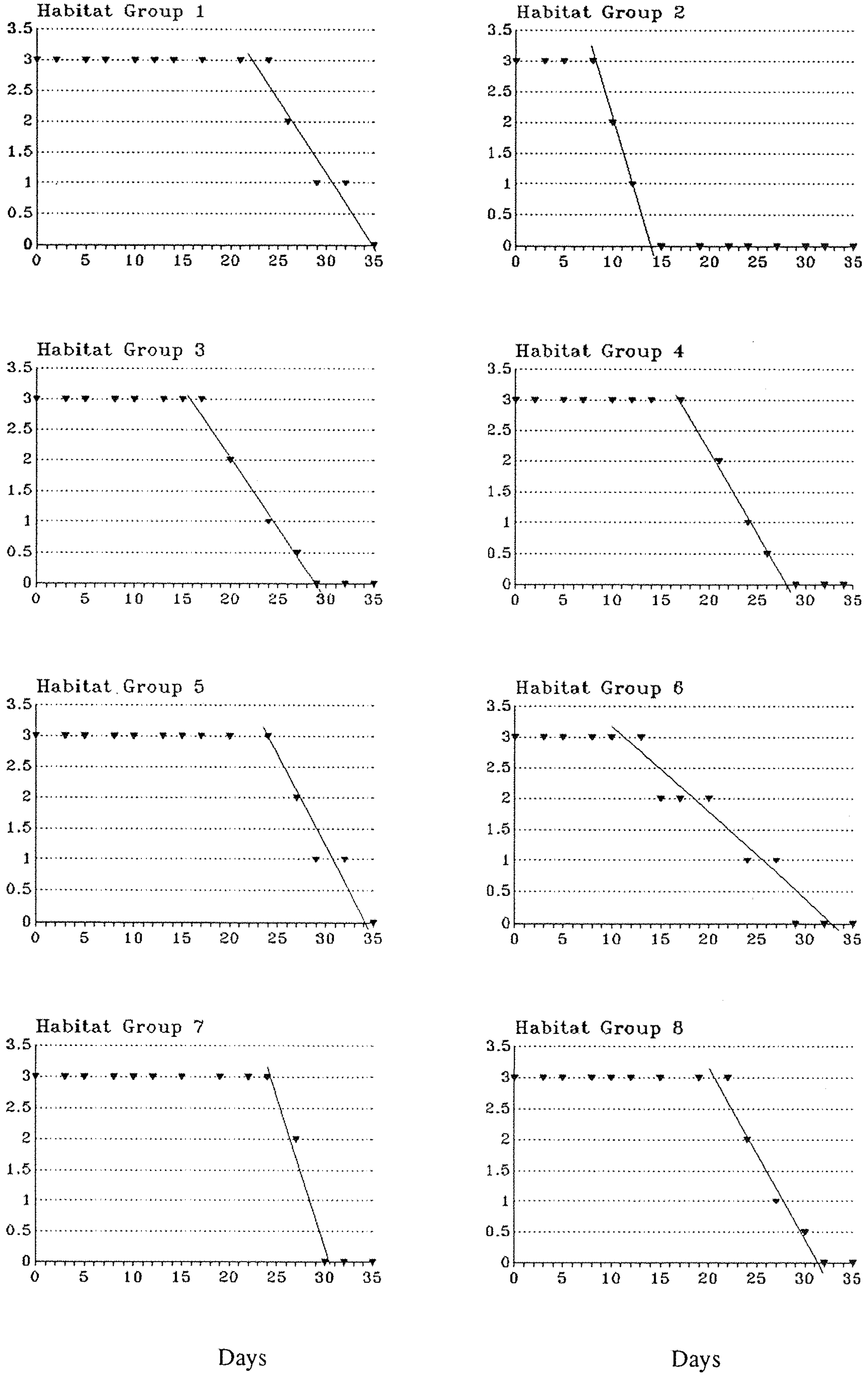


Table 4.4 *Coefficients of correlation between number of roe observed and adjusted number of faecal pellet groups, by site, in three-month blocks*

Site	Aug-Oct	Nov-Jan
Holmsley	0.768 **	0.504
King's Hat	0.780 **	0.747 **
Salisbury Trench	0.419	0.095
Shave Green	-0.073	0.894 **
Milkham	-	0.311
Knightwood	0.725 **	0.540 *

Notes: (i) * denotes $0.01 < p < 0.05$; ** denotes $p \leq 0.01$
(ii) insufficient data for a result for Milkham Aug-Oct.

There is clearly good overall agreement between the estimates of habitat use derived from the visual transects and from the adjusted faecal pellet group counts. Agreement of these two independent methods of assessing patterns of habitat use permits some confidence in the more detailed results presented below from direct observations.

4.5.3 Patterns of habitat use in the New Forest inclosures: all sites

Ecological consistency between the two levels of habitat classification was investigated by repeating the earlier correlation analyses (Chapter 3) of roe numbers against sites' habitat characteristics, but this time using habitat classes rather than habitat types. Two habitat classes were found to correlate significantly with roe numbers. Food-depleted conifer stands (habitat class III) correlated significantly negatively ($r = -0.6513$, $p < 0.05$) with roe numbers, in agreement with the negative correlation obtained for its major habitat type component, mature conifer stands with a bracken understorey (habitat type 11).[2] Food-bearing conifer stands (class IV) also correlated significantly positively with roe numbers

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[2] In the remainder of this chapter, both habitat types and habitat classes are referenced by use of abbreviated descriptions followed by the identity of the habitat category in square brackets; habitat types are indicated by Arabic numerals and habitat classes by Roman numerals. It is hoped that this will assist readability, and at the same time allow cross-reference back to tables where the habitat categories have been identified only numerically.

Table 4.5 *Number of faecal pellet groups found at six study sites over August 1989 - January 1990.*

(i) Holmsley

Habitat Type	Aug	Sep	Oct	Nov	Dec	Jan
2	10	5	5	0	4	0
5	4	2	0	0	0	0
7	2	0	0	0	0	2
10	2	1	0	0	0	0
11	0	0	0	0	0	0
12	2	1	1	1	0	3
13	2	0	0	1	0	0
14	0	0	0	0	2	1
16	0	0	0	0	0	1
19	0	2	0	0	0	0
20	0	0	0	0	0	0

(ii) King's Hat

Habitat Type	Aug	Sep	Oct	Nov	Dec	Jan
4	0	0	0	0	0	0
6	4	1	0	1	0	4
7	2	0	0	0	0	0
9	3	0	0	0	0	1
10	2	0	0	0	0	1
12	3	1	0	1	3	1
13	1	1	0	0	0	0
19	3	1	0	0	1	1
20	1	0	0	0	0	0

(iii) Salisbury Trench

Habitat Type	Aug	Sep	Oct	Nov	Dec	Jan
1	1	5	0	0	1	0
2	1	2	1	0	0	1
4	5	2	0	0	3	2
5	0	1	0	0	1	1
6	0	0	0	0	0	2
7	0	0	0	0	0	0
9	0	0	0	0	0	3
10	0	2	0	0	0	0
11	0	0	0	0	1	2
12	4	3	0	0	0	3
13	2	2	0	0	0	2
14	1	0	0	0	0	0
16	1	1	0	0	0	0
17	0	0	0	0	0	0
19	0	2	0	0	0	0
20	0	0	0	0	0	0

Table 4.5 *continued.*

(iv) Shave Green

Habitat Type	Aug	Sep	Oct	Nov	Dec	Jan
5	6	0	2	0	0	0
6	1	2	0	0	0	0
7	2	0	0	0	0	0
10	1	1	0	0	0	2
12	2	3	0	0	1	0
17	2	1	0	0	0	0
19	3	1	0	1	1	0
20	0	0	0	0	0	0

(v) Milkham

Habitat Type	Aug	Sep	Oct	Nov	Dec	Jan
1	0	0	0	0	0	1
3	0	0	0	0	0	0
4	0	0	0	0	0	0
7	0	0	0	0	1	1
9	0	0	0	0	0	0
10	0	0	0	0	0	0
11	0	0	0	0	0	0
12	0	0	0	0	0	0
17	0	0	0	0	0	1
18	0	0	0	0	0	0
20	0	0	0	0	0	0

(vi) Knightwood

Habitat Type	Aug	Sep	Oct	Nov	Dec	Jan
1	0	0	0	0	0	0
3	0	0	0	0	0	0
4	2	0	1	1	0	0
5	0	0	0	0	0	0
7	0	0	0	0	0	0
8	2	0	0	0	0	0
10	0	0	0	1	0	0
11	1	0	0	1	0	0
12	2	1	1	1	0	0
14	0	0	0	0	0	0
17	1	0	0	0	0	0
18	0	0	0	0	0	0
19	0	0	0	0	0	0
20	0	0	0	0	0	0

($r = 0.767$, $p < 0.01$), in agreement with the earlier correlation obtained for its largest constituent habitat type, food-bearing mature conifer woodlands (type 12). The third significant positive correlation found in the earlier analyses against roe numbers, food-bearing broadleaf woodlands, was not supported significantly in the present analysis. Overall, however, the results suggested a reasonable measure of consistency between the two habitat schemes.

As an initial step in evaluating habitat use, data for all study sites were pooled to examine the overall pattern of habitat use by roe in the New Forest inclosures, and to see if these patterns of habitat use differed between seasons and from the pattern of habitat availability. For these comparisons, the broadleaf woodland (habitat class V) was divided into food-depleted (class Va) and food-bearing areas (class Vb), based upon the original habitat type classification (Table 3.3): i.e. the food-depleted class comprised habitat types 14, 15, 17 and 18, and the food-bearing class comprised habitat types 16 and 19. (This division was not feasible for other site-level analyses as it would have made impossible comparisons of broadleaf woodland use between individual sites.) Levels of use and indices of selection for the year, and for each season are presented in Table 4.6.

In the New Forest inclosures, roe make high use of the three most extensive habitat classes, mature conifer stands (food-depleted and food-bearing), and food-bearing broadleaf areas. Each of these accounts for close to a third of the total observations of roe. Moderate use is made of prethicket and establishment areas that offer forage, and of food-depleted broadleaf woods, but little use is made of rides or food-depleted open / prethicket.

It is clear from the different extent to which the habitat classes are present, however, that roe are expressing a net degree of selection for certain habitats. All food-bearing habitat classes are selected, most notably the establishment / prethicket areas. The food-depleted broadleaf woodlands are also selected, but to a lesser extent than the food-bearing equivalent. In contrast, food-depleted conifer woodland types are all avoided, and rides are neither selected nor avoided. Patterns of annual use and habitat availability differed very significantly ($\chi^2 = 142.4$, $p < 0.001$).

Table 4.6 *Annual and seasonal levels of enclosed woodland habitat class usage and selection by roe deer (all sites' data combined)*

Habitat Class:	I	II	III	IV	V*a*	V*b*	VI
AREA (Ha.):	34	40	270	115	33	100	32
LEVELS OF USE (Number of observations):							
Winter	7	19	38	44	4	54	1
Spring	2	23	39	57	11	37	5
Summer	5	23	32	37	8	29	18
Autumn	0	5	23	12	18	22	5
All year	14	70	132	150	41	142	29
SELECTION (Goodall's coefficient):							
Winter	-0.14	0.28	-0.31	0.18	-0.38	0.34	-0.8
Spring	-0.65	0.35	-0.32	0.28	0.09	0.14	-0.28
Summer	-0.25	0.41	-0.35	0.14	0.0	0.08	0.40
Autumn	-1	-0.04	-0.23	-0.13	0.60	0.23	0.07
All year	-0.39	0.31	-0.31	0.17	0.15	0.20	0.0

The seasonal picture of use and selection shows a number of interesting features. Food-depleted conifer stands [I and III] are avoided in every season, while food-bearing conifer areas [II and IV] are selected from winter through to summer (and appear to be slightly avoided in autumn). Rides are selected strongly in summer, slightly in autumn and avoided at other times, but it is the broadleaf woodlands which dominate overall use and which are selected very strongly in autumn, whether food-depleted [Va] or food-bearing [Vb].

Patterns of use and availability in all sites when correlated by rank (Spearman's rank test) showed positive correlations for winter, spring and summer ($p < 0.05$), but not for autumn ($p = 0.15$). Significant differences were found, however in all numerical analyses of seasonal patterns of use against habitat availability, and when comparing patterns of use between seasons (χ^2 test: $p < 0.001$ in all cases, except spring use compared with winter and summer use, $p < 0.05$).

Together, these analyses suggest that underlying pattern of habitat use is (as would be expected) related to habitat availability (Spearman's rank results), but that roe are also showing significant selection of habitat (chi-square result), i.e. both contribute to the observed patterns of habitat use.

4.5.4 Use of habitats in relation to availability: individual sites

The results of chi-square tests comparing the use of habitat classes in relation to the use expected by availability are presented below in Table 4.7.

On the basis of the analyses over the year as a whole, all sites show that habitat classes overall are not used in simple proportion to their availability ($p < 0.01$). All sites except King's Hat also show significant differences between patterns of habitat use and availability ($p < 0.05$) for at least two seasons, although only Salisbury Trench shows a significant difference between pattern of use and availability in all seasons. There is no clear predominance of any one season over another across all sites.

Table 4.7 *Comparisons of patterns of habitat use and availability; entries show probabilities to 3 decimal places of patterns differing by chance*

Site	Winter	Spring	Summer	Autumn	Year
Holmsley	0.050 *	0.068	0.000 **	0.091	0.000 **
King's Hat	0.005 **	0.061	0.061		0.002 **
Salisbury Trench	0.000 **	0.000 **	0.037 *	0.000 **	0.000 **
Shave Green	0.087	0.010 *	0.000 **	0.400	0.000 **
Milkham	0.235	0.029 *		0.042 *	0.000 **
Knightwood	0.030 *	0.586	0.078	0.048 *	0.000 **

Notes: ** highlights $0.01 < p < 0.05$; * highlights $p < 0.05$; blank denotes too few data for calculation

(As noted earlier, some tests could not be done because of small sample sizes, and the lack of significant differences overall would appear to due to this in some measure. At all sites few observations were made over late August through early October, and the most likely explanations for this are that the roe were resting after the period of the rut, and, perhaps,

Table 4.8 *Habitat use by roe deer in the New Forest inclosures, showing number of observations by season and habitat type for each site ('.' indicates zero).*

(i) Holmsley

Habitat Type	Winter	Spring	Summer	Autumn
2	5	17	16	1
5	.	3	7	1
7	5	.	2	2
10	6	18	6	3
11	2	.	.	2
12	13	23	9	5
13	1	.	.	.
14	.	2	2	1
16	.	.	.	.
19	.	2	4	.
20	.	.	1	4

(ii) King's Hat

Habitat Type	Winter	Spring	Summer	Autumn
4	1	.	1	.
6	2	.	.	.
7	1	2	3	.
9	.	.	.	.
10	.	.	.	.
12	17	24	12	2
13	.	.	.	.
19	2	8	3	1
20	.	4	5	.

(iii) Salisbury Trench

Habitat Type	Winter	Spring	Summer	Autumn
1	2	.	.	.
2	.	1	1	2
4	7	4	2	.
5	.	.	1	.
6	1	.	.	.
7	.	.	.	.
9	1	.	2	1
10	.	.	4	.
11	.	.	.	.
12	3	6	10	.
14	.	.	.	.
16	15	12	5	8
17	.	5	2	4
19	17	2	5	.
20	.	.	.	.

Table 4.8 *continued.*

(iv) Shave Green

Habitat Type	Winter	Spring	Summer	Autumn
5	1	1	.	.
6	.	.	.	2
7	2	.	.	.
10	4	.	.	4
12	3	2	2	1
17	2	2	2	.
19	20	13	12	13
20	.	1	11	.

(v) Milkham

Habitat Type	Winter	Spring	Summer	Autumn
1	3	2	.	.
3	1	.	1	.
4	2	5	.	.
7	5	1	.	1
9	2	.	.	.
10	.	.	.	2
11	7	6	1	6
12	.	2	.	.
17	.	.	.	6
18	2	.	.	4
20	.	.	.	1

(vi) Knightwood

Habitat Type	Winter	Spring	Summer	Autumn
1	.	.	1	.
3	1	.	3	.
4	4	6	3	2
5	.	.	.	.
7	.	1	.	.
8	.	.	.	.
10	2	4	6	.
11	1	4	2	2
12	2	.	2	1
14	.	.	.	.
17	.	2	2	3
18	.	.	.	.
19	.	.	.	.
20	1	.	1	.

that feeding on acorns meant they spent less time feeding / moving, and more ruminating.)

4.5.5 Seasonal patterns of habitat use within sites

Table 4.8 (above) shows the numbers of roe observed by habitat type in each season for each of the separate study sites; from these data and the correspondence between habitat types and classes (Table 4.2), the patterns of habitat use (percentage use of each habitat class) can be derived (Table 4.9).

Table 4.9 *Patterns of percentage usage of habitat classes by roe deer in the New Forest inclosures, by site and season*

Habitat Class:		I	II	III	IV	V	VI
HM	Winter	-	16	44	41	0	0
	Spring	-	13	38	42	7	0
	Summer	-	34	32	19	13	12
	Autumn	-	5	42	26	5	21
KH	Winter	-	4	4	83	9	0
	Spring	-	0	5	63	21	11
	Summer	-	4	13	50	13	21
	Autumn	-	0	0	67	33	0
SA	Winter	4	15	2	11	68	0
	Spring	0	17	0	20	63	0
	Summer	0	9	16	38	38	0
	Autumn	0	13	0	7	80	0
SG	Winter	-	-	22	9	69	0
	Spring	-	-	5	11	79	5
	Summer	-	-	0	7	52	41
	Autumn	-	-	20	15	65	0
ML	Winter	18	9	55	9	9	0
	Spring	13	33	40	13	0	0
	Summer	50	0	50	0	0	0
	Autumn	0	0	45	0	50	5
KN	Winter	9	36	27	18	0	9
	Spring	0	35	53	0	12	0
	Summer	20	15	40	10	10	5
	Autumn	0	25	25	13	38	0

In turn, these data and the availabilities of each habitat class (Table 4.3) permit Goodall's selection indices for seasonal selection of habitat classes to be calculated; values are given in Table 4.10.

Table 4.10 *Goodall's indices of selection for habitat classes by roe deer in the New Forest inclosures, by site and season*

Habitat Class		I	II	III	IV	V	VI
HM	Winter	-	0.54	-0.02	0.18	-1	-1
	Spring	-	0.46	-0.09	0.19	-0.37	-1
	Summer	-	0.76	-0.18	-0.19	-0.10	-0.42
	Autumn	-	0.06	-0.05	-0.03	-0.50	0.60
KH	Winter	-	-0.42	-0.63	0.29	-0.35	-1
	Spring	-	-1	-0.57	0.16	0.07	0.28
	Summer	-	-0.41	-0.20	0.05	-0.19	0.54
	Autumn	-	-1	-1	0.18	0.29	-1
SA	Winter	0.69	0.05	-0.86	-0.31	0.36	-1
	Spring	-1	0.10	-1	-0.01	0.33	-1
	Summer	-1	-0.18	-0.31	0.29	0.09	-1
	Autumn	-1	0.00	-1	-0.51	0.43	-1
SG	Winter	-	-	-0.14	-0.38	0.20	-1
	Spring	-	-	-0.69	-0.33	0.27	0.09
	Summer	-	-	-1	-0.48	0.07	0.81
	Autumn	-	-	0.18	-0.17	0.17	-1
ML	Winter	0.17	0.39	-0.10	0.49	0.05	-1
	Spring	0.01	0.79	-0.25	0.62	-1	-1
	Summer	0.59	-1	0.14	-1	-1	-1
	Autumn	-1	-1	-0.19	-1	0.72	-0.01
KN	Winter	-0.27	0.73	-0.37	0.52	-1	0.23
	Spring	-1	0.72	-0.06	-1	0.24	-1
	Summer	0.11	0.44	-0.19	0.27	0.16	-0.07
	Autumn	-1	0.62	-0.41	0.36	0.67	-1

The way in which habitat use varies with season between the 6 different study sites is clearly diverse. There were significant differences between patterns of use at Holmsley in all but one seasonal comparisons, but no significant differences were found for either King's Hat or Knightwood (see results of the Fisher exact test comparisons of patterns of habitat usage within sites, Table 4.11). Salisbury Trench and Shave Green were found to have precisely the same pattern of difference between seasonal usage, a finding in line with the similarity in their habitat structure (Section 4.5.2 above). This finding was also seen (though not quite as closely) between Milkham and Knightwood, the two 'poor' sites. While a degree of habitat similarity was also found earlier between Holmsley and King's Hat, this was not so well exhibited in the pattern of significant differences of seasonal habitat use by roe.

Table 4.11 *Seasonal comparisons of patterns of habitat use by roe within sites; entries show probabilities to 3 decimal places of patterns differing by chance.*

Site	Season:	Winter	Spring	Summer
HM	Spring	0.552	-	-
	Summer	0.017 *	0.015 *	-
	Autumn	0.029 *	0.018 *	0.014 *
KH	Spring	0.158	-	-
	Summer	0.067	0.328	-
	Autumn	0.488	1	0.844
SA	Spring	0.662	-	-
	Summer	0.002 **	0.026 *	-
	Autumn	1	0.631	0.016 *
SG	Spring	0.289	-	-
	Summer	0.000 **	0.018 *	-
	Autumn	0.828	0.506	0.000 **
ML	Spring	0.339	-	-
	Summer	0.717	0.743	-
	Autumn	0.003 **	0.000 **	0.177
KN	Spring	0.103	-	-
	Summer	0.630	0.159	-
	Autumn	0.366	0.170	0.458

Note: ** highlights $p < 0.01$; * highlights $0.01 < p < 0.05$.

Holmsley

More significant differences between seasonal patterns of use emerged here than at other sites. The patterns of use over winter and spring were not significantly different, both seasons being typified by high use of both food-depleted and food-bearing conifer stands, [III] and [IV] respectively; of these, however, the food-bearing conifer stands [IV] were moderately or strongly selected by the roe, whereas food-depleted conifer stands [III] were more available but generally slightly avoided. The summer habitat usage showed a dramatic increase in the use of food-bearing establishment / prethicket [II], which was very strongly selected; in contrast, the use of food-bearing conifer stands [IV] fell. Food-bearing establishment / prethicket [II] was selected moderately in winter and strongly in spring. Broadleaf woodland [V] was avoided to differing extent all year, and roe used rides [VI] only in the autumn.

At Holmsley, habitat classes and habitat types are simply related. Two of the selected habitat classes each contain only a single habitat type: food-bearing establishment / prethicket [II] contains only food-bearing open ground [2], and food-bearing conifer stands [IV] have only food-bearing mature conifer [12]. Further, some 80% of the broadleaf woodland [V] consists of food-bearing mature broadleaf [19]; some food-depleted immature broadleaf [14] and food-bearing immature broadleaf [16] are also found at the site, but no use was observed of the latter of these two. Food-depleted conifer stands [III] comprise a mix of five different habitat types: none was selected over the year as a whole more strongly than 'neutral', although food-depleted pole-stage conifer [7] was selected moderately in both spring and autumn.

King's Hat

At this site no significant differences were found between any seasonal patterns of habitat usage. Overall, the most abundant habitat class, food-bearing conifer stands [IV], was also the one subject to the highest usage and to a degree of positive selection in all seasons. In contrast to the finding at Holmsley, food-bearing establishment / prethicket [II] appeared to be consistently avoided at this site at all times: this result was surprising, but may be the result of the particular difficulty of observing roe in this habitat class at King's Hat (discussed later in Section 4.6.1). Food-depleted conifer stands [III] were, as at Holmsley, consistently avoided all year, but at King's Hat even more strongly. The use and selection of rides [VI] varied greatly, from their being totally avoided in winter and autumn, to being strongly selected in summer; this agrees with the use of rides by roe at Shave Green but at no other site.

As at Holmsley, food-depleted establishment / prethicket [I] is not present at this site. Food-bearing establishment / prethicket [II] consists only of food-bearing prethicket [4] (in contrast with Holmsley, where it is food-bearing open ground [2]), and food-bearing conifer stands [IV] at King's Hat are largely - about 65% - composed of food-bearing mature conifer [12], which was the habitat type within the class where most use (over 95%) occurred. Broadleaf woodland [V] is entirely made up of food-bearing mature broadleaf [19]. Food-depleted conifer stands [III] are almost entirely (some 85%) pole-stage [7], in which habitat type all the use for that habitat class occurred.

Salisbury Trench

Patterns of use when compared showed that summer usage differed significantly from all other seasons, but that other seasons did not differ from each other significantly. Food-depleted establishment / prethicket [I] was used only in winter, although its apparently strong selection is a reflection of its low availability (less than 1% of the site area) than high usage. Food-bearing establishment / prethicket [II] was used in all seasons in proportion to its availability. In summer, the season when usage did differ significantly from others, food-depleted conifer stands [III] were used to some extent (but still moderately avoided), and food-bearing conifer stands [IV] were selected slightly, in contrast to their being avoided at other times. In addition, broadleaf woodlands [V] were not selected strongly, though still used heavily, in distinction from greater use and selection in all other seasons. Rides [VI] were not seen to be used at any time.

Habitat class [I], food-depleted establishment / prethicket, equates at Salisbury Trench to food-depleted open ground [1]. Food-bearing establishment / prethicket [II], however, is made up of food-bearing open ground [2] and food-bearing prethicket [4] in about equal measure: of these two, the latter was used and selected more. Food-depleted conifer stands [III] comprise a mixture of 5 habitat types, but food-depleted mature conifer [10] dominates (about 60%), and use of the others was either limited (as with food-depleted thicket [5] and dense thicket [13]) or zero (for food-depleted pole-stage conifer [7] and food-depleted mature conifer with bracken [11]); even then, food-depleted mature conifer [10] was still strongly avoided for the year overall. Food-bearing conifer woodland [IV] is nearly 80% made up by food-bearing mature conifer [12], which was also the most heavily used component. Food-bearing immature broadleaf [16] and food-bearing mature broadleaf [19] make up some three-quarters of broadleaf woodlands [V]; the former of these two habitat types was the more consistently selected generally, although both food-depleted mature broadleaf [17] and food-bearing mature broadleaf [19] for the year as a whole still emerged as positively selected habitat types.

Shave Green

Neither food-depleted [I] nor food-bearing establishment / prethicket [II] is present at this site, yet the pattern of habitat use for other habitat classes as revealed by seasonal comparisons, was similar to that found at Salisbury Trench. Conifer stands, whether food-depleted [III] or food-bearing [IV] were used but avoided all year. By comparison broadleaf woodland [V] was, as at Salisbury Trench, heavily used and consistently subject to moderate selection in all seasons except summer, when it was used in proportion to its availability. Rides [VI] show great differences in usage across seasons, being unused in winter and autumn, but very strongly selected in summer, and slightly so in spring: almost all of the observations on rides were made at one area of particularly lush grass growth, and roe were seen clearly to be taking advantage of the grazing offered.

Food-bearing conifer stands [IV] at Shave Green are composed mainly of food-bearing mature conifer [12], which was used but actually somewhat avoided at this site (other components of this habitat class were selected positively in particular seasons). Food-depleted conifer stands [III] are again a mixture of habitat types, comprising food-depleted stands of thicket [5], pole-stage conifer [7] and mature conifer [10], but all components were little used and to some degree avoided. Broadleaf woodland [V] is almost entirely food-bearing mature broadleaf [19], although the small amount of food-depleted mature broadleaf [17] was appeared to be more strongly selected.

Milkham

Comparisons of patterns of habitat use between seasons showed most not to be significantly different; the exceptions were autumn against both winter and spring. Only two observations of roe were made during the summer, and little can be concluded for habitat use over that season. Much use was made all year of food-depleted conifer stands [III], although this habitat class had high availability and was still slightly avoided in all seasons. Food-bearing establishment / prethicket [II] was used and very strongly selected in spring, and moderately selected in winter, but appeared to be unused otherwise; this pattern also applied to the use and selection of food-bearing conifer stands [IV]. Broadleaf woodland [V] was used only in autumn and winter; in autumn it became the most heavily used habitat class and was very strongly selected. Use of rides [VI] was minimal, being observed only once (in autumn).

At Milkham, food-depleted establishment / prethicket [I] is made up of food-depleted open ground [1] and food-depleted prethicket [3] in about equal measure, with the former habitat type being by far the more heavily used. Food-bearing establishment / prethicket [II] is entirely food-bearing prethicket [4], and food-depleted conifer stands [III] are a mix of pole-stage conifer [7], mature conifer [10] and mature conifer with bracken [11], with the last making up some 65% of the total: all three were avoided for the year as a whole. Food-bearing conifer stands [IV] are present at Milkham only to a small extent, of which most is food-bearing pole-stage conifer [9]. Broadleaf woodland [V] is made up of food-depleted mature broadleaf [17] and food-depleted mature broadleaf with bracken [18] in equal (but small) amounts.

Knightwood

No significant differences between seasonal patterns of habitat use were found at this site, which in its habitat composition is very similar to Milkham. Overall, as at Milkham, food-depleted conifer stands [III] were used throughout the year but were slightly or moderately avoided in relation to their high availability. In contrast, food-bearing establishment / prethicket [II] was not only highly used but also strongly / moderately selected over the whole year. Food-bearing conifer stands [IV] were also selected in all seasons except for spring (when they were unused), and broadleaf woodland [V], again as at Milkham, was particularly heavily used in the autumn. Only two observations were made of roe using rides [VI], while food-depleted establishment / prethicket [I] was seen to be used to any extent only during the summer.

Although food-depleted establishment / prethicket [I] here, as at Milkham, is made up of food-depleted open ground [1] and food-depleted prethicket [3], at Knightwood it was the latter which was used and selected more. Food-bearing establishment / prethicket [II] at this site consists only of food-bearing prethicket [4], while all food-bearing conifer stands [IV] were mature [12]. Of the five components of food-depleted conifer stands [III], food-depleted mature conifer [10] was the most heavily used, but food-depleted pole-stage conifer [7] the most strongly selected for the year; food-depleted thicket [5] and food-depleted pole-stage conifer with bracken [8] were unused, and food-depleted mature conifer with bracken [11] was slightly avoided overall. Finally, broadleaf woodland [V] is largely (73%) made up of food-depleted mature broadleaf [17], its only component where roe were observed.

4.5.6 Bracken as a factor in habitat selection

Examination of the selection coefficients calculated for individual habitat types (Table 4.12) permits a further general analysis, the comparison for all sites between two types of food-depleted habitats at the same site, those with and without bracken. This may then be examined in relation to the earlier significant negative correlations obtained (Chapter 3) between roe density and bracken. From the sites' composition (Fig. 4.1) it can be seen that 4 sites contain similar food-depleted woodland categories without and with bracken: Holmsley and Salisbury Trench contain mature conifer [10 and 11], while Milkham and Knightwood contain both mature conifer [10 and 11] and broadleaf woodland [17 and 18]. Using the sign test to compare the selection indices for all these habitat types across seasons reveals no significant difference in selection ($p = 0.12$), failing to substantiate the earlier result.

