UNIVERSITY OF SOUTHAMPTON

VARIATION IN SOCIAL SYSTEMS OF FALLOW DEER

by

SIMON JEREMY THIRGOOD

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To my parents
for their support and encouragement
over the years

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ABSTRACT

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The thesis investigates intraspecific variation in grouping patterns and mating systems in free-ranging populations of fallow deer Dama dama inhabiting two distinct environments. The New Forest in southern England consists of large continuous woodlands adjacent to large areas of heathland and grassland. The southern English agricultural landscape is typified by small, discontinuous woodlands interspersed with pasture and arable crops. Fallow populations occur at a range of densities in both environmental types.

Despite occurring in environments markedly different in habitat composition and structure, habitat use patterns showed great similarity between sites in terms of utilization of woodland and open habitats. In all study sites, deer predominantly utilized woodlands. Differences between the two main environmental types were more pronounced in respect of population characteristics. Densities were much higher in the New Forest populations, and there was considerable variation in sex ratio within and between environmental categories. These two characteristics appeared to influence the extent of winter and spring sexual segregation exhibited by the populations. Males joined female groups when male numbers were low. In the New Forest, mixed-sex groups were the result of temporary aggregations of females and young males. In contrast, mixed-sex groups in the agricultural sites contained males of all ages.

The size of social groups was strongly influenced by season, habitat openness, habitat structure and population density. A common seasonal pattern existed across all sites, with female groups largest in winter and spring, decreasing during parturition in early summer, and increasing again during the autumn rut. Male group size was smallest during the rut and varied little throughout the year. In common with most ungulates, fallow group size was largest in open habitats. Between different populations, variation in the extent of group size between woodland and open habitats may have been influenced by habitat structure and population density. High density populations inhabiting large continuous woodlands were characterised by small groups in woodland and large groups in open habitats. In contrast, in low density populations inhabiting small discontinuous woodlands group size was less variable.

The flexibility in fallow grouping patterns was matched by the variation in mating systems. Males adopted a range of mating strategies which could be broadly classified according to the degree and type of territoriality during the autumn rut. In the low density agricultural populations, male territoriality was reduced and males followed groups of females throughout their range. In the higher density New Forest populations a variety of male mating strategies existed including leks, multiple stands, single territories, temporary territories, and non-territorial following. Increased territoriality and the development of multiple territory mating systems was associated with an increase in male and female density. Lekking may be initiated by locally high densites of females aggregating near favoured feeding resources. In one population in the New Forest, lekking occurred as an alternative strategy to single territory defence and non-territorial following. In this population, copulatory success was highest on the lek, but unsuccessful lek males achieved less copulations than some single territory males away from the lek.

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1. GENERAL INTRODUCTION

In recent years it has become clear that the social systems of many mammals and birds are highly flexible and closely related to environmental characteristics. The concept of a social system has been succinctly defined by Petrie (1986) as 'a description of two main aspects of animal existence: 1) the spacing pattern of the individuals (eg. whether they form groups) and 2) the form of the mating system (eg. whether individuals are monogamous or polygamous)'. A social system is the sum of the behaviours of the individual animals in the population and as such represents a level at which natural selection does not act (Gosling & Petrie 1981), since natural selection acts on individuals or genes rather than groups or populations (Hamilton 1964; Williams 1966; Dawkins 1976). This thesis describes a three year investigation into variation in social systems of a common European cervid, the fallow deer *Dama dama*, concentrating upon the two parameters outlined above, namely social grouping and reproductive behaviour. The first section of this introductory chapter presents the theoretical framework within which the remainder of the thesis should be considered by asking three fundamental questions:

1. Why do animals live in groups?
2. Why do animals have different mating systems?
3. Why do social systems vary within species?

1.1. WHY DO ANIMALS LIVE IN GROUPS?

In a review of the origins of animal sociality, Alexander (1974) argued that the ecological factors favouring the evolution of social groups fall into two main classes, predation pressure and resource distribution. The essence of his argument is that grouping invariably confers disadvantages in terms of increased competition and susceptibility to parasites and disease. Even where the resource distribution allows animals to form groups at low cost, positive benefits must exist to outweigh these inevitable costs. With rare exceptions all such benefits come from either escaping predators or acquiring resources. Alexander further suggested that social behaviour within groups evolved to enhance the original advantages of grouping.

The view that predation and resource distribution are the two principal factors responsible for variation in social grouping has received wide acceptance (eg. Bertram 1978; Pulliam & Caraco 1984; Krebs & Davies 1987). Wrangham & Rubenstein (1986) suggest that it is useful to recognize a third major category of factors responsible for the formation of groups, namely interactions between conspecifics. Like predation and resource distribution, the effects of interactions between conspecifics are expressed in different ways in different species, are mediated by ecological constraints, and can account for the evolution of social groups even when no other factors favour grouping. The following three sections will deal with each of these factors in turn.

Escaping predators

Potential prey animals may benefit in a number of different ways from being in a group. Grouped prey often detect an approaching predator sooner than do solitary individuals. For example, goshawks *Accipiter gentilis* are less successful when they attack larger flocks of wood pigeons *Columba plumbus* largely because bigger flocks take flight at greater distances from the hawk (Kenward 1978). This occurs even though each individual in a group usually spends less time in vigilance behaviour and can therefore allocate more time to other activities. In ostrich *Struthio camelus* flocks, for example, Bertram (1980) found that each individual spends a smaller proportion of its time scanning than when alone but that the overall vigilance of the group increases with group size. Similar results have been demonstrated for a range of large mammalian herbivores, for example, bighorn sheep *Ovis canadensis* (Berger 1978), pronghorns *Antilocapra americana* (Lipetz & Bekoff 1982), ibex *Capra pyrenaica* (Alados 1985) and eastern grey kangaroos *Macropus giganteus* (Jarman 1987).

Prey may aggregate in an attempt to place conspecifics between themselves and an attacking predator (Hamilton 1971). However when individuals on the periphery of the group experience greater predation, it is difficult to invoke this mechanism as the sole selective force favouring sociality (Pulliam 1973). A more plausible explanation is that individuals take advantage of the 'dilution effect' of being only one of a large group of potential prey items. If prey are capable of taking evasive action, and predators only kill a single victim on a successful hunt, then the larger the group of prey animals the smaller the chance that any individual will be the victim (Hamilton 1971). Schaller (1972) and Kruuk (1972) showed that lions *Panthera leo* and spotted hyaena *Crocuta crocuta* rarely catch more than a single animal from the prey group they were hunting, the rest of the herd escaping. Prey aggregations may attract predators, but it is unlikely that the increase in predation will be proportional to the size of the group.

Tightly aggregated prey may confuse an attacking predator, if the predator is prevented from focusing its effort on a particular prey target. Similarly, Jarman (1974) suggests that the 'explosion' in all directions of a herd of impala *Aepyceros melampus* when startled has a confusing effect on a predator trying to catch one. Finally, it is possible that groups of some prey species can deter or thwart the predator's attack, whereas a single prey animal would be unable to do so. For example, musk oxen *Ovibus* *moschatus* threatened by wolves *Canis lupus* form into a defensive formation with an array of horns facing the predators and vulnerable animals in the middle (Mech 1970).

Acquiring resources

Group size can influence the rate at which patches of food are discovered in temporally and spatially uncertain environments. Laboratory studies with great tits *Parus major* have demonstrated that the time required to discover a patch of food decreases significantly as group size increases (Krebs et al. 1972). Since the location of food by one individual alerts other group members, per capita search time can be lower in large groups. This effect can be particularly important if the food patches are large in relation to individual requirements (Pulliam & Caraco 1984).

The type and distribution of food eaten clearly determines the advantages of foraging in a group (Jarman 1974). When animals feed on small discrete highly nutritious food items, relatively abundant in a small area, the most advantageous tactic may be to forage solitarily and defend an exclusive territory to reduce intraspecific competition. Such a foraging strategy is adopted by many of the smaller antelope, as for example the dik-dik *Rhynchotrgus kirki* (Jarman 1974). When food supplies are more patchily distributed, larger foraging groups are able to search over a wider area, and take advantage of the relative richness of individual food patches. Red colobus monkeys *Colobus badius* feed selectively on young shoots, fruit and flowers; these resources are highly clumped in space and time, difficult to find, but once located are sufficiently abundant to feed a large group (Clutton-Brock 1975). When animals feed unselectively and food is thus abundant and relatively available, as for many large savannah-dwelling ungulates, foraging may no longer be a limiting factor influencing group size. These animals have gained flexibility from their feeding style, allowing them to respond to other environmental variables (Jarman 1974).

Once food is located, the decreased vigilance time of individuals in groups may increase foraging efficiency. Eastern grey kangaroos in larger groups spend more time feeding and less time surveying than do those in smaller groups (Jarman 1987). An alternative explanation of the positive correlation between group size and feeding time is that feeding in a group environment is less efficient due to mutual interference, as has been shown for large groups of starlings by Feare (1984) and suggested for some antelope species by Underwood (1982a).

Finally foraging in a group may allow individuals to exploit particular types of food that they would be unable to obtain on their own. This is the usual explanation given for group hunting in social carnivores such as lions and hyaenas (eg. Schaller 1972, Kruuk 1972, Caraco & Wolf 1975). Recent re-analysis of sociality in lions however, casts doubt on the idea that grouping in lions evolved in response to selection for cooperative hunting (Packer 1986). Rather it is suggested that lion sociality results from group defence of carcasses against scavenging conspecifics in high density populations.

Interactions between conspecifics

Ecological influences favouring sociality may not act alone; they may be mediated by the pattern of interactions between conspecifics. In the lion example given above, Packer (1986) suggests that females allow their kin to share the foraging range because the costs of sharing large carcasses are low in comparison to the costs of dispersal in a high density population. Thus group living is favoured not only by the distribution of resources but also by the effect of intraspecific competitors on resource distribution. Additionally, female lions may benefit from each others assistance in reducing the rate of infanticide by males.

Certain types of intraspecific interactions may promote sociality even in the absence of ecological benefit. In eastern grey kangaroos, females in oestrus increase their range and attract a retinue of courting males, advertising themselves to ensure fertilization by the dominant male in the population (Jarman & Southwell 1986). In lekking species such as sage grouse *Centrocercus urophasianus*, female movements appear to determine male distributions and may influence male behaviour within mating aggregations (Gibson & Bradbury 1986). In summary, it seems that interaction between conspecifics, like predation pressure and resource distribution, may act either by itself or in combination with other factors to influence patterns of social grouping (Wrangham & Rubenstein 1986).

The comparative approach: socioecology of antelope

The preceding account has summarised how individual animals might benefit from being members of a group. For simplicity of presentation, the ecological and behavioural factors influencing sociality were largely presented in isolation. However, a number of studies have attempted to show how food, predation and other factors may interact to influence group size and other aspects of the social organisation of a range of closely related species. The instigator of this comparative approach to investigating adaptation in the early 1960's was Crook, with his now classic studies on weaver birds and primates (Crook 1964, Crook & Gartlan 1966). However, perhaps the most influential work, and most relevant to the current project, was Jarman's review of social organisation in the African antelope (Jarman 1974), which now be considered in some detail.

Jarman surveyed the literature on the behaviour and ecology of 74 species of antelope and suggested that each could be assigned to one of five classes, distinguished largely by the strategies used by males to secure mating rights, and the effects of those strategies on other social castes. He demonstrated that these strategies were appropriate to each class because of the effects of ecological aspects on their ways of life. Jarman's argument can be followed as a series of logical steps.

1. Larger species with lower metabolic requirements per unit body weight will tolerate lower quality food than smaller species.
2. Low quality food items are more abundant and evenly dispersed than high quality food items.
3. Individuals of smaller species have to seek carefully their scarce, scattered food items; individuals of larger species are more likely to find with little searching, abundant, evenly dispersed items.
4. A single food item may form a greater proportion of a day's intake for an individual of a smaller species than a larger species.
5. Smaller species are more capable of selecting plant parts of high food value.
6. Food items in a given dispersion will be more widely spaced relative to the size and movements of an individual of a small species than a larger species.
7. Smaller species are less likely than larger species to be able to defend themselves against or outrun predators, therefore individuals of smaller species must avoid being detected by predators.
8. Individuals of larger species avoid predation by group defence, group alertness, dilution, and speed.
9. Group-living individuals must remain in communication to maintain group cohesion.
10. Dense vegetation and broken terrain disrupt visual communication, flat open country favours it.

Putting these hypothetical points together, large species feed on abundant, evenly dispersed, low quality food items, and are more likely to form groups for defence against predators. Such groups are more likely to be found in the open where visual communication is favoured. In these herds there is potential for the strongest males to monopolize several females by defence of a harem or dominance hierarchy of mating rights. In contrast, small species feed on scarce, scattered, high quality food items, lead a solitary existence, and avoid predators by hiding. Because the females are dispersed, the males must also be dispersed and the commonest mating system is for a pair to defend a territory. Antelope of intermediate size show aspects of the ecology and behaviour of these two extremes. The essential point of Jarman's hypothesis was that whilst predation pressure sets the lower limits on group size in antelope, food dispersion and foraging style sets the upper limits.

Jarman (1974) then presented data extracted from the literature to test his hypotheses; in general the predictions and the data were well matched. An elegant study by Wirtz & Lorscher (1983) on eight antelope species occurring in Lake Nakuru National Park, Kenya, offers supporting evidence: browsers had smaller group sizes than grazers, group size was positively correlated with body weight of the species, and open grassland species were found in larger groups than those of dense scrubland.

1.2. WHY DO ANIMALS HAVE DIFFERENT MATING SYSTEMS?

As stressed in the first paragraph of this chapter, the evolution of a particular mating system must be considered in terms of individualistic reproductive maximization (Williams 1966), the currency in which natural selection operates. Individuals may maximize their reproductive success either directly through producing surviving offspring, or indirectly through helping the reproductive efforts of close relatives who share a large proportion of their genes (Hamilton 1964). An important development was the suggestion by Trivers (1972) that the sexes invest differently in reproduction. In most vertebrates, females invest more in individual progeny than males. For example, in mammals the male invests a small amount of time in courtship and copulation whereas the female invests heavily during pregnancy and lactation. The number of offspring a female can produce is therefore smaller than that of a male. Consequently males can increase their reproductive success by mating with a number of females whereas most females cannot increase theirs by mating with several males. Trivers argued that when one sex invests more in the rearing of offspring than the other, members of the latter will compete for members of the former.

It is clear from the above argument that polygynous breeding will usually be to a male's advantage but may be to the disadvantage of the female, whose offspring may receive less paternal investment than if their mother had bred monogamously. Verner & Willson (1966) and Orians (1969) argued that in those species where polygynous breeding occurs, it must also be to the female's advantage to breed polygynously, otherwise she would chose a monogamous male. In Orians's model, all males are presumed to adopt a strategy of defending a resource that females need. When the partitioning of resources by territorial males is unequal, females may do better to mate polygynously with an already mated male on a good territory than to mate monogamously with an unmated male on a poor territory.

Maynard Smith (1977) extended this argument to consider the evolution of mating systems other than polygyny in terms of a game in which the optimal behaviour of one parent depended on the behaviour of the other. He argued that whether or not one parent should withhold parental care depends on how likely the other parent is to continue caring for the offspring. Maynard Smith's idea was to determine the pair of strategies, one male and one female, which when performed together, produced an "evolutionarily stable strategy" (ESS). An ESS would occur when it would not pay either sex to change strategies as long as the other sex also did not change. Whether there is parental care, and which sex should provide it, is determined by the relative effectiveness of uni- or biparental care, the likelihood of a deserting partner finding another mate, and the extent to which a female's ability to provide care reduces her ability to produce future offspring. Maynard Smith's model is particularly useful in identifying the factors which will lead to different patterns of parental investment and mating systems.

Most studies of polygyny focused on birds, and the relevance of the polygyny threshold model of Verner & Willson (1966) and Orians (1969) to many mammals is debatable (Armitage 1986). Implicit in the polygyny threshold model is the assumption that females are free to disperse and choose mating partners on the basis of phenotype or territory quality, preferring polygynous matings to monogamous ones when their fitness is increased by doing so. Among mammals however, females are often bonded to other females and interactions between females may often determine the size of the breeding group. Additionally, in the majority of social mammals, females seldom disperse far from their natal group and males typically impose themselves on pre-existing female distributions (Greenwood 1980).

Emlen and Oring (1977) suggested that polygyny will occur either where males can monopolise resources sufficient to attract several females ('resource defence polygyny') or where they can defend groups of females ('female defence polygyny'). The feasibility of defending either resources or females will be affected by their distribution in time and space. The 'environmental potential for polygyny' depends on the degree to which multiple mates, or the resources critical to gaining multiple mates, are economically defensible. Whether polygyny occurs will be also be affected by the amount of time and energy that the male can invest in defence of mating access and the degree of female synchronization in reproductive receptivity. What Emlen and Oring's model lacked was an understanding of how ecological factors affected female distribution. The relationships between ecology, social organisation and mating systems in mammals were clarified by studies on antelope (Jarman 1974), bats (Bradbury & Vehrencamp 1976, 1977) and primates (Clutton-Brock & Harvey 1977) which demonstrated that female distributions were adapted to the environment and depended largely on the needs of females to seek food and safety from predators (see preceding section).

There is now a general consensus that the mating strategies of many male mammals are influenced by the spatial and temporal distribution of receptive females, which are in turn affected by variation in resource distribution, predation pressure, the costs of social living and the activities of other males (Jarman 1974; Bradbury & Vehrencamp 1976, 1977; Emlen & Oring 1977; Clutton-Brock & Harvey 1978; Lott 1984; Gosling 1986; Rubenstein & Wrangham 1986; Wrangham & Rubenstein 1986). A detailed review of mammalian mating systems has recently been published by Clutton-Brock (1989) and what follows is extracted from this paper. Clutton-Brock argues that much of the variation in male mating behaviour is related to the effect of male assistance in rearing young and differences in the economic defensibility of females by males. The three main factors which influence the economics of female monopolization are the size of female ranges, the size of female groups, and the density and distribution of females in time and space.

The basic framework of Clutton-Brock's model can be best presented as a series of hypothetical scenarios, each of which leads to the evolution of a particular type of mating bond and defence system. Details and examples of each category are given in Clutton-Brock (1989), who stresses that categories clearly intergrade and that species may show several different mating systems.

1. Obligate monogamy. Females cannot rear offspring without the assistance of their mating partner or assistance raises breeding rate. Males mate with a single female and defend a territory.

Where breeding success does not require male assistance, female range size and grouping characteristics have an important influence upon the polygyny potential.

2. Facultative monogamy/polygyny. Females are solitary and occupy ranges small enough to be defensible by males, and males defend territories overlapping one or more females.
3. Unimale groups with spatial defence by males. Female ranges or core areas are small enough to be defensible and females live in small social groups. Males defend the range of the female group.
4. Multimale groups with spatial defence by males. Female ranges or core areas are defensible and female live in large social groups. Several reproductively active males live in the group and cooperate in territorial defence of the female range.
5. Unimale groups without spatial defence by males. Female ranges are too large to be defended or male territoriality is precluded for other reasons. Females live in small stable groups and males defend an exclusive harem.
6. Multimale groups without spatial defence by males. Female ranges are too large to be defended and female groups are large and typically contain several breeding females. Several reproductively active males live in the group, although they seldom co-operate in group defence.
7. Mating territories. Females range over areas too large to be defensible and female groups are unstable in composition. Males defend individual mating territories considerably smaller than the female range in areas regularly visited by females.

8. Clustered mating territories or leks. As above but large numbers of females share a common range and local density is very high. In some species male territories are very small and mating systems are analogous to the leks of some bird species.
9. Temporary harems, territories, or leks. Females live in large, unstable groups and mating may take place during migrations. Male behaviour appears very flexible.
10. Roving males. Females range widely and are solitary or live in small groups that are unpredictably distributed at low density. Males range widely in search of oestrous females, consorting with them and defending them against other males.

Whilst Clutton-Brock's review is controversial, and likely contains some anomalies, it demonstrates how the diversity of mammalian mating systems can be interpreted within a relatively simple framework of ecological relationhips.

1.3. WHY DO SOCIAL SYSTEMS VARY WITHIN SPECIES?

Implicit in many early assessments of avian and mammalian social grouping and mating systems was the assumption that a species social system was a fixed product of natural selection. Such an approach is apparent, for example, in the well known comparative reviews of antelope social organisation by Jarman (1974) and Estes (1974), relating feeding style and habitat choice with body size, group size and behaviour. Variation in social systems within a single species were referred to by both authors, for example the observed variation in territoriality between sedentary and migratory populations of wildebeeste. However as Alcock (1979) states:

'The co-existence within a species of several alternative strategies is probably far from uncommon, although this is not widely recognized because ethologists have tended to sweep intraspecific variations in social behaviour under the rug.'