Table 4.12 *Coefficients of habitat selection by roe deer, for pairs of food-depleted woodland habitat types without and with bracken at same site.*

Site		Winter	Spring	Summer	Autumn
HM	*Food-depleted mature conifer*				
	Without	-0.06	0.22	-0.25	-0.14
	With	-0.08	-1.00	-1.00	0.17
SA	*Food-depleted mature conifer*				
	Without	-1.00	-1.00	-0.17	-1.00
	With	-1.00	-1.00	-1.00	-1.00
ML	*Food-depleted mature conifer*				
	Without	-1.00	-1.00	-1.00	-0.01
	With	-0.16	-0.05	0.07	-0.18
	Food-depleted mature broadleaf				
	Without	-1.00	-1.00	-1.00	0.73
	With	0.44	-1.00	-1.00	0.70
KN	*Food-depleted mature conifer*				
	Without	0.03	0.16	0.28	-1.00
	With	-0.39	0.02	-0.38	0.06
	Food-depleted mature broadleaf				
	Without	-1.00	0.38	0.30	0.75
	With	-1.00	-1.00	-1.00	-1.00

4.5.7 Differences in patterns of habitat use between sites

The results presented in this section are also based upon patterns of seasonal habitat use and selection previously given (Tables 4.8, 4.9 and 4.10). The results of the comparisons of these patterns of use between sites by season, based upon the Fisher exact test / chi-square test, are presented in Table 4.13 below.

From Table 4.13 it can be seen that most comparisons of patterns of habitat use between sites were found to be significantly different in any given season. However, the two poor sites, Milkham and Knightwood, showed no significant differences for any season; these sites were also those with the most similar habitat structure (Section 4.5.1). A similar result was also found (to a lesser extent) for another pair of similar sites, Salisbury Trench

Table 4.13 *Comparisons of seasonal patterns of habitat use by roe between sites; entries show probabilities to 3 decimal places of patterns differing by chance.*

Season	Site:	HM	KH	SA	SG	ML
WINTER	KH	0.000 **	-			
	SA	0.000 **	0.000 **	-		
	SG	0.000 **	0.000 **	0.043 *	-	
	ML	0.036 *	0.000 **	0.000 **	0.000 **	-
	KN	0.118	0.000 **	0.000 **	0.003 **	0.214
SPRING	KH	0.000 **	-			
	SA	0.000 **	0.000 **	-		
	SG	0.000 **	0.000 **	0.244	-	
	ML	0.079	0.000 **	0.000 **	0.000 **	-
	KN	0.002 **	0.000 **	0.000 **	0.000 **	0.228
SUMMER	KH	0.000 **	-			
	SA	0.003 **	0.019 *	-		
	SG	0.000 **	0.000 **	0.000 **	-	
	ML	1.000	0.320	0.021 *	0.036 *	-
	KN	0.516	0.012 *	0.001 **	0.000 **	1.000
AUTUMN	KH	0.200	-			
	SA	0.000 **	0.076	-		
	SG	0.000 **	0.174	0.176	-	
	ML	0.001 **	0.012 *	0.002 **	0.069	-
	KN	0.079	0.503	0.069	0.810	0.077

Note: ** highlights $p < 0.01$; * highlights $0.01 < p < 0.05$.

and Shave Green, which showed no significant differences in spring and autumn. Against this, Holmsley was found to show no significant difference in the pattern of habitat use in three seasons with Knightwood and in two with Milkham. Most significant differences were found for winter and spring, and fewest for autumn: this may be due in part to the low number of observations at King's Hat in autumn and Milkham in summer.

Winter

More significant differences were found between sites for this season than for any other. Roe were seen in food-bearing establishment / prethicket [II] at all sites where it occurs, and this habitat class was selected at all sites except King's Hat. At Salisbury Trench, food-depleted establishment / prethicket [I] was selected far more strongly - but this reflects its very low availability rather than high usage - and this habitat class was used more at Milkham, where it has rather greater availability than food-bearing establishment / prethicket [II]. Food-depleted conifer stands [III] were used but avoided to varying degrees at all sites, from near 'neutral' avoidance at Holmsley to extreme avoidance at Salisbury Trench. The levels of usage also varied widely, and no consistent pattern of use between good and poor sites was apparent. Food-bearing conifer stands [IV] showed a far clearer picture: they were used little and avoided moderately at both Salisbury Trench and Shave Green, but were selected at other sites, most strongly at the poorer sites (Milkham and Knightwood). The usage at these poorer sites, however, still fell far short of the levels seen at both Holmsley and King's Hat. Broadleaf woodland [V], in contrast, was selected to any degree only at the two sites where food-bearing conifer stands [IV] were avoided, Salisbury Trench and Shave Green, and was used but little at other sites.

Spring

It was for this season that, overall, the clearest patterns of habitat selection were seen across sites. Food-bearing establishment / prethicket [II] was subject to extreme selection at both Knightwood and Milkham, and levels of use exceeded those at all other sites. Food-depleted conifer stands [III] were used to a greater extent at the poor sites, and to differing degree elsewhere, but, as in other seasons, they were avoided. Food-bearing conifer stands [IV] and broadleaf woodland [V] showed somewhat complementary patterns of use and selection across sites, suggesting they may be used as alternatives. Levels of usage were higher at Holmsley and King's Hat for food-bearing conifer stands [IV], but higher at Salisbury Trench and Shave Green for broadleaf woodland [V], very much in line with the availabilities at the sites. The availability of both food-bearing conifer stands [IV] and broadleaf woodland [V] is limited at both poor sites, and at neither does the usage of either approach that of whichever is the more highly used habitat class at the other sites.

Summer

The occurrence of food-depleted establishment / prethicket [I] is limited to three study sites, and so patterns of similarity and difference are difficult to infer. Food-bearing establishment / prethicket [II] was selected more strongly at Knightwood (and also very strongly at Holmsley), while food-depleted conifer stands [III] were avoided to a similar (slight) extent at all sites, the comparatively high use at the two poor sites being a reflection of its high availability. As in spring, the high levels of use of broadleaf woodland [V] at Salisbury Trench and Shave Green suggested not only the high availability of that habitat class, but also a degree of selection; at Knightwood too, broadleaf woodland [V] was selected slightly, though not at Milkham. Finally, the use of rides [VI] was found to differ widely between sites: they were selected strongly at King's Hat and Shave Green, but avoided at other sites.

Autumn

As in other seasons, food-bearing establishment / prethicket [II] was selected strongly at Knightwood, with levels of use higher than at any other site. This use was not seen at Milkham, where the roe used food-depleted conifer stands [III] and broadleaf woodland [V] more heavily. In autumn, it was broadleaf woodland [V] that provided the most revealing usage. High use of this habitat class was made at all sites except Holmsley, and most of all at Salisbury Trench and Shave Green, but the strongest selection by far was seen at the two poor sites, Milkham and Knightwood, where the levels of use reached those at Shave Green but not Salisbury Trench. Once again, roe at Milkham and Knightwood made use of food-depleted conifer stands [III]. Food-bearing conifer stands [IV] were also strongly selected at Knightwood.

4.5.8 Habitat use and selection by roe in New Forest inclosures: a summary

In this final section of the results, the findings from the analyses of patterns of habitat use and selection, both within and between sites and in relation to habitat availability, are summarised, and are also examined for evidence of roe practising compensatory selection of habitats. Complementing the previous sections, presentation of the overall patterns of usage and selection is here organised by habitat class.

Food-depleted establishment / prethicket [I]

This habitat class occurs at only three of the 6 sites where observations of roe were made, and at one, Salisbury Trench, makes up less than 1% of the available area. Only at the two 'poor' sites, Milkham and Knightwood, does it occur significantly. This, coupled with the inevitably few observations of roe at those sites, means that little pattern in its usage can be discerned. The habitat class is used to some extent, but does not appear to be selected more than weakly at the poorer sites, the single instance of apparently strong selection at Milkham in summer deriving from only one observation of the two obtained for that season.

Food-bearing establishment / prethicket [II]

This is found at all sites except Shave Green, but nowhere in high availability, the maximum being some 14% of site area at Salisbury Trench. Usage levels vary seasonally from always very low (at King's Hat) to consistently high (at Knightwood), with most use at the sites of lowest roe density in spring, continuing to some extent through to autumn.

The pattern of selection is very distinct. At both Holmsley and Knightwood, there was strong selection at almost all times of year. Selection was strongest at the 'poorer' sites, Milkham and Knightwood, the sign test showing that overall selection at these sites was significantly greater ($p < 0.05$) for the year than at the other sites. The high levels of usage at Milkham and Knightwood suggest that roe at those sites may be trying to make maximum use of the habitat through compensatory selection; neither site has high availability of any alternative food-bearing habitat class. Only at King's Hat was this picture contradicted, as roe appeared to show some avoidance of this habitat class.

At most sites, this habitat class is made up largely of food-bearing prethicket [4]; at Holmsley, in contrast, it is entirely food-bearing open ground [2], which suggests that both its constituent habitat types may be of value to roe. It is also noteworthy that at Salisbury Trench, where it comprises both in approximately equal measure, it is food-bearing prethicket [4] that appears to be the more strongly selected of the two.

Food-depleted conifer stands [III]

This habitat occurs with generally high availability at all sites, from a minimum of 19% (King's Hat) to 67% (Milkham). Its higher availability is a characteristic of sites with low roe density (Table 4.3). Use of this habitat class is generally high throughout the year, particularly at the 'poorer' sites (Milkham and Knightwood) but also at Holmsley, the site with the highest roe population.

The pattern shown by the selection indices is unique: this habitat class was avoided by roe in relation to its availability at all sites in all seasons, an avoidance varying in degree from extreme to about neutral. While no clear seasonal pattern is evident, the sign test shows that roe at the two low density sites avoided the habitat class less strongly for the year taken overall than did roe elsewhere ($p = 0.01$), suggesting that at those sites, roe have to make more use of such food-depleted habitats. Neither food-bearing conifer [IV] nor broadleaf [V] is available in large quantity at the 'poorer' sites. There is no evidence of significant differences in selection between the habitat types within this habitat class (sign test, $p > 0.05$), nor in the relative amounts of resource species in food-depleted mature conifer stands with and without bracken (sign test, $p > 0.05$).

Food-bearing conifer stands [IV]

Comparison of the usage of this habitat class with the previous one provides a direct contrast of a food-bearing against a food-depleted woodland class, in this case both containing thicket, pole and mature stage conifer woodland stands. In overall availability, food-bearing conifer stands [IV] are less common than the previous habitat class [III], varying from 3% and 6% of site area at the two 'poorer' sites to a maximum of 45% at King's Hat. They are used at all sites and in almost all seasons, with a slight tendency towards higher winter usage.

The pattern of selection is very different from that for food-depleted conifer stands [III]. The clearest overall difference was seen between the two sites bearing most broadleaf woodland (Salisbury Trench and Shave Green) and the others; at these two sites, this habitat class was avoided in winter, when it was selected at other sites. In the same season the greater selection displayed at the two 'poor' sites compared to the other sites was significant (sign test, $p < 0.01$). However, the levels of usage at Milkham and Knightwood did not reach the levels at Holmsley and King's Hat, presumably because of the very low availability of this habitat class.

Although mainly composed of food-bearing mature conifer [12], it is unclear whether there was any preference between this and food-bearing pole-stage conifer [9] overall ($p = 0.07$, perhaps suggesting a trend towards the stronger selection of more mature conifer stands). As may be expected, a within-site comparison of the relative amounts of resource species (excluding grasses) in the mature phase [12], compared to the thicket and pole-stage stands, [6] and [9], shows that there is a significant difference in their resource levels, with the mature stands [12] the richer (sign test, $p < 0.05$).

Broadleaf woodland [V]

As with food-bearing conifer stands [IV], Milkham and Knightwood have the lowest availabilities of broadleaf woodland (approximately 8% of the inclosed area at each). Usage is highest at Salisbury Trench and Shave Green, where proportional availability is also much higher than elsewhere (32% and 46% respectively), and is also very high at the 'poorer' sites in the autumn, when it approaches similar levels to those at the 'better' sites.

Selection for this habitat class is consistently strong across sites, most clearly in autumn. In that season the selection at Milkham and Knightwood was significantly stronger than at other sites (sign test, $p < 0.01$). At both Salisbury Trench and Shave Green, this habitat class was positively selected in all seasons, and the high usage at these sites suggests a strong dependence on this habitat class. Usage at Holmsley and King's Hat was not so high as at other sites, roe appearing to select food-bearing conifer stands [IV] instead.

There is a revealing difference in the habitat type composition of this habitat class between sites. At most sites, the class is all or mostly food-bearing mature broadleaf [19] or food-bearing immature broadleaf [16], i.e. food-bearing habitat types. At the two low-density sites, Milkham and Knightwood, it is mostly food-depleted mature broadleaf [17] (including some with bracken [18] at Milkham). This 'food-depleted' habitat type composition at Milkham and Knightwood may explain why the habitat class is used at those sites heavily in autumn and only little at other times.

Rides [VI]

At all sites rides cover some 5% of the inclosure area, but it should be stressed that rides vary in composition (both within and between sites) from being comparatively rich grazing with some edge vegetation from the adjacent compartments to being bare gravel. There is little usage overall, and roe were found to avoid rides at all sites in most seasons. Only at King's Hat and Shave Green in summer was there strong selection for rides.

4.6 DISCUSSION

4.6.1 Methodological considerations

Estimating large herbivore population numbers in closed and semi-closed habitats is notoriously difficult. Even estimates by experienced rangers and foresters in familiar areas have been shown to be unreliable, often underestimating true numbers considerably (e.g. Andersen 1953, Loudon 1978, Staines and Ratcliffe 1987). Ratcliffe (1989) reported estimates red deer in commercial forests to be 'commonly' underestimated by a factor of 4, and sometimes more (in one instance by a factor of 17). For studies of comparative habitat use, absolute population numbers are not required, but reliable measures of occupance of the different habitat types are essential. While the original plan in the present study had been to utilise two methods for independent assessments of habitat and site use, circumstances beyond my control (i.e. the severe damage to the study sites from the January 1990 storms) resulted in reliance on one method (visual transect observations) with the second (faecal pellet group counts) used only to substantiate the first.

All visual methods suffer from inherent potential bias from differential habitat visibility (Mitchell *et al.* 1977, Putman 1990). This bias may be reflected between different habitat types, between seasons for the same habitat type, or between different blocks of the same habitat type. In general, visibility through mature and pole-stage woodland habitats was broadly comparable, and the habitat types within the Forest inclosures most likely to be affected by restricted visibility (undersampled) were stands of prethicket and thicket. Rides, in contrast, were likely to be oversampled by their shape and unobstructed nature, but may also be undersampled as the habitat type most likely to suffer disturbance by visitors and Forestry Commission activities. Other habitat types were seasonally affected by growth of bracken or foliage on shrubs. In this study, an effort to compensate for restricted visibility was made by routing the transect through some of the denser / darker habitats, and making occasional incursions of approximately 10 - 20 m. into prethicket, thicket, shrub and bracken when surveying from adjacent rides: this permitted better vision into the areas and occasionally 'flushed' roe resting close to the habitat edge. In the case of thickets, routing the transect through the habitats often gave visibility comparable to that for more open types.

It is recognized, however that such methods may not fully compensate for visibility differences and some allowance has to be made during interpretation of the results, particularly in the case of prethicket habitats. At King's Hat, the large block of food-bearing prethicket was particularly impenetrable, and is likely to have been undersampled (roe were seen entering and leaving the block). At all other sites prethicket was more accessible. This difficulty may well have accounted for the apparent 'avoidance' of this habitat type by roe at the King's Hat site. While other workers have attempted to use compensatory factors derived from e.g. visibility boards (de Vos and Mosby 1971, Suring and Vohs 1979), this approach was not adopted in this study, as the use of a second method to assess usage (faecal assessment) would act as a cross-check, and sufficient allowance could be made during the interpretation. A further consideration was that, following correction of the numbers of deer actually seen, the numbers would then be in effect estimates of a sample, and not properly open to statistical analysis comparing patterns of habitat use.

As already stated, the results of the habitat usage studies based upon visual observation were corroborated by use of a second technique, faecal pellet group counting. The substantial degree of agreement obtained between the measures of habitat use from the two methods - notwithstanding that only six months' data for the faecal method were collected - gives grounds for confidence in the results. Other workers who have conducted parallel studies on deer populations using two or more methods (including faecal assessment) have come to similar conclusions, e.g. Dasmann and Taber (1955), Harris (1959), Edge and Marcum (1989), and Aulak and Babinska-Werka (1990).

Visual transects were conducted evenly over the available daylight hours, but this is still likely to give an incomplete picture of habitat use (e.g. Beyer and Haufler 1994). From personal night time and early morning observations, it was clear that some roe leave the enclosed woodlands to feed on (often better) vegetation on roadsides and in adjacent fields during the hours of darkness. The important question for the present study was whether nocturnal and diurnal patterns of habitat use within the enclosed woodlands were different.

Once again, however, the agreement found between patterns of habitat use from direct observation and the assessment of dung (which presumably accumulates over the entire diel period), suggests that the differences are not likely to be serious.

4.6.2 Interpretation of habitat use and selection by roe

This study has examined patterns of habitat use and selection within the enclosed woodlands of the New Forest, and has shown that roe select habitats within the New Forest inclosures largely on the basis of their levels of food availability.

In the present day Forest inclosures, most silvicultural stands are coniferous. The more mature stands (i.e. including thicket and pole stage) total some 62% of the area, of which over two-thirds is food-depleted according to the definition used here. Mature broadleaf woodland accounts for another 21% of the inclosures, and the remainder mostly comprises food-depleted prethicket, rides and food-bearing prethicket in near-equal amounts. Using aggregated data from all sites shows the annual pattern of habitat use to be in broad agreement with availability in rank order, but also shows strong habitat selection. Selection indices calculated for annual use across all sites show all food-bearing habitat classes to be consistently selected, while corresponding food-depleted coniferous areas are avoided. This result corroborates those from the correlation studies reported earlier (Chapter 3, Table 3.6), where all food-bearing woodland habitat types correlated more positively than the corresponding food-depleted woodland habitat type. In the case of food-depleted broadleaf woodland, heavy autumnal use results in its being a selected habitat (though not as strongly over the year as the food-bearing equivalent). The strongest selection is seen for the food-bearing prethicket woodlands, with proportional use twice their relative availability. Indeed, as the number of roe observed is, if anything, likely to have been underestimated through visibility bias, the actual levels of use and selection of these areas by roe may actually be even greater. Other food-bearing woodland areas have levels of use around 1.5 times that in proportion to their availability. Rides showed neither selection nor avoidance for the year.

Such a picture is repeated seasonally, with habitat usage conforming more closely to availability over the winter and spring, slightly less in summer, and least in autumn, when the nut-producing broadleaf areas are used particularly heavily. It also appears that selection for food-bearing prethicket is in all seasons stronger than selection for food-bearing mature conifer; while this could be due to either the additional value as cover of prethicket, or to differences in resource levels, the former is thought to be more likely as vegetation levels overall do not differ significantly between the two habitats (sign test, $p > 0.05$). Patterns of selection across all sites on a seasonal basis show a significant selection ($p < 0.05$) for food-bearing mature conifer woodlands in winter, food-bearing prethicket over winter and spring, and broadleaf woodlands in autumn. All food-depleted conifer stands were avoided in all seasons.

Such an overview using data combined for all sites gives essentially a qualitative picture of habitat use and selection, and may mask conflicting patterns at specific sites. Within most sites patterns of use change seasonally, and patterns of both use and selection also differ markedly between sites. Similar patterns of use and selection are found at sites with closer habitat composition. In the present day inclosures, food-bearing prethicket habitat is comparatively scant and sites of higher roe density are characterised by greater availability of resource in the more mature woodlands, whether coniferous or broadleaf. These food-bearing woodlands are subject to higher levels of use at 'better' sites throughout the year, whereas roe at 'poorer' sites are found more often in food-depleted areas. At all sites roe make high use of food-bearing areas of establishment or prethicket where they are available. While selection of habitat types is practised by roe at all sites, it is in the differential degree of selection of habitats shown by roe in poor compared to good sites that the effects of different habitat and resource availability on roe behaviour become most noticeable.

This differential selection is again evident both seasonally and between use and availability at 'better' sites; roe at poor sites try and make the best use of fewer habitat types offering forage throughout the year, and show greater seasonal changes in the intensity of selection of those habitats. The strongest degree of selection was seen at the poor sites for food-bearing prethicket in all seasons, but particularly over the winter and spring, when this habitat type accounted for between 55% and 73% of the total use of all food-bearing habitats. These habitats offer the best shelter as well as food, a consideration that may be important to the roe in the New Forest for minimising energy expenditure. Grace and Easterbee (1979) found that the rate of heat loss by Highland red deer in severe wind-exposed conditions could be as much as double that in shelter; while the New Forest has a far milder climate, the rather limited fat reserves of the roe (Holand and Staaland 1992) in combination with the marginal nature of the poorer quality sites may increase the need to avoid heat loss through habitat choice at such sites. It is also over winter that roe at the poorer sites appear to be not only heavily reliant upon food-bearing prethicket, but also show stronger selection of food-bearing mature conifer. In Chapter 2, we saw there was a significant negative correlation between mean daily temperature over November - February and roe numbers over time. Over summer, differences in selection between good and poor sites are less clear, but the autumnal patterns of selection once again show a significantly greater selection of broadleaf woodland by roe at poor sites.

By selecting more strongly those food-bearing habitats to which they have access, roe at poorer sites appear to be trying to compensate for the lower overall availability of food-bearing habitats. Habitat types selected in this way, as has been noted, include food-bearing prethicket [4] which is selected heavily for much of the year (but especially in winter and spring), food-bearing mature conifer [12] in winter, and mature broadleaf woodlands [16 and 19] over the autumn. Combined use of all food-bearing habitats (i.e. of all woodland types and growth stages) compared between sites shows that at poor sites roe fail to match levels of usage at the better sites for winter, spring and summer (sign test, $p < 0.05$). The data do not permit any one of these seasons to be singled out clearly as particularly deficient. In contrast, the high autumnal selection of broadleaf woodlands, including otherwise food-depleted types [17 and 18] as well as food-bearing ones [16 and 19] does appear to achieve a level of usage comparable to that at other sites (not significantly different, $p > 0.05$).

Implicit in this disparity in the levels of usage of good (food-bearing) habitats is that for much of the year roe at poorer sites also make more use of poor quality (food-depleted) habitat types. This is indeed found to be the case: the levels of both <u>usage</u> ($p < 0.05$) and <u>selection</u> ($p < 0.01$) of such habitats types (dominated by the food-depleted conifer stands [10 and 11], which occur in quantity at all sites) are significantly higher at poorer sites in all seasons. It is apparent, then, that roe at poorer sites are unable to compensate fully for the non-availability of food-bearing habitat types, despite attempting to, and are forced to make significantly more use of poorer quality, food-depleted areas.

Some workers have also argued that the edges or boundaries of habitats may be of disproportionate importance to animals, e.g. Leopold (1932), Julander and Jeffery (1964), Porter and Church (1987). No surveys were carried out in the present study specifically to investigate the use of inclosure edges; however, there was no association apparent from the earlier spatial correlation studies (Chapter 2). There is evidence to suggest that the response to boundaries is related to the strength of the distinction between the two adjacent habitats concerned (Kremsater and Bunnel 1992). Within the New Forest inclosures, the boundaries between adjacent woodland habitat types generally do not have any distinct features of their own, although the woodland edging with the open Forest or major rides may be somewhat more strongly characterised. Equally, it has been suggested the juxtaposition of habitat types may be of importance to roe, a food-bearing habitat close to cover being used in preference to one not so close (Prior 1968, Porter and Church 1987); unfortunately, this would be extremely difficult to quantify and evaluate, especially in the irregular mosaic of stands found within the New Forest inclosures, and the extent to which this juxtaposition is perceived by and influences the patterns of habitat use of roe remains open. However, these characteristics do not appear to differ between sites and nor are they likely to have changed over the period of the decline in the roe population, and it is considered unlikely they play a significant role in explaining the pronounced differences in present day patterns of habitat use.

5. DIETARY PATTERNS OF NEW FOREST ROE DEER

Chapter summary

Work related in previous chapters has suggested that in areas of low roe population in the New Forest enclosed woodlands are forced to make greater use of more food-depleted habitats. In this chapter, therefore, studies are described which have examined dietary intake of roe in the Forest, to see what the overall food intake is, how it changes over seasons, how it differs between better and poorer roe sites, and whether it has changed overall since reported earlier by Jackson (1980) for the period 1970-1973. The latter contrast allows, in effect, a comparison of the diet of the New Forest roe before and after the prolonged period of population decline.

Dietary investigations were based on faecal pellets sought at the 6 sites used for earlier studies of habitat use (Chapter 4), once a month over a 12 month period. Faecal samples were not found at all sites in all months, fewest being located at sites of lowest roe density.

Dietary composition was determined by the proportion of plant epidermal fragments in the faecal samples belonging to each of 12 categories: pines, other conifers, broadleaf trees/shrubs, holly, ivy, heathers, bilberry, graminoids, forbs, bramble, fern and mosses.

Diet of roe generally differed significantly between samples collected at each site between seasons, and between sites in each season. Overall New Forest roe at the present time rely heavily on conifer browse (mainly over winter and spring) and broadleaf material (summer through autumn), and take graminoids, forbs, heathers and fern in moderate amounts. In contrast, the diet of 1970-1973 comprised far more bramble and more forbs, suggesting there has been a drop in dietary quality over the period of the population decline. This change is well reflected by the differences between present day good and poor sites: roe at poorer sites appear to have a diet of lower nutritional quality than roe at better sites, with a higher intake of fibrous / cellulose material (heathers and graminoids) and lower intake of bramble and forbs.

These findings are consistent with the earlier differences noted in patterns of habitat use by roe in sites of high and low roe density, and, in conjunction with results presented in previous chapters, suggest the decline in the roe population of the New Forest to be the result of food-limitation.

5.1 INTRODUCTION

In recent years much has been learned about what determines diet selection in ungulates. Body size and the type of digestive system (ruminant or caecal digestion) have been shown to be major determinants of overall time-energy constraints (Hungate *et al.* 1959, Bell 1970), while mouth size enables or restricts the degree of selection of plant items (Jarman 1974, Illius and Gordon 1987, Gross *et al.* 1993). Within the ruminants, a range of feeding strategies is recognized, from selective feeding on high quality, 'concentrated' plant material rich in nutrients or energy (such as leaf-browse, seeds and fruit), to reliance on the bulk intake of cellulose-based (typically graminoid) and fibrous material of poorer nutritional quality (Hofmann 1985). The typical characteristics of the digestive system of a selective, concentrate-feeding ruminant include large salivary glands, a small rumino-reticular volume relative to body weight, and a comparatively short small intestine. While the roe deer has all of these features (Westerling 1975, Hofmann 1985), it is unique among cervids in also having a capacious and well-vascularised caeco-colon, giving it the potential for efficient digestion of cell-wall carbohydrates after their passage through stomach and small intestine (Drescher-Kaden 1976, Lackhoff 1983 [cited in Hofmann 1985]). Why the roe should have this dual capacity is not clear (Hofmann 1985).

That the roe is, in practice, very much a concentrate selector has been supported both by the composition of its ruminal microflora, which are amylolytic rather than cellulolytic (Prins and Geelen 1971), and by the many reported investigations of its diet and food preferences. These studies cover both the Continent (e.g. Bulgaria: Kolev 1966; Poland: Siuda *et al.* 1969, Szmidt 1975, Borowski and Kossak 1975, Drozdz 1979, Gebczynska 1980; Finland: Helle 1980; France: Maizeret 1988; Czechoslovakia: Holisova *et al.* 1982, 1984), and Britain (Cumming 1966, Henry 1978, Jackson 1980, Nakhasathien 1980, Hosey 1981, Diakite 1983, Hearney and Jennings 1983, Forde 1989). The actual detailed species composition of the diets reported by these studies varies greatly from study to study, reflecting the differences in vegetational composition and local plant availability across the range of the roe. What all of the studies show is that the roe is a highly opportunistic and adaptable feeder which, in every case, selects high quality, concentrate items (Hosey 1981). Indeed, several of these studies have also shown that roe are selective not only in the species eaten but choose parts of the plant and growth stages of most nutritional value (e.g. Holisova *et al.* 1982, 1984). Dietary choice in roe does not appear to be age-related

(Gebczynska 1980, Nakhasathien 1980), and neither is there evidence of dietary difference between the sexes, in contrast with other species of deer which show greater sexual dimorphism (e.g. red: Staines, Crisp and Parish 1982; fallow: Putman *et al.* 1993).

From 105 rumina of animals killed in the New Forest between November 1970 and March 1973, Jackson (1980) compiled a detailed dietary profile of the New Forest roe. He showed monthly changes in the consumption of food species, of which bramble and rose were by far the most important components throughout the year, comprising 20 - 45% of items recorded. Coniferous browse (mostly Scots pine) was used heavily between late autumn and spring, being replaced by broadleaf and shrub over summer. Graminoids and dwarf shrubs (heathers and bilberry) were both taken throughout the year, the latter especially in the spring. Herbs formed up to 30% of the diet over the summer months. Ivy formed an important food item over winter and spring, and new holly was taken during June. Fruit and nuts (particularly acorns) made up a significant part of the intake over autumn and winter, and a variety of other species were also ingested, including fungi (mainly over winter), ferns (mostly in May) and small amounts of bark and mosses.

The dietary profile described by Jackson (1980) provides an extremely useful picture against which to compare findings from this study detailing the present day diet of the New Forest roe, some 20 years on. The two studies essentially reveal the diet of the New Forest roe before and after the decline in the population. The underlying questions here are whether the roe in the present day New Forest show the same high quality of diet as did the roe reported by Jackson (1980), and whether there are discernable and consistent differences in dietary quality between areas of good and poor roe performance. In this chapter therefore, we ask:

- what is the overall pattern of diet of the present roe population in the New Forest: which species are taken and what is their relative importance?
- what seasonal differences are there in the diet of the roe?
- how does the diet compare with that reported by Jackson (1980)?
- do present day dietary patterns differ between 'good' and 'poor' roe sites, and can these patterns be related to differences in known food availabilities and to the observed patterns of habitat use of roe in those sites?

5.2 METHODS

In contrast to Jackson's (1980) study, which employed ruminal content analysis, dietary investigations in this study were based on faecal samples collected from the six study sites used for assessment of habitat use (Chapter 4). Use of rumina was not possible, as few roe are culled in the Forest at present, and none is taken from any area of low density.

At each of the six study sites samples of fresh pellets were collected each month and placed in bags labelled with site and date information. Ten pellets were collected from up to 5 separate pellet groups at each site, where this was possible; at some sites in some months, fewer than 5 pellet groups - sometimes none at all - were found. Faecal pellets for dietary analysis were collected from all the study sites for a period of one year. After collection, the pellets were dried gently in warmed air and stored for later analysis.

In order to identify plant fragments recovered within faecal samples, a reference collection was prepared of epidermal tissues using as many potential food items as possible from within the bounds of the New Forest; these species included all broadleaf and conifer trees, shrubs, graminoids and forbs, as well as ferns and bryophytes. Leaves and other shoot material were collected, air-dried and mechanically macerated before being boiled in an 0.1 N solution of potassium hydroxide for 30 minutes in a water bath. After cooling, the samples were washed with distilled water and teased apart or ground further (where necessary) in order to show the epidermal cell characteristics under a microscope. Permanent slides suitable for photography were prepared by drying samples spread on standard microscope slides on an air dryer, prior to fixing with xylene and mounting in DPX. The slides were then labelled and photographed under a microscope at x100, with at least two photographs of each slide taken to encompass the range of variation found in tissue morphology (Zyznar and Urness 1969). The printed photographs formed the standard reference collection, although the original slides were also retained for reference.