Much of the attention of early socioecologists was directed towards description of species-specific behaviour patterns as an essential first step in understanding the adaptive significance of behaviour. Groups or individuals which differed from 'typical' behaviour were either ignored or treated as deviants destined for removal from the population by natural selection. As wild vertebrates are increasingly studied in more than one area or at more than one time, however, intraspecific variations in social systems have been increasingly observed (Rubenstein 1980; Dunbar 1982; Lott 1984).

The recent review by Lott (1984) lists nearly 200 instances of intraspecific variation in social systems of vertebrates recorded in the literature up until 1982, and the last decade has almost certainly seen an increase in such reports. Lott catalogues intraspecific variation in numerous aspects of vertebrate social systems. Amongst mammals, individuals within a species may be solitary or group living (eg. spotted hyaena (Kruuk 1972)). Their spacing system may be territorial or lekking (eg. Uganda kob *Adenota kob* (Beuchner 1961)), territorial or undefended home range (eg. otter *Lutra lutra* (Kruuk & Hewson 1978)), or territorial or dominance hierarchy (eg. pronghorn antelope (Kitchen 1974)). They may breed monogamously or polygynously (eg. yellow-bellied marmot *Marmota flaviventris* Armitage & Downhower 1974)) or polygynously or promiscuously (eg. deer mouse *Peromyscus maniculatus* (Mihok 1979)). Either both parents or a single parent may care for the young (eg. brown hyaena *Hyaena brunnea* (Mills 1982)) and the parents may or may not have helpers (eg. black-backed jackal *Canis mesomelas* (Moehlman 1979)). Parents may or may not pool their young and care for them communally (eg. red fox *Vulpes vulpes* (MacDonald 1979)).

Numerous studies have now identified ecological correlates of alternative social systems in different populations of single species. These variables are generally those currently considered to be important in interspecific socioecological analysis: the level of predation and its avoidance, the distribution and abundance of food, and the level of population density and habitat saturation (Lott 1984). Such explanations only account for variation between populations, and it is now clear that individuals may adopt markedly different social strategies even within the same population. This flexibility has been particularly well studied with respect to alternative male mating strategies, and current theory suggests that there are two main reasons for such variation within populations (Rubenstein 1980; Dunbar 1982). The first explanation is that the best strategy for an individual to adopt may depend upon the strategies adopted by other males in the population. This explanation assumes that the payoff between the two strategies is similar in terms of the number of copulations acheived, and a mixture of strategies evolves by frequency-dependent selection. The second explanation is that some males in the population are poorer competitors than others, for reasons of size, age, nutrition and so on, and are simply forced to 'make the best of a bad job' in an inferior strategy. It is quite probable that there are intermediate stages between these two extremes.

The consideration of mechanisms that produce intraspecific variation in social systems highlights a fundamental difference between interspecific and intraspecific socioecology (Lott 1984). Interspecific differences are typically assumed to be caused by genetic differences resulting from distinct natural selection histories in the species under consideration. Intraspecific differences, on the other hand, often involve facultative switching between alternative strategies that are clearly not due to genetic differences. For this reason, intraspecific comparisons are extremely useful for testing sociobiological theory without the masking effects of profound genetic differences implicit in interspecific comparisons (Jarman 1982).

The second section of this chapter introduces the study animal, the European fallow deer *Dama dama*, briefly reviewing existing knowledge of its social system before proceeding to outline the aims and approach of this thesis.

1.4. THE FALLOW DEER

History and distribution

Fallow deer are the most widely distributed deer in the British Isles, occurring in the wild in nearly all the English counties and parts of Wales, Scotland and Ireland. Originally widespread throughout Europe, the species became extinct in the last glaciation except for a few relic populations in Southern Europe, from which reintroduction to Britain occurred, probably during the Norman period. In addition to wild populations, fallow deer are maintained in park herds on many private estates; indeed escapes from such deer parks have helped to re-establish many wild populations. The history and distribution of fallow deer both in Britain and world-wide is reviewed in detail by Chapman & Chapman (1975, 1980).

Physical description

Fallow are medium sized deer, adult males standing up to 90 cm at the shoulder and weighing up to 110 kg in early autumn. Females are considerably smaller at 80 cm height with weights up to 60 kg. Coat colour varies from white to nearly black, with the most typical summer coat a reddish fawn with white spots along the flank and back. In winter coats become greyish with indistinct or no spots. Males' antlers are palmate and vary in size depending upon age, condition, and genotype. Antlers are cast April - June, older animals casting before younger ones; regrown and clear of velvet August - September; younger animals cleaning before older ones. A detailed physical description is given in Chapman & Chapman (1975) and Chapman & Putman (1990).

Habitat use

In the wild state, fallow are characteristic of mature deciduous woodland, however their flexibility of behaviour and habitat demands have enabled them to colonise a variety of environments ranging from coniferous plantations to agricultural land with small woodland copses. Patterns of habitat use change throughout the year as seasonal availability of different forage alters. Patterns of habitat use within the New Forest show selection for deciduous woodland during September - April and more open habitats during May - August (Jackson 1974; Parfitt in Putman 1986a).

Diet

Fallow are preferential grazers and anatomical considerations based on the structure of the gut suggest that they are adapted as relatively unselective bulk feeders. In all populations, grasses form >60% of forage intake during spring and summer, with fruit crops and deciduous browse taken more commonly in autumn and winter. Even during winter however, grass still contributes >20% of diet stressing that the deer are preferential grazers throughout the year (Jackson 1977; Caldwell et al. 1983; Putman 1986a; Waterfield 1986).

Reproduction

Breeding is highly seasonal with most mating activity concentrated in a short period, the 'rut', in late October. Conceptions before and after this date do however occur and copulations have been observed as late as February. Does are polyoestrus and can breed as yearlings. Most fawns are born in June after a gestation period of approximately 230 days. Single young only are produced, and are able to follow their mothers soon after birth. Reproductive physiology is reviewed in detail by Sterba & Klusak (1984) and Asher (1986).

Social system

In many populations the sexes remain spatially segregated for much of the year, with adult males forming separate 'bachelor' groups from females and young (including yearling males). Males move into female areas early in autumn to rut but remain only until November before returning to their own ranges (Jackson 1974; Chapman & Chapman 1975). This strict segregation does not however occur in all cases. In some populations males remain in female areas after the rut and mixed-sex groups persist until late spring (Heideman 1973; Schaal 1982; Langbein 1985; Waterfield 1986). Fallow are non-territorial outside the rut and home ranges show extensive overlap. Data on range size is limited, and is restricted to populations in extensive woodlands where summer ranges for females and males are approximately 70 ha and 110 ha respectively (Rand in Putman 1986a).

Group size of both sexes is variable and is affected by season. Most males are solitary during the autumn breeding season and are found in small groups of less than five throughout the rest of the year (Jackson 1974). Female groups show more variation throughout the year, and range from solitary individuals to aggregations of up to 200 on favoured feeding areas. Parturition in June is associated with a decrease in group size which increases again during the autumn (Jackson 1974; Parfitt in Putman 1986a). Female group size appears strongly influenced by habitat openness, with larger groups occurring on open grassland or agricultural crops than in woodland (Heideman 1973; Putman 1981; Schaal 1982; Waterfield 1986).

Mating systems appear equally variable. The conventional interpretation is that mature males compete to establish noncontiguous reproductive territories called 'rutting stands' to which they attract females by calling or 'groaning' (Chapman & Chapman 1975). The extent of territoriality varies greatly between and within populations however and it is now clear that 'rutting stands' are only one of several different mating strategies adopted by fallow bucks. Non-territorial reproductive behaviour during the main autumn rutting period has been recorded by Schaal (1985a, 1987) in which males defend exclusive unimale harems. In other populations, males defend small clustered mating territories analagous to the 'leks' of some antelope (Schaal 1986, 1987; Pemberton & Balmford 1987; Clutton-Brock et al. 1988; Apollonio et al. 1989). The ecological relationships influencing such pronounced variation have not been clarified.

1.5. AIMS AND APPROACH OF THE THESIS

It is clear from the above account that social systems of fallow deer are highly variable and appear strongly influenced by the environment. This study emphasizes the ecological relationships linking characteristics of the vegetational environment and population structure to grouping patterns and mating systems in wild populations of fallow deer.

Comparisons within species, either between populations living in different environments, or within populations in different circumstances, are a common way of testing sociobiological attributes without major differences between species masking subtle responses to environmental variation (Jarman 1982). There are three primary ways of conducting such studies:

1. Comparing populations in different parts of the species range in order to see whether differing environmental factors affect their sociobiological attributes.
2. Similar comparisons can be made between the attributes of a single population living under differing circumstances (eg. between seasons or between years).
3. Studying the behaviour of individuals to see how individual differences contribute to overall behaviour.

This study employs all three methods but concentrates in the main on the first approach of inter-population comparisons. To this end, eight study populations were established in two distinct environmental types: the extensive woodlands of the New Forest and the mixed arable-woodland complexes typical of agricultural areas in Southern England. Chapter 2 gives a general description of each site and discusses the sampling methods common to each of the data chapters.

In order to assess and interpret population differences in grouping patterns and mating systems in relation to environmental parameters, it was first necessary to quantify the availability, structure, and patterns of use of vegetational resources in each study site. Chapter 3 introduces the habitat classification scheme used in the study and provides linear measures of habitat composition and structure for each site. Patterns of habitat utilization are examined in Chapter 4, with emphasis on the level of resolution of habitat categories. The chapter presents comparative data on seasonal variation of both habitat use and selection and determines whether observed differences in utilization are due to changes in habitat availibility or selectivity.

A second factor potentially influencing fallow social systems is the population structure itself. Chapter 5 initially presents comparative data on population density, dispersion, and sex ratio, then going on to quantify the extent of sexual segregation in each study site. Sexual segregation, or the lack of it, is then related back to the population parameters previously introduced.

Season and habitat openness have been identified as important factors influencing social grouping in many ungulates, including fallow deer. Chapter 6 picks up this theme and examines it in considerable detail. After an initial discussion of the suitability of available group size measures, the effects of season and habitat on group size and flexibility are examined in each of the eight study populations. Comparisons of group size are then drawn between sites both as an overall measure and within individual habitats and seasons. The final section attempts to explain group size variation in terms of the environmental and population parameters introduced in the preceding three chapters.