Faecal samples were prepared for dietary analysis by being soaked in water overnight, and then thoroughly macerated using a pestle and mortar. Samples were analyzed on the basis of site and month, and where more than one sample had been collected at a site in one month, an equal number of pellets from each sample were mixed (for poorer sites there were often only one or two samples found). The macerated mixture was then centrifuged, the suspension poured off, and the sample washed 2 or 3 times to remove fine (unidentifiable) particles; the centrifuging and washing were repeated. The sample was then agitated (for even mixing) and some 2 ml. of it spread evenly within a Petri dish, under the base of which a grid had been marked. Under a dissecting microscope at x100, the sample was then carefully scanned along the grid lines, and the first 100 identifiable epidermal fragments were matched against the reference collection and recorded.

Where material was sufficient three platings were carried out on each sample. To derive some measure of the accuracy of analysis of the plant composition for individual faecal pellet groups, and how representative that estimate was of the pellet group as a whole, a series of correlation analyses was undertaken on a large subsample of the data - 44 of the total of 52 samples analyzed - comparing the relative composition by rank of each dietary category recognised in the initial plating of any faecal pellet group with that recorded in subsequent platings from the same pellet group. A second series of correlation analyses were also carried out to compare results from the second and third platings, to see if greater accuracy and consistency had been gained.

Epidermal fragments were not recorded to species level in all cases, but were classified appropriately for evaluation against the vegetation surveys carried out at the study sites (Chapter 3), and for comparison with the results of Jackson (1980). Accordingly, 12 classes of vegetation were recognized (Table 5.1), and the observed fragments were recorded in these classes.

The percentage of recovered fragments too thick or opaque for the cell pattern to be visible for potential identification varied between samples, ranging between 5 - 15%. As identification was carried out to one of 12 defined food categories, rather than to species level in all cases (see below), it was possible to attribute almost all other fragments to a category; of those fragments, i.e. those which had a discernable cell pattern, under 2% (in total) could not be matched with any reference photograph or slide: as any one type of fragment made up a small portion of this (under 0.5% of the total), these were discounted.

Table 5.1 *Dietary categories used for identification of plant epidermal fragments in faecal samples*

Category	Plant species included
Pine	Pines
Ocon	Conifers excluding pines
Bdlf	Broadleaf trees / shrubs (excl. holly)
Holl	Holly
Ivy	Ivy
Heth	Heathers
Bilb	Bilberry
Gram	Graminoids
Forb	Forbs
Bram	Bramble
Fern	Ferns
Moss	Mosses

Plant species compositions of the faecal collections were compared between sites and months using G-tests (Sokal and Rohlf 1981).

5.3 RESULTS

As noted, samples of roe faecal pellets were not located at all sites in all months, the inevitable (and ironic) consequence of studying a rare animal. Those months for which faecal collections were made are shown by site in Table 5.2; fewest pellet groups were discovered at poor sites.

Of 44 faecal samples analyzed for consistency of identification, 11 of the correlations between initial and second runs were significantly positive at $p < 0.01$, and 23 others at $p < 0.05$; 10 samples did not correlate significantly. This suggests a degree of inconsistency during analysis of the same faecal samples on the two occasions as I was learning the technique. In contrast, from the 44 correlations between the second and third platings there were 38 positive correlations at $p < 0.01$ and 6 others at $p < 0.05$, i.e. all were positively correlated significantly, showing a far greater consistency. On the basis of these findings, only the results from the second and third platings were used for the subsequent analyses of dietary patterns, and were aggregated for this purpose. (For the other 8 samples of the total of 52, the material available did not permit re-examination, and only the data from the first run are used.)

Table 5.2 *Months and sites in which roe deer faecal pellet groups were located (shown as 'x')*

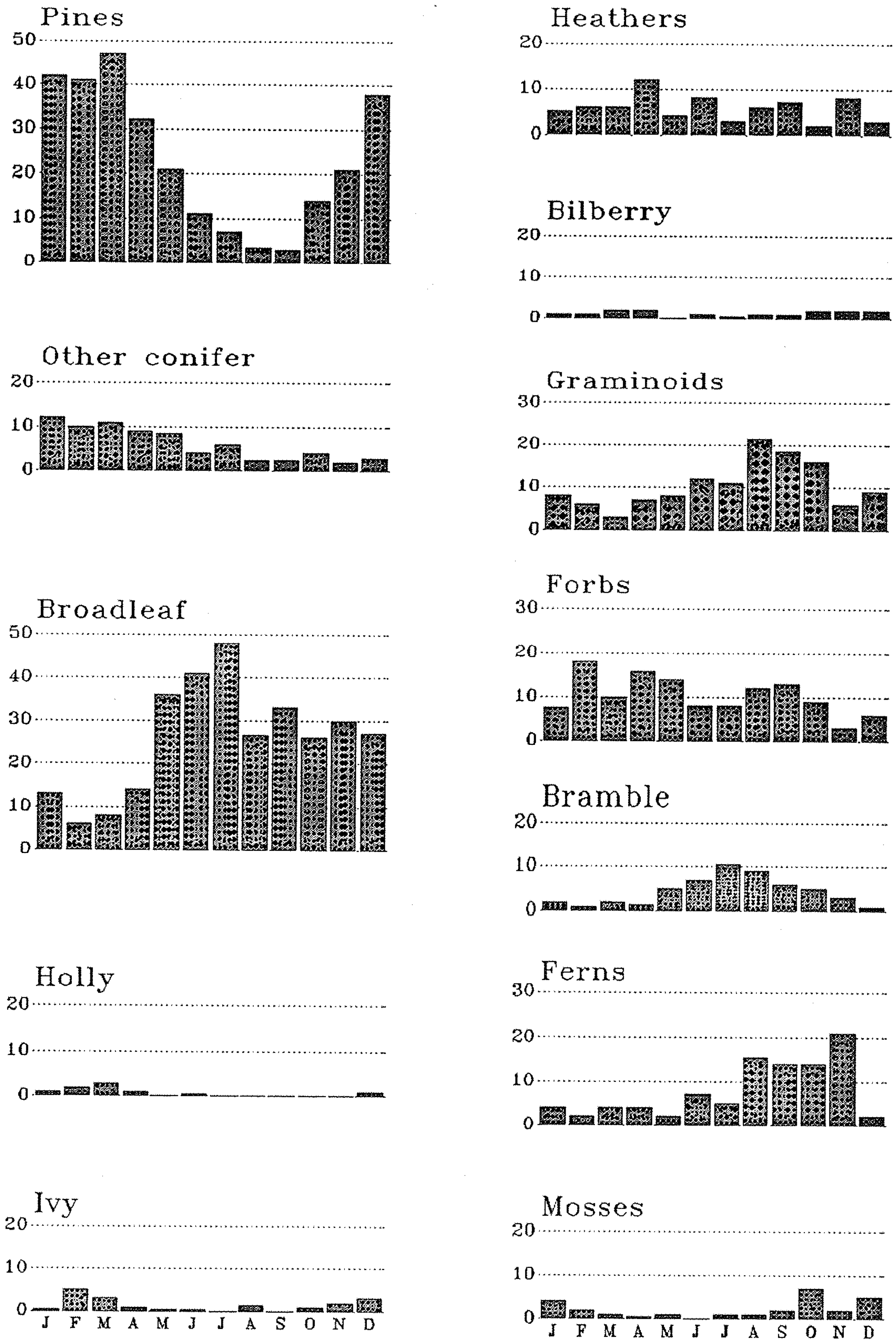
Site	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
HM	x	x	x	x	x	x	x	x	x	x	x	x
KH	x	x	x	x	x	x	.	x	x	.	x	x
SA	x	x	x	x	x	x	x	x	x	x	.	x
SG	x	x	.	.	x	.	x	x	x	.	x	x
ML	x	x	x	x	.	x	x	.	.	.	.	x
KN	.	x	.	.	.	.	.	x	.	x	x	.

Dietary composition

An impression of the monthly dietary composition for the New Forest roe deer population as a whole, calculated from the average percentage composition for all of the study sites at which faecal samples were found, is presented in Fig. 5.1. As all samples have been aggregated on a month by month basis, the overall dietary pattern is thus biased to a degree towards 'better' sites, as most samples were located in those areas.

The diet of roe in the New Forest at the present time, from Fig. 5.1, showed clear differences in both the amount of use made of different plant categories in the annual diet as a whole, and seasonal change within most categories. Two categories dominate the diet: broadleaf / shrub foliage, and pine needles, together comprising some 50% of the annual intake. Grasses, forbs, ferns, heathers and 'other conifers' (here used to mean 'other than pine') are of moderate importance over the greater part of the year, while bramble becomes a significant item only briefly over the summer. Detailed presentation of the use of individual food categories at each site is also given below in Table 5.3.

Fig. 5.1 *Foliage diet of roe deer in the New Forest 1989 - 1990, showing percentage composition of diet by month; data for all sites aggregated.*



Pine and other coniferous browse

Coniferous browse (including pine) was taken heavily from late autumn through winter, forming over half the observed diet, then declining in use during spring (but remaining important), and used slightly over summer. It is clear that pine is by far the most important item of coniferous browse taken by roe. Roe at all the study sites used coniferous browse heavily: use was highest at Salisbury Trench, and least at the poor sites (based largely on Milkham); this distinction may, however, apply more to 'other conifer' rather than pine which, if anything, may have been used slightly more at the poor sites.

Broadleaf / shrub foliage

The use of broadleaf / shrub material showed a complementary pattern to that seen for coniferous browse, reaching a peak in the summer, when it formed almost half the epidermal matter identified in the faecal samples. It was present over the whole of the year, however, and remained an important component throughout autumn into winter, and was taken in smaller quantities in late winter. Similar usage occurred at all sites.

Heathers

The heathers appeared to be taken fairly evenly over the year, amounting to some 6% of the overall annual intake. The peak usage occurred in April. There was some indication that use of heathers was higher at the poor sites: the highest usage for any month by far occurred at Milkham, and for all 4 months for which data are available for Knightwood the usage at that site exceeded that at any other.

Bilberry

Bilberry appears to be an item of very minor importance in the diet, with slight use observed only between late autumn and spring.

Graminoids

The graminoids - grasses, rushes and sedges together, but made up in practice almost entirely of grasses - remain of limited importance over almost the entire year, contributing 11% of the identified epidermal fragments. There is an increased use from late spring through summer, with a level close to 20% of the diet maintained well into autumn. Usage varied greatly between sites, with suggestions of highest use at the poor sites: the highest absolute levels of use were seen at Milkham and Knightwood over the summer months.

Forbs (herbs)

As with graminoids, forbs were taken over the whole year and to a similar extent overall (some 10%), but the usage was spread more evenly from the end of winter through mid-autumn. There may be a slight peak of usage in spring, perhaps reflecting new shoot growth for the year. The data suggest that very little use is made of forbs at poor sites at any time, dietary levels for those sites when data were available being lower than levels at other sites. The greater portion of the forb component of the diet was clover (*Trifolium* spp.).

Holly and Ivy

Both holly and ivy are represented poorly in the faecal samples, at only 1% and 2% respectively for the year. Nearly all intake occurs over winter and the start of spring, but even peak usage barely reaches 5%. The data do not show any clear differences in usage between sites.

Bramble (and rose)

Bramble is currently an item of very limited importance in the diet of the roe in the New Forest. It comprised only 5% of the diet overall, and even at its peak over the summer barely reached 10%, before falling to below 5% by late autumn. Nearly all use of bramble occurs at sites of higher roe density, as poor sites contain little or none.

Ferns

Most intake of ferns was found to occur during the period from August through November when this item comprised between 15-20% of the diet; much less use was made at other times of the year. This pattern is seen at all sites, but highest use appears to be at the 'better' sites, especially Holmsley and King's Hat.

Mosses

Finally, mosses were found at low levels in the faeces over the whole year, apparently taken slightly more over the period from mid-autumn to early spring. Their contribution to the diet overall was under 3%. No difference in consumption was noted between sites.

Table 5.3 *Dietary composition by percentage of epidermal fragments counted each month, for New Forest roe deer from 6 study sites*

(i) Holmsley

Month	Food category											
	Pine	Ocon	Bdlf	Holl	Ivy	Heth	Bilb	Gram	Forb	Bram	Fern	Moss
Jan	53	7	26	1	1	2	0	4	7	0	0	1
Feb	25	12	7	1	4	2	0	2	42	6	2	0
Mar	36	8	13	5	4	4	3	1	18	5	4	1
Apr	34	9	10	2	1	16	4	4	18	2	3	0
May	11	8	39	1	2	6	0	4	24	4	1	2
Jun	22	5	32	1	2	3	4	5	16	7	6	0
Jul	15	2	38	0	0	4	0	9	6	23	4	0
Aug	1	4	10	1	2	7	0	6	4	17	51	0
Sep	2	1	16	0	0	21	6	7	18	13	15	1
Oct	3	3	27	0	0	1	6	10	12	6	21	13
Nov	29	1	10	0	9	11	10	3	7	7	13	0
Dec	63	6	17	0	0	1	2	2	5	2	3	0

(ii) King's Hat

Month	Food category											
	Pine	Ocon	Bdlf	Holl	Ivy	Heth	Bilb	Gram	Forb	Bram	Fern	Moss
Jan	36	9	14	1	1	10	4	5	7	4	11	1
Feb	38	11	7	0	5	6	1	7	25	0	2	1
Mar	29	9	8	4	5	14	5	7	9	2	10	1
Apr	21	12	28	2	3	6	0	9	12	4	4	2
May	6	4	53	0	0	9	0	9	9	6	5	0
Jun	6	4	46	0	0	16	0	8	70	12	3	0
Jul	-	-	-	-	-	-	-	-	-	-	-	-
Aug	3	1	51	1	5	6	5	9	8	8	6	0
Sep	6	5	47	0	0	5	0	6	11	5	17	0
Oct	-	-	-	-	-	-	-	-	-	-	-	-
Nov	35	3	8	0	0	3	0	3	1	0	46	2
Dec	30	2	30	3	0	11	1	3	18	2	2	1

Table 5.3 *continued.*

(iii) Salisbury Trench

Month	Food category											
	Pine	Ocon	Bdlf	Holl	Ivy	Heth	Bilb	Gram	Forb	Bram	Fern	Moss
Jan	16	29	4	2	0	2	0	18	14	6	2	10
Feb	57	13	7	2	1	2	1	4	12	1	2	1
Mar	51	10	9	2	3	6	2	3	12	2	3	0
Apr	39	11	11	1	0	2	0	4	31	1	2	0
May	46	9	15	0	0	1	0	9	15	4	1	2
Jun	5	7	49	0	1	8	0	8	4	6	14	1
Jul	7	13	57	0	0	0	1	9	7	5	1	1
Aug	2	1	27	0	1	2	0	30	24	11	2	2
Sep	4	1	27	0	0	1	0	21	15	5	23	4
Oct	8	5	43	0	2	0	0	21	7	4	8	4
Nov	-	-	-	-	-	-	-	-	-	-	-	-
Dec	22	2	23	0	0	0	5	23	3	0	3	21

(iv) Shave Green

Month	Food category											
	Pine	Ocon	Bdlf	Holl	Ivy	Heth	Bilb	Gram	Forb	Bram	Fern	Moss
Jan	61	3	8	0	0	0	0	8	4	2	7	7
Feb	52	4	12	0	0	9	2	13	2	0	1	5
Mar	-	-	-	-	-	-	-	-	-	-	-	-
Apr	-	-	-	-	-	-	-	-	-	-	-	-
May	22	13	36	0	0	2	0	11	9	8	1	1
Jun	-	-	-	-	-	-	-	-	-	-	-	-
Jul	2	7	49	0	0	3	1	11	13	10	6	1
Aug	6	4	38	0	0	5	0	8	19	7	11	4
Sep	2	4	39	0	0	2	0	40	8	0	3	4
Oct	-	-	-	-	-	-	-	-	-	-	-	-
Nov	11	1	53	0	4	5	2	4	5	3	11	4
Dec	22	6	32	2	16	3	2	11	4	0	1	3

Table 5.3 *continued.*

(v) Milkham

Month	Food category											
	Pine	Ocon	Bdlf	Holl	Ivy	Heth	Bilb	Gram	Forb	Bram	Fern	Moss
Jan	64	4	9	4	2	8	0	4	0	0	0	5
Feb	42	16	0	4	1	10	0	9	2	0	9	5
Mar	75	17	2	0	0	0	0	1	1	0	1	3
Apr	35	6	7	0	1	27	3	12	4	0	7	0
May	-	-	-	-	-	-	-	-	-	-	-	-
Jun	14	0	30	1	0	5	0	44	3	0	3	0
Jul	5	4	49	1	0	4	0	16	5	5	11	1
Aug	-	-	-	-	-	-	-	-	-	-	-	-
Sep	-	-	-	-	-	-	-	-	-	-	-	-
Oct	-	-	-	-	-	-	-	-	-	-	-	-
Nov	-	-	-	-	-	-	-	-	-	-	-	-
Dec	56	1	33	0	0	2	0	5	1	0	1	1

(vi) Knightwood

Month	Food category											
	Pine	Ocon	Bdlf	Holl	Ivy	Heth	Bilb	Gram	Forb	Bram	Fern	Moss
Jan	-	-	-	-	-	-	-	-	-	-	-	-
Feb	41	2	0	5	22	14	1	10	3	0	0	2
Mar	-	-	-	-	-	-	-	-	-	-	-	-
Apr	-	-	-	-	-	-	-	-	-	-	-	-
May	-	-	-	-	-	-	-	-	-	-	-	-
Jun	-	-	-	-	-	-	-	-	-	-	-	-
Jul	-	-	-	-	-	-	-	-	-	-	-	-
Aug	7	4	3	0	1	12	0	55	8	4	8	1
Sep	-	-	-	-	-	-	-	-	-	-	-	-
Oct	32	4	8	0	0	7	0	21	5	5	15	6
Nov	16	4	39	0	0	13	2	12	1	3	11	1
Dec	-	-	-	-	-	-	-	-	-	-	-	-

Seasonal differences in diet between sites: a summary

In spring, roe at poor sites appear to take slightly more pine foliage and ericaceous shrub; they also consume less 'other conifer' browse than do roe at sites of higher density, a trait that persists into the summer. Over both summer and autumn, roe at better sites eat less grass and more bramble in comparison with roe at poorer sites and, as autumn progresses, make more use of fern. In contrast, roe at poorer sites begin eating more heather in late summer, continuing through autumn and winter and into the next spring. At all times of the year, roe at the poor sites consume less forb than do roe at better sites.

Statistical exploration of variation in diet between months and sites

Comparisons of the epidermal fragment composition of the samples from the 6 study sites using G-tests showed clear differences both between months at each site, and between sites in any month. In only two instances were differences between adjacent months not statistically significant ($p < 0.05$): those at King's Hat for May / June, and Salisbury Trench for February / March. Further, all 85 comparisons between sites (within months) showed significant differences between samples at $p < 0.01$ (except for two, $p < 0.05$).

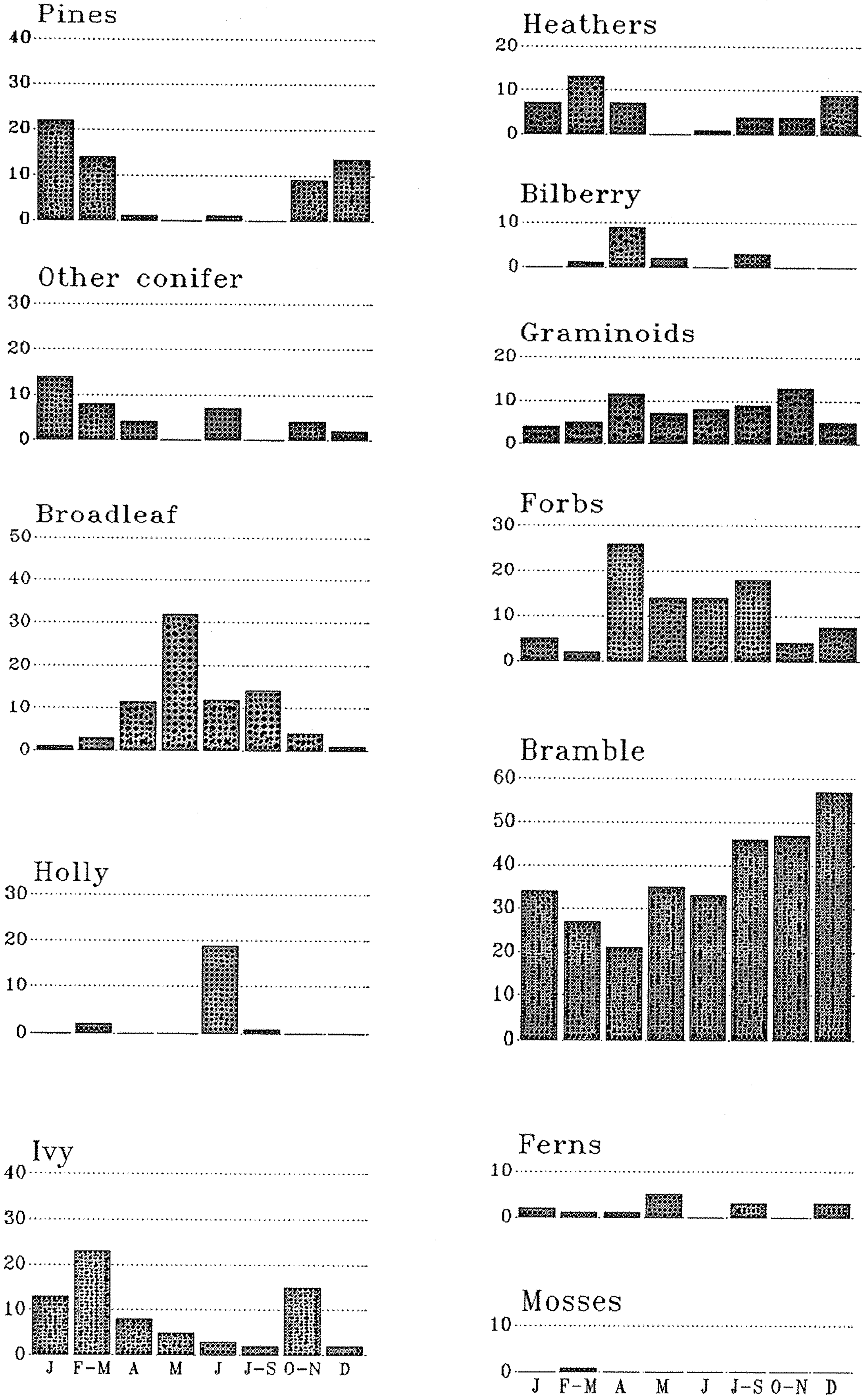
5.4 DISCUSSION

Microhistological analysis of faecal pellets of roe deer collected over August 1989 to July 1990 suggest the (foliage) diet to be strongly based on pine and broadleaf material: each category accounts for some 25% of the annual diet. Other food categories which contribute moderately (each between 5% and 11%) to the total diet include, in order of decreasing importance, grasses, forbs, ferns, heathers (mostly *Calluna*), other conifer browse and bramble.

As noted, an important aspect of this study is the comparison between the diet of roe in the present day Forest and that reported by Jackson (1980) for roe from the early 1970s in the early stages of the population decline. However, for such a comparison, a number of differences between the two studies' methods must be accommodated. (The most obvious question, to what extent dietary composition from faecal and ruminal epidermal fragments can be compared, even for identical actual diets, is discussed in detail below.) Specifically, for the two studies in question, three other matters need to be considered. Firstly, certain materials cannot effectively be assessed at all using faecal material, notably bark, nuts, fungi and other fruits. Jackson, on the other hand, included all of these in his calculations of percentage dietary composition. Secondly, Jackson used slightly different categories from those defined in this study. In particular, he lumped all conifers (whereas I have distinguished pines and others), and also lumped heathers and bilberry as 'dwarf shrubs'. Finally, Jackson observed, after Siuda, Zurowski and Siuda (1969), that a more realistic pattern of dietary composition is obtained by multiplying the mean percentage composition (from counted fragments) by the 'percentage occurrence in samples', to give an index of importance, which he then used to determine relative dietary composition. In this study such a correction was not made as samples for one site in a month were mixed. However, Jackson (1980) presented all his raw data as an appendix to his paper. This permits a recalculation of the dietary composition of his results in accordance with the procedures of this study, with respect to all three differences, thereby allowing closer comparison of 'like with like'. Jackson's recalculated results (which do not actually differ greatly overall from his own presented results) are presented below as Fig. 5.2, which follows the form of Fig. 5.1 for the results from this study.

There are clear differences between the findings of the present study and those for 1970 - 1973 reported by Jackson (1980). Jackson found bramble (with rose) to be by far the most important item in the diet of the roe, accounting for some 40% of the annual intake. Other workers in the south of England have also reported similar (or higher) dietary prevalence of bramble (Nakhasathien 1980, Hosey 1981, Diakite 1983). By contrast, food categories which were found to make up a greater part in the diet of the roe in the present study include both broadleaf and conifer (especially pine) foliage, and grasses, ferns and heathers. Both broadleaf and pine foliage are taken to a greater degree in their respective 'peak' months and over a greater period of the year. The main difference in the amount of grasses taken is seen in the high present level of intake over late summer, when it reaches double the level reported by Jackson. Ferns, in contrast, appear as an important dietary item only in this study, some 8% of the overall foliage diet (compared to 1% reported by Jackson). The slight increase in the levels of heathers is of interest as it also represents a real increase in the bulk, ligninous component of the diet. Jackson (1980) himself noted that many of these items were available in good quantity at that time, which suggests that at that time they were deliberately not being selected by roe.

Fig. 5.2 *Foliage diet of roe deer in the New Forest 1970 - 1973; axes as Fig. 5.1 (some months combined as shown). Data from Jackson (1980).*



On the basis of the roe's digestive system, it must be presumed that roe in the New Forest are currently subsisting on (for them) a poorer quality diet than was the case twenty years ago. Such a shift in diet is not only likely to be a qualitatively poorer (protein-reduced) one (Drozdz 1979), but may reduce nutrient intake further by both increasing retention time (Hofmann 1985), and (perhaps) reducing digestive efficiency by higher intake of phenolics (Feeny 1969, Freeland and Saladin 1989). As roe are essentially concentrate selectors, neither their stomachs nor ruminal microflora are ideally suited to cellulose decomposition (Hofmann 1985, Prins and Geelen 1971). As mentioned, however, roe do appear to have a capacity for cellulose digestion from the presence of a large caeco-colon (Hofmann 1985). While some authors feel roe can make little use of cellulose (Hofmann and Herzog 1980), this view is disputed; Dissen and Hartfiel (1985) claimed that roe are able to digest cellulose with an efficiency similar to that of domestic goats. However, roe deer are, as noted earlier, highly selective and flexible feeders able to adapt to plant resource availability, and it seems that cellulose material is not a preferred food item.

As stated, to some extent the differences in dietary composition from this study and Jackson's may be explained by differences in methodology. Jackson (1980) used point-frame sampling of ruminal contents (after Chamrad and Box 1964) and the present study has been based on the examination of epidermal fragments in faecal material (Storr 1961, Stewart 1967). Each method has its own methodological limitations. Dietary estimation from ruminal contents is considered biased towards browse matter which is retained for greater time (Anthony and Smith 1974). As a method, it may also suffer to an extent from the choice of sieve size for washing samples (McCaffery *et al.* 1974), and from requiring larger sample sizes, perhaps 2 - 5 times the number of faecal samples (Cochran 1967). Dietary estimation from faecal matter inherently has several potential sources of bias, notably those of differential digestibility and fragmentation (reviewed in Putman 1984, but see also Dickman and Huang 1988). Fibrous and cellulose rich intake, including both evergreen and deciduous trees and shrubs, would be digested less completely than softer, forb material. In consequence, and as for ruminal analyses, these items are likely to be overestimated in proportion to the total diet (Anthony and Smith 1974). The technique is further limited to (and biased towards) the identification of the more distinct epidermal fragments (Dearden *et al.* 1975), and does not permit the estimation of bark, fruits or flowers. (Jackson found bark and nuts other than acorn to be relatively minor items in the diet, however). Several workers have also pointed out that the dietary mix of fibrous and non-fibrous material itself affects ruminal retention time and digestibility (Prins and Geelen 1971, Drozdz and Osieki 1973, Gill *et al.* 1983), and therefore that relative digestibility is itself subject to seasonal change with diet (Hanley 1984, Holand and Staaland 1992).

Notwithstanding these criticisms, the use of faecal material remains widely used and, indeed, it is often the only technique available for dietary assessment (Putman 1984). Moreover, several comparative studies of diet based on both faecal and ruminal analyses suggest that the results from both methods are broadly comparable (e.g. Anthony and Smith 1974, Kessler *et al.* 1981, McCullough 1985), an opinion also expressed by Jackson (1980). A more likely explanation of the observed differences in the diet between the two studies may be changes in the availability of plant species or in their selection by the roe: in either case it would very likely influence the animals' patterns of habitat use, and also be reflected in contemporary differences in diet of present day roe in different areas of the Forest.

The patterns of habitat use for roe at the six study sites, described in the previous chapter, may here be related to differences in dietary composition of roe from the same sites. High use and selection of food-bearing establishment / prethicket for much of the year were characteristic of the poorer sites, where that habitat class consists largely of pine and contains high levels of ericaceous shrub. These items appeared to form greater dietary intake for roe from those sites than for roe at better sites. However, it is not clear if the pine foliage itself was taken, as the dietary material appeared to consist largely of Scots pine rather than Corsican pine, and it is the latter which forms the prethicket. More likely, Scots pine is the far more strongly selected by roe (as shown by Jackson), and this is mostly taken elsewhere, from thinnings and self-sown individuals (pers. obs. of both). Selection of food-bearing establishment / prethicket in summer was also noted at Holmsley, where bramble levels in such habitats are higher than in other habitat types. Also in summer, use of mature food-bearing woodlands was found to increase at all sites, consistent with the greater availability of ground vegetation; food-bearing mature conifer woodland is particularly strongly selected at King's Hat, where its level of bramble is higher than in mature woodland at any other site. Broadleaf woodlands are also used more during summer, a finding consistent with the increase in broadleaf and shrub material found in the diet. It is unfortunate that the consistent high autumn use and selection of broadleaf woodland at all sites cannot be positively ascribed to the intake of nuts (because of methodological limitations), although casual observation of several ruminal contents supported this (pers. obs. of rumina of 6 roe). Although a broad picture, the conclusion is that the differences in dietary patterns between roe at good and poor sites is consistent with the use and selection of habitats found earlier, and consistent with the changes over time since Jackson's study.

For some food categories, such as holly, ivy and bilberry, there appears to be little difference in usage between sites. Ivy has been reported as being used in substantial amounts over winter (Diakite 1983, Maizeret *et al.* 1989), despite bearing toxic glycosides (Lieutaghy 1969). While both holly and ivy are available today in moderate quantity, and are presumably not selected by roe, bilberry is somewhat rarer (Chapter 3) and the very low incidence of it in the diet may be the result of this. The differences in the usage of ferns, both between the two studies and between sites today is of interest. Bracken is abundant today throughout the New Forest, as it was 20 years ago, and several other fern species occur, although to a far lesser extent (e.g. hard fern *Blechnum spicant*, lady fern *Athyrium filix-femina*, and *Dryopteris* spp.). Fern dietary components were not identified to species, either by Jackson or in this study, but roe have been known to take several of the species listed above (Cadman 1966, Henry 1978). The low level of fern consumption reported by Jackson suggests that they are not preferred items, and that the ferns consumed today are taken to some extent from necessity, although why the levels of intake are higher at better sites is not clear: there may be differences in availability between sites of species other than bracken.

Differences in diet, both between 'good' and 'poor' sites and in the New Forest overall between 1970 and 1990, may be attributed to changes in the availabilities of food types or to altered patterns of forage selection by roe, or to both. The vegetation surveys carried out within the New Forest inclosures for the present study were not intended to be detailed assessments of the availability of forage, rather to characterise the chosen study sites for investigations of association (Chapter 3) and habitat use (Chapter 4). For this reason formal analyses of resource use in relation to availability have not been possible in the present chapter. Instead consideration of this topic must be restricted to a rather speculative consideration of whether the relative (ranked) occurrence of the food categories in the present day diet of roe across sites can be related to the relative availability of those food items which were included in the surveys.

From the survey data at the six study sites (Chapters 3 and 4), the percentage compositions of the surveyed area of three tree species-groups (pines, other conifers and broadleaves), and seven characters of the inclosure ground vegetation (holly, ivy, heathers, bilberry, graminoids, bramble and bracken) were calculated and ranked. These were then correlated against the ranked occurrence of the same items in the overall annual diet (above) across all six sites. Significant and positive correlations were obtained for other conifers ($r = 0.94$, $p < 0.05$) and broadleaves ($r = 0.89$, $p < 0.05$), suggesting that these materials may be taken in some measure as they occur, while others are more actively selected or avoided. Further to this, taking the ratio of proportional usage to proportional availability for each food item (Hunter's (1962) index of selection), three food items were 'selected' at all sites where they occurred (in more than negligible amounts): ivy (at 2 sites), heathers (at 5 sites) and bramble (at 3 sites). All other items showed a mix of selection and avoidance. Although rather simple analyses, these findings are broadly consistent with those from the earlier correlation studies (Chapter 3).

For the New Forest roe, the consequences of an enforced poorer quality diet may be various, for instance by reducing body condition and reproductive performance and survival: these and other possible effects on the New Forest roe are examined in detail in Chapter 7. Skogland (1988) reported that a similar change in diet in reindeer, i.e. an increase in the amount of grass and fibrous material, resulted in greater tooth wear. This in turn, he speculated, may lead to an increase in chewing / food retention time, and thereby reduce food intake further. Tooth wear has also been linked to an increase in mortality in other deer (mule deer: Klein and Olson 1960) and to senescence in roe (Gaillard *et al.* 1993b).

6. ROE AND OTHER LARGE HERBIVORES: ECOLOGICAL SEPARATION OR CONFLICT?

Chapter summary

The likelihood of resource competition between roe and the other principal large herbivores of the New Forest was assessed, considering (where data permitted) both the potential for competition from resource use overlap, and any evidence of actual competition. This was based largely on published data for the other herbivores, the data on roe presented in Chapters 2-5, and some additional data on habitat use by fallow deer collected for this study.

Habitat and dietary overlaps between roe and both cattle and ponies were very low throughout the year; moreover, the absence of a significant negative correlation between the changing populations of either species with roe over the period of decline (Chapter 2) suggested there had been little if any impact on roe from these species.

Similarly, overlaps in habitat use and diet between roe and both red and sika deer were also low; while there were significant negative correlations between roe and both of these species in the earlier correlation analyses, the very restricted ranges of both red and sika in the New Forest make the chance of actual competition remote.

Fallow deer, perhaps the most likely potential competitors with roe from range considerations, was considered in more detail. Data on habitat use and selection by fallow in the enclosed woodlands showed significant differences in patterns of habitat use from roe, and demonstrated fallow did not select the same habitat types; there was no resource overlap pattern consistent with roe density across the study sites. Fallow strongly selected rides for grazing, and used mature woodland without regard to its food status (as defined in Chapter 3). Dietary overlap between the two species was moderate over 1970-1973, but appears actually to have decreased over the period of the roe's decline and is currently low. Fallow did not appear to select the preferred food item of roe, bramble, and were judged unlikely to have caused a decline in its availability. There was no evidence of interference between the two species from patterns of presence and absence at the study sites.

Changes in the New Forest's fallow population over the period of the decline in the roe were examined with respect to environmental variables according to the methods used for roe (Chapters 2 and 3). Results suggested that the censussed rise in the fallow population may be related to habitat changes over the period, notably the increase in mature woodland in both the inclosures and on the Open Forest: this, it is suggested, may offer increased cover in close proximity to the grazing on rides and the Forest's other grassland areas. Thus the correlated changes in both the roe and fallow populations of the New Forest (Chapter 2) may be independent responses to changes in the Forest's woodland and unenclosed habitats.

6.1 THE LARGE HERBIVORE POPULATIONS OF THE NEW FOREST

This study has for the most part explored interactions between the roe deer population of the New Forest and its vegetational environment. The analyses carried out have suggested that roe numbers may be strongly influenced by the availability of suitable vegetational resources. This is based upon evidence from both the initial correlation studies between roe numbers and changing vegetational characters (Chapters 2 and 3), and the subsequent corroborative evidence from patterns of habitat use (Chapter 4) and diet (Chapter 5). Roe numbers over the period of the decline also correlated with several climatic factors for the 12 month period before the census: these were February precipitation, mean daily March temperature, the precipitation and mean daily temperature over May - June, and the mean winter temperature (Chapter 2).

However, the early investigation of environmental changes coincident with the decline in the roe population (Chapter 2) also revealed significant negative correlations between the changing numbers of roe deer and the population levels of the Forest's red, sika and fallow deer over the period 1972 - 1988. In addition, Putman and Sharma (1987) reported a significant negative correlation between the numbers of censussed roe over 1961 - 1986 and total numbers of domestic cattle and ponies depastured on the Open Forest over the previous three years.

In this chapter, therefore, I explore whether the observed decline in the roe population over 1972 - 1988 may also be in some measure the result of competition from these other species, either directly (via physical interference) or indirectly (through resource exploitation).

6.2 THE POTENTIAL FOR COMPETITION BETWEEN LARGE HERBIVORES

Competition and competitive exclusion in nature are extremely difficult to prove. Wiens (1989) proposed a stringent set of criteria, based upon the earlier set of Reynoldson and Bellamy (1971), for the detection of interspecific competition under field conditions:

Strength of Evidence:	Criteria:	
Weak	1.	Observed patterns consistent with predictions
↓	2.	Species overlap in resource use
↓	3.	Intraspecific competition occurs
Suggestive	4.	Resource use by one species reduces its availability to another species
↓		
↓	5.	One or more species is negatively affected
Convincing	6.	Alternative process hypotheses are not consistent with patterns.

In fact, to demonstrate the satisfaction of all of these criteria would require manipulation of both the resource and the population in question and, as Krebs (1994) has noted, few studies actually investigate more than the first two. Certainly the application of all these criteria was not practicable for the present study: time was not available for detailed studies on intraspecific competition, and direct manipulative experiments on the herbivores of the New Forest would have been impossible. A more realistic approach was to adopt the logic de Boer and Prins (1990) used in their evaluation of the potential for interspecific competition between four species of large herbivores occurring in Lake Manyara National Park, Tanzania (African elephant *Loxodonta africana*, Cape buffalo *Syncerus caffer*, wildebeest *Connochaetus taurinus* and Burchell's zebra *Equus burchelli*). De Boer and Prins (1990) argued that interspecific competition between any two species of the herbivores was only possible when three conditions were met: (a) there must be habitat overlap, (b) there must be common diet between the two species in those overlapping habitats, and (c) the shared dietary resources must be limiting. (It should be stressed that the satisfaction of these conditions does not establish that competition is actually occurring; de Boer and Prins' protocol can merely establish the potential for competition.)

Various measures of overlap in resource use between two species have been proposed. For instance, Levins' (1968) suggested an asymmetric index of overlap, which is useful for cases where the overlap of resource use by species A on B may not be the same of that of species B on A; interpretation of this index is made somewhat difficult, however, as it is not clearly bounded in its range of values. An alternative index of resource overlap is the symmetric niche overlap index of Pianka (1973), for which values range from 0 (no overlap) to 1 (identical niche patterns). Putman (1986b) uses both of these indices in his earlier study of resource overlap of the New Forest large herbivore species; for this study, however, to avoid excessive duplication only Pianka's index is used. This is expressed by (α_{ij}), the overlap between two species (*i* and *j*) for a given resource (e.g. habitat use or dietary intake), where:

$$\alpha_{ij} \quad = \quad \sum p_{ia}\, p_{ja} \ \ / \ \ [\, (\sum p_{ia}^{2}) \ (\sum p_{ja}^{2})\,]^{1/2}$$

and where p_{ia} represents, for species *i*, each component's proportion *a* of the resource in question. Though widely used in the literature, interpretation of such measures of niche overlap is contentious. Reviewing competition and niche theory, Pianka (1981) considered that overlap is a necessary but, in itself, insufficient condition for exploitation competition. However, just as high overlap does not necessarily indicate competition, and may occur through tolerant sharing of non-limiting resources (Colwell and Futuyma 1971), it has been pointed out that aggressive exclusion (i.e. intense competition) could result in low perceived overlap (Schoener 1983) - for a recent review see Putman (1994: pp. 73-79). This difficulty with interpretation has also been noted with specific reference to large mammalian herbivores: de Boer and Prins (1990) suggested that interspecific competition between species effects a separation of the niche use, resulting in a small observed overlap, while others (e.g. Jarman 1971) have associated competition with large niche overlaps. The underlying questions, i.e. to what extent competition is able to 'force' large herbivore species apart along a resource spectrum, and how much (or how little?) overlap there must be before competition may be inferred, remain largely unanswered; the answers are likely to depend upon, among other things, the dynamics of the populations, the carrying capacity of the environment, and the number of interacting species present. Schoener (1983) suggested that in large herbivores (and perhaps for mammals more generally) species are not readily shifted as a response to competitive pressure, which may thus be assessed by large values of index overlap.

In this study, patterns of overlap are examined in a broader context of evidence for competitive interaction between roe and the other species of deer and domestic stock occurring in the New Forest. This evidence encompasses consideration of overlaps in habitat use and diet, patterns of site usage, and geographic distribution of the different species within the Forest as a whole, as well as evidence from correlation studies such as those described for roe in Chapters 2 and 3. More specifically, this chapter addresses several questions:

(a) What is the potential for resource competition between roe and the other species of large herbivores in the New Forest from consideration of niche overlap (habitat and diet)?

(b) Is there any evidence of interference interaction between roe and the other species within the Forest's enclosed woodlands?

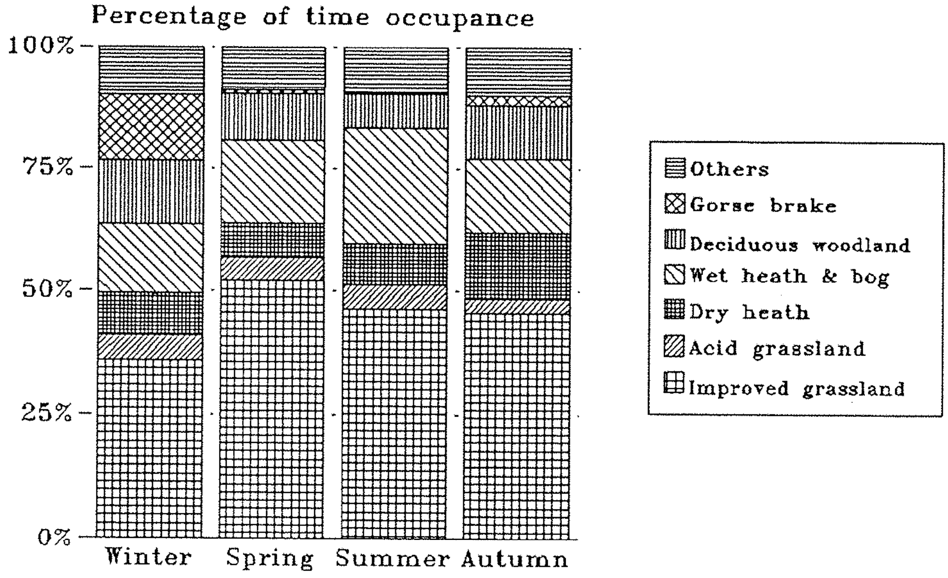
(c) Is there any evidence to suggest that actual competition between roe and the other species might be taking place in the New Forest, and are there plausible alternative interpretations for that evidence?

Much of the material cited in this chapter is taken from other published works, or data already described in earlier chapters of this report. Relatively few new data are introduced, and the chapter therefore differs from others in this report as being more in the nature of an assessment or discussion.

6.3 RESOURCE USE BY CATTLE AND PONIES AND THE POTENTIAL FOR COMPETITION WITH ROE

Several recent studies have documented the patterns of habitat use and diet for both cattle and ponies in the New Forest (Pratt *et al.* 1986, Putman *et al.* 1987; summarised in Putman 1986a, b). Both species are preferential grazers and make much use of the Forest's better grasslands (including the streamside lawns as well as the reseeded lawns and other artificially improved grasslands of the Open Forest described in Chapter 1). Ponies make extensive use of these areas throughout the year, spending approximately half their total time on them; they use the Forest's acidic grasslands far less, despite the fact that these comprise a larger area of the Open Forest. From late spring through to early autumn ponies also make increasing use of both wet and dry heathland habitats and, over the winter, greater use of sheltered areas of gorse brake. Use of deciduous woodland is moderate throughout the year, though generally higher over the autumn and winter period. In contrast, coniferous woodlands are little used at any time. Seasonal patterns of habitat use by ponies are summarised in Fig. 6.1 (data from Putman 1986b).

Fig. 6.1 Open Forest habitat use by New Forest ponies

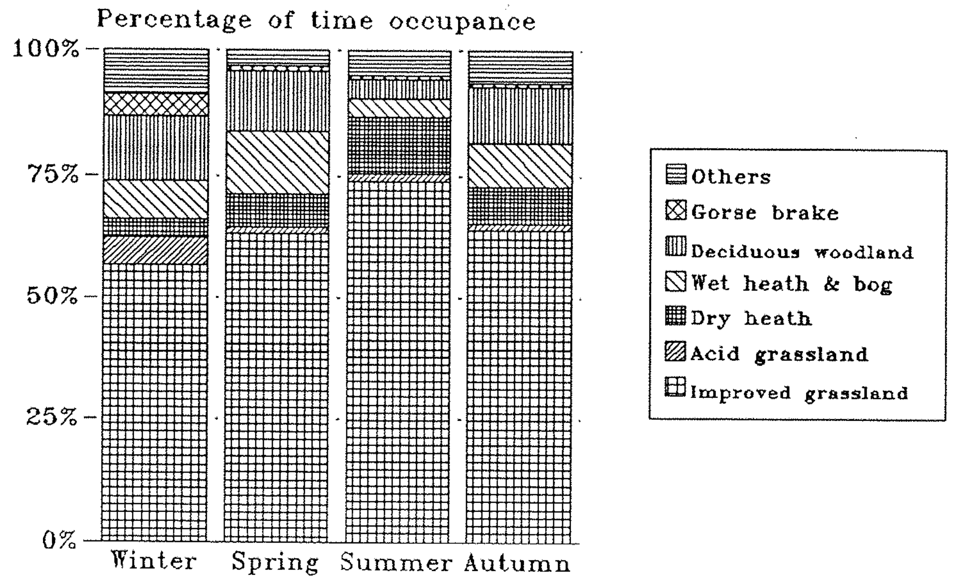


Data from Putman (1986b), seasons as defined in this study

Over the year, cattle make even greater relative use of the improved grasslands and lawns, which account for some 59% of all observations of these herbivores (Putman 1986b). By comparison with ponies, they make more use of dry (rather than wetter) heath, and less use of the wetter grasslands, such as those by streams. Cattle also make moderate use of deciduous woodlands over the spring months and, like ponies, make very little use of conifer woodland. Overall, though broadly similar, the pattern of habitat use of cattle (Fig. 6.2) shows less seasonal variation than that of ponies.

It is Forestry Commission policy to exclude all domestic stock from the enclosed woodlands, as rights of common apply only to the Open Forest. The extent and degree to which this exclusion is effected varies between keepers and over the year according to the keepers' other duties. However, during the 12 months of the transect fieldwork, a few records were made of domestic stock within the study inclosures. Where ponies were

Fig. 6.2 Open Forest habitat use by New Forest cattle



Data from Pratt et al.(1986), seasons as defined in this study

observed within the inclosures, over half of were on rides, and most others were in broadleaf woodlands, a pattern of inclosure habitat use much closer to that of fallow deer than of roe (see below). Though not formally calculated for the enclosed woodlands, the amount of overlap in habitat use overall between roe and either cattle or ponies is considered low to moderate.

As noted, both cattle and ponies are preferential grazers. Typically, grasses comprise some 65-80% of the total diet of cattle, and over 70% of that of ponies between May and November, dropping to 35-50% for winter and spring. The remainder of the diet of cattle is mostly heather, while ponies eat more holly and broadleaf browse, with some gorse over winter and spring. (While the published work suggests that cattle and ponies appear to eat very little bramble (Putman *et al.* 1987), this may be because bramble has recently been in very limited supply in the Forest - as found in this study, Chapter 3 - and because the published diet for ponies is for individuals on the Open Forest rather than those which spend more time in the Forest inclosures.)

Indices of seasonal dietary overlap for both cattle and ponies with roe, based upon the studies of Putman *et al.* (1987) for the domestic stock and Jackson (1980) for roe, have been presented by Putman (1986b) and are reproduced here (Table 6.1).

Table 6.1 *Indices of overlap (Pianka 1973) between seasonal diets of roe deer and those of cattle and ponies in the New Forest*

	Winter	Spring	Summer	Autumn
Ponies	0.14	0.14	0.14	0.17
Cattle	0.16	0.20	0.14	0.20

Note: Seasons as defined in Putman (1986b) with winter (Nov-Jan), spring (Feb-Apr), summer (May-Jul) and autumn (Aug-Oct). Data as credited in text.

Actual index values of dietary overlap for both species with roe are consistently low, ranging from 0.14 to 0.20, with the higher values in autumn, when all the large herbivore species tend to make more use of the nut and mast available in broadleaf woodlands. The major dietary item for both species of domestic stock (grasses) is of very limited importance to roe (Jackson 1980, and Chapter 5), and is also available in good quantity within the inclosures (i.e. it appears not to be limiting). Thus, according to the criteria of de Boer and Prins (1990), on the basis of current habitat and food usage the likelihood of resource competition between roe and both cattle and ponies appears slight.

As noted, comparisons of patterns of habitat use and diet, and derivation of high values for symmetric indices of niche overlap such as that of Pianka (1973), cannot in themselves be taken to indicate that competition is actually taking place. Similarly, low calculated indices of overlap do not in themselves demonstrate the absence of competition. For one thing, such measures take no account of the actual numbers of domestic stock on the Forest (Pianka's (1973) indices of overlap are calculated simply for the 'average' individual of each species, unweighted by the respective population sizes). The actual population levels of both cattle and ponies are, in practice, influenced by owners' requirements and Forest regulations. Individual commoners may remove animals from the Forest over winter (especially in the case of cattle) or give them supplementary winter feed while on the Forest, and many of the year's foals are sold following the autumn 'drifts'. The New Forest Verderers may (and do) remove animals from the Forest considered to be in poor condition. During the 12 months of transect fieldwork, when records were maintained of the numbers of cattle and ponies see within the study inclosures, cattle were seen only on three occasions. Ponies were seen more frequently, but were entirely absent from some areas, such as Milkham, for almost the entire year. The highest level of use by ponies at any site was seen in Salisbury Trench, which contained some 6 individuals over the greater part of the year.

In this study, we are also able to enquire whether or not there is evidence of any temporal association between the population changes of the roe and the number of cattle and ponies on the Forest over the period of the decline in the roe population. As noted, in an earlier investigation, Putman and Sharma (1987) found no clear relationship between the censussed New Forest roe deer population numbers over 1961 - 1986 and the numbers of cattle or ponies depastured on the Open Forest in the same year; they did, however, report a significant negative correlation between the annual census number of roe and 'grazing pressure over the past three years' from cattle and ponies together. That initial analysis, as has also been noted, was based on the censussed population changes of roe over the whole period 1961 - 1986 and was carried out prior to the detailed evaluation of the census data discussed in Chapter 1. We have seen that when the correlation analysis was repeated using only the more reliable roe census data from the period 1972 - 1988 (Chapter 2), no such relationship emerged. In consequence, the findings of that earlier (1987) study for all correlations between roe and other Forest herbivore populations should be treated with caution, and for now we should rather accept the analyses presented in Chapter 2 which showed no significant correlation between the censussed roe deer population and the numbers of licensed cattle and ponies on the Forest.

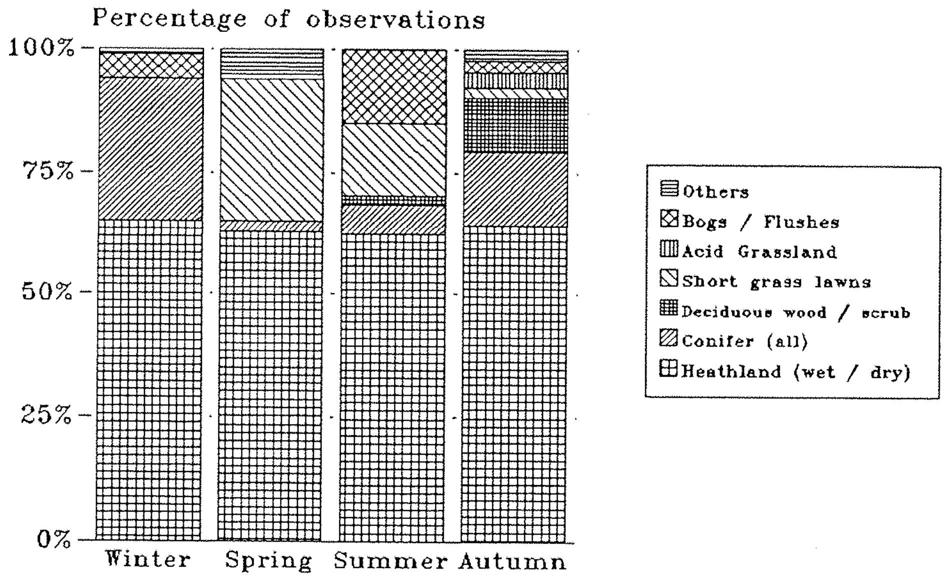
6.4 RESOURCE USE BY RED AND SIKA DEER AND THE POTENTIAL FOR COMPETITION WITH ROE

While there is thus no good evidence for resource competition between roe and domestic stock turned out on the Open Forest grazing, the analyses of Chapter 2 revealed a number of significant negative correlations between the censussed (whole Forest) roe population and the estimated abundance of fallow, red and sika populations within the Forest ($p < 0.01$ in each case). Beat level replication was possible only for fallow deer over the period 1976 - 1988, and this failed to support the significant negative correlation apparent for figures at the whole Forest level.

As noted in Chapter 1, both red and sika deer are found only in certain localities within the Forest, and in fairly low numbers - indeed, over the period of the decline each species has (according to the spring censuses) been restricted almost entirely to a single beat.

There are no published studies on habitat use or diet of New Forest red deer. Long-term data on habitat use have, however, been presented in an unpublished report by Payne (1987). Over the year, 51% of observations of red deer were made on dry heathland, 13% on wet heathland, 7% on each of short grass (lawns) and self-sown conifer patches, some 5% in mature conifer and some 6% in deciduous scrub / woodland. Seasonally, use of heathland (especially dry heath) remained consistently high at all times, but the relative use of other habitat types varied. Payne's (1987) data are summarised by season in Fig. 6.3.

Fig. 6.3 Habitat use by red deer in the New Forest



Data from Payne (1987), seasons as defined in this study

Payne (1987; and pers. comm.) points out, however, these data may be biased towards higher use of heathland, both through differential habitat visibility and also by seeking deer on heathland more frequently.

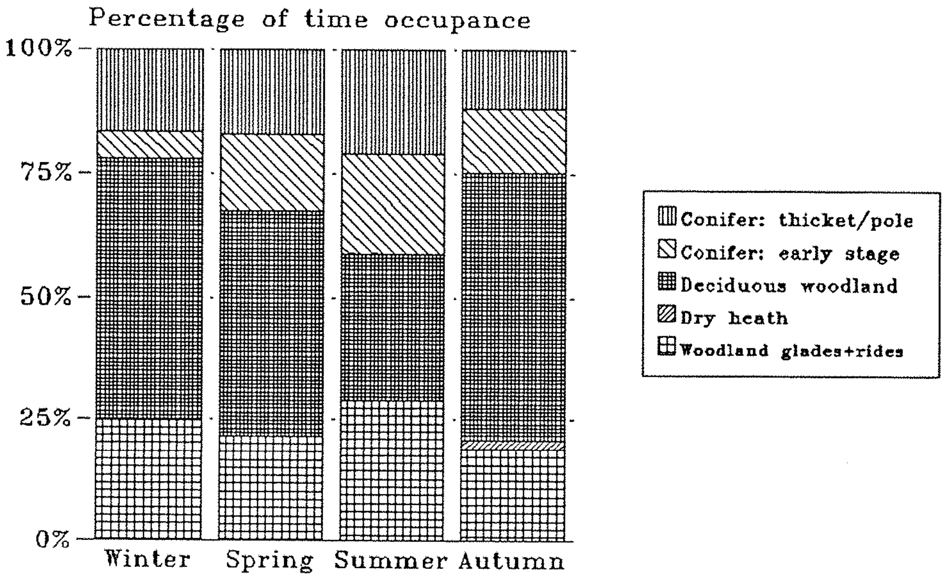
Payne also recorded observations made on red deer feeding in different habitats, again, not systematically, but subsequent (unpublished) faecal pellet analysis has in some measure supported the overall dietary picture presented below (Payne 1987, and pers. comm.). Heathers were the principal items noted for the year overall, and accounted for 38% of the feeding records; *Molinia* was also taken a great deal (22%), while conifer browse (14%), deciduous shrub (10%), grazing on short lawns (8%), rushes (5%) and 'others' (3%) made up the remainder. Although heathers remained important at all times of year, other items varied in importance seasonally. In winter conifer browse (44%) was second to heathers (53%), but *Molinia* accounted for 23% - 30% of feeding observations over the remaining seasons. In spring the deer were observed feeding more on short lawns (24%), but used this habitat less over the summer and autumn (6% in each season). Deciduous shrub was taken most in autumn (13% of observations). Using these dietary data and those for roe in this study (Chapter 5), the seasonal coefficients of dietary overlap between the two deer species are very low: winter (0.22), spring (0.20), summer (0.12) and autumn (0.18).

It may be noted, in passing, that the diet of the New Forest red deer appears to differ somewhat from that reported for the species elsewhere in Britain. Highland red deer consume much greater amounts of broad-leaf grasses (e.g. bents and fescues), which may comprise over 90% of intake in some areas in spring and summer. Although Highland red take more heather in eastern areas (where it is more abundant) than in the western Highlands, nowhere do they take *Molinia* in the quantity reported for New Forest animals (diets summarised in Clutton-Brock and Albon 1989).

When the very different patterns of habitat use and diet between New Forest red (above) and roe (Chapters 4 and 5) are considered, along with the restricted range of the larger species over the Forest, it seems unlikely that there is any significant potential for competition between the two species.

Mann (1983) studied habitat use and diet of sika in the New Forest, where the species is effectively restricted to one inclosure; this area largely comprises broadleaf woodland, but there are some conifer and mixed stands. Patterns of habitat use of sika in the Forest are summarised in Fig. 6.4.

Fig. 6.4 Habitat use by sika deer in the New Forest



Data of Mann (1983) [in Putman (1986b)], seasons as defined in this study

Sika are predominantly grazers. Mann's (1983) studies suggested that grasses make up around 40-50% of their dietary intake over the late spring and summer, and >20% at other times. The other principal component of their diet is heather, which consistently forms around 25-35% of intake. Broadleaf material (excluding holly) is taken moderately all year at about 10-15% (with a slight increase in autumn), and the remainder of the diet is composed of conifer browse (over late autumn to mid-spring), and small amounts of gorse, fruits and other items. Calculated indices of dietary overlap between roe and sika from the work of Jackson (1980) and Mann (1983) (taken from Putman 1986b), are moderately low: winter (0.37), spring (0.53), summer (0.32) and autumn (0.31).

From all these considerations, the correlations between roe and both red and sika deer may be considered to have little relevance to the question of the decline in the roe population.

6.5 RESOURCE USE BY FALLOW DEER IN THE NEW FOREST INCLOSURES

The potential for competition between roe and fallow deer, by contrast, cannot be discounted so simply. As noted, both species range over the whole Forest, and have shown opposite trends in population levels in recent years (Table 1.1), the census numbers for roe and fallow over 1972 - 1988 showing a significant negative correlation (Chapter 2). While this result was not supported by the beat level correlations over 1976 - 1988, census returns from successive years suggest fallow herds may range between beats, and this may have confounded that analysis. Moreover, Jackson (1980) suggested the two species may compete for food in winter if resources were limiting, and the published dietary overlaps between fallow and roe (Putman 1986b, and given in full in the next section) do show at least a moderate overlap in winter (November - January: index value 0.68). The possibility of interaction between roe and fallow thus needs to considered in greater detail. To this end, much of the remainder of this chapter explores the evidence for possible competitive interaction between these species in the New Forest.

In this section, from my own studies on habitat occupance, and published accounts of dietary overlap between fallow and roe deer in the New Forest, the potential for significant interspecific competition between the two species is assessed (after de Boer and Prins 1990). As a subsidiary analysis, alternative explanations are then considered which might account for the observed negative correlation between roe and fallow deer population numbers. If, for example, changes in the censussed fallow deer population may be related independently to changes in the vegetation of the New Forest, or to variation in other coincident factors such as climate - as has already been found for roe - then the observed negative association between roe and fallow numbers may simply be coincident effects of a single, other common cause, and the case for competitive interaction between the two species would be weakened (Section 6.6).

In order to assess resource overlap between roe and fallow in the New Forest, data on habitat use and diet of fallow are necessary comparable to those for roe presented earlier (Chapter 4). While carrying out the direct observational transects on roe deer, and in accordance with the methodology described in Chapter 4, records were also kept on all fallow deer sighted. As only five fallow deer in total were seen at the King's Hat site over the entire year this site has been excluded from analyses presented in this chapter, which are thus restricted to five of the full six sites.