Mating system variation between populations is examined in Chapter 7. For each of five sites, three in the New Forest and two in agricultural land, a detailed description of male mating strategies is given. This account is then interpreted in the light of complimentary work on enclosed fallow populations (Langbein 1990) and an overall framework is presented to clarify the wide range of male mating strategies observed. From this basis, mating system variation in wild populations is related to characteristics of the population and vegetational environment already presented.

In Chapter 8 emphasis is shifted to the individual in an intensive study of the reproductive success of males adopting the alternative mating strategies of lekking, single territory defence, and non-territorial following within a single fallow population in the New Forest. This chapter also analyzes the behaviour of lekking males and determines the correlates of male mating success.

Finally, Chapter 9 provides an overview of the implications of this study for a wider understanding of the complex interactions between the social and ecological environment and the social systems of large mammals.

2. STUDY SITES AND FIELD METHODS

2.1. INTRODUCTION

The first section of this chapter gives a basic qualitative introduction to the eight study sites in terms of general appearance, vegetational diversity, land use, and mammalian fauna. A more detailed quantitative analysis of habitat composition and structure will be presented in Chapter 3. The remainder of the chapter briefly describes the sampling methods common to the data chapters which follow.

2.2. STUDY SITES

For convenience and ease of presentation, this section is divided into the two main 'environment types': the New Forest sites, and the agricultural sites.

The New Forest sites

The New Forest in southern England is an area of some 37500 ha of mixed vegetation, first set aside as a royal hunting preserve in the 11th century. Set in the Hampshire Basin, the area enjoys a mild oceanic climate. Mean minimum and maximum daily temperatures recorded in nearby Hurne Airport, Bournemouth for the period 1968-1985 were 1.2 and 7.9°C respectively in January and 11.4 and 21.6°C in July. There was an annual average of 102 days with ground frost. Average annual rainfall was 785 mm distributed throughout the year, with the wettest period from November to January (All climatic data from Putman & Sharma 1987).

Out of a total area of 37500 ha, some 9000 ha are occupied by villages or agricultural land; the remainder forms a mosaic of deciduous and coniferous woodlands, natural and improved grasslands and open heathland and bog. There are currently 9200 ha of woodland enclosed for timber production, of which 4850 ha is coniferous (primarily Scots pine *Pinus syslvestris* with smaller amounts of Douglas fir *Pseudotsuga menziesii* and Corsican pine *Pinus nigra*) and 4350 ha deciduous or mixed (primarily beech *Fagus sylvatica* and oak *Quercus robur*). The enclosed woodlands are bisected by gravelled roads and grassy rides. Of the remaining 19000 ha of so-called 'open forest', some 4000 ha are woodland (primarily oak and beech with an understorey of holly *Ilex aquifolium*, with smaller amounts of naturally regenerated Scots pine), and the remainder a mixture of 7500 ha of *Calluna*-dominated dry heath, 2000 ha of *Erica*-dominated wet heath, 1350 ha of bog, with some 4200 ha of grasslands. Of these grasslands, some 800 ha have been managed to improve their productivity by fertilizing and/or reseeding. The area and its vegetation is described in more detail in Putman (1986a) and Tubbs (1986).

The Forest is an area of outstanding natural beauty, and is now the largest area of semi-natural vegetation remaining in lowland England. Over the last 50 years it has come under increasing pressure, from commercial interests, tourism and recreation. Forestry operations remain an important source of income for local inhabitants, as does the pasturing of cattle and ponies on the Forest under ancient rights of common. Tourism, currently standing at 8 million visitor days per year (New Forest Review Group 1988) is of increasing importance in the local economy, particularly during the summer months.

The area currently supports populations of five deer species: fallow, red *Cervus elaphus*, roe *Capreolus capreolus*, sika *Cervus nippon*, and muntjac *Muntiacus reevesi*; domestic cattle and ponies are also pastured in the Forest under ancient rights of common. Population levels of all deer species have fluctuated markedly over the centuries as management aims have altered (Putman & Sharma 1987). Fallow deer were undoubtedly much more numerous in earlier centuries, such records that do exist indicate that populations were maintained at 6000-7500 animals from the 17th century to the 1850s. Populations were drastically reduced after the Deer Removal Act of 1851, and an estimate in 1900 gave a figure of 200 head (Lascelles 1915, quoted in Putman & Sharma 1987). Since that time the population has increased to its current stable levels estimated at about 2000 animals. The deer have no natural predators in the Forest and management is undertaken by the Forestry Commission who undertake an annual cull of 20-25% (Putman & Sharma 1987). Fallow deer numbers are not uniform throughout the Forest and seasonal movements of deer may result in locally high densities. Study sites were established in five locations differing markedly in habitat composition and structure.

Denny (Grid ref. SU 340050)

Situated in the east of the Forest, this area consists of a single large block of enclosed coniferous and deciduous woodland with the adjacent open Denny Wood and heathlands (Fig 2.1). Primarily a female deer area, Denny was one of the principal study sites for the two previous fallow deer research projects within the New Forest (Jackson 1974, Parfitt in Putman 1986a) and there remain a few marked individuals and an extensive body of comparable data. The heathlands and unenclosed woodlands are used by domestic stock.

Brinken (Grid ref. SU 275055)

Centrally located between the towns of Lyndhurst and Brockenhurst, Brinken consists of a large area of unenclosed deciduous woodland adjacent to the narrow heathlands of Warwickslade and Poundhill (Fig 2.2). A 10 ha field known locally as Queens Meadow is mown and fertilized annually and fenced to restrict public access. Predominantly a female deer area, Brinken holds very high densities of fallow and smaller numbers of red and roe deer.

Dames Slough (Grid ref. SU 250050)

Located in the west of the Forest, this area largely comprises a single enclosed mixed coniferous and deciduous woodland, with adjacent fields of improved grasslands at Burley Lodge (Fig 2.3). These grasslands are frequently grazed by domestic stock. Dames Slough was also included in the studies of Parfitt (in Putman 1986a) and a single marked animal remains. As well as containing substantial numbers of female deer, this area is included in the range of one of the Forest buck groups.

South Oakley (Grid ref. SU 220050)

Situated on the south-western edge of the Forest, adjacent to the village of Burley, South Oakley presents a mixture of enclosed coniferous and deciduous woodland, natural deciduous woodland, extensive heathlands and bog (Fig 2.4). This site also infringes onto the agricultural holdings in Burley village. Primarily a male deer area, South Oakley contains one of the larger Forest buck groups. The heathlands and roadside verges to the south and west of the study area are extensively utilized by domestic stock.

Blackensford (Grid ref. SU 230070)

Approximately 2 km to the north of the preceding two sites, Blackensford is situated on the western edge of the largest continuous woodland block in the New Forest (Fig 2.5). This site consists of a mixture of enclosed and open forest coniferous and deciduous woodlands, extensive heathlands, bog and scrub birch, and improved grasslands. This area has limited public access and receives little disturbance with the exception of the autumn rut. Primarily a small deer area throughout the year, occasionally males remain in Blackensford for two or three months after the rut.

The agricultural sites

Lockerley (Grid ref. SU 310280)

The area is one of mixed agricultural land approximately 15 km NW of Southampton, contained within the adjacent Lockerley and Mottisfont estates, and consisting of a mosaic of woodland copses managed for commercial forestry and pheasant *Phasianus colchicus* rearing, and of arable fields and pasture (Fig 2.6). The woodlands are a mixture of coppiced hazel *Corylus avellana,* mature stands of oak and beech, and mixed age plantations of conifers, largely Scots pine and Norway spruce *Picea abies.* The woodlands are surrounded by farmland of varying use: grass crops for hay or silage, cattle pasture, cereals (mainly wheat and barley), and root crops and legumes. Modern agricultural practises result in crops in rotation throughout the year.

The estates are intensively managed for both agriculture and game, hence public access is minimal and disturbance outside of the shooting season limited. Most estate work is performed from a vehicle. Estate woodsmen are limited in number, hence forestry operations tend to be very localised. Cattle and horses are depastured on various fields across the estate.

The estates support populations of both fallow and roe deer, and occasional sighting of muntjac have been reported. The size of the fallow and roe populations is unknown, as is their history in the area. As in all of the agricultural sites, there are no natural predators of deer. Deer management is undertaken by the estate gamekeepers and private stalkers, however the combination of highly mobile deer populations and two separately owned estates make population control difficult.

Tollard Royal (Grid ref. ST 950190)

This is an area of largely open agricultural land with isolated woodland copses, situated on the chalk downs of Rushmore Estate straddling the Dorset and Wiltshire border, and approximately 50 km NW of Southampton (Fig 2.7). The agricultural land includes extensive areas given over to arable crops, primarily cereals such as wheat and barley, and root crops and kale grown as winter feed for livestock. The upper downlands and valley bottoms are used as summer pasture for cattle and sheep. The woodlands are a mixture of currently managed and overgrown hazel coppice, mixed deciduous scrub, and conifer plantations, largely Scots pine, Norway spruce, and western hemlock *Tsuga heterophylla.* Towards the end of the study the estate initiated a major programme of coppice clearance.

The estate is managed very intensively for game; pheasants are reared in all woodlands and shoots are held on more than 70 days of the year. The intensity of shooting is likely to have an effect on deer populations. Similarly, forestry operations were more pronounced here than in the other two agricultural sites. Large numbers of sheep are pastured both on the lower fields and the upper downlands, and occasionally horses are grazed on the lower fields.

Large numbers of fallow deer are present on the estate, although estimates of total population size are not available. Roe deer are occasionally seen in the area and populations have apparently decreased in recent years. The fallow population is a remnant of the once extensive herds of the old Royal Forest of Cranbourne Chase which was reported to have exceeded 1000 head. Deer management is the responsibility of a single deer warden, and culling intensity has increased in recent years as a result of changing management policy. Deer regularly move off the estate and are subject to less selective culling. Road accidents and poaching account for an unknown number of deer each year.

Tadley (Grid ref. SU 610580)

Tadley is an area of mixed agricultural land and small woodland copses approximately 50 km north of Southampton (Fig 2.8). The study site is an amalgamation of several adjoining farms and small estates. The agricultural land is a mixture of arable crops, largely cereals, and pasture for the extensive cattle stocks on these properties. The woodland copses are largely coppiced hazel, although much is overgrown, with the remainder either young conifer plantations, predominantly Norway spruce, and birch *Betula pendula* scrub.