Patterns of habitat use by fallow

Patterns of habitat use by fallow at all sites differed significantly from those expected on the basis of habitat availability, both for the year in total (χ^2, $p < 0.001$), and seasonally (χ^2, all $p < 0.001$). Patterns of usage also differed significantly within sites between most pairs of seasons (21 of 30 comparisons: χ^2, $p < 0.05$) and between sites for all seasons (27 of 40 comparisons: χ^2, $p < 0.05$). Habitat usage and corresponding coefficients of habitat selection for fallow deer are presented in Table 6.2 for all sites data aggregated, and in Tables 6.3 and 6.4 giving details of individual sites.

Table 6.2 *Annual and seasonal levels of enclosed woodland habitat class use and selection by fallow deer (all sites' data combined)*

Habitat Class:	I	II	III	IV	V*a*	V*b*	VI
AREA (Ha.):	34	33	257	85	33	88	28
LEVELS OF USE (Number of observations):							
Winter	7	4	34	15	18	58	36
Spring	14	11	51	18	26	24	37
Summer	7	13	30	10	12	4	30
Autumn	7	5	56	7	43	19	56
All year	35	33	171	50	99	105	159
SELECTION (Goodall's coefficient):							
Winter	-0.20	-0.04	-0.40	-0.27	0.27	0.36	0.61
Spring	0.12	0.03	-0.24	-0.21	0.41	-0.09	0.60
Summer	0.04	0.34	-0.24	-0.24	0.31	-0.61	0.70
Autumn	-0.26	-0.40	-0.22	-0.62	0.58	-0.23	0.71
All year	-0.06	-0.08	-0.28	-0.33	0.43	0.01	0.66

Table 6.3 *Use of habitats by fallow deer in the New Forest inclosures, showing number of deer observed at each study site by season and habitat class*

Habitat Class		I	II	III	IV	V	VI
HM	Winter	-	2	6	3	20	0
	Spring	-	0	4	0	4	7
	Summer	-	2	0	5	0	2
	Autumn	-	0	1	0	5	3
SA	Winter	0	0	0	5	40	0
	Spring	0	2	2	14	22	3
	Summer	2	6	5	3	3	1
	Autumn	0	0	2	5	12	2
SG	Winter	-	-	4	0	0	6
	Spring	-	-	8	0	10	6
	Summer	-	-	1	0	3	5
	Autumn	-	-	8	0	3	0
ML	Winter	2	2	6	5	16	26
	Spring	14	5	31	4	10	15
	Summer	5	5	14	0	7	9
	Autumn	4	0	21	2	28	45
KN	Winter	5	0	18	2	0	4
	Spring	0	4	6	0	4	6
	Summer	0	0	10	2	3	12
	Autumn	3	5	24	0	14	6

Approximately half the total observations of fallow were in either food-depleted conifer stands [III] or rides [VI]. Broadleaf woodlands account for nearly a third of total usage, equally divided between food-depleted [Va] and food-bearing [Vb] areas, and other habitat classes fairly evenly make up the remainder. This pattern of usage in relation to actual habitat availability suggests that, for the year overall, two habitat classes appear to be positively selected, food-depleted broadleaf woodland [Va] (moderately), and rides [VI] (very strongly). In contrast, food-bearing broadleaf woodland, along with establishment and prethicket stage conifer stands (irrespective of food status), appear to be neither selected nor avoided. Mature conifer woods in general, again whether food-depleted or food-bearing, show a high level of use but are in practice used somewhat less than would be expected in relation to availability.

Table 6.4 *Goodall's indices of selection for habitat classes by fallow deer in the New Forest inclosures, by site and season*

Habitat Class		I	II	III	IV	V	VI
HM	Winter	-	0.15	-0.40	-0.49	0.61	-1
	Spring	-	-1	-0.26	-1	0.26	0.80
	Summer	-	0.65	-1	0.32	-1	0.62
	Autumn	-	-1	-0.61	-1	0.56	0.73
SA	Winter	-1	-1	-1	-0.29	0.48	-1
	Spring	-1	-0.49	-0.73	0.23	0.24	0.25
	Summer	0.86	0.38	-0.08	-0.15	-0.35	0.08
	Autumn	-1	-1	-0.51	0.08	0.29	0.38
SG	Winter	-	-	0.16	-1	-1	0.86
	Spring	-	-	0.07	-1	-0.05	0.70
	Summer	-	-	-0.45	-1	-0.16	0.85
	Autumn	-	-	0.43	-1	-0.25	-1
ML	Winter	-0.58	-0.06	-0.73	0.47	0.54	0.80
	Spring	0.15	0.24	-0.26	0.24	0.20	0.58
	Summer	-0.02	0.52	-0.31	-1	0.36	0.63
	Autumn	-0.47	-1	-0.52	-0.23	0.54	0.79
KN	Winter	0.03	-1	0.02	0.09	-1	0.41
	Spring	-1	0.55	-0.33	-1	0.47	0.67
	Summer	-1	-1	-0.24	0.13	0.22	0.77
	Autumn	-0.47	0.25	-0.13	-1	0.58	0.33

The patterns of habitat use and selection in individual seasons may be seen broadly to reflect the annual picture. Thus, establishment and prethicket areas are moderately avoided in autumn, but otherwise neither strongly selected or avoided (although there appears a slight tendency to select food-bearing areas in summer), and mature conifer stands are always subject to a degree of avoidance. The simplest explanation for these differences is that fallow are selecting whatever convenient wooded cover happens to be available for rest / rumination after foraging (usually on nearby rides, pers. obs.), rather than selecting specific woodland types. For all coniferous woodlands, fallow appear to make little if any distinction in selection of the food-depleted and food-bearing areas.

As may be expected, highest use of the nut producing broadleaf woodlands overall is over autumn and winter, especially the latter. In the light of the uniform selection of conifer areas, the apparent selection of food-depleted over food-bearing broadleaf woodlands is unexpected: the former are consistently selected in all seasons, but the latter are avoided more strongly except for the winter (but see patterns at site level, below). This may, however, be resolved by examination of habitat selection at individual sites at the level of the (more finely resolved) habitat type scheme (Table 6.5).

Table 6.5 *Coefficients of habitat selection by fallow for broadleaf stands, at the three sites containing both food-depleted and food-bearing habitat types.*

Site		Winter	Spring	Summer	Autumn
HM	*Food-depleted immature broadleaf [14]*	-1	-1	-1	-1
	Food-bearing immature broadleaf [16]	0.69	-1	-1	-1
	Food-bearing mature broadleaf [19]	0.63	0.34	-1	0.66
SA	*Food-depleted immature broadleaf [14]*	-1	-1	-1	-1
	Food-bearing immature broadleaf [16]	0.91	-1	-0.02	0.56
	Food-depleted mature broadleaf [17]	-0.17	-0.63	-0.12	-0.14
	Food-bearing mature broadleaf [19]	-1	0.24	-1	0.03
SG	*Food-depleted mature broadleaf [17]*	-1	-1	0.51	-1
	Food-bearing mature broadleaf [19]	-1	-0.01	-0.28	-0.19

Excluding Knightwood, which bears only a trivial amount (0.5 ha.) of food-bearing broadleaf woodland, three sites can be considered. At Holmsley the food-bearing habitat types are the only ones used, while at Salisbury Trench fallow select food-bearing pole-stage broadleaf [16] more in winter, autumn and summer, but food-depleted mature broadleaf [17] in spring; there is no consistent selection of any either habitat type at Shave

Green. While there is an overall tendency to equalise selection of all broadleaf woodland habitat types over autumn / winter, there remains no other clear pattern, and no distinction which may be related to site 'quality' for fallow. By contrast, the strong selection of rides is consistently shown in all analyses.

By and large, these patterns of habitat use are in accord with those reported for the New Forest by Thirgood (1990), who, like Jackson (1974) and Parfitt (in Putman 1986a), noted the strong selection of deciduous woodlands and rides by fallow. Differences between Thirgood's results and those presented here are that, in my study sites fallow used conifer woodland less in winter than in other seasons, and used rides more in autumn; Thirgood found less use of rides in autumn, and higher use of closed conifer woodland for the rut. During my transect walks I noted fallow rutting stands only at one site, Milkham.

Comparison of habitat use and selection by roe and fallow

The patterns of habitat use by fallow deer presented above may be compared directly with patterns of habitat use expressed by roe at the same sites (data from Chapter 4). These comparisons show that the two species differ significantly in their patterns of habitat use - at all sites in winter and at most sites in other seasons (Fisher Exact test / χ^2 as appropriate, $p < 0.05$ in all cases, Table 6.6).

Table 6.6 *Comparisons of patterns of habitat use by roe and fallow in New Forest enclosed woodlands; entries show probabilities of patterns differing by chance.*

Site	Winter	Spring	Summer	Autumn
Holmsley	0.000 **	0.000 **	0.007 **	0.011 *
Salisbury Trench	0.010 **	0.106 *	0.018 *	0.096
Shave Green	0.000 **	0.006 **	0.213	0.013 *
Milkham	0.000 **	0.011 *	0.550	0.006 **
Knightwood	0.008 **	0.058	0.007 **	0.139

Note: ** highlights $p < 0.01$; * highlights $0.01 < p < 0.05$. Analyses by Fisher Exact Test / chi-square.

Formal indices of overlap may also be calculated (Table 6.7.)

Aggregating data across all sites, the overlap indices for all seasons are almost identical, ranging from 0.84 to 0.86. Although formal statistics cannot be performed on these indices individually, or in pairwise comparisons, the overall pattern across sites (or seasons) can be examined using the sign test. Across sites, thus, both Holmsley and Salisbury Trench - the two 'best' roe sites - have indices of overlap significantly different from the remaining sites as a whole ($p < 0.01$ in each case). Yet these differences are not consistent: Holmsley shows significantly lower overlap than other sites, and Salisbury Trench significantly higher overlap. A similar 'opposing' result (though not statistically significant) also applies to the two 'poor' sites, Milkham and Knightwood, with the latter showing greater overlap. Thus, no reliable general conclusion can be based upon these differences, as there is no finding consistent with either site 'quality' for roe or vegetational similarity of the sites (Chapter 4).

Table 6.7 *Indices of overlap (Pianka 1973) of habitat use by roe and fallow deer in the New Forest enclosed woodlands using data collected in this study*

Site	Winter	Spring	Summer	Autumn
Holmsley	0.32	0.35	0.56	0.41
Salisbury Trench	0.97	0.94	0.70	0.92
Shave Green	0.17	0.76	0.92	0.60
Milkham	0.30	0.76	0.69	0.67
Knightwood	0.63	0.77	0.64	0.81

It is also clear that the two deer species are expressing very different patterns of habitat selection: roe show distinct selection of habitats on the basis of the availability of forbs, whereas fallow tend to select grazing areas such as rides. Although both species avoided the food-depleted mature conifer stands in all seasons, they differed markedly in their selection of food-bearing mature conifer. Fallow avoided these habitats in a similar manner to the food-depleted mature conifer, whereas roe showed strong positive selection for them (especially over the winter but also to some extent through spring into summer). In winter and spring roe also selected food-bearing prethicket very strongly, which fallow tended to avoid in favour of the broadleaf woodlands. Most notably, roe made little effort to use rides, strongly avoiding them at most sites for most of the year, whereas fallow showed more consistent and strong selection of rides than of any other habitat type all year round. While both species selected broadleaf woodlands, for most of the year roe were again selecting them preferentially when they were food-bearing rather than food-depleted, a distinction not made by fallow. Both species selected all broadleaf woodlands more uniformly over autumn and winter.

As has been noted, the shared use of habitats within the inclosures of the New Forest does not form a complete study of habitat usage; both species make use of the Open Forest habitats, but roe would seem to do so to a far lesser extent than fallow (Chapter 3 analyses, and pers. obs.). The actual shared use of habitats for the Forest as a whole is likely to be rather less than that reported here.

Comparison of diets of roe and fallow

Complementary to these patterns of habitat use and selection are the actual dietary patterns of the two species. Data presented here are based upon the detailed studies from rumen content analyses carried out on New Forest fallow by Jackson (1977b). Jackson (1977b) reported that graminids form the major component of the diet in all months, varying from 21-33% over late autumn and winter to between 55-70% during spring and summer. Conifers, heather and some holly make up the bulk of the remainder of the diet from early winter through to spring, and some bramble is taken over autumn and winter. Other items such as ivy and bilberry are also eaten in small quantities over the year (but again slightly more over the winter), and broadleaf material is consumed to a moderate extent over the summer months.

This pattern may be compared with that for roe (Jackson 1980, and this study). Putman's (1986b) presentation of Jackson's (1977b, 1980) monthly data of the two species' diets, permits calculation here of indices of their seasonal dietary overlap at the start of the decline (1970 - 1973): winter (0.69), spring (0.32), summer (0.49), autumn (0.60).

The higher values for autumn and winter reflect the more diverse diet taken by fallow in those seasons, when they share a number of food species with roe. Indices of overlap between roe and fallow using present data for roe (Chapter 5) and Jackson's (1977b) data for fallow (adjusting the latter by removing 'fruits') are: winter (0.69), spring (0.27), summer (0.60) and autumn (0.65), i.e. slightly more overlap for summer and autumn.

However, this increase in overlap assumes that fallow diet has not changed substantially over the period of the decline. Recently published data for fallow diet in the New Forest from faecal pellet analysis (Putman, Culpin and Thirgood 1993) allows some test of this assumption. The diet of New Forest fallow deer reported by Putman *et al.* (1993) suggests that, when compared to Jackson's (1977b) study, fallow now take less conifer browse, heathers, bramble and moss, and may also have slightly increased their intake of graminoids (even after 'correcting' for fruits). Indices of overlap calculated using data from this study (Chapter 5) for roe, and for female fallow (as 70% of fallow seen within the inclosures were does), from Table 2 in Putman *et al.* 1993, suggest present day seasonal overlaps in diets between roe and fallow may be lower than over 1970 - 1973: winter (0.20), spring (0.14), summer (0.34) and autumn (0.34).

Although comparison here is between roe and female fallow, Putman *et al.* (1993) noted that, when comparing overall diets of male and female fallow, i.e. without regard to occurrence of the sexes in sympatry or otherwise, there were no significant differences between the sexes in month by month comparisons. The data presented by Putman *et al.* (1993) were from faecal pellets collected at 10 separate sites over 1988 - 1989, and may indicate that fallow, like roe, have adapted their diet over the past twenty years, perhaps also as a response to changes in relative plant species availabilities. One consequence of this appears to have been to reduce the total overlap in diet between the two deer species.

Site avoidance and interference between roe and fallow

As a final consideration of the ecology of the two species within the New Forest inclosures, we can consider briefly the evidence for whether the presence of either species at a site affects the use of that site by the other, and whether there is direct interference between the two species (as was suggested by Carne (1954) and Delap (1955)). From the transect data, the expected values of the number of transects on which (i) no deer were seen, (ii) only roe were seen, (iii) only fallow were seen, and (iv) both roe and fallow were seen, at any site were calculated from the overall frequencies with which roe and fallow were encountered. The observed values of (i) to (iv) were then compared against these using a χ^2 test for goodness-of-fit, with the null hypothesis that the presence or absence of either species has no effect of the presence or absence of the other. No test showed significance for any sites, whether by season or for the year (all tests $p > 0.3$). Thus there is no direct evidence that either species makes any attempt to avoid any site because of the other species. During the transect surveys, only two observations (both at Milkham) were made of the two species in close proximity; in each case the resident roe doe was feeding within 30 m. of fallow (on one occasion a group of four does, and on the other a fallow buck), and the two species were seen to observe but otherwise ignore the other.

Assessment of competition between roe and fallow deer

Based upon the comparison of habitat use and dietary patterns of roe and fallow in the New Forest, we can see that there is limited potential for competition between the two species according to the first two criteria of de Boer and Prins (1990). Their final criterion, that the shared resource should be limiting, is now considered. Assessment of resource availability is necessarily incomplete, as full knowledge of the vegetation availability within the individuals' ranges is not available. Most of the major items of the diet of fallow, i.e. grasses, heathers, conifer and (perhaps) holly, appear to be present in quantity in the New Forest. Acorns are also likely to be available in sufficient amount for both species, and in Chapter 4 it was suggested that compensatory use of broadleaf woodlands by roe did indeed appear to restore levels of use of that habitat to parity between good and poor sites. Neither holly nor ivy is a major item of roe diet, either before or after the period of the decline (Jackson 1980, and Chapter 5), and there was no evidence of stronger selection of these species at poorer sites. The item of most interest in this context is bramble, not only the former dominant item in the diet of the roe (Jackson 1980), but now in very short supply and still strongly selected by roe at all sites where it occurs (Chapter 5).

Jackson (1977b), reporting analyses carried out on rumina collected from November 1970 to March 1973, found that fallow took bramble in moderate amount between October and February (around 10% of dietary intake). It did not appear to be a preferred food item as it was not taken when more abundant in spring and summer (when it comprised 3-6% of intake). In their recent study, Putman, Culpin and Thirgood (1993), found bramble to be an even less significant item in the diet of fallow than reported by Jackson (1977b) - presumably reflecting its lower availability in the Forest. In contrast, roe still clearly try to maximise their use of bramble, making most use of it over the summer (Chapter 5) and would presumably use it all year if they could (Jackson 1980). The possibility remains that the increasing fallow population of the Forest may have taken a significant amount of the little bramble that is available, but if fallow take bramble in relatively low amounts simply as it occurs, it seems unlikely that it would have declined so dramatically. More likely, the decline of bramble would be expected in line with forest growth as reduced light levels reach the ground layer; we may also note that roe have declined in the King's Hat site and other areas within the same Forest beat over the past twenty years even in the relative absence of fallow (census data).

Other workers who have considered resource use by roe and fallow, have also concluded competition between the two species to be unlikely. Petrak *et al.* (1991), for instance, saw their resource use as complementary rather than conflicting. In an early study looking at roe, red and fallow in Scotland, Batcheler (1960) also felt that roe and fallow did not compete. He emphasized that the species (and also red deer) are characteristically associated with different developmental stages in commercial forestry. Roe numbers, Batcheler noted, increased in the later establishment / prethicket stage, and then declined, while those of red, and then fallow, increased during the thicket stage through pole and mature woodland development; indeed, fallow deer were specifically associated with areas of grasses and mature conifer (Batcheler 1960). For roe these associations between population numbers and forest growth stages have been confirmed (e.g. Loudon 1978, Ratcliffe and Petty 1986), and are also entirely consistent with the findings of this study.

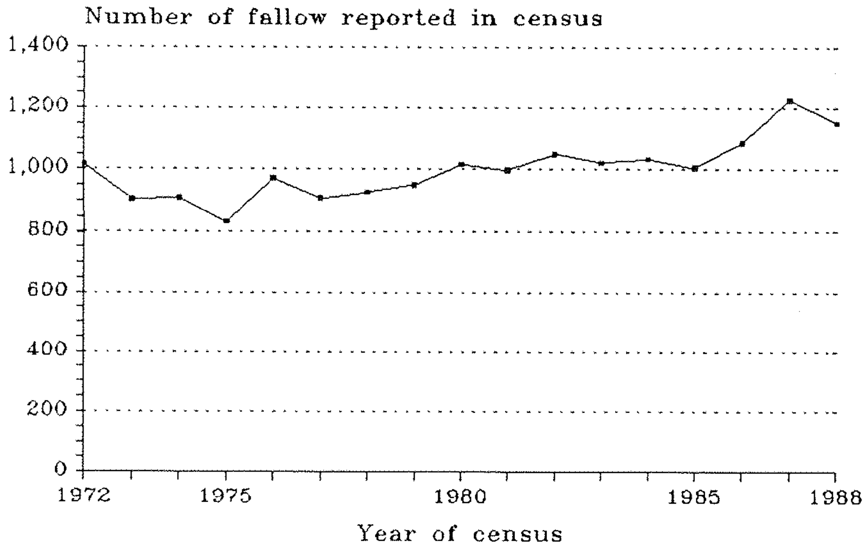
6.6 CHANGES IN THE FALLOW POPULATION DURING THE DECLINE IN THE ROE

The above evaluation of possible competition between roe and fallow has argued that any competitive interaction between the two species is likely to be minimal. It is therefore considered extremely unlikely that the presence of fallow deer has influenced to any significant extent the decline in roe numbers in the New Forest over 1972 - 1988. Yet there was, as noted, a highly significant negative correlation between temporal changes in the two deer populations over that period (Chapter 2). To be more certain that the change in the roe population was not in fact directly linked to the rise in fallow, we can seek a plausible alternative cause for this correlation. If it can be shown that the change in the fallow population over 1972 - 1988 can itself be related to other changes in the New Forest environment over the same period, then it can be argued that the correlation between the two deer population changes is the coincidental result of independent responses of each species to environmental changes. Thus, applying the methods described in Chapters 2 and 3 for roe, we can seek associations between fallow deer abundance and environmental characteristics in both temporal population change over the period 1972 - 1988, and differences in present day local abundance of fallow in relation to site vegetation.

Temporal change in the New Forest fallow deer population in relation to environmental characters

Census data for the period 1972 to 1988 for fallow deer in the New Forest were previously presented in Table 1.1, but for convenience are shown here graphically (Fig. 6.5.)

Fig. 6.5 Census data for New Forest fallow 1972 - 1988



Source: Forestry Commission census data (Table 1.1)

As already stated, these census data should be taken as an index of population change rather than as absolute population levels, which may actually be at least 2 or 3 times higher (Strange 1976, Putman and Sharma 1987).

Fallow deer numbers for the whole Forest over 1972 - 1988 correlated significantly negatively not only with roe (above) but with numbers of previous year's cattle ($r = -0.533$, $p < 0.05$), ponies ($r = -0.491$, $p < 0.05$), the number of cattle and ponies combined ($r = -0.618$, $p < 0.01$), and the accumulated number of cattle and ponies over the previous three years as 'recent grazing pressure' ($r = -0.593$, $p < 0.05$). The negative correlations of fallow with cattle and ponies are of interest: as noted, all of these species are predominantly grazers, and calculated dietary overlaps reflect this (Table 6.8, data from Jackson (1977b), Putman *et al.* 1981, quoted in Putman 1986b).

Table 6.8 *Indices of overlap (Pianka 1973) between seasonal diets of fallow deer and those of cattle and ponies in the New Forest*

	Winter	Spring	Summer	Autumn
Ponies	0.63	0.92	0.94	0.88
Cattle	0.65	0.96	0.94	0.86

Note: Seasons as defined in Putman (1986b) with winter (Nov-Jan), spring (Feb-Apr), summer (May-Jul) and autumn (Aug-Oct). Data as credited in text.

However, habitat usage overlaps between fallow and both cattle and ponies on the Open Forest are relatively low: fallow make more use of acidic than improved grasslands - although some shared use does occur (Edwards and Hollis 1982, Putman 1986a) - and much more use of both broadleaf and conifer woodlands. Indices of habitat overlap between fallow and the domestic stock are actually low, ranging between 0.06 - 0.50 (Putman 1986b). Putman (1986b) considered both habitat use and dietary overlaps of all of these species and concluded that despite high overlap in diet, actual competition was unlikely. Dietary overlap was highest when food availability was maximal (spring and summer) and food resources were not considered limiting; in time of lowest food availability, the fallow are able to adapt their diet to include more browse material, as might be predicted from their classification as more 'intermediate' feeders on anatomical evidence (Hofmann 1985).

At the beat level, census data for fallow are available only from the year 1976. These data do however, permit temporal correlation analyses to be carried out of fallow population change with a range of environmental characters, as described for roe in Chapter 2. (The criteria applied to the analyses in order to identify significant and consistent correlates were the same as those specified for roe in Chapter 2: there should be at least two significant correlations ($p < 0.05$) across the beats agreeing in sign, or one significant correlation must be supported by 9 or more of the 12 beats agreeing in sign (sign test equivalent $p <= 0.054$), and in either case none of the remaining beats should be correlated significantly with the opposite sign.)

Using data for the 12 Forest beats as replicates, correlation analyses were performed of numbers of censussed fallow deer over 1976 - 1985 against characters of the Forest inclosures' gross vegetational structure derived from the Forestry Commission forecasting model. These vegetation characters, fully described in Chapter 2 (Table 2.4), divided each of 7 tree 'species-groups' (Scots pine, other pines, firs, spruces, other conifers, oaks, and other broadleaves) into 5 height classes (<2m, 2-5m, 5-15m, 15-20m, >20m). Fallow numbers were found to be consistently and significantly correlated positively with the availability of mature (>20m) fir plantations (2 correlations at $p < 0.05$), and negatively with prethicket (2-5m) spruce (3 correlations at $p < 0.05$).

Investigation of fallow population changes by beat over 1976 - 1988 in relation to climatic factors over the same period (listed in Table 2.5) revealed additional correlations. The population of fallow over the period 1976 - 1988 was significantly and consistently correlated with three measures of climate, all from the 12 month period immediately prior to the April census: negatively with immediately previous February rainfall (9 of 12 beats, two at $p < 0.05$), and positively with both mean temperature over May - June (10 of 12, two at $p < 0.05$) and April rainfall (9 of 12, one at $p < 0.05$).

April rainfall appears to promote grass growth and increase plant biomass (Roberts and Dunbar 1991), and influences birth weight of calves in red deer (Albon, Guinness and Clutton-Brock 1983, Albon, Clutton-Brock and Langvatn 1992), and this may also apply to fallow. Vegetation growth may be further promoted by warmer May-June temperatures, and adversely affected by heavier February rain, which may act through waterlogging (as suggested by Putman and Langbein 1992). Examination of the climatic pattern over the period 1972 - 1988, suggests few consistent trends and much 'noise': only two climatic variables show significant regressions with time over the period. Total annual rainfall (positive) and mean temperature over January - February (negative) ($p < 0.05$ in each case); a positive but weak (insignificant) trend was found for April rainfall. Thus, as in the case of roe, while there may well be some yearly influence on fallow deer numbers by climate, there is no strong evidence that climate change has influenced any trend over the longer term.

Spatial association between fallow habitat occupance and vegetational characteristics

Correlation studies were also carried out exploring spatial association between present day fallow deer distribution and habitat characters, using detailed field data for both the inclosures and the Open Forest, as described for roe in Chapter 3. As fallow range widely and are not as obviously attributable to specific sites as are roe, estimates of local populations are taken from the number seen at each site during the transect studies. However, the census figures for fallow at the level of the whole beat were used for correlation analyses against characters of the Open Forest using the English Nature Open Forest survey data; although fallow movement between beats does occur, it is proportionately less than between sites, and beat census data remain the best available of spatial distribution of fallow over the Forest.

For the enclosed woodlands, as before (Chapter 3) analyses were carried out based on three sets of characters describing the Forest inclosures:

(i) woodland categories closely equivalent to those used in the previous (temporal) investigations i.e. tree species groups by specified height classes (as in the temporal analyses described above)

(ii) characters of the ground vegetation (Table 3.2)

(iii) habitat types composed from features of the woodland, shrub and herb layer in combination (Table 3.3).

Significant and corresponding correlations emerged between fallow deer numbers and habitat characters from all three analyses (Table 6.9); it is emphasised once again, however, that these analyses are based upon the same data, and are very much 'alternative views' rather than independent and complementary studies.

Table 6.9 *Significant correlation results from spatial analyses of fallow use and vegetation of sites: (* denotes 0.01 < p < 0.05; ** denotes p < 0.01).*

Site character	Correlation coefficient
(a) Gross habitat characters	
Scots pine > 20 m.	0.902 *
Other pines 0-2 m.	0.897 *
Oaks 0-2 m.	0.865 *
Other conifers > 20 m.	0.865 *
(b) Characters of ground vegetation	
Availability of grass (excl. *Molinia*)	0.873 *
(c) Composite habitat types	
Mature conifer with bracken	0.922 **
Mature broadleaf with bracken	0.905 *
Rides	0.930 **

It can be seen that, of the 'simple woodland' categories (i), a pattern of positive correlations was found for open 'establishment' areas (both broadleaf and conifer) and also pole-stage conifer. Of the vegetational features of the ground level, only the available area of grasses (excluding *Molinia*) correlated significantly positively, a result repeated by the significant positive correlation with the 'rides' habitat type. Two other habitat types gave significant positive correlations with fallow usage, mature conifer with bracken and mature broadleaf with bracken. Taking these results together, we can note the association between fallow and grass availability (principally on rides), and mature woodland.

The results from both temporal and spatial analyses show good agreement. Importantly, they are supported in good measure by the studies on habitat use and selection described earlier (Section 6.5). Rides were the most consistently and strongly selected habitat type in the inclosures, and available broadleaf woodland was also selected to a moderate extent (but strongly over winter.) Mature conifer was not found to be selected, though it did appear to be used for cover. Chapman and Chapman (1980) noted that in England, broadleaf woodland was the typical fallow habitat, although the species occurred in a diverse range of habitat types. Results from this study agree, also showing that mature conifer is readily used but not as strongly selected as broadleaf woodland. The rides within the New Forest inclosures provide a significant amount of grazing in addition to that provided by the Open Forest. From the inclosure surveys described in Chapter 3, rides make up some 5% of the total inclosure area. They vary widely in vegetational composition but, on average, bear some 37% grass cover (excluding *Molinia*). Thus, given some 8640 ha. of enclosed woodland, rides give some 160 ha. of grassland, equivalent to almost 15% of the improved grasslands on the Open Forest. Further grazing in the inclosures is also available on establishment / clear-felled areas and patchily within the other woodlands, and in total, we may reasonably estimate the additional grazing provided within the inclosures at a minimum of 200 ha., much of which is of good quality, and thus forms a significant addition to the grasslands of the Open Forest.

For the Open Forest, using the data from the English Nature survey and their defined Open Forest habitat types (Table 3.4), censussed fallow numbers correlated significantly positively with bracken-bearing dry heathland ($r = 0.647$, $p < 0.05$) and closed-canopy Scots pine woodland ($r = 0.711$, $p < 0.01$).

While no independent confirmation of the value of these characteristics of the Open Forest to fallow is available from the present study, this result shows agreement with the work of Chapman *et al.* (1985), who found the presence of mature forest (Scots pine in particular) the best single predictor of fallow distribution in the compartments of the King's Forest, Suffolk, and with Batcheler (1960), who also noted that fallow appeared to select Scots pine areas at Drummond Hill, Scotland. The spread of Scots pine on the Open Forest has been identified as a consequence of the decline in commoning over recent years by the New Forest Review Group (1988). While the evidence remains circumstantial, it may be that fallow have been able to benefit from an increase in cover (and winter browse?) from the Open Forest Scots pine, the lack of which could have been one factor acting to restrict the rate of spread of fallow. This may, for instance, explain the comparative absence of fallow until recently from King's Hat, which is somewhat isolated from other inclosures. If true - and it should be stressed that this scenario is proposed tentatively - then it may be that it is the increase in forest cover, rather than the fact that Scots pine is the species involved, which is significant: re-analysing the habitat use of fallow within the inclosures from this study for pole-stage and mature conifer woods divided into 'Scots pine' and 'all other conifers' showed no significant preference by fallow for the former over the latter.

6.7 CONCLUSION

Consideration of overlaps in range, habitat usage and diet has suggested that there is only limited potential for competition in the New Forest between roe and four of the other large herbivores species (cattle, ponies, red deer and sika deer); in the case of fallow deer, however, the evidence at first appeared to be less clear. While both roe and fallow share the whole Forest range, the populations of both species over the period of the decline in the roe (1972 - 1988) appear to have been affected by changes in their vegetational environment. Changes in both the woodland structure and the associated ground vegetation in the New Forest inclosures have influenced both species, although each has responded to quite distinct aspects of that change. Climatic influence appears to have an impact on numbers of both species on a year-by-year basis, although the two species are impacted by different factors, presumably mediated via vegetation. However, none of the climatic variables found to be correlated with changes in either species has itself demonstrated a significant trend over the period of the decline. Roe have suffered through lowered forage availability (especially of bramble) throughout the inclosures, most likely brought about following canopy closure in an increasing mature forest profile, and the lack of early stage (prethicket) woodland which offers both forage and shelter. Fallow, by contrast, have benefitted by increasing cover availability in the maturing woodlands, an ample supply of grazing in close proximity within the inclosures, and possibly by the additional Scots pine regeneration on the Open Forest permitting an increase in range and more ready access to previously unfrequented inclosures.

7. BODY CONDITION AND REPRODUCTIVE SUCCESS OF NEW FOREST ROE

Chapter summary

This chapter presents evidence of how food limitation on the New Forest roe may have affected individuals so as to effect the observed reduction in population performance. Data available were limited to body weights and measures of reproductive success of culled New Forest does, which were compared with animals culled in two neighbouring areas which have healthier roe populations, Ringwood Forest and Roydon Woods.

New Forest does were found to have a significantly lower mean body weight than does from either Ringwood or Roydon.

No significant differences were found between New Forest roe and those from the other areas in either the proportion of does ovulating successfully or the mean number of ovulations per doe. A significantly lower proportion of New Forest does were found, however, to be pregnant when compared to Ringwood does (65% and 81% respectively), and (though not statistically significant) New Forest does had fewer foetuses per pregnant doe.

The censussed New Forest fawn:doe ratio over 1976-1988 was also examined. No significant difference between years was found. Between beats however, there was a significant difference in the fawn:doe ratio of two beats (N3 and N5) and, consistent with this, a strong significant positive rank correlation of the fawn:doe ratio with beat roe density with respect to area of enclosed woodland. This was interpreted as resource depletion having resulted in both lower reproductive success (which, it is speculated, may be combined with higher fawn mortality) and lower roe densities.

7.1 INTRODUCTION

In earlier chapters, we have seen that changes in the New Forest roe population over time, and local variation in the roe population density over the present day Forest, may be associated with corresponding changes in habitat quality and resource availability. Such a response by a population to differences in resources must be mediated through changes in one or more of the rates of immigration, emigration, births or deaths. This chapter examines the evidence available to see if it is possible to determine which of these may be implicated in the decline of the New Forest roe population.

Unfortunately, data are not available either on movements of individual roe in the New Forest, i.e. on immigration or emigration (including normal dispersal), or on adult mortality, and so these cannot be directly examined further. However, data are available on the body weight and reproductive status of female roe culled in both the New Forest and other nearby areas (collected as part of normal management practice) and these allow comparison of body condition and reproductive success between roe from the New Forest and these other forests.

Previous workers have used the persistence of *corpora lutea* within the ovaries of roe as evidence of fertilisation, on the basis that these bodies persist only when the released ova have been fertilised (Borg 1970, Strandgaard 1972b). However, Aitken et al. (1973) pointed out that although persistence is extended following fertilisation, the *corpora lutea* may remain for 5 months whether or not the animal is pregnant. Thus, the presence of *corpora lutea* in a doe killed during the open season (November - February) may be taken as evidence of sexual maturity or fertility (i.e. capacity for ovulation), though not necessarily of fertilisation. Implantation of the embryos themselves takes place around the end of December, and in southern England most births occur around late May and early June (Prior 1968).

In deer, as in mammals generally, body weight (or condition) appears to be a crucial factor influencing both reproductive performance and mortality. The achievement of a certain critical, or threshold, body weight is essential for the onset of sexual maturity: see review for mammals by Frisch (1984), with instances from deer, red: Hamilton and Blaxter (1980); moose: Sæther and Heim (1993); reindeer: Reimers (1983), Skogland (1983);

white-tailed: Verme (1969); fallow: Langbein and Putman (1992b); roe: Loudon (1987). However, Bronson (1989) cautioned about assuming any simple relationship between body weight and the onset of sexual maturity, noting that, in practice, the actual threshold weight required for sexual maturity in a given population may be a complex dynamic function of body weight, density and age. Indeed, in roe, as in red deer (Clutton-Brock and Albon 1989), this threshold value has been shown to vary between populations and with age-class. Hewison (1993) found variation in threshold body weights across his 15 study sites, with fawns at some better sites even heavier, on average, than yearlings and even adults at other, poor performance sites. However, while roe fawns may occasionally become sexually mature and conceive (Borg 1970, Ratcliffe and Mayle 1992), such pregnancies are rarely successful (Hewison 1993).

After puberty, body weight may continue to play an important role in determining fecundity in deer, affecting the frequency of ovulation and thus of breeding, e.g. in red: Mitchell (1973), Hamilton and Blaxter (1980), Albon, Mitchell and Staines (1983); reindeer: Reimers (1983), Skogland (1985, 1985); moose: Sæther and Haagenrud (1983); white-tailed: Mundinger (1981), Ozoga and Verme (1982), Ozoga (1987). In multiparous species, such reduced ovulation may constrain actual or potential litter size (white-tailed: Ozoga and Verme 1982; roe: Blant 1987).

Many studies have also reported the importance of body weight in survivorship, both in juveniles (white-tailed deer: McCullough 1979; red: Clutton-Brock *et al.* 1982, fallow: Putman and Langbein 1992) and adults (mule deer: Klein and Olson 1960; white-tailed: Cook 1984; red: Clutton-Brock *et al.* 1982; roe: Gaillard 1988, quoted in Gaillard *et al.* 1993b). Thus, in addition to its role as a direct contributor to differences in reproductive success of roe between forests, the data available on body weight for this study allow a (speculative) assessment of its potential effect on mortality.

As has been noted, the data available in this study are restricted to information collected as part of normal management practice, either from culled animals (body weight, numbers of *corpora lutea* and implanted embryos), or from the annual census carried out in the spring on the New Forest roe (numbers of fawns and does in each beat). From these data the following questions may be addressed.

(i) Do roe from the New Forest differ from those of neighbouring forests in body weight?

(ii) Do roe from the New Forest differ from those of neighbouring forests in apparent reproductive performance (specifically with respect to success of ovulation and implantation), and if so are the differences significant after allowing for differences in bodyweight between populations?

(iii) Is there any evidence from the census returns of changes in the fawn:doe ratio in the New Forest over the period of the decline, or of differences in the fawn:doe ratio between beats? If so, in the latter case, do these differences correspond to differences in overall roe densities for the beats or with beat 'quality'?

7.2 METHODS

The study areas

Within the New Forest no comparisons of body weights, or of ovulation and implantation rates for roe between 'better' and 'poorer' sites are possible, as cull records do not record the precise locality of the kill. Such comparisons can only therefore be carried out between roe from the New Forest and other areas. Only local forests were chosen for comparison with the New Forest in order to minimise likely differences in roe population characters from genetic or climatic causes. Appropriate data from two such nearby areas were made available for this study; although other local estates with roe were contacted none appeared to keep comparable data on culled deer.

The first, Ringwood Forest, is situated approximately 3 km. to the west of the New Forest and covers an area of 3650 ha. About one-third of this is in private ownership, and the rest is managed by the Forestry Commission, with some 95% of it devoted to Scots or Corsican pine woodland and the remainder to oak forest. Woodland management practices at Ringwood differ from those in the New Forest inclosures, with more clear-felling and replanting of stands, resulting in a more mixed-age forest profile.

The second area, Roydon Woods, is a 380 ha. nature reserve owned by the Hampshire and

Isle of Wight Naturalists' Trust and located to the south-east of Brockenhurst; the reserve actually adjoins the Forest land at several places. It consists mainly of broadleaf woodland, much of which is ancient in character, with some open pasture and heathland and a small amount of coniferous woodland. The area harbours red, sika and fallow deer in addition to roe (Boxall 1990).

Unfortunately, no census data for roe are available for either Ringwood or Roydon, but both support substantially higher density roe populations than are found in the New Forest.

Data on body weights, ovulation and pregnancy rates

Data on every adult female roe culled at all three forests were collected by the responsible keepers (in this context including rangers and warden) during the subsequent processing of the carcasses. For this study the term 'adult' includes yearlings but excludes fawns: more specific details of age were not available (the precise mix of yearlings and older adults in any cull is unrecorded). The data recorded included the date shot, the animal's clean weight (i.e. as shot, less viscera but head and feet on), number of *corpora lutea*, and number of embryos present. For this study, cull data for both the New Forest (1982-1984) and Ringwood Forest (1983-1990) were made available by the Commission's research branch at Alice Holt, and for Roydon Woods (1984-1990), from the personal records of the reserve warden, Mr. M. Boxall. From the cull data it was possible to derive measures of reproductive success for each forest by year as

(i) percentage of does ovulating
(ii) percentage of does carrying embryos
(iii) mean number of ovulations per doe
(iv) mean number of embryos per pregnant doe.

For assessment of (ii) and (iv), the number of embryos, only deer shot after the end of December were included as implantation may not have occurred earlier. Data available are summarised in Table 7.1; the quantity of data varied between forests and, as noted earlier, few roe have been culled in the New Forest in recent years precisely because the population has been declining.

Table 7.1 *Sample sizes for deer culled at three forest sites*

Year	19-	82	83	84	85	86	87	88	89	90
New Forest		20	13	5	-	-	-	-	-	-
Roydon		-	-	6	10	1	5	1	2	4
Ringwood		-	30	25	21	23	31	21	18	25

All data presented here are for female roe only, shot during the open season for does from November to February. A preliminary regression analysis showed no significant regression of clean body weight against date shot within season ($r = -0.003$, $p > 0.2$), so all further analyses have ignored the actual date of death. In addition, a preliminary analysis of variation in both clean body weight and reproductive success between years within each forest showed no significant differences (for all forests: $p > 0.05$) and so analyses presented below are also based on data for all years combined.

Censussed numbers of fawns and does

In addition to data from culled roe, the New Forest census returns specify the number of adult does and number of fawns (actually 10 - 11 months of age) at the time of the census count. This allowed the calculation of the mean fawn:doe ratio for each of the Forest's 12 beats for each year from 1976 - 1988, giving a further measure of recruitment rate combining rates of both actual births and neonatal survival.

Data analyses

One-way ANOVA (Sokal and Rohlf 1981) was used to investigate differences in fawn:doe ratio within the New Forest, both between beats and between years, and contemporary differences in clean body weights between forests. The Scheffé procedure for multiple comparisons was used to determine pairwise differences between forests.

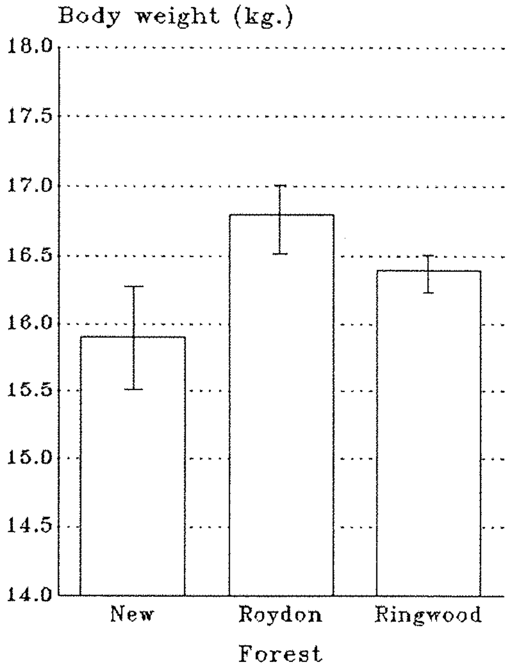
Differences in reproductive success between forests, carried out separately based on the mean number of ovulations and implanted embryos, were investigated by two-way ANOVA using clean body weight as a covariate (as differences in reproductive success may be due in some measure to differences in body weight alone).

7.3 RESULTS

Differences in body weight of roe between forests

The clean body weight of roe does culled within the New Forest was found to be significantly less than those from either Ringwood or Roydon ($p < 0.05$); roe from Ringwood and Roydon were not significantly different (Fig. 7.1).

Fig. 7.1 Mean clean body weights of roe from three forests



Bar lines show standard errors

Differences in reproductive success of roe between forests

Roe does at all three forests achieved an extremely high level of ovulation in all years. No significant differences were found between forests in the percentage of adult does ovulating, with over 99% of adult does ovulating in each location (all years combined). Neither were significant differences found between forests in mean number of ovulations per doe, whether or not bodyweight was used as a covariate: $p > 0.05$ in all cases.

However, significant differences were found between the percentage of adult pregnancies occurring in the New Forest (65%) compared with Ringwood (81%); F=6.68, p=0.011. The mean number of embryos per pregnant doe also found to be lower in roe from the New Forest (1.59) than roe from both Roydon (1.67) and Ringwood (1.68), but was not statistically significant (F=1.47, $p>0.05$): however, inspection of the results suggests that the lack of significance may be due to limited data availability as the pattern agrees with those seen for both bodyweight and percentage pregnancies. Thus, does in the New Forest do appear to have a lower probability of becoming pregnant than do does from 'better' areas, and may also suffer a lower mean number of embryos per doe (Table 7.2).

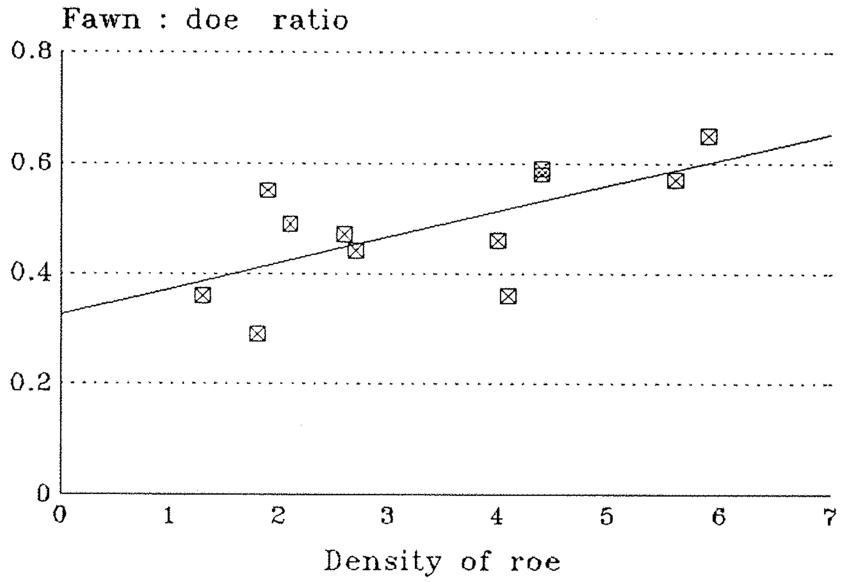
Table 7.2 *Mean numbers of ovulations per adult doe, embryos per pregnant adult doe, and overall percentage of adult does pregnant, at three forest sites*

	Ovulations per adult doe		Embryos per pregnant doe		Percentage pregnancies
	Mean	*SE*	*Mean*	*SE*	
New Forest	1.78	0.08	1.59	0.11	65
Roydon	1.70	0.12	1.67	0.13	71
Ringwood	1.80	0.04	1.68	0.05	81

Differences in fawn:doe ratio between years and beats

No significant difference was found in the fawn:doe ratio within the New Forest between years over 1976 - 1988 (F=1.12, $p>0.3$). When examining differences between beats however (using annual data over 1976 - 1988 as replicates), a significant difference was found between beats N3 and N5 ($p<0.05$), the former having a greater mean value (0.70, SE=0.13) compared with beat N5 (mean of 0.29, SE=0.04). The two beats have mean overall roe densities of 5.9 and 1.7 roe per 100 ha. of enclosed woodland respectively (1986 census data). As a check on this result - which may have emerged as a chance occurrence from the high number of comparisons between beats - a Spearman rank correlation analysis of the fawn:doe ratio with overall beat roe density was carried out (based on the mean beat values over 1976 - 1988). This showed a significant positive result, $r_s = 0.653$, $p < 0.05$, suggesting that, overall, does in 'better' beats within the Forest do have relatively more fawns entering the yearling phase (Fig. 7.2). It should be noted that, although Fig. 7.2 may appear to show that performance in the roe population increases with density i.e. that the population is not subject to density-dependence, it is actually a reflection of the fact that resource-depletion has resulted in both a lower density of roe and a lower fawn:doe ratio (through greater suppression of performance).

Fig. 7.2 Fawn:doe ratio against beat density of roe



Density as mean number censussed per 100 ha. enclosed woodland

7.4 DISCUSSION

In a wide-ranging and detailed study of factors affecting reproductive performance in 15 roe populations across Britain (using the same measures of ovulation and implantation as used in this chapter), Hewison (1993) looked at variation in reproduction in relation to age, body condition, habitat quality and climate. Ovulation was extremely high in adults and very high in yearlings at all sites, but, across sites, variation in yearling ovulation rate was influenced to a degree by mid-winter temperature. Fawns achieved sexual maturity at some sites, but were only rarely successful at implanting foetuses. Hewison (1993) found that, within populations, maternal body weight was the major factor affecting differences in reproductive success, both between age-classes and between years, confirming a threshold pubertal body weight in roe (Loudon 1987) but one which varied between populations. In addition, analysis of differences in reproductive performance between populations suggested that, although body weight continued to be of significance, both the proportion of animals implanting foetuses successfully (both adults and yearlings) and the average number of foetuses per pregnant doe (again in both adults and yearlings, but especially in the latter) were influenced by winter temperature or rainfall; indeed, Hewison (1993) found that climatic factors supplanted body weight in yearlings as the primary influence on successful implantation. Hewison's findings are detailed further in Chapter 8 of this report.

Results from the present study are consistent with Hewison's findings. Body weight of roe from the New Forest were found to be significantly less than from neighbouring forests, most likely attributable to poorer resource availability (Chapters 4 and 5). Both the high percentage of does ovulating and the mean number of ovulations per doe observed in the New Forest agree with the range of rates reported by others (Gaillard *et al.* 1992, Hewison 1993), and do not appear to be substantially affected by the reduction in bodyweight. However, the percentage of New Forest does successfully implanting embryos (65%) was just beyond the lower end of the range for adult does (67% - 94%) and lower than that for yearlings at all but four of Hewison's (1993) Scottish / northern England Forestry Commission sites (with at least 10 individuals' data), as well as being significantly lower than that at Ringwood (81%). Similarly, the mean potential litter size for does (number of embryos per pregnant doe) in the New Forest was lower than (though not significantly different from) those in the neighbouring populations. While these comparisons show that the New Forest population is one of poor performance, the lack of age-class data for the Forest limits full quantitative assessment.

However, these results are necessarily based on the limited data available, and they may well be underestimating the difference between the New Forest and neighbouring areas of better habitat quality for roe. Firstly, as a consequence of the declining population, data from the New Forest only represent roe from 'better' localities within the Forest, and may include peripheral animals that spend some time off the Forest. No animals are culled in poorer quality sites, where roe may suffer further reduction in body condition. Secondly, as the population levels at both Ringwood and Roydon are unknown, the possibility remains that reproductive success at either forest, or both, is itself suppressed through density-dependent effects, as has been reported in roe and other cervids (discussed further in Chapter 8.)

Reduced body condition in adult females may also have important consequences for survival as well as reproductive success. In red deer, for instance, calf birth-weight is related to the weight of the mother in the spring (Clutton-Brock *et al.* 1982), and lower weight calves have higher mortality rates both in their first summer (Guinness *et al.* 1978) and in their first two winters (Clutton-Brock *et al.* 1982). In white-tailed deer, Verme (1963, 1967, 1969, 1977) also showed that the nutritional plane of an adult doe, especially in the later stage of pregnancy, greatly influences foetal growth and its survival at birth. Thus, low birth weights in roe may be expected to result from poor maternal body condition either through under-nutrition of the foetus(es) during the latter stages of pregnancy (Sadleir 1969), or insufficient milk production by does, or both. Lactation makes extremely heavy energy demands on the mother (Pond 1977, Hanwell and Peaker 1977, Loudon 1985), females with lower fat reserves produce less milk (in caribou: Allaye-Chan and White 1992), and demands on milk production are heaviest in polytocous species (Kirkwood 1981) such as the roe. Ellenberg (1978) considered that population regulation in roe occurred largely through maternal body condition in spring / summer affecting subsequent post-natal mortality; even healthy populations may suffer heavy losses (50% - 65%) at that time (Ratcliffe and Mayle 1992). The agreement between the fawn:doe ratio and roe density over the 12 Forest beats may further suggest that fawn / juvenile mortality may be a significant mechanism through which population decline has been effective in the New Forest, with roe in the poorer beats tending to have a significantly lower proportion of their fawns entering the yearling phase.

Gaillard *et al.* (1993b) noted a ‘critical stage’ for juvenile roe, after which their survivorship was similar to that of adult roe. The length of the critical stage differed between Gaillard *et al.*’s (1993b) two study populations, at Trois Fontaines and Chizé (described in Gaillard *et al.* 1993b). Juveniles at Trois Fontaines (where roe were at lower density) had a critical stage of under 8 months (the youngest age studied), and had a mean body weight at that age of 69% that of adults. Eight month old juveniles at Chizé, by contrast, had a mean body weight of 61% adult weight, and a critical stage of 20 months. The New Forest is, as noted, a poor quality habitat, and we may expect roe to develop more slowly (i.e. have a longer critical stage), with correspondingly lower survivorship in juveniles than in adults, although this does not exclude high post-natal mortality occurring as well. It is, of course, the cumulative effects of lowered recruitment (percentage pregnancies, potential litter size) and survival (post-natal, late juvenile) which may result in a net population decline. Population regulation in roe is discussed further in Chapter 8, and another possible consequence of reduced body condition (an increase in parasite load) is explored further in Appendix 2.

8. FINAL DISCUSSION

While the main purpose of this study has been to identify environmental factors limiting the performance of the New Forest roe population over 1972 - 1988, the study's wider interest lay in analysis of how those environmental factors might influence the dynamics of roe deer populations more generally, and how population performance may be related to individual performance. Such an examination must, of course, be set within the context of current knowledge of the population dynamics and reproductive biology of this and other deer species.

In any such analysis it is important to make clear distinction between those factors limiting population size, and those regulating numbers to that level. The terms 'limiting' and 'regulating' are here used after Messier (1991). All factors which affect population growth may be termed *limiting*, and they may act either stochastically or in some density-related manner. The effect of a subset of those factors may be to tend to stabilise the population level within certain limits, i.e. by depressing population growth more strongly as density increases. Such factors are termed *regulating*, and are of necessity *density-dependent* (Howard and Fiske 1911). In contrast, as emphasized by Sinclair (1989), the other, or *density-independent* factors (Andrewartha and Birch 1954) may affect the *persistence* of animal populations, but cannot contribute to regulation. In practice, over a period of time the actual dynamics of a given population may well be constrained by either type of factor, or by a combination of both, to determine the actual population distribution and abundance.

The influence of specific factors of either type on the dynamics of populations in any situation may not be independent of the actual population density; for instance, the effects of density-independent factors could, by chance, be crucial on populations at low density (Lawton 1991). In large mammals in particular, a relationship with population density may also be a consequence of social organisation (Clutton-Brock and Albon 1985), perhaps mediated through stress (e.g. Woolf and Harder 1989). The effect may be manifest, for example, by a depression of reproductive performance in yearlings despite adequate food availability (Ozoga and Verme 1982), or by changing patterns of juvenile dispersal (e.g. in roe: Bideau *et al.* 1993). Similar considerations of density may also apply to the impact of diseases (McDiarmid 1978). By far the most common causal factor of regulation in large mammals is food-limitation (Sadleir 1969, Laws 1981, Fowler 1987, Sinclair 1989), and this may affect populations across a wide range of densities, as it is primarily the food available per individual to which those individuals respond (Klein 1970, Klein and Strandgaard 1972).

Where animals are food-limited, i.e. occur at high density relative to the available or accessible resources, many studies have documented an impact on growth or body weight (e.g. in deer: white-tailed: Cook 1984, McCullough 1985; sika: Kaji *et al.* 1988; red: Albon, Mitchell and Staines 1983, Staines 1978; reindeer: Reimers *et al.* 1983; and roe: Klein and Strandgaard 1972). As noted in Chapter 7, body weight in turn is a crucial determining factor in deer of both reproductive performance and survivorship (e.g. Mitchell and Brown 1974, Reimers 1983, Verme 1969, McCullough 1979, Loudon 1987, Putman and Langbein 1992, and others cited in Section 7.1).

In the present study the data available on body weight and reproduction of New Forest does were presented in Chapter 7. These data showed that, in comparison with roe from neighbouring forests, New Forest animals had a significantly lower body weight and lower reproductive performance, expressed by a significantly lower proportion of New Forest does becoming pregnant. While some of this latter difference was attributable to the differences in body weight, when allowance was made for this the difference remained very close to being significant (with $p=0.07$).

Beyond such 'local' comparisons, the findings from the present study on a declining roe population may be more fully evaluated in the context of Hewison's (1993) investigations into the mechanisms through which reproductive performance in roe may be limited. Hewison examined reproductive performance in roe does across 15 sites spanning almost the entire latitudinal range, and therefore environmental conditions, of Britain; he looked particularly at variation in reproductive performance in relation to maternal age, body weight, habitat quality and climate. Measures of performance considered by Hewison were those used in the present study (Chapter 7), i.e. percentage ovulation, mean ovulations per doe, percentage pregnancies and mean number of foetuses per pregnant doe. Hewison's data were derived from deer culled by Forestry Commission rangers (9 sites) and Ministry of Defence stalkers (6 sites) over a number of years (range 6 - 21). Using these extensive data sets, Hewison analyzed reproductive performance for: fawns (<12 months), yearlings (12-24 months) and adults (>24 months) as separate age-classes, having previously confirmed that variation in reproductive performance within the adult age class was not significant (as also reported by Gaillard *et al.* 1992). In the present, New Forest, study data on reproductive performance of yearlings and adults were not available separately.

In virtually all of Hewison's sites the proportion of adult animals ovulating was close to 100% - as was also found for New Forest animals - and for yearlings was between 92% - 100%. At any one site, average body weights of yearlings and adults were within 15%, and differences between ovulation rates within sites could be attributed to differences in body weight. Thus in roe, once sexual maturity has been achieved, does continue to ovulate each year. In the New Forest the mean number of ovulations per doe (a measure of potential litter size) of 1.78 was very close to that for Ringwood (1.80) and higher than that for Roydon (1.70). Hewison reported a range of approximately 1.27 - 2.18 for adult does across his Commission sites, and found a significant positive correlation with body weight, which also emerged as the principal explanatory variable of differences in 'mean ovulations per doe' between yearlings and adults. Hewison also found some association between ovulations per doe and habitat quality in year of birth within sites (as reflected by mandible length or diastema height), but the relationship was not consistent across sites. The pattern of variation between sites, however, showed a clear positive association between mean ovulations per doe and site quality (reflected in body weight) for both adults and yearlings, suggesting an influence of habitat conditions upon potential litter size; the value for the New Forest deviated only minimally from the trend identified by Hewison (1993). Hewison did not find a direct significant relationship between site population density and ovulation rate.

In the New Forest roe both the percentage of does implanting successfully (65%) and the mean number of foetuses per pregnant doe (1.59) were lower than in Ringwood - 81% and 1.68 respectively - although in the latter case the difference was not significant. Values for the same measures across Hewison's sites were (for only those sites with a minimum of 10 animals' data): 35% - 96% for percentage of yearlings implanting and 67% - 94% for adults, and a range of 1.12 - 1.98 foetuses per pregnant adult doe. (High values for percentage pregnancies were also reported by Gaillard *et al.* (1992), with 87% of yearlings and >98% of adult does pregnant at Chizé.) The low proportion of New Forest does implanting foetuses, as a population limited by its food supply to the point of population decline, is consistent with Hewison's suggestion that there might be a density dependent effect on the proportion of adult does becoming pregnant. There is the need for a caveat, however, in that the data for the New Forest are not age-class specific: Hewison's data for yearlings (range 35% - 96% implanting) are more variable. It may be, however, that the cull sample from the New Forest does indeed consist wholly or largely of adult does. Klein (1970) argued that there may be a change in the age structure of a deer population towards a higher proportion of adults in poor quality range, as both production and survivorship of fawns decreases; this may be made slightly more pronounced by an increase in longevity of individuals as a result of a reduced food supply (Wood, Cowan and Nordan 1962).

Whether the low body weight of New Forest roe has also reduced the average number of foetuses implanted per pregnant doe is unclear from the data available. Hewison found some evidence for a density-dependent effect on this parameter in yearlings but not in adults, and also noted that body weight was a significant contributory factor to variation in the average number of foetuses per doe. The effect of low body weight on litter size in the New Forest, if any, appears slight.

Climate was shown to have a significant association with year by year changes in the New Forest roe population, but, as there was no evidence of a strong climatic trend over the period of the decline, the climatic change was not considered in itself to be an important factor responsible for that decline (Chapter 2). The influence of those climatic factors which were most significantly associated with changes in the roe population in the New Forest was also considered more likely to act through vegetation availability (that is, mediated through body weight) than directly.

Hewison (1993) also looked at variation in reproductive success in relation to climatic variation. He found no significant relationship between climate and ovulations per doe for adults, but for yearlings did find significant associations between both the proportion of does ovulating and ovulation rate with a number of climatic factors, in particular with the mean monthly mid-winter temperature. Hewison suggested that yearlings, being closer to the threshold weight for ovulation, may be more sensitive than adults to climatic influence. At the time of implantation, over mid-winter, direct effects of climate were apparent on both yearlings and adults, even after allowance for the effect of body weight. Climatic factors supplanted body weight as the primary variables accounting for variance in the proportion of does implanting (mean mid-winter temperature in adults, winter precipitation for yearlings), suggesting an impact on the animals' thermoregulatory requirements. The average number of foetuses per pregnant doe was associated primarily with body weight (and thus habitat quality) in adults but, in yearlings, the mean mid-winter temperature again emerged as a more significant explanatory variable.

While a significant positive correlation between changes in the New Forest roe population over 1972 - 1988 and mean winter temperature was found in this study, this is not interpretable as a reflection of Hewison's result that the mid-winter temperature affected reproductive performance. In the present study, the correlation was obtained between the total (April) population and the immediately previous winter, not that of two years ago. No significant result emerged in this study when either the number of roe in total, or the number of yearlings censussed, were correlated with mean winter temperature of two years ago. Indeed if, as suggested, there is a high proportion of adults in the New Forest roe population, then only a limited effect would be expected from direct climatic influence. It may also be worth reiterating that from multiple regression analyses, described in Chapter 2, the influence of vegetation change upon the New Forest roe population was far more pronounced than that of any climatic factor directly. Further, any direct effect by climate on population performance through pregnancy rates of New Forest roe may be masked by subsequent events such as juvenile mortality or emigration. We have already seen that ratios of fawns:does in the Forest, as derived from April census data, are very low (range 0.29 - 0.70 across beats); while this may reflect low reproductive rates, it also prompts the question about what other mechanisms of population change may be operating in the New Forest roe.