In common with the other agricultural sites, pheasants are reared in most of the woodlands, although sporting activities are not practised as intensively as in other areas. Forestry operations were very limited during the time of study. Several public rights of way pass through the farms and are commonly used by walkers and riders. Cattle and horses are grazed on several of the pastures.

Fallow deer numbers fluctuated greatly throughout the study on a short term basis suggesting that animals ranged widely off the study site. Total population size was not known, nor was the history of the herd. Roe deer were regularly seen on the site. Deer management was initially under the control of a single stalker, however in the second year of the study private stalking was leased on a commercial basis. Few deer were shot on the study site during the duration of the project.

2.3. FIELD METHODS

Data collection to assess patterns of habitat use (Chapter 4), population structure and sexual segregation (Chapter 5) and social grouping (Chapter 6) was by direct observation from fixed transect routes in each site and the methodology is presented in detail here to avoid later repetition. Methods and analysis specific to individual chapters are presented in the relevant chapters.

Transects

This method involves walking a set route regularly throughout the day, viewing animals on either side of the transect line, visibility being determined by the physical features of the vegetation. One route was developed in each study site during initial observations in November and December 1986 with the aim of including a representative sample of all vegetation types available in the site. The length of the route varied from one study area to another but on average took approximately two hours to complete, dependent on the numbers of deer seen and activity recorded. The transect routes are marked on the study site maps (Figs 2.1 - 2.8). Because of the large distances between woodland copses in the agricultural sites, some sections of the transects were completed in a vehicle. In these cases open fields were surveyed from vantage points at approximately 100 m intervals along the roads or farm tracks. On each sampling day, at least one transect was completed in each of three time periods:

1. Dawn. Within three hours of first light.
2. Day. From three hours after first light until three hours before last light.
3. Dusk. Within three hours of last light.

Observations were initially continued at night by spotlight, however a combination of poor visibility in woodland habitats and great disturbance of both deer and deer-rangers led to their termination. Spotlighting continued on a casual basis throughout the three years of the study, but was confined to arable land and grassland at Dames Slough, South Oakley, Lockerley, and Tollard Royal. Each study site was visited two or three times monthly. Transects were conducted at Denny, Dames Slough, South Oakley, Lockerley, Tollard Royal, and Tadley from January 1987 to December 1988, at Blackensford from October 1987 to September 1989, and at Brinken from October 1988 to September 1989.

Data recorded

For each group of deer encountered, the following details were recorded and later transferred onto computer files:

1. Weather conditions. The weather conditions at the time of sighting each group were recorded as follows: *temperature*, *cloud cover*, *wind speed* on the Beaufort Scale and the presence or absence of *precipitation.*
2. Number and sex/age composition of group. Individual deer were classified into the following six categories. *Bucks* were adult males judged to be 5+ years of age on the basis of antler development described in Chapman & Chapman (1975). Young bucks *(Yobs)* were males of 2-4 years of age, recognizable on the basis of non-palmate antlers typical of this age class. *Prickets* were yearling males identified on the basis of the unbranched spike antlers. The ageing of male fallow deer on the basis of antler development is controversial; clear differences exist between populations in antler size at particular age classes (Chapman & Putman 1990). Total accuracy can only be guaranteed distinguishing prickets from other age classes. For this reason, in most analyses, bucks and 'yobs' were combined and simply referred to as mature males. Female deer were referred to as *does* and included all adult and yearling animals. *Fawns* are easily recognizable by their small size and were considered to become yearlings in June during parturition. No distinction was made between male and female fawns. In some instances, observations of animals was brief, and accurate age class distinctions could not be made. In these cases, all individuals not carrying branched antlers (including prickets) were referred to as 'small-deer' after the classification of Jackson (1974)
3. Activity of individuals. The activity of each animal in the group was assessed and classified into one of the following categories. *Grazing*, *Browsing*, *Lying*, *Standing*, and *Moving* are all self-explanatory. *Alert* included all instances when the deer were alarmed by the observer, as frequently happened. *Rutting* activities included all male-male or male-female interactions observed during October or early November. *Other* activities included all other actions seen.
4. Location. The location of the group was recorded and logged onto a 4 ha grid superimposed on a 1:10000 map of each study area.
5. Habitat of occupance. The habitat classification scheme used in this study is described in detail in Chapter 3. The habitat of current occupance of each group was recorded at the time of first sighting. If animals were moving at this time, the habitat from which they came was considered to be the habitat of occupance. For example, the observation of fallow crossing a forest ride from open conifer to open deciduous was considered as an open conifer sighting.

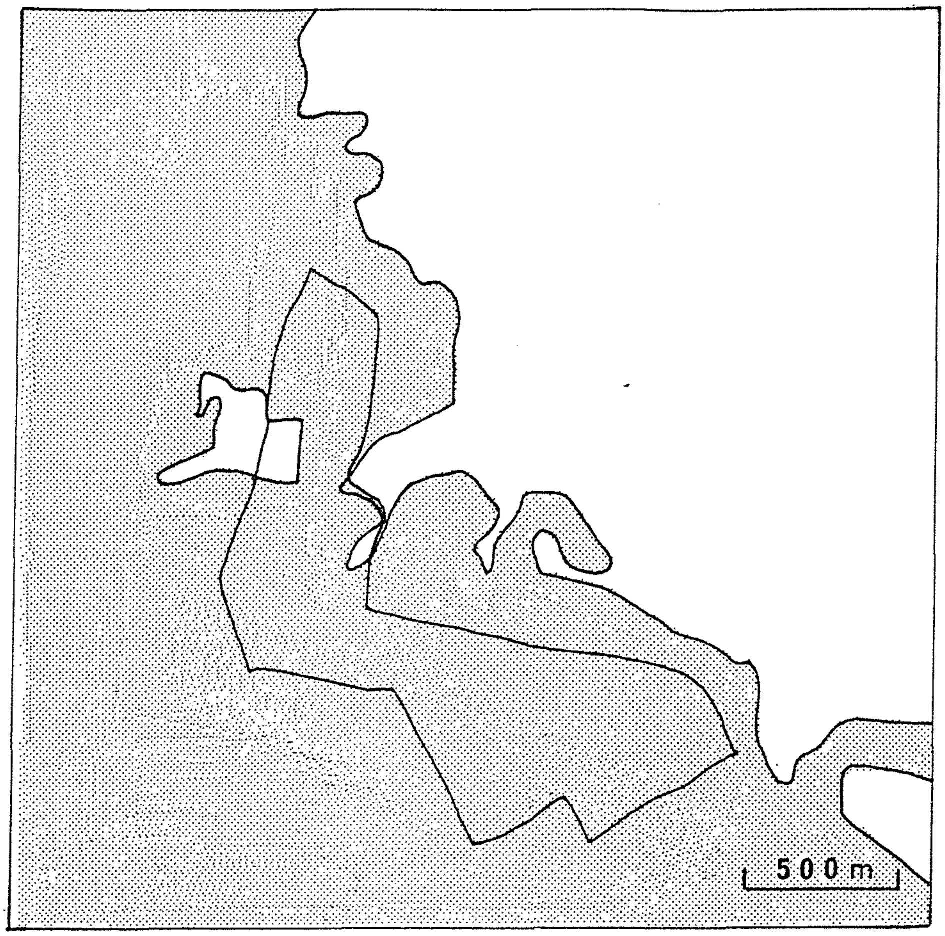


Fig 2.1 Map of Denny study site showing transect route as solid line. Woodland habitats shaded, open habitats white.

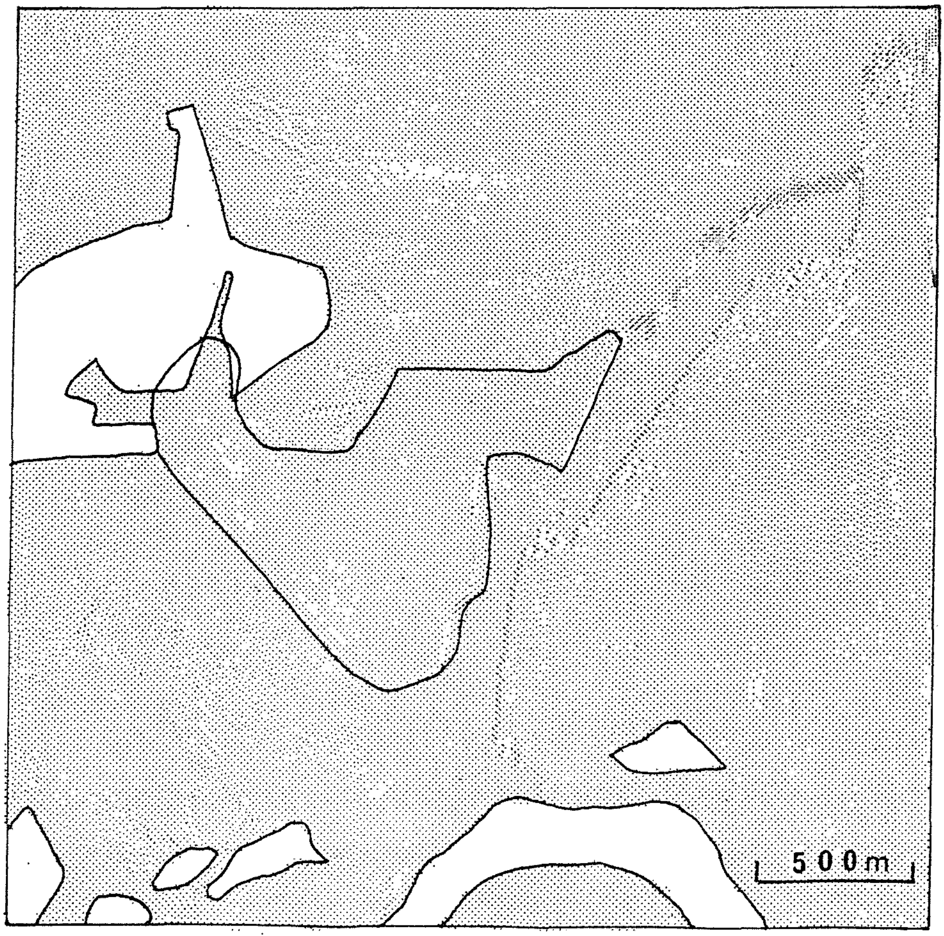


Fig 2.2 Map of Dames Slough study site showing transect route as solid line. Woodland habitats shaded, open habitats white.