Hanks (1981) proposed a modification of Eberhardt's (1977) sequence of events which could be used as measures of progressively decreasing 'demographic vigour' in a population of large mammals:

1. Juvenile mortality rate increases
2. Age at first reproduction increases
3. Fecundity declines
4. Adult mortality increases.

Such changes may accompany, for instance, a rise in population density. According to this progression, juvenile survival provides a sensitive measure of the state of the population 'condition', while adult mortality, as the last parameter to 'give way' provides the key to the population's persistence. In northern temperate deer, juvenile mortality is often the stage of greatest loss, especially during severe winters (Bartmann and Bowden 1984, Skogland 1985, Clutton-Brock *et al.* 1985, Putman and Langbein 1992).

Recent work by Gaillard *et al.* (1993b), previously outlined in Chapter 7, has provided valuable information of survival patterns in the roe. In their study, Gaillard *et al.* collected and analyzed long-term data of survival at two sites of male and female roe in each of three age classes: juveniles (8-20 months), adults (20-92 months) and senescent adults (over 92 months). (As animals were caught when a minimum of 8 months old, survival of younger fawns could not be studied.) Gaillard *et al.* found overall that survival of adults at both sites was fairly constant for adults between 2 - 7 years, with females generally having slightly higher annual survival rates (0.95) than males (0.85). After the age of 7 years (or 92 months), both sexes' survival decreased, but again, that of males declined more steeply. The rate of decline in survivorship of senescent roe was higher at Trois Fontaines, the site of greater winter severity. While no differences between survival rates of juveniles (8-20 months) and adults were found at Trois Fontaines, juveniles of both sexes had lower survival rates than adults at Chizé, where density-dependent effects on reproduction and body weight had earlier been demonstrated (Gaillard *et al.* 1992). Severe winters affected survival of roe, and mortality of juveniles showed some evidence of a density-dependent response at the site of higher density, Chizé. It should be pointed out that emigration by roe at either of Gaillard *et al.*'s sites was impossible and both populations were controlled, with between 100 and 200 animals removed annually from each. Thus, it could be argued that their results may not be applicable to unrestricted and unmanaged populations. However, Gaillard *et al.* argued that such removals would not have affected the observed survival rates overall, pointing out the large sizes of their two study areas (1360 ha. and 2660 ha.), and that adult roe are sedentary so that only yearlings normally emigrate. Moreover, Gaillard *et al.* supported these assertions by consistent results from repeating their analyses on Strandgaard's (1972a) 16-year data set of an unmanaged population.

From the results of Gaillard *et al.*s' (1993b) study, we might expect higher mortality in such juveniles in the New Forest. While this may be true, certain other considerations must also be taken into account. Firstly, it is possible that the New Forest roe suffer high mortality in the first few weeks or months of life (Ratcliffe and Mayle 1992), from lower maternal body weight and the high energetic demands of late pregnancy and lactation (as discussed in Chapter 7, and see below). Secondly, the New Forest is surrounded by estates and agricultural areas to which juvenile roe could disperse (unlike the situation at either of the sites studied by Gaillard *et al.*). Density-dependent emigration has been reported in deer and other ungulates (elk: Houston 1982; horses: Berger 1986; moose: Tomek 1977), and may be expected to occur in roe through territory-induced expulsion of juveniles (Bramley 1970a).

Hanks (1981) also observed that, in addition to measures of reproduction and mortality, there were behavioural traits which could be used as indicators of population 'condition'. These, he suggested, could be broadly grouped under (i) the rate and quality of social interaction, (ii) density, and (iii) feeding strategy. Other authors have also noted changes in forage intake as populations increase in density relative to the available food supply (e.g. Klein 1970, Skogland 1988, Maizeret *et al.* 1989). In the present study, while no work on the species' social behaviour was carried out, roe in the New Forest were found to attempt to compensate for poorer quality forage through habitat selection (Chapter 4), In addition, when the present diet was compared to that described by Jackson (1980), roe in the Forest now were found to subsist on a poorer quality diet, containing higher amounts of fibre / cellulose material and less bramble and forb (Chapter 5). In this respect, Klein (1970) observed that as deer food quality and quantity diminishes, there is an accompanying fall in both the production and survivorship of fawns.

Unfortunately, no data on natural mortality are available for New Forest animals. While there is a mortality component implicit in the fawn:doe ratio measurement investigated earlier (Chapter 7), that measure cannot be compared with values from other studies (e.g. Klein and Strandgaard 1972, Maizeret *et al.* 1989) as the latter relate to other times of year. However, within a population, the fawn:doe ratio measured at the same time of year over a number of years may fall as the population increases relative to the resources available. Thus, Maizeret *et al.* (1989) recorded a reduction in the fawn:doe ratio from 1.62 to 1.3 to be associated with a drop in mean body weight of 1.5 kg. for roe at Chizé between 1978 and 1985. In reindeer, Crête and Huot (1993) suggested regulation of their study population by a limitation of protein and available energy in summer, affecting both calf and adult mortality. Carroll and Brown (1977) also considered that the high neonatal fawn mortality of white-tailed deer in Texas was the major factor stabilising the population, while Logan (1973; cited in Carroll and Brown 1977) noted that fawn mortality increased with density, and was highest during the period of population decline. The change in the fawn:doe ratio across the New Forest beats (Chapter 7) is striking, and again appears to relate positively to likely resource availability (Chapters 3 and 7).

Studies on declining ungulate populations - indeed on declining populations in general - are uncommon, and often those studies aim only to identify the cause of the decline in a particular population (e.g. caribou over late 1800s: Bergerud 1974; Serengeti Thompson's gazelle *Gazella thomsoni* over 1972-85: Borner *et al.* 1987; caribou in British Columbia during the 1930s and 1940s: Bergerud and Elliot 1986). While the majority of studies have concerned populations declining steadily over a period of years, in some cases the decline has taken the form of a sudden, dramatic crash. This has been observed, for instance, when disease has been the responsible factor - e.g. rinderpest in African buffalo (Sinclair 1977), or (less severely) pneumonia in bighorn sheep *Ovis canadensis* (Festa-Bianchet 1988, 1989). Similarly, the combined effects of when several factors may result in a pronounced change in numbers, e.g. Klein's (1968) documentation of the crash in the reindeer herd on St. Matthew Island, a population introduced in 1944 and which fell drastically from an estimated 6000 in the summer of 1963 to a mere 42 animals counted in 1964, the result of a combination of the animals over-exploiting their food resources and very severe winter conditions.

Among the Cervidae, there are many species and subspecies which have declined in numbers to the point that they are now regarded as 'threatened' or 'endangered': 29 were listed by Cowan and Holloway (1978; updated in Putman 1988). Reasons for these declines were given variously as habitat change, over-exploitation (legal hunting and poaching), the introduction of domestic stock, and disease - or in many cases, a combination of these. (Such attributions should, however, be treated with some caution: cattle grazing may, in some cases, actually improve pasture quality for deer, e.g. Gavin *et al.* 1984). Data on rare animals tend to be sparse and, with conservation sensitive species, such data must often be restricted to those which can be obtained through non-destructive means.

One example of such an endangered deer is the southernmost subspecies of the venado, the Argentinean pampas deer (*Ozotoceros bezoarticus celer*), one of the world's most threatened cervids (Cowan and Holloway 1978) and listed as endangered in the IUCN Red Data Book (Thornback and Jenkins 1982). Numbers currently stand at around 300 (Jackson and Giulietti 1988). An Odocoiline, the venado is similar to the roe in size (males stand some 70 cm. at the shoulder and weigh around 25 kg.) and, like the roe, is a concentrate selector (Hofmann 1985, Jackson and Giulietti 1988). Jackson relates the decline of the venado in Argentina (Jackson 1978; Jackson and Langguth 1987) and Uruguay (Jackson *et al.* 1980). Once abundant throughout the Argentinean pampas, the species suffered heavily from exploitation for hides, but remained numerous - according to accounts of hunters and pioneers (Jackson and Langguth 1987) - until late in the 19th century. At that time, the rapid settlement of the pampas, changes in drainage and agricultural practice, and great increases in stocking rates (and the possible effects of disease such as foot-and-mouth) resulted in the deer population declining. Today the Argentinean subspecies remains in only two widely separated areas of Argentina, at San Luis and the Bay of Samborombon. Few detailed studies of the species' biology have been published (e.g. diet: Jackson and Giulietti 1988, and antler cycle: Jackson 1986), but Jackson (1978) observed the reproductive rates to be very low. Although Jackson attributed this to disruption of the social system, he cited no supporting evidence (Jackson 1978) and, as noted, a lowering of reproductive rates can also result from other causes, such as resource limitation affecting body condition.

In other food-limited ungulates, results broadly consistent with those found for the New Forest roe have been reported. Wilson and Hirst (1977) looked at the decline in the sable *Hippotragus niger* and roan *H. equinus* antelopes in the Transvaal, following the introduction of the species in a number of areas. They found animals in poor body condition and suffering high juvenile mortality in their study populations, with animals also showing more signs of disease than animals in control areas. Wilson and Hirst (1977) attributed the populations' declines to the low grade soil of the areas into which the species had been introduced; this in turn resulted in forage low in protein and minerals (notably phosphorus and selenium), and calves receiving poor milk and suffering from severe nutrient deficiency. The two species may also have suffered in competition with other large herbivores in the areas. Reproductive capabilities of males, judged from semen samples, were not apparently impaired, but the reproductive performance of females was not examined.

Similarly, in birds, a study of resource-limited blue grouse *Dendragapus obscurus fuliginosus* on Hardwicke Island, British Columbia, was reported by Zwickel *et al.* (1988), who examined the change in nesting parameters associated with a steep decline in the population over 1979 - 1984. Zwickel *et al.* found, in comparison to a stable population at Comox Burn, Vancouver, a smaller clutch size, lower egg fertility (93% compared to 96%) and (consequent) lower egg hatchability. These differences did not account for the observed decline, however, and Zwickel *et al.* suggested (but had not then examined) a lower proportion of birds to be breeding at Hardwicke Island.

For a contrast with populations suffering from resource limitation, we can also examine one which declined from a different cause and for which the population properties were measured. Staines (1978) studied a declining population of red deer in Glen Dye in north-east Scotland, after counts by the Red Deer Commission suggested the population had declined from 846 to 426 over the period 1961 to 1966. Of particular interest in this study is that Staines looked at the population reproductive and mortality properties as well as verifying and establishing the cause of the decline. Carcasses (located and shot) supplied data on growth, body condition and reproductive status of hinds. While there was some evidence of stags mixing with others outside the study area, there was no evidence of immigration of hinds, despite the relatively low density of animals following the decline. The decline in the population, Staines (1978) concluded, was due to heavy shooting, in excess of the population recruitment. The deer themselves - in contrast with results for the food-limited roe of the New Forest - were heavier than red deer from comparable hill areas elsewhere, with adults of both sexes and calves showing better growth. Yearling hinds also showed a high annual fertility rate (64% compared to 7% elsewhere), and most older hinds bred every year (cf. Mitchell 1973, who noted that red hinds at higher density from similar areas tended to breed in alternate years). Overall, the Glen Dye herd grew faster, reached puberty sooner, had higher fertility and lower natural mortality than red deer from other open-hill areas in Scotland. If the New Forest roe had declined primarily through the imposition of a heavy culling regime, the observed differences in bodyweight and reproductive performance would not be expected; whether predation or culling may have been a factor responsible for the decline in the New Forest roe population is discussed further in Appendix 2.

It is clear from the studies cited, and others, that there are many factors which may precipitate a population decline. As noted earlier, however, only some of those factors are able to regulate populations, and of these the most commonly recorded is food-limitation (Fowler 1987). Most studies on food-limited populations have concerned populations at increasing density which have been experiencing a decrease in growth rate rather than a decline in numbers. However, these two situations may not be fundamentally different, as in both cases the individual animals are in a situation of decreasing food per capita (Klein 1970), and the physiological consequences for those individuals which remain in the depleted area may be similar. Where the quality or quantity of the resource in question is itself diminishing, the population may decline and yet remain at high density relative to that changing resource base and thus continue to be subject to regulation.

Such a situation may arise when a reduction of the species' required food species occurs, associated with, for example, a gradual increase in forest cover - as was the case of the Columbian white-tailed deer (*Odocoileus virginianus leucurus*), for instance, because white settlers in the late 19th century stopped the periodic burning of the species' former prairie range by native Amer-Indians (Gavin 1978). For the New Forest roe, we have also noted that the decline within the Forest has been associated strongly, and perhaps entirely, with the areas enclosed for commercial, mostly coniferous woodland, where the roe have been shown to be food-limited. Yet roe are often reported as being at their most numerous in such forests (Prior 1968, Loudon 1982), and indeed, roe in other conifer forests throughout southern Britain do appear to be thriving (Ratcliffe and Pepper 1987). Thus, it is necessary to ask why the New Forest roe population should be exceptional. To answer this question it is necessary to examine how the New Forest differs from other forests in its woodland management.

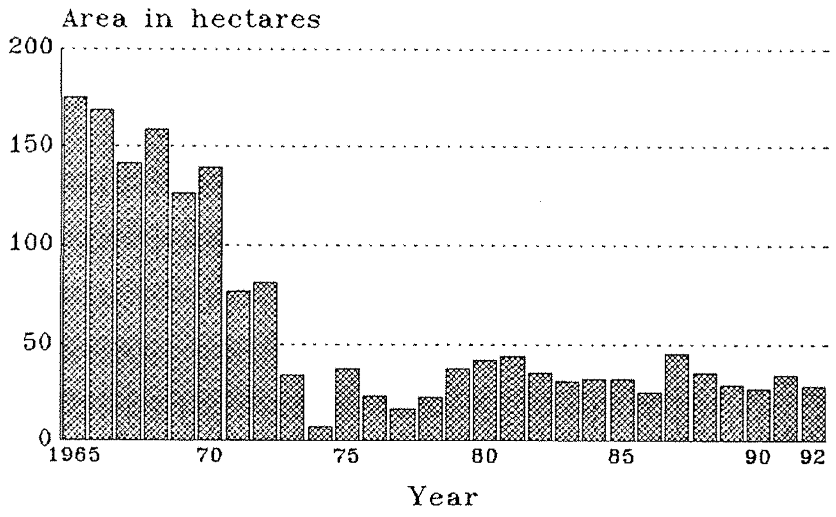
As noted throughout this study, managed commercial woodlands in Britain may be structurally described as a succession of growth stages generally recognised by foresters: establishment, prethicket, thicket, pole and mature woodland (Ratcliffe, Hall and Allen 1986). As a consequence of tree development and changes in tree spacing following thinning, each growth stage is characterised by the level of light penetrating to the forest floor, and a corresponding change in the relative abundance and richness of the ground flora (Ehrenreich and Murphy 1965, Hill 1979a, Tyler 1989). Many animal populations follow similar patterns of change in population levels, e.g. rodent numbers rise during the planting / establishment stage and diminish over prethicket development, thereafter remaining low, but increasing gradually again during extended rotation or reestablishment (Charles 1981), and bird communities also show changes over commercial forest development (Petty and Avery 1990).

The roe deer occurs at greatest density in the early forest growth stages (Batcheler 1960, Prior 1968, Loudon 1978, 1982, Staines and Welch 1984). Ratcliffe and Petty (1986) have described this association, starting with the colonization by roe of establishment areas, initially by bucks seeking territories and subsequently by does. As prethicket develops, roe benefit from the increase in cover and reach their maximum densities in forests of 12 - 15 years of age, with trees around 5 m. (Loudon 1982). During late prethicket and the following thicket stages (canopy closure), roe numbers decline as food on the forest floor becomes scarce. After thinning during the pole and mature stages, there is again an increase in the population level of roe, although not to the previously high level (Loudon 1982). The patterns of habitat use and selection found in this study conform to this pattern of use, but have related use of areas by roe directly to ground vegetation availability as well as the forest growth stage.

The rotation period for commercial conifer forests in lowland Britain is, in general, similar to the 45 - 55 years for uplands cited by Ratcliffe and Petty (1986), although will vary according to the species planted, yield class and windblow risk (Hibberd 1986). In forests on second or subsequent rotation, there may be as much as between a quarter and a third of this in the early growth stage (under 15 years of age) favoured by roe, with about 10% of the total at a stage vulnerable to damage (Gibson and MacArthur 1965). Extending the crop rotation period will correspondingly reduce the proportion of trees at the younger growth stage. While these figures are averages, and based largely on upland practice, considerations regarding the use of forest growth classes by roe in conifer woodland appear to be similar throughout the country (Prior 1968). However, as described in Chapter 1, the New Forest is uniquely subject to many pressures, and an important strand of the Forest's history has been the tension between the demands of silviculture and those of other land usage.

While Acts of Parliament after the Second World War had observed the earlier restrictions on the area of woodland which could be enclosed for silviculture (Chapter 1), they also left considerable scope for increasing timber production. Forestry Commission policy during the 1950s and 1960s favoured a relative increase in conifer planting at the expense of broadleaf trees within the inclosures, as well as increased exploitation of the Forest's unenclosed broadleaf woods. This policy was reaffirmed in a 1963 Working Plan by the Commission (Tubbs 1986). However, public outcry in the late 1960s, after the 'thinning' of Rushpole Woods on the Open Forest, led to the then Minister of Agriculture immediately banning the further felling of any broadleaf trees, and subsequently, in May 1971, issuing a Mandate to the Commission restricting their future silvicultural policies. The Mandate stipulated that the unenclosed broadleaf woods were to be managed on a 'minimum intervention' basis, and that the enclosed broadleaf woodlands were to be managed on a rotation of not less than 200 years, with felling restricted to single trees or small groups of trees. Further, there was to be no increase in the area planted with conifers beyond that already present or prepared for planting. The Mandate was reaffirmed in 1982 and 1992, and will remain in effect until at least the year 2003.

Fig. 8.1 Replanted area in New Forest inclosures 1965 - 1992



Source: Forestry Commission data

The implementation of these directives meant that conifer restocking of the inclosures was greatly diminished and has subsequently remained low through the 1970s and 1980s (Fig. 8.1). The overall area of establishment and early prethicket growth stages favoured by roe has consequently decreased, a change found to be correlated strongly with the change in the censussed roe population (Chapter 2). The remainder of the conifer woodland has been through thicket and canopy closure, and many of the present pole and mature stands are, as seen from the vegetation survey described in Chapter 3, severely food-depleted in character.

Present practice in the New Forest is to grow conifers on a 60-year rotation, with a few amenity blocks left for 120 years (Perry 1990). Retention felling at 20%, or 50 stems per hectare, has been practised since the Mandate was issued, but is now being superseded by improved landscaping (Mr. Harry Oram, Head Forester, pers. comm.). The low level of replanting through the 1980s has resulted in only some 2-3% of the Forest's enclosed woodlands currently at the establishment / prethicket growth stage. However, this replanting, though low, has been fairly consistent and, on these grounds, the decline in the roe population may be expected to level off in due course. The present population trend is not yet clear. Recent census data (presented below) at first suggest there has been a slight increase in the population since 1988.

Year:	1989	1990	1991	1992	1993	1994
Roe census:	265	296	351	369	351	303

However, it should be stated that over 1989 to 1994 there have been several changes of keeper on the Forest beats, and thus the pre-1989 assumption of methodological consistency may not be valid. There has also been an increase in culling as a result of the initial apparent recovery (especially since 1991 / 92). Some increase in the ground vegetation would be expected following the storm damage in 1987 and 1990, with the 'opening' of those areas to increased light levels, and it may be that roe are making at least some local recoveries, but may also be continuing to decline in other areas. In the longer term, as the woodlands become more mature, there will need to be more thinning and clear-felling, and this may be expected to lead to a more widespread increase in the New Forest roe population.

APPENDICES

A1. HABITAT CLASSIFICATION FOR STUDY OF HABITAT USE

A1.1 INTRODUCTION

To explain the distribution and abundance of any animal it is essential to have an understanding of its resource requirements and preferences. In practice, this understanding is most readily achieved by initially relating the observed occurrence of the study animal to different types of habitats, that is, areas predefined in terms of either the resources they contain or the extent to which they may satisfy particular needs (see Duncan 1983 and Chapter 4 for further exposition). Such an approach has been adopted in this study (Chapters 3 and 4). Although such habitats would ideally be defined functionally and dynamically, in terms of the commodities offered to the animal at any given time (Duncan 1983, van Horne 1983), in practice most studies of the distribution of mammals between different habitats assess dispersion between habitat categories arbitrarily defined *a priori*.

This method does have several advantages: it is generally simple and quick to devise, the categories can usually be universally recognized, and the results readily understood and communicated; in addition all the available information can be taken into account, irrespective of its 'form' (nominal, interval, binary data etc.). The main problems with this approach are in the location and classification of habitat boundaries or the problem of 'edge effects' (Patton 1975, Porter and Church 1987, Aebischer *et al.* 1993) - especially for animals that may specifically select ecotones (e.g. red deer: Mitchell *et al.* 1977) - and that the "human orientation" of the classification may not reflect accurately the animals' own perception of the resources available (see Morris 1984, 1987). These difficulties can result in the artificial distinction between two areas viewed by the animal as homogenous, and the lumping together of habitats viewed by the animal as distinct. Further, the very act of classification necessitates the choice of certain environmental factors to act as 'separators' between habitats, and may further require the arbitrary division of continuously varying characteristics, such as the abundance levels of certain species.

In many studies of ungulate ecology these problems are of more theoretical than practical importance, and habitat types are sufficiently broad and obviously distinct to be undisputable. However, within the New Forest's enclosed woodlands the situation is less straightforward. All gross vegetation types (with the exception of rides) are managed commercial woodlands, whose boundaries are more likely to have been determined by human action than by changes in the natural features of the area. Indeed, there is little underlying variation in altitude, aspect, general topology, or drainage within the Forest, and the pattern of soil types does not necessarily accord with sub-compartment boundaries (i.e. with selected tree plantings).

Accordingly, an attempt was made as a part of this study to see if a more objective definition of habitat types could be derived, by taking individual geographical sub-compartments and using as many as possible of the variables for which data were collected (Chapter 3, Table 3.2). Two multivariate classification methods for such objective determination of habitat groupings were originally considered, cluster analysis (e.g. Everitt 1980) and TWINSPAN (Hill 1979b). Further investigation however, revealed that the latter method was unsuitable for the 'percentage-cover' type data collected during the vegetation surveys: the method is based upon reciprocal averaging ordinations, which calculate chi-square distances and it should thus be used only on independent species-count type data (Greenacre 1984). Cluster analysis techniques were thus considered the more appropriate for this study. Several broad criteria were defined to judge the validity of any habitat classification scheme derived.

(i) Using the vegetation survey data as collected (i.e. without pre-transformation) the habitat scheme derived should encompass all or nearly all (preferably over 95%) of the sub-compartments in 16 - 24 categories.

(ii) The method should be fairly robust: simple parameter changes, or omitting or adding one variable should not result in excessive change to the pattern of clustering. Though arbitrary, we can take a measure of the 'similarity of clustering' of above 90% as 'very robust' and 80% as 'fairly robust' (a simple measure of this is proposed below).

(iii) The resulting scheme of habitat classification must be field-workable. In other words, categories should be sufficiently clear so that other workers using simple guidelines could allocate any sub-compartment to a specific category in the field.

It should be stated that the scope of the investigations described here was strictly limited. Extensive evaluative investigations of clustering methods, though of interest, would form a major study in their own right and, as the use of cluster analysis for habitat classification in this study was ultimately rejected, such treatment would be inappropriate. Neither is this Appendix intended as a review of methods of habitat classification; its purpose, rather, is to present and discuss the attempt made to apply cluster analysis methods to the range of woodlands found in the New Forest inclosures.

A1.2 METHODS

A brief overview of cluster analysis techniques

Cluster analysis techniques in general are used to compute the similarity or differences between a number of objects, quantifying those differences in some way as measured "distances". Those objects (sub-compartments in the present study) must be defined by a range of variables which are all either measured on at least an interval scale, or expressed as binary variables. Having computed the distances between all pairs of objects from the total of the differences in the values of all the measured variables, the analysis then proceeds to place the objects into groups (clusters).

There are two broad categories of clustering techniques: non-hierarchical and hierarchical. Both serve to identify clusters, but non-hierarchical methods do not attempt to relate the clusters to one another; they are, however, better at handling noise in the data and assigning outliers to clusters (Gauch 1979, 1982). By contrast, hierarchical methods reveal the relationships between clusters as part of the stepwise process of forming groups (see below). For this study, hierarchical methods were chosen as the hierarchical pattern of clusters would permit 'cutting' at an appropriate resolution or level.

Mathematically, the process of clustering may be achieved in a variety of ways. In 'agglomerative' mode, the method works by first assigning each object to a separate cluster, and pairs the two closest clusters into one; the distance of this cluster from the remaining objects is then calculated. This procedure of combining and recalculation is then repeated, reducing the number of objects or clusters by one at each step, until ultimately there is only one cluster. Alternatively, the clustering may be derived using a 'divisive' process, that is by starting with one large cluster and repeatedly dividing it into more clusters, so that each object ultimately forms a separate cluster. The latter approach is generally preferred, as it is the less affected of the two by sampling error (Gauch and Whittaker 1981) and has been adopted in this study. Either way, the user may choose the requisite degree of resolution (i.e. number of clusters) appropriate to his or her study, and will know which of the original objects fall into each cluster. Cluster techniques are very widely used (see Blashfield and Aldenderfer 1978), and are described further in many works, such as Everitt (1980) and Romesburg (1984). Gauch (1982) and Jongman, ter Braak and van Tongeren (1987) specifically examine the application of clustering techniques to community ecology. For the present study the clustering program used was part of the SPSS-X analysis package v.3 (Norušis 1985).

When executing a cluster analysis, the user may specify certain parameters. Essentially these cover three areas.

- Any data transformations required: typically all variables are rescaled so as to carry equal weighting (as they may originally have been measured in a range of units). In this study all variables were rescaled on a range of 0 - 1.

- The measure used for calculating the 'distances' between objects: again a variety of options is available, including Euclidean, cosine, block, Chebychev and power transformations (details are given in works cited above). For this study the 'squared Euclidean' measure was used in all analyses (i.e. measuring the distance between two objects X and Y is given by $\sum (X_i - Y_i)^2$ over $i = 1 \ldots n$ variables describing those objects): this measure was chosen as it is the most widely used measure of distance, and is closest to the standard statistical measure of calculating deviation by least squares; it is also the only measure compatible with certain clustering methods such as Ward's (Norušis 1985, and see below).

- The method used to measure distances between objects when combining or dividing them during the clustering operation: in the clustering program used here seven options are available. Of these the 'default' method is Baverage (average linking between groups), and the others are Waverage, Single, Complete, Centroid, Median and Ward's. The Baverage method was chosen as the basic one, but three analyses were carried out to see the extent to which choosing alternative methods affected the clustering result, and these used the Single linking (nearest-neighbour), Complete linking (furthest-neighbour), and Ward's method (which minimises the total within-cluster distances at each step; Ward 1963). Further algebraic details of all of these methods may be found in Norušis (1985).

Clearly, the number of different types of cluster analyses that could be performed on any one data set is vast, given the number of combinations of parameter values. For this investigation, the number of different types tried was kept to the minimum consistent with the stated objectives. In total eight separate analyses were performed: a 'control' analysis (chosen arbitrarily, but adopting the most widely used parameter values for the method of clustering and including all data variables), three analyses using changes in the method of clustering (as described above), and four analyses where each omitted a single data variable from the variable set used in defining sub-compartments (Table A1.1).

Data used

The data used for these investigations was the vegetation survey data collected from the study sites, derived as in Chapter 3. Of the total of 549 sub-compartments surveyed (Chapter 3), a subset of 499 of them was used for this work (in scope these do not differ substantially from the complete data set and all the 'subjective' habitat types are represented). Clearly, only the variables with suitable numeric attributes within the data set could be used for this analysis, and nominal variables were excluded. The full set of variables entered comprised: height of dominant tree, average spacing between trees, canopy cover, and percentage cover of each of: brash, litter, bramble, holly, ivy, heathers, scrub, bilberry, grasses (excluding *Molinia*), *Molinia*, and bracken.

Table A1.1 *Cluster analyses carried out to investigate variation in clustering resulting from single changes in operational parameters or data variables entered*

Analysis Description

(i) Control analysis

Distance measure = Squared Euclidean
Method = Average linking between groups (Baverage)

Data variables entered:	height of principal tree species
	average spacing between trees
	percentage cover of canopy
	percentage ground cover of:
	- brash
	- litter
	- bramble
	- holly
	- ivy
	- heathers
	- scrub
	- bilberry
	- grasses (excluding *Molinia*)
	- *Molinia*
	- bracken

(ii) - (viii) are test analyses, each differing from (i) in the single detail specified

(ii) Method = Single clustering
(iii) Method = Complete clustering
(iv) Method = Ward's

(v) Omit percentage cover of brash
(vi) Omit percentage cover of bracken
(vii) Omit height of principal tree species
(viii) Omit percentage cover of bramble

Notes: Data used in analyses from surveys described in Chapter 3.
Algebraic details given / referenced in text.

Control analysis

This analysis served as the 'fixed' point against which other cluster analyses were compared. As noted, it used the squared Euclidean measure of distance calculation (as did all test analyses) and the Baverage method of clustering. These are the most commonly used measures, and are offered as the program defaults (Norušis 1985). All data variables listed in the previous paragraph were included in the analysis. Although this analysis has been chosen as the control, the choice is, as noted, somewhat arbitrary, but adequate for the purpose of this comparison; the intention is to investigate the variation (robustness) of the method when changing parameters or variables, rather than seeking an evaluation against a separate system of classification.

As explained in Chapter 3, the number of clusters deemed suitable for the habitat classification of the New Forest's enclosed woodlands was initially set at 20. However, examination of the cluster pattern obtained at this resolution in the control analysis showed that many resultant clusters actually comprised only one or two sub-compartments. Accordingly, the resolution chosen for detailed examination was that at which there were 20 clusters of at least 4 sub-compartments in each. This level of resolution was then taken as the basis for comparisons against the results of the other cluster analyses, which were all examined at the same level of resolution. It is recognised, however, that other criteria for comparison could have been chosen.

Test cluster analyses and method of evaluation

It would be impractical, and inappropriate, to present the full output from all analyses, as each occupies many pages of computer printout and direct comparisons would be extremely difficult. Instead, summary statistics have been calculated from the outputs of the analyses which allow the results to be more readily assimilated and compared, in particular the 'test' analyses (ii) - (viii) of Table A1.1 to be compared with the control analysis (i), which is sufficient for present requirements.

Each of the seven 'test' analyses was examined in two ways. Firstly, in the pattern of clusters produced: for a specific level of resolution, did the test analysis produce a few large clusters and many small ones, or a moderate number of evenly-sized clusters? Secondly, in comparison with the control analysis, how well did the test analysis retain the relationships between specific cases as identified by the control analysis?

To obtain a measure of the 'similarity of clustering' between the control analysis and any test analysis, I compared the way 80 specific sub-compartments were assorted into clusters in each case. From each of the 20 clusters in the control analysis which contained 4 or more sub-compartments, 4 individual sub-compartments were selected which represented the range of cases present. These 80 sub-compartments were then viewed as (i) 4 sets of 20, which had been separated in the control analysis, and (ii) 20 sets of 4, whose sub-compartments had been clustered together in the control analysis. These 80 sub-compartments were then located in the pattern of clustering resulting from each test analysis. The mean proportion (of the 4 sets of 20) which remained in separate clusters in a test analysis was used as a measure of the consistency of separation of sub-compartments, 'p'. Similarly, a measure of the extent to which sub-compartments placed within the same cluster in the control analysis were kept together in the individual test analyses was derived from the 20 sets of 4 sub-compartments identified in the control analysis. If all 4 fell within the same cluster, a score of 1 was recorded; if 3 of the four did, the score was 0.75, and if two did, the score was 0.25 (i.e. the two pairs could score a total of 0.5). These scores were tallied and taken as a proportion of the maximum of 20 to give 'q'. Both p and q ranged from 0 - 1, and their product expressed the degree of correspondence between a test analysis and the control analysis.

Evaluation of habitat clusters for 'field use'

As well as the sensitivity analyses outlined above, it was also considered necessary to have some measure of the correspondence of the clusters produced by the analyses with respect to an independent scheme of habitat classification. This was done by examining the composition of the largest cluster from each analysis in terms of the habitat classes actually used in the study (designated [I] through [VI], and described in Chapter 4). If the cluster showed a high proportion of two or more habitat classes, then it would be doubtful if the habitat categories would be practical for field use.

A1.3 RESULTS

Comparison of cluster analyses

The results of all eight cluster analyses are presented below in summary form. Table A1.2 gives the values of the calculated statistics for the similarity of clustering, and Figure A1.1 shows the distributions of sub-compartments between clusters for all analyses.

Table A1.2 *Results of test cluster analyses showing patterns of clustering and differences from control analysis*

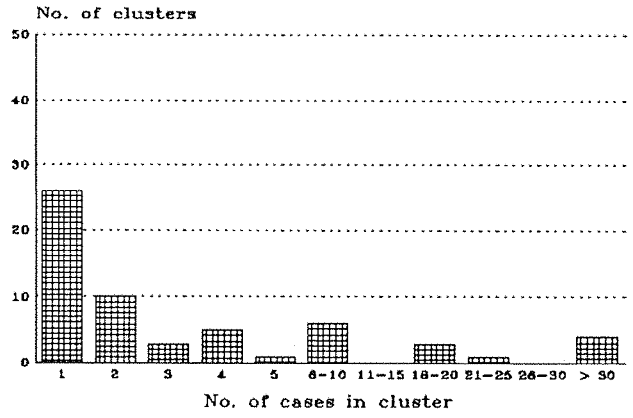
Analysis No.	p-value	q-value	pq	Largest cluster Size	Largest cluster % of cases	Outlying clusters No.	Outlying clusters % of cases
Control analysis							
(i)	1.00	1.00	1.00	142	28.5	55	11.0
Test analyses							
(ii)	0.28	0.89	0.25	423	84.8	65	13.0
(iii)	0.86	0.66	0.57	64	12.8	49	9.8
(iv)	0.91	0.69	0.63	30	6.0	28	5.6
(v)	0.79	0.90	0.71	183	36.7	59	11.8
(vi)	0.76	0.79	0.60	152	30.5	54	10.8
(vii)	0.76	0.76	0.58	139	27.9	58	11.6
(viii)	0.83	0.79	0.66	127	25.5	62	12.4

From these results it can be seen that, for the control analysis, the criterion that there should be 20 clusters which contained 4 or more sub-compartments was met at the 59 cluster resolution level. This level of resolution therefore was the one used during the comparison of results from all test analyses. (The problem of the many small clusters comprising 'outlier' sub-compartments is discussed later).

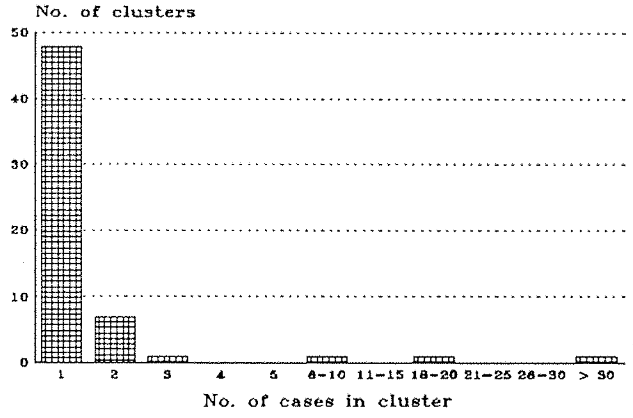
Figure A1.1 and Table A1.2 show the differences in clustering that result from even small changes in the way the analyses are performed, or when single variables are omitted from the data matrix. While the level of resolution of the control analysis was deliberately set to produce 20 clusters with 4 or more cases in each, the distributions of cases in the test

Fig. A1.1 *Distribution of cases (subcompartments) in clusters*

Control analysis (i)



Test analysis (ii): Method = Single



Test analysis (iii): Method = Complete

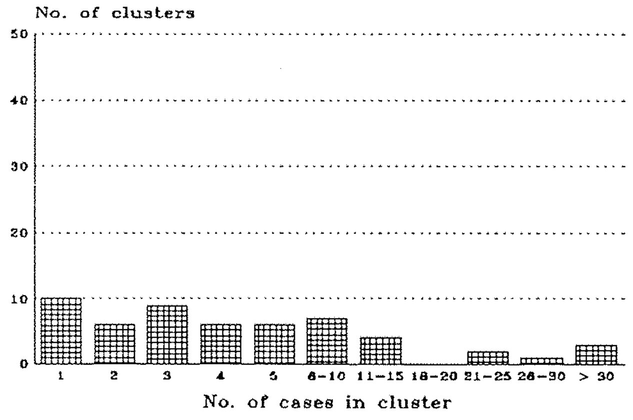
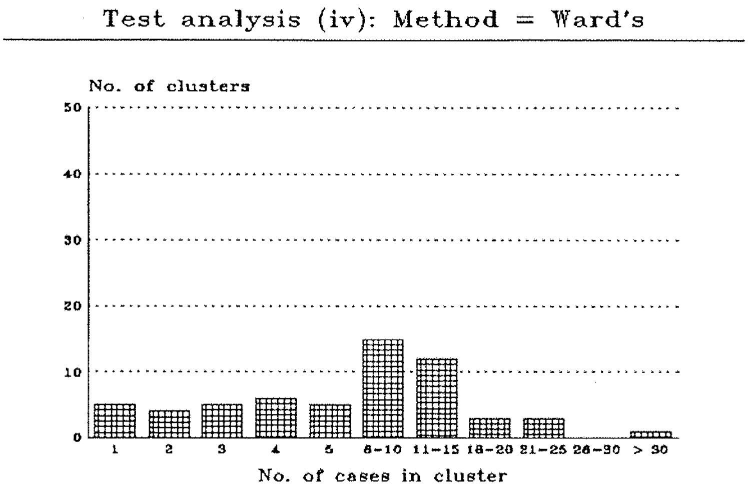
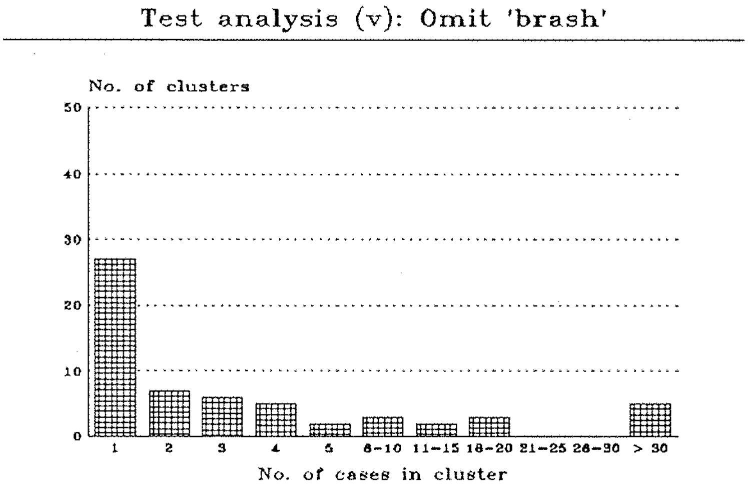


Fig. A1.1 *continued*


Test analysis (iv): Method = Ward's


Test analysis (v): Omit 'brash'

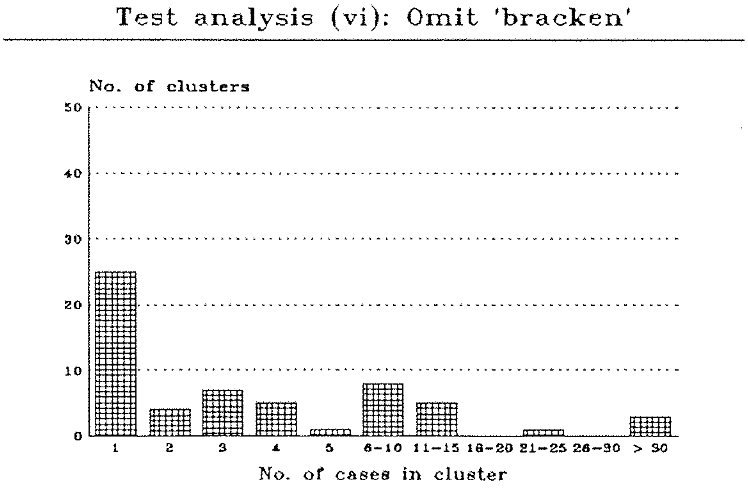
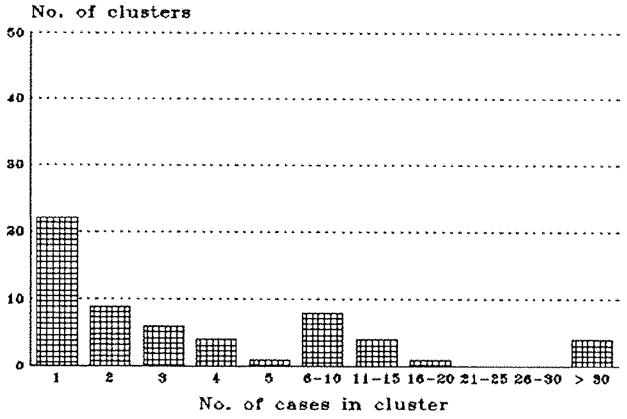
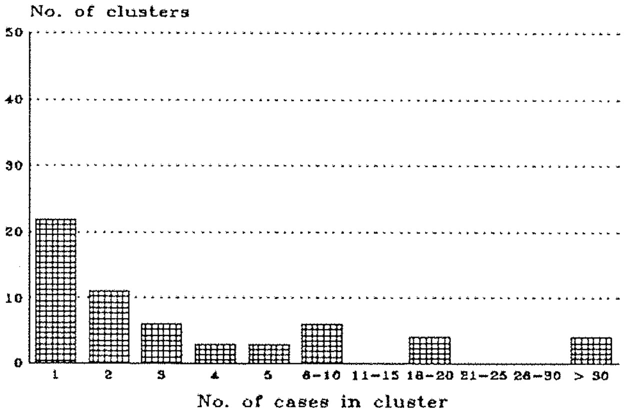

Test analysis (vi): Omit 'bracken'

Fig. A1.1 *continued*

Test analysis (vii): Omit 'height of principal tree'



Test analysis (viii): Omit 'bramble'



analyses suggest that a very different level of resolution for each analysis would be needed to satisfy this criterion. The number of clusters with 4 or more cases varied from 3 to 45 in the test analyses, with the number of sub-compartments which were contained within the single largest cluster ranging from 30 in analysis (iv) to 423 in analysis (ii) i.e. from 6% to 85% of the entire dataset occurred in one cluster. A major problem which results from all of these analyses (including the control one) is the high number of outliers, those cases that have been placed in isolation or in very small clusters (here taken as consisting of 3 or fewer sub-compartments). The proportion of cases placed as outliers ranges from 5.6% in analysis (iv) to 13% in analysis (ii). Such outliers must be considered in any scheme of habitat classification, and this aspect of the problem is discussed further below. In general, the more extreme outcomes arose by the use of different operational parameters, whereas the omission of a single data variable had a more constant (though still sizeable) effect.

The calculated measures of similarity between the control and test analyses (Table A1.2) suggest that the resulting habitat schemes are very sensitive to changes in methodology and the actual variables entered. On average, it seems that the difference of the inclusion or omission of a single variable results in around 30% - 40% change in the segregation of cases (omitting bramble, for instance, gave a 66% similarity in clustering in comparison with the control analysis). Clearly such a change is significant, and the method cannot in this respect be considered as robust; the outcome of clustering is strongly influenced by what environmental variables / characteristics the observer chooses to record in the first instance. In this study, for example, the percentage covers of fern (other than bracken) and mosses were not recorded: had either been included in the data set, then the resulting clustering would most likely have been quite different. Similarly, some variables represented individual species (such as holly and bilberry) while others were aggregates (grasses, heathers) and this is equivalent to the inclusion or omission of variables.

Comparison of cluster analyses with subjective habitat classification scheme

Table A1.3 presents an analysis of the composition of the single largest cluster resulting from each of the analyses. This is intended as a way of assessing the extent to which the cluster analyses give 'field-workable' patterns of habitat types. In this case, the cluster is broken down with respect to the habitat class categories [I] - [VI] used for the analyses of habitat use / selection described in Chapter 4.

The largest cluster from every analysis except that using Ward's method (iv) combines into a single vegetational category sub-compartments from the three most widespread habitat classes used in the study: mature conifer without and with food, [III] and [IV], and broadleaf woodland [V]. One analysis (single linkage (ii)), contains in addition establishment / prethicket classes [I] and [II], and embraces over 84% of sub-compartments within the one cluster; moreover, the constituent proportions of habitat classes [III], [IV]

Table A1.3 *Composition of largest single cluster from all analyses, as percentage of cases by 'habitat classes' (Chapter 4)*

Analysis No.	Habitat class I	II	III	IV	V	VI
Control analysis:						
(i)	0	0	38	14	48	0
Test analyses:						
(ii)	3	1	56	17	23	0
(iii)	0	0	38	14	49	0
(iv)	0	0	97	3	0	0
(v)	0	0	46	17	37	0
(vi)	0	0	43	16	41	0
(vii)	0	0	32	17	51	0
(viii)	0	0	31	16	53	0

and [V] in that cluster do not differ significantly from those in the data set as a whole ($\chi^2 = 4.4$, $p > 0.1$). The outcomes of all other analyses do differ significantly from the data set ($p < 0.001$); only Ward's method (iv), however, has managed to separate mature conifer from broadleaf woodlands, while also achieving the best separation between mature conifer stands with and without food, which arguably is more important (29 of the 30 sub-compartments belong to the former habitat class [III]); Ward's is also the method of clustering that gives the most even distribution of sub-compartments and fewest outliers (Fig. A1.1 and Table A1.2). All other analyses show high proportions of both mature conifer (with and without food) as well as broadleaf woodlands occurring within the same individual (largest) cluster, and would be unsuitable for field use. Further work would be necessary evaluating Ward's method, but it appears to be the least unsuitable of the range of cluster analyses tried.

A1.4 DISCUSSION

Multivariate techniques are used increasingly in community ecology to reveal pattern and order in large data sets otherwise beyond human comprehension (Jongman *et al.* 1987, Jackson and Somers 1991). Classification methods in particular have often been used for the identification of community assemblages of both plants and animals, often in combination with ordination techniques to achieve more understanding of the underlying determinants of the perceived species pattern. Despite numerous studies, it is recognized that the application of such complex methods is fraught with potential problems, and that instances of misapplication and invalid interpretation abound (see review by James and McCulloch 1990). In the case of cluster analyses, areas of concern have included: the identification of suitable variables upon which to base the classification, the criteria for determining optimal clustering (including the method of clustering, the number of clusters required, and the treatment of outliers), and the ecological evaluation of the result (Pielou 1977, Gauch 1982, Popma *et al.* 1983, Jongman *et al.* 1987). The underlying problem is one of knowing how to maximise the ecological understanding gained relative to the effort expended in using the technique (Moore *et al.* 1970).

Gauch (1982) pointed out that (not surprisingly) the most satisfactory clustering outcomes are achieved when the samples under analysis naturally comprise groups of alike and differing groups. Unsatisfactory outcomes in habitat classification using multivariate methods have been attributed to the existence of clines (Holmes *et al.* 1993). The New Forest enclosed woodland assemblages are not, of course, natural assemblages, but have been largely determined artificially by management practices; to some extent this may have obscured any community pattern typical of a natural habitat. The imposition of management has also been identified as the dominant determinant of habitat in other studies (e.g. Rushton and Eyre 1992). In commercial woodlands, there is, partly as a result of management practices, an 'unnatural' compound of ecological scales (e.g. with ground vegetation present at the start and in the later stages of the management cycle, and sudden events such as woodland thinning which are not reflected by the ground flora). The correct identification of an appropriate scale may be crucial for adequate description of the habitats available (Morris 1987, Aebischer *et al.* 1993). In addition, attempts to express the habitat characteristics purely in terms of geometric measures (such as Euclidean distances) have been found by other workers not to be robust (Faith *et al.* 1987), and make it hard to separate differences in ecological scale from methodological artifact (Allen 1987). Although suitable data transformations may counter these problems, they may again necessitate the introduction of the very subjective influences the use of multivariate methods may be intended to avoid in the first place.

According to the criteria as applied in this study, simple application of hierarchical cluster analysis was judged to be unsuitable for the derivation of a useful scheme of habitat categories of the New Forest's enclosed woodlands. Large variation in the clustering profiles, and in the segregation of sub-compartments between analyses differing by one operational parameter, or by the inclusion / exclusion of a single variable, suggested a lack of robustness in the method in generating consistent habitat categories. Further examination of the composition of the largest cluster for all but one case also showed that clear guidelines for field-use of the habitat categories were difficult to formulate, thus greatly diminishing their usefulness. A few other workers have reported similar problems (e.g. Holmes *et al.* 1993), although attempts which proved unsuccessful are unlikely to appear in the literature.

All the cluster analyses carried out gave a significant number of ‘outliers’, sub-compartments which were not readily fitted into the main clusters. Here too, arbitrary decisions have to be made regarding the acceptability and fate of such outliers. In this study, where outliers were defined as cases falling within clusters of 1 - 3 cases at the 59 cluster level, some 5.6% - 13% of sub-compartments fell into this category. The decision of what to do about them, such as ignoring them (Gauch 1982) or lumping them into a category of ‘others’, may be of critical importance to the study and must be evaluated in that context; unfortunately, general rules for such evaluation do not exist. In the case of a rare animal, such as the roe of the New Forest, it may be in terms of the use and selection of just such unusual or rare habitats that its ecology may be understood. If so, then they cannot be ignored, while lumping them together into a single heterogeneous habitat category of "others" will risk neutralising any apparent patterns of use / selection. Alternatively, they may be assigned to other clusters, either those that are nearest up the classification hierarchy or via a second, perhaps non-hierarchical, cluster analysis. The consequences of this are not predictable, although this course of action may represent the most objective one.

However useful (or otherwise) in the generation of a scheme of habitat classification, it is also apparent that cluster analysis cannot justifiably be termed an ‘objective’ method. The investigator makes many arbitrary choices, such as the selection and measurement of variables, the rescaling or transformation of data, the methods of defining similarity or differences between cases, and the method of clustering to be used. In the present study, I surveyed several habitat characters as species (bilberry, bracken) and chose to assess others at a higher taxonomic level (grasses, heathers). While the use of higher level groupings is not invalid (Dale and Clifford 1976), mixing different levels would be certain to affect greatly the resulting habitat categories, by comparison with surveys in which everything was recorded at the species level. Giving all data variables equal weighting (by suitable rescaling) has been termed objective (Gauch 1982), but this is not actually the case: the underlying form of the data (whether count of individuals or percentage cover) is not in itself any measure of 'equality', as other measures of species availability (e.g. biomass) may be just as valid.

One way of selecting the clustering variables would be to use those which have been identified by separate analyses. These may include discriminatory, statistical methods which focus on vegetation characteristics and their underlying determinants, such as ordinations (already mentioned), or correlation and regression techniques, to suggest suitable, biologically meaningful variables relevant to the study animal (e.g. Hill 1981). In this study, for instance, the environmental characters which had been found to correlate significantly with the presence of roe (Chapters 2 and 3) may have been used. The resulting habitat classification would not have been 'objective' in a true sense, and would have removed the independence between those correlation studies and the subsequent habitat use studies; the benefit would be that the correlations would have inherently chosen an appropriate 'scale' for the roe, and perhaps have given a more accurate representation of the animals' perception of the woodlands. In this study, the variables used for clustering would have been woodland stage, bramble, holly, ivy, *Molinia*, and bracken. A more restricted list of variables would also give less 'fuzzy' clustering (Gauch 1982); Curry and Slater (1986) also suggest omitting rare species from the data matrix, and Hill (1981) noted that adding variables served only to confuse the classification of his habitats.

A2. PARASITES AND PREDATION ON NEW FOREST ROE DEER

A2.1 PARASITIC LOAD OF NEW FOREST ROE

Parasites and disease have been shown to be important, even predominant, factors affecting both reproductive performance and mortality in some animal populations e.g. in birds (Hudson 1986, Davis *et al.* 1972, May 1983). In ungulates, the effects of parasitic infection on performance have been less well studied generally (Festa-Bianchet 1989), but has been recognized as an important cause of death in specific cases e.g. lungworm *Prostostronglylus* spp. in bighorn sheep (Forrester 1971). While easily recognized in times of epidemics, such as the devastating effect of rinderpest on African buffalo, as noted (Sinclair 1977), in many cases both the causal role and the effect of parasitic infection on performance may be difficult to assess as the infection often appears in conjunction with other factors, such as inadequate nutrition (Klein and Olson 1960, Wilson and Hirst 1977, Fowler 1987).

Roe, like other deer in Britain, carry a range of parasites (McDiarmid 1973). Common ectoparasites include keds *Lipoptena cervii*, sucking lice *Solenopotes burmeisteri*, biting lice *Damalinia meyeri*, and ticks *Ixodes ricinus*, while endoparasites reported include liverfluke *Fasciola hepatica* and lungworm *Dictyocaulus* spp. New Forest roe have also been found to carry *Borrelia burgdorferi,* the agent of Lyme disease (Muhlemann and Wright 1987). Lungworm causes some local mortality of roe in Britain (McDiarmid 1974) but the effect of liver-fluke is less certain (see Gibson and MacArthur 1965, McDiarmid 1974, Staines and Ratcliffe 1991).

The Forestry Commission collects data on parasites on culled deer as part of its standard deer management procedures. During the processing of deer carcasses, keepers (or rangers) are required to note the presence and extent of any parasites and signs of diseases and other abnormalities. Specifically the keepers look for the presence of ticks, keds, lice, lungworm and liver-fluke. These data are available from the Commission for a number of years, both for the New Forest and for other forests throughout the country. In practice, the amount and quality of information recorded varies and in a few cases it is not possible to carry out an examination. However, these records do provide some indication of the parasitic load of New Forest roe, and this can be compared with that in other forests; these analyses are restricted to comparisons of the proportions of the respective populations infected, as there are no data on the extent of parasite loads carried by individual animals.

Over the periods 1982 - 1984, and 1986 - 1988, data for 50 roe from the New Forest are available, and these were compared with similar data from 140 roe from Ringwood Forest over 1983 - 1985. Within each population considered there were no significant differences between years in the proportions of animals infected with either ticks or keds, and so data for all years within a forest were aggregated for specific infections. No significant differences were found in the levels of ticks ($\chi^2=0.96$, $p > 0.32$) or keds ($\chi^2=1.31$, $p > 0.25$) between the forests; 89% of roe at Ringwood carried ticks, compared with 94% in the New Forest, and the corresponding figures for keds were 49% and 58% respectively. There was, however, a significant difference in the percentage of animals infected with lungworm (Fisher's Exact test, $p < 0.01$): about 1% of roe at Ringwood had lungworm, compared to 14% in the New Forest, although only one of the latter cases was recorded as severe. Other conditions were rarer, with 8% of New Forest roe recorded as carrying liver-fluke and some 10% with lice (none was recorded for Ringwood). A single case of pleurisy was also recorded in the New Forest in 1984, although this represents a lower proportion than the average figure for roe over the south-east of England over 1986 - 1988 of some 4% (Adams and Dannatt 1989).

The findings for the New Forest roe may also be compared to levels of parasitic load of other deer in southern England. Jackson (1975) noted that the New Forest fallow appear healthy despite a much heavier parasitic load than that found on the Forest roe. In addition, data collected for a detailed survey of deer from many forests in the south and east of England, including the New Forest, did not suggest that the New Forest roe were carrying an abnormally high parasitic load overall. Some 16% of all fallow examined had liver-fluke, and nearly 4% had lungworm (Adams and Dannatt 1989).

Levels of parasitic infection of course may themselves be a consequence (rather than cause) of loss of body condition from poor nutrition (Wilson and Hirst 1977). Indeed, populations of large mammals suffering from high levels of infection are also often food-limited (Fowler 1987), as animals shift limited resources from the immune to the reproductive system (Festa-Bianchet 1989). Maizeret *et al.* (1989) recorded that roe populations at high density in Germany and Austria were frequently reported by hunters as being in poor condition, including suffering from parasites and disease, and Boutin (1986) also considered that mortality in juvenile roe from coccidiosis was a secondary consequence of limited food availability. Altogether, it seems that the New Forest roe may carry a slightly higher burden of internal parasites than roe at Ringwood, but levels remain fairly low, and in themselves are unlikely to be responsible for the observed drop in performance. More likely, they are a consequence of poorer body condition from food-limitation.

A2.2 EFFECTS OF PREDATION AND CULLING

Natural predation can exert a profound effect on deer population performance. Predation by wolves *Canis lupus* on moose (Messier and Crête 1985, Messier 1991, Gasaway *et al.* 1992), and on white-tailed deer (Bergerud and Elliott 1986), and by coyotes *Canis latrans* on white-tailed deer (Garner *et al.* 1976, Cook *et al.* 1971, Messier *et al.* 1986) have been shown to limit population levels. However, it is not clear whether predators can also regulate prey populations. Some authors have suggested this to be the case (e.g. Keith 1974, Yoaciel 1981, Bergerud 1988), but the evidence remains ambiguous, not least because to demonstrate such regulation would necessitate controlled predator removal and restoration (Sinclair 1989).

In the case of the New Forest roe, the only potential natural predator is the fox *Vulpes vulpes*, which in other populations has been recorded as taking young fawns (e.g. Ratcliffe and Rowe 1985), although some additional casualties may be caused by domestic dogs. There is no direct evidence of predation on New Forest roe by foxes, which are themselves not common in the Forest (Insley 1977), and it is unlikely they have a significant effect upon the roe population. At Kalø, in Denmark, Andersen (1961) also noted that loss of fawns to foxes was rare. Loose dogs certainly do harass deer on occasion (pers. obs. and keepers' reports) and, despite the Commission's regulations, some 97% of dogs walked within the inclosures are off-lead (pers. data for 1989 collected during habitat use studies).

However, killing of roe by dogs appears to be very rare and is unlikely to affect the population as a whole (a single record of such a killing was noted during on the New Forest cull data sheets over 1982 - 1984).

Casualties through road traffic accidents and poaching are also thought to be negligible for roe (Commission keepers, pers. comm.), and certainly insignificant when considered against the potential of the roe to increase its population (Chapter 1). In any case, any known mortality from any of these causes has been offset against the Commission's own annual cull. Indeed, for many years, it is this cull which has been by far the major source of imposed mortality on the roe population in the New Forest.

For the last 30 years the Forestry Commission has calculated its cull target for each deer species according to a standard formula. On the assumption that two-thirds of the censussed population of adult females (one year and older) will produce offspring in any year, in a 1:1 sex ratio, the number of individuals likely to be recruitment to the population in that year can be calculated. Estimated losses due to poaching and road traffic accidents can then be deducted, and the resulting culling level required to retain the target population established. The current target for roe is set at 300, and in practice, as censuses through much of the 1980s have returned a population less than this, there has been a negligible level of culling of roe since 1984.

The likely effect of culling can be assessed by consideration of other species, both in the New Forest and elsewhere. The total imposed mortality (that is, from accidental death, poaching and culling operations) in the New Forest over 1975 -1985 has been of the order of 40% - 50% of the censussed population for fallow and sika deer, which may be assumed to have a major impact on population levels. Such a calculation, however, assumes that the censussed population each April approximates to the true population total and that the mortalities from poaching and road traffic accidents can be accurately assessed.

As we have seen, underestimating actual population levels of deer is common and often severe (Staines and Ratcliffe 1987). In his studies of population change in New Forest fallow deer, Strange (1976) considered that estimates of road traffic losses and poaching may well be reasonable. However, the census figure on which the cull is first calculated may be a considerable underestimate of true population size. Strange's figures for 1970 -

1975 suggest that while the Commission estimated a total population of 914 fallow deer within the New Forest (mean over the five years), the true population was probably nearer to 1800. Mann's (1983) figures for sika deer populations between 1979 and 1982 suggest numbers of 175 - 200, once again around twice the censussed level of 74 - 95 for the same period (Putman and Sharma 1987).

Such figures suggest that the New Forest roe deer population may also be underestimated in a similar way to the other species; certainly other studies on roe support this, with Andersen (1953) reporting that the true number of deer at Kalø was over three times the level estimated by experienced local game keepers. Thus, the true culling levels for the three species over the period 1975 - 1985 are more likely to have been in the region of 20% - 25% for fallow and sika deer, but only 6% - 10% for roe. An imposed mortality of even 20% may well be sufficient to have a disruptive effect on deer populations. Clutton-Brock, Guinness and Albon (1982) found that the numbers of red deer on Rhum increased substantially following the relaxation of a 17% cull in 1973; Houston (1982) considered that human predation on elk populations in the Yellowstone National Park at an average level of 21.5% was the major factor responsible for changes in population numbers. In roe, Vincent and Bideau (1992) noted that, at St. Arnoult-en-Yvelines (some 40 km. from Paris), the previously stable population level rose after 1980 with cessation of hunting, which had accounted for an estimated 22% of the population each year (mortality from other causes was not given).

Ratcliffe and Mayle (1992) calculate the levels of culling needed to achieve stable populations at different Commission sites, using reliable data on numbers, recruitment and mortality in age-class specific population models. They note that different forests require different cull levels to achieve zero population growth. Thus at Alice Holt, a 25% cull resulted in zero growth, compared with 17% at Kershope, 21% at Chedington, and 26% at Pickering. Ratcliffe and Mayle (1992) noted the importance of using accurate fawn:doe ratios in these models, as low values (i.e. when there has been heavy fawn loss) could reduce the following year's required cull to zero, e.g. at Kershope. Such a picture makes it difficult to predict the effect of even such a low cull as 6% - 10% on the New Forest roe population. However, we should observe that in the later years of the decline (certainly 1982 onwards) the actual cull in the New Forest was even lower (e.g. some 6% of the censussed population in 1982, thus perhaps only 2-3% of the actual population, and even less thereafter) but the decline in the roe population continued. It not only seems unlikely that such a low cull would have any effect on a roe population that was not limited by some other factor (such as some resource limit, or high density), but a decline precipitated by non-selective heavy culling would also not be accompanied by reduced body condition and reproductive performance (e.g. Staines 1978). Moreover, even if this imposed mortality has had some effect upon the roe population, the demonstrated relationships between roe deer and the vegetation of the New Forest remain.

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