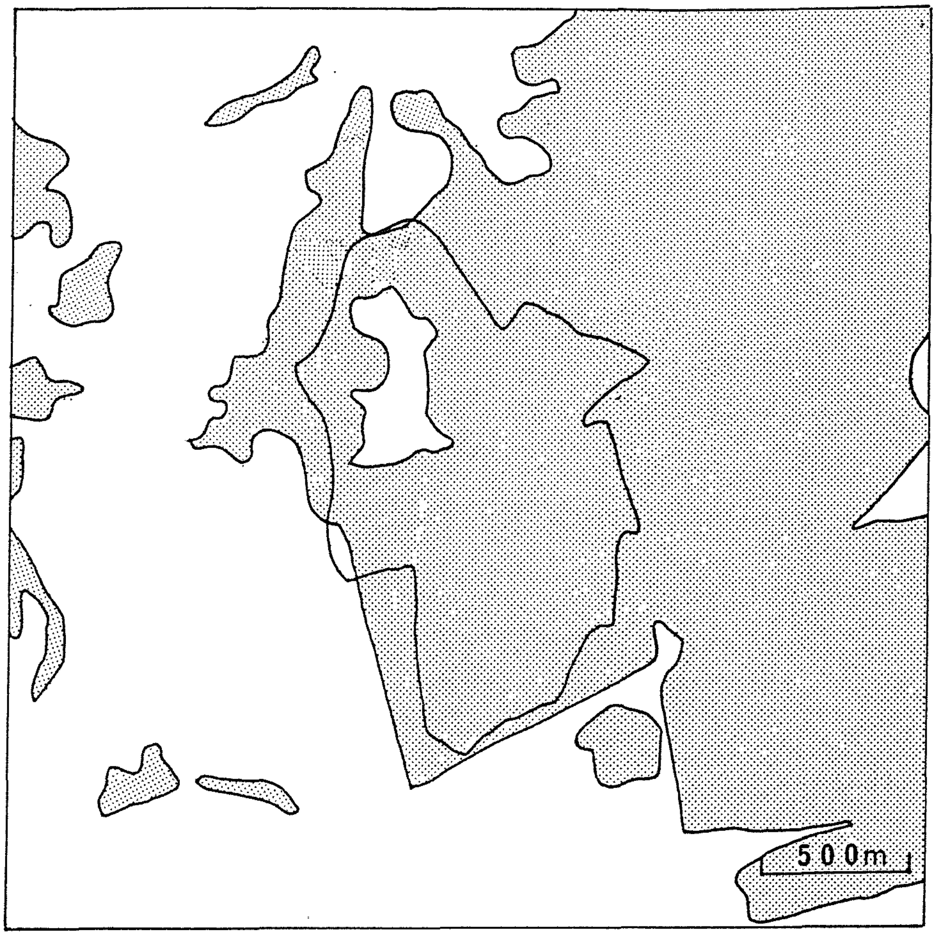


Fig 2.3 Map of South Oakley study site showing transect route as solid line. Woodland habitats shaded, open habitats white.

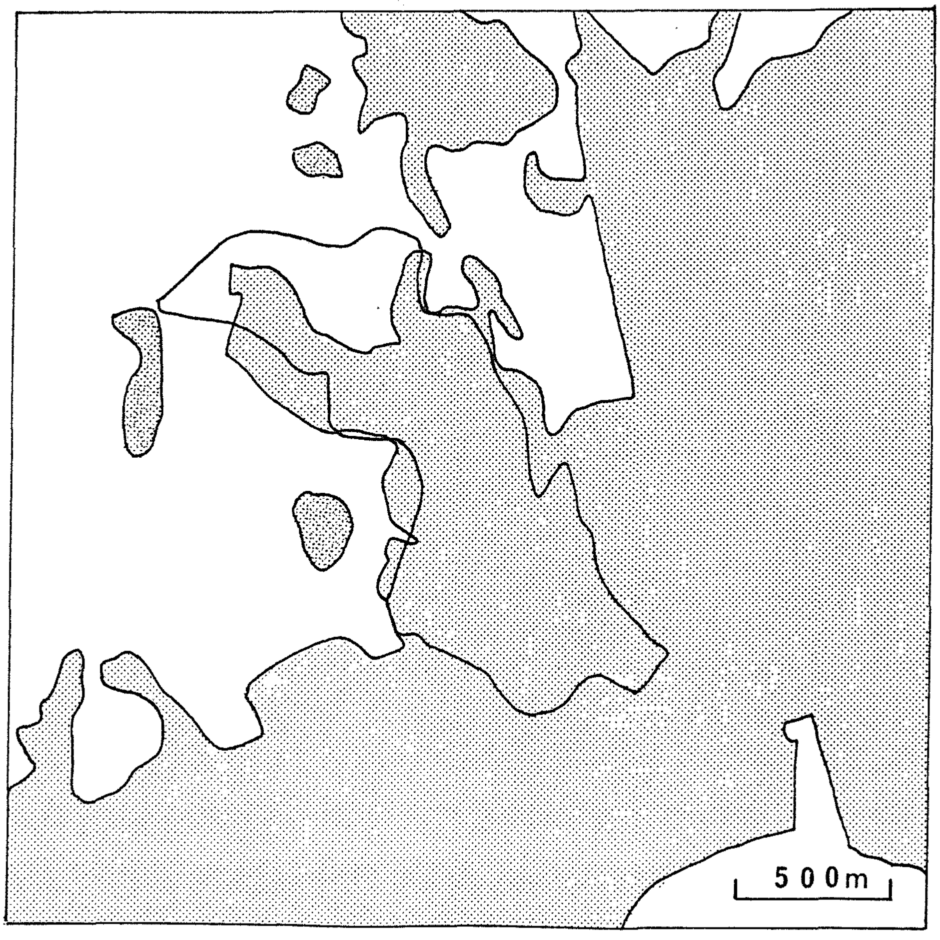


Fig 2.4 Map of Blackensford study site showing transect route as solid line. Woodland habitats shaded, open habitats white.

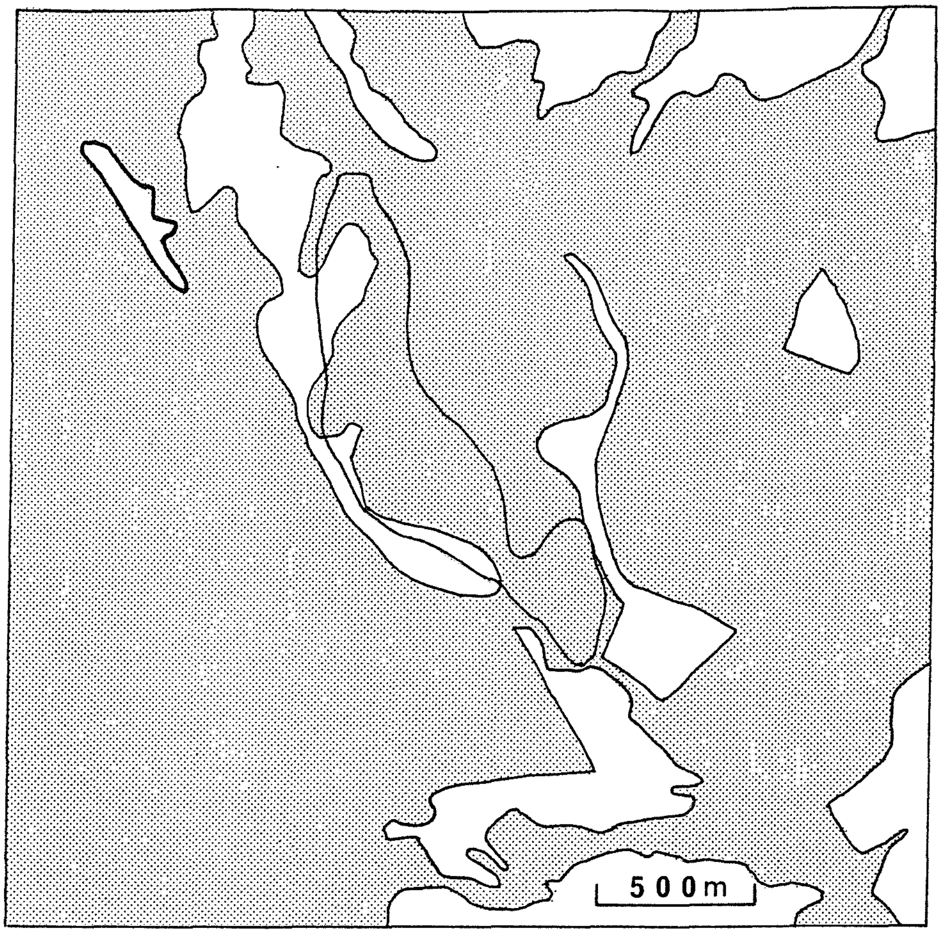


Fig 2.5 Map of Brinken study site showing transect route as solid line. Woodland habitats shaded, open habitats white.

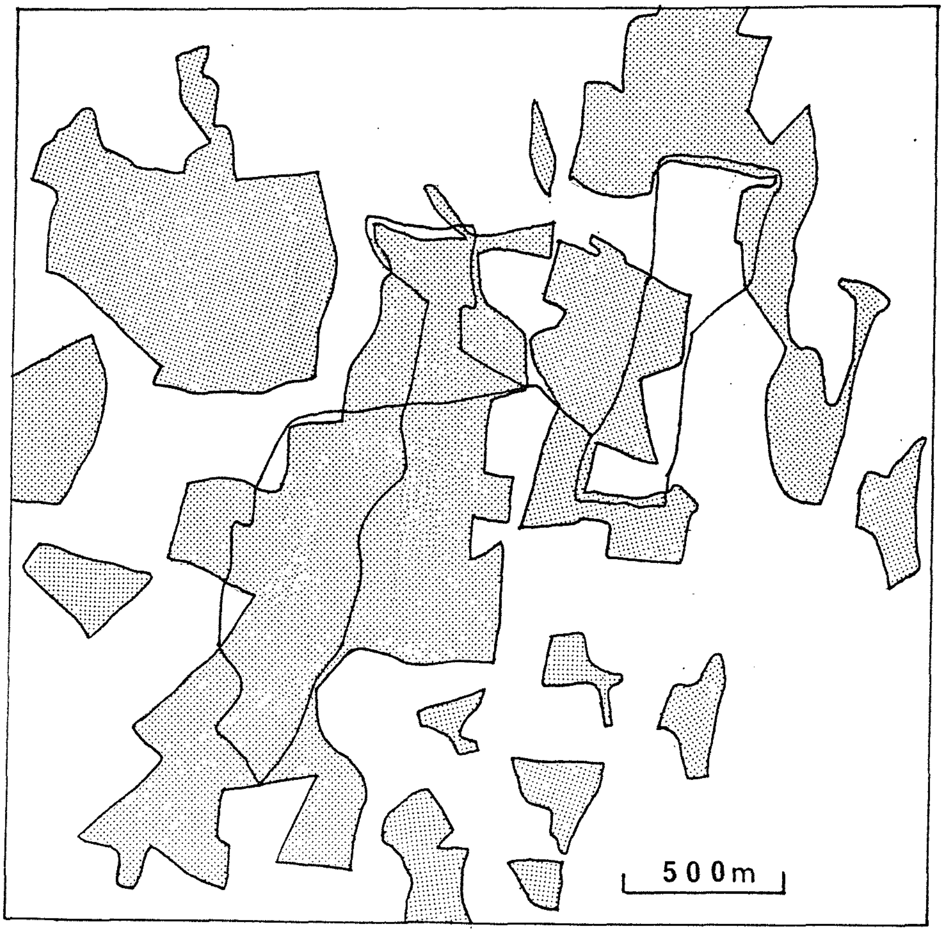


Fig 2.6 Map of Lockerley study site showing transect route as solid line. Woodland habitats shaded, open habitats white.

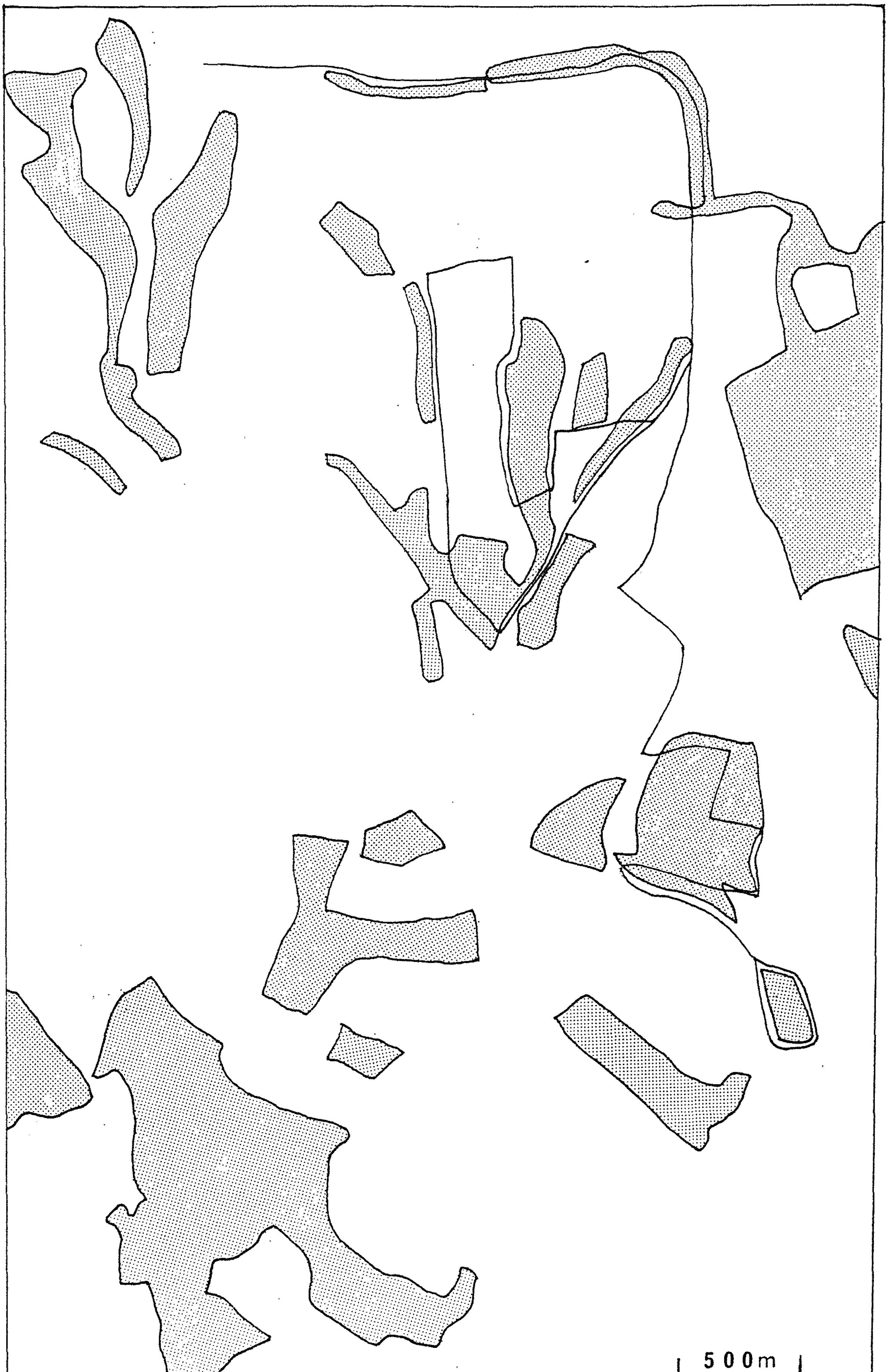


Fig 2.7 Map of Tollard Royal study site showing transect route as solid line. Woodland habitats shaded, open habitats white.

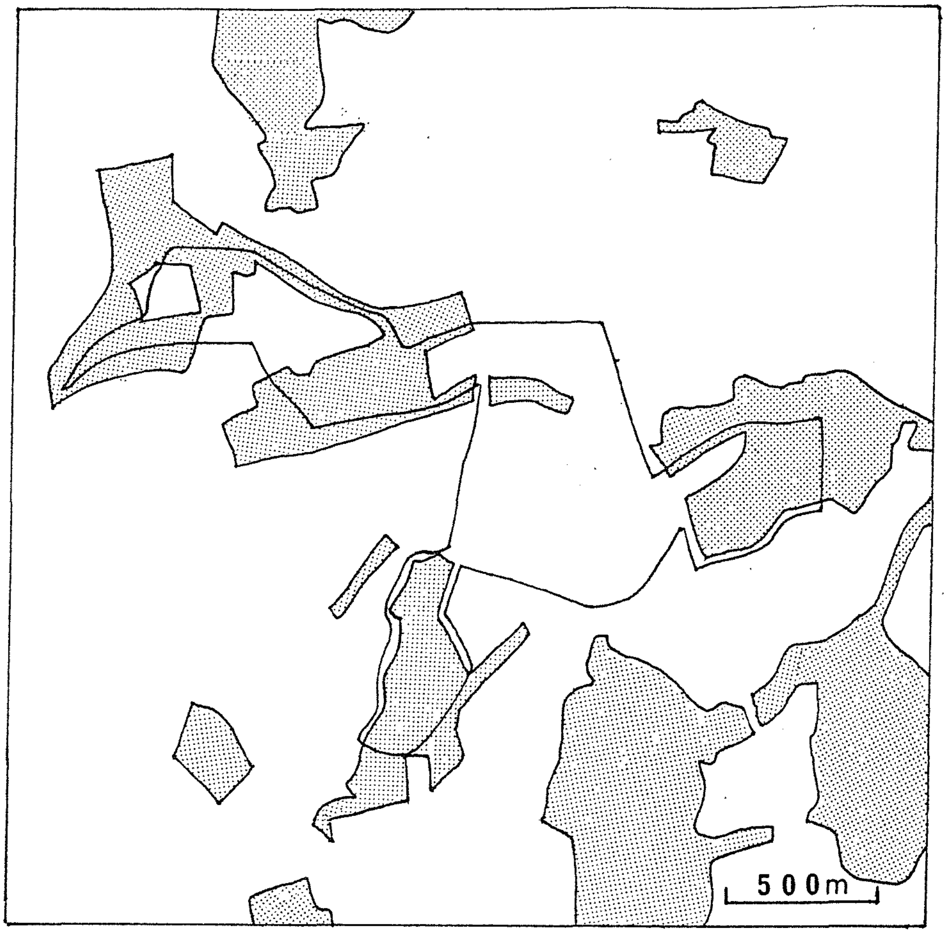


Fig 2.8 Map of Tadley study site showing transect route as solid line. Woodland habitats shaded, open habitats white.

3. HABITAT CHARACTERISTICS

3.1. INTRODUCTION

The purpose of this chapter is to describe, in a quantitative fashion, the vegetational characteristics of the eight study areas. The reasons for this are two-fold, initially to establish that the vegetational environment experienced by the deer differs significantly from site to site, and secondly to present the habitat variables that will ultimately be used to explain some of the variation that exists in the social organisation and mating systems in fallow deer.

Some preliminary information has already been presented in the previous chapter on the general appearance of the study sites, in addition to a more detailed catalogue of the species present on the sites. It is not intended to duplicate such a qualitative description here, nor is it logistically possible in the context of the current study to present a quantitative species-specific description of the vegetation for each of the eight study sites. Rather an attempt has been made to simplify these data into a number of broadly recognisable discrete habitat categories, on the basis of which sensible comparisons can be made between study sites. Throughout, the approach taken has been to try, as far as possible, to visualise the environment from the point of view of the deer using the resources available, rather than from a more human perspective.

3.2. METHODS

Vegetation Mapping

Vegetation maps were prepared at a scale 1:10000 with the aid of Ordinance Survey maps, Forestry Commission stocking maps, Nature Conservancy Council vegetation maps, and detailed ground surveys. Measures of surface area and distance were obtained from maps using standard cartographic instruments (planimeter and ibsometer).

Habitat Categories

As previously explained, in order to permit any realistic comparison of one site with another, it was necessary to condense the number of different species present on the study areas into a series of broader habitat categories. Such an approach will inevitably lose some of the resolution of a species-specific description, and as such the number of categories chosen must be a balance between the desired level of accuracy and the difficulties of interpretation of complicated data sets. Additionally, this task is made more difficult by the fact that for any particular analysis, different degrees of resolution are appropriate in different kinds of analyses. For this reason three levels of resolution have been chosen, each of which will be used for different stages of the analysis (Table 3.1).

At the finest level of resolution nineteen habitat types have been recognized , based on a modified version of the classification system of Putman (1986a) for use in studies of habitat use and feeding behaviour of cattle, ponies and deer in the New Forest. The woodland categories have been divided into ten simple types, based on structural differences as well as species composition. The heathland and grassland categories have been condensed in relation to the previously mentioned study for simplicity, and categories for cereal and other arable crops included.

At the middle level of resolution the divisions between grasslands, arable, and other open communities are maintained, however an attempt is made to divide the woodland communities purely on a structural basis rather than distinguish between coniferous and deciduous woodlands. The structure of a woodland in terms of canopy closure, and its subsequent effect upon ground flora and hence presence or absence of food, may possibly be more important in influencing social grouping of deer than simple differences in species composition.

At a final gross level of resolution, relationships between social organisation of the deer and habitat use are explored in relation merely to the open/closed nature of the environment. For such analysis, all woodland habitat types are lumped together into one category, and a similar approach is taken to the open habitat categories.

Analytical Approach

The principal features of the environment that have been quantified are habitat composition and habitat structure. Throughout attempts have been made to linearize all variables, in order to make further statistical analyses possible, although this has not been feasible in all cases. In some of the following sections the analytical approach taken has been described in considerable detail, contrasting where necessary with alternative techniques. The final discussion of this chapter will be concerned primarily with the results that are relevant to fallow deer social organisation, and will not consider methodology.

Habitat Composition

Composition is a very difficult variable to linearize because by its very nature it is a multifaceted value. Numerous other studies have resolved this problem by simply referring to the percentage composition of certain individual habitat types in relation to the total study area, an approach that has also been followed here. A major drawback of this approach is that one is restricted to considering the affects of individual habitat types in isolation, for example the effect on typical group size of the amount of cereal crops within a study site. Realistically, group size should be examined in relation to the whole array of habitat types available to the deer within a site.

An alternative approach to investigating habitat composition is through the use of various measures of diversity. A useful distinction between two different aspects of diversity has been made by Whittaker (1960) who differentiates between:

α -diversity: the diversity of species within a community

ß -diversity: a measure of the rate and extent of change in species diversity along a range or between two communities.

In the context of this study, habitat diversity is a measure of both the number of habitat types present in a study site, and the evenness or 'equitability' of area between them, equivalent to species richness and abundance in more common calculations of species diversity. The distinction between α and ß diversity is a useful one in this context and allows us to calculate a measure of habitat diversity for each study site, and then contrast the habitat composition and abundance between the various sites.

For studies of α diversity, Magurran (1988) advises the use of a few of the better known indices, whose properties are well tested and understood. The Shannon Index (Shannon & Weaver 1949) is widely used in studies of habitat diversity (eg. Tapper & Barnes 1986) and is a measure of the evenness of abundances of habitat types. It is calculated from the equation:

$H = - \Sigma p_i \text{ In } p_i$ where p_i is the proportion of the $_i$th habitat type in the sample

An alternative approach to investigating α diversity is through the use of dominance measures, which are weighted towards the abundance of the commonest species rather than providing a measure of species richness (Magurran 1988). One of the best known of these is the Simpson Index (Simpson 1949) which gives the probability of any two individuals drawn at random from an infinitely large community belonging to the same species. This index is also frequently used in the context of habitat diversity (Magurran 1988) and is calculated as:

$D = \Sigma p_i^2$ where p_i is the proportion of the $_i$th habitat type in the sample

Careful consideration should be made of the results of analysis of diversity indices before too much biological significance is attached to them. In the current context, both the Shannon and the Simpson indices simply tell us something about the evenness and spread of different habitat types around the study sites, and do not take any spatial factors into consideration.

ß diversity is essentially a measure of how different (or similar) a range of sites are in terms of the variety and abundance of habitats found in them. One approach to the measurement of ß diversity is to investigate the degree of association or similarity of sites using the standard ecological techniques of ordination and classification (Grieg-Smith 1983; Kershaw & Looney 1985). However the easiest way to measure the ß diversity of pairs of sites is by the use of similarity coefficients (Magurran 1988). A vast range of similarity indices exists, but as Southwood (1978) suggests, the ecological insights gained are by no means proportional to the mathematical sophistication and complexity of the models. Some of the oldest and simplest similarity coefficients are also the most useful (Magurran 1988). Particularly widely used are the Jaccard index and Sorensen index. However, these coefficients take no account of the abundance of habitat types and tend to place too much significance on the rarely occurring habitats (Southwood 1978). This consideration has led to the development of similarity measures based on quantitative data, of which the most widely used is the version of the Sorenson index modified by Bray & Curtis (1956). However, recent comparative studies of a range of quantitative similarity indices (Wolda 1981; Smith 1986) found that all but one, a modified version of the Morisita-Horn index (Morisita 1959), were strongly influenced by species richness and sample size. The Morisita-Horn Index is calculated as:

$C_{mh} = 2\ \Sigma\ (an_i bn_i\ /\ (da + db)\ aN * bN$

where aN = total area in Site A
bN = total area in Site B
an_i = area of the $_i$th habitat type in Site A
bn_i = area of the $_i$th habitat type in Site B
$da = \Sigma\ an_i^2\ /\ aN^2$
$db = \Sigma\ an_i^2\ /\ aN^2$

Similarity indices may by sorted by classification or ordination (Southwood 1978). Many complicated multivariate techniques exist (reviewed in the plant ecology texts previously cited) but it was felt that they were unnecessarily sophisticated for the relatively simple task of demonstrating that certain study sites are more similar than others. Two extensively used old methods from Southwood (1978) have been used, those of descriptive trellis diagrams and quantitative dendograms. The latter technique has the disadvantage that much information about relationships between sites is lost, as dendograms utilize only the highest similarity coefficients. However, the level of resolution is fine enough to distinguish between distinct groups of sites.

Habitat Structure

Habitat structure is equally difficult to quantify and linearize in terms that are of biological significance to the subject of study, that is social systems in fallow deer. The approach that has been taken is to concentrate on the size of habitat blocks within the range of study sites.

The mean patch size for specific habitat types may be quite easily determined for each study site. These 'mean' values rarely follow a normal distribution, hence analysis thereafter must rely upon non-parametric statistics. This problem is exacerbated when investigating the patch size of the combined or lumped habitat categories. This is clearly illustrated by the problems of determining the average size of woodland blocks, in environments of such different overall character as agricultural land and the New Forest. A 'mean woodland size' is of some value in an environment where there are many small woodland blocks and the mean and variance accurately describe the range of sizes. However, in the typical situation in the New Forest, where there are at most two or three big blocks of continuous woodland, with additional small copses, any 'average' figure is of limited value. A partial solution to this problem is the calculation of the cumulative woodland area which is simply the accumulated total area of woodland with increasing number of woodland blocks. This method provides clear graphical resolution between the two main environmental types; unfortunately, however, statistical interpretation is difficult.

A single measure of the size-scale of the environment as a whole can be obtained by calculating the average patch size irrespective of habitat type at the finest level of resolution. To clearly distinguish from the above measures this parameter has been called the habitat grain size. In some study sites there was a great contrast between grain size in the woodland and open areas, and therefore data has been presented separately for woodland grain size and open grain size.

An alternative method of investigating the scale of the environment from more of an animal-based point of view, irrespective of habitats involved, is to examine the frequency of change in habitat type along a predetermined transect line. For simplicity this measure has been termed habitat change, and is calculated as the number of changes in habitat types per kilometer along regularly spaced grid lines covering the entire study area. A similar value may also be calculated for the frequency of changes from an open to a closed habitat type. These two figures probably most accurately represent the situation experienced by the deer as it moves through its environment.

Another feature of habitat structure which may be important to deer is the amount of edge in the environment. For simplicity this has been restricted to consideration of the amount of edge between open and closed environments in each study area. Patton (1975) has suggested a diversity index based on the relative amount of edge or perimeter of a irregular shaped vegetation block in relation to a similar sized circular block. This method, whilst appealing at first, has a basic assumption that entire blocks of vegetation are always sampled, and these conditions are not met in the current study. Instead, the relatively simple method of determining the amount of edge over the entire study area and presenting it in the form edge(m) / area (ha) has been adopted.

Final features of the structural environment worth considering briefly are the spatial characteristics of habitat: juxtaposition and interspersion. Whilst undoubtedly important in affecting the behaviour of the animals, their conversion into a linear measure remains unresolved. Porter & Church (1987) state that the diversity index of Patton (1975) quantifies these parameters. However, closer examination of the original paper reveals that his analysis is restricted to the affect of shape of internal subdivisions within habitats, and is not concerned with spatial relationships between habitat types. To my knowledge this parameter remains unquantifiable.

3.3. RESULTS

Habitat composition

Percentage composition

The habitat composition of the eight study areas at each of the three levels of resolution adopted here are given in Figs 3.1 - 3.8. This is expressed both in terms of the area of each habitat type in hectares: a) individual habitats, c) combined habitats, e) woodland/open; and in percentage of total study site: b) individual habitats, d) combined habitats, f) woodland/open. There are clear differences in the area and percentage cover of the various habitat types within each study site, including total absence of certain habitat types from some sites (eg. arable cereal in all New Forest sites excluding S.Oakley, heathland in all agricultural sites). For ease of comparison between sites, the composition data at the two coarser levels of resolution can be presented in summary figures. In Fig 3.9a, these data are presented at the middle level of resolution, and clear contrasts can be made between the New Forest and agricultural sites. Fig. 3.9b simply summarizes the data in terms of % area of open and closed habitats, and ranks the sites in order of increasing openness.

Comparisons between sites in habitat composition may not be made statistically, as essentially it is not a statistical problem. Statistical analyses usually test hypotheses about populations, based on samples of a certain number of individuals (Sokal & Rohlf 1981). The results of such analysis demonstrate, with a specified level of significance, that the samples are drawn from different populations. Clearly in this case, the data on habitat composition describe a complete population, more specifically, the composition of the total study area. Therefore, each site is simply different from every other in terms of habitat composition.

ß-Diversity

Clearly, however, there are certain sites which are more similar in terms of habitat composition than others, and it is of considerable importance to quantify this relationship. As previously mentioned, several multivariate ordination and classification techniques exist, of which the best known and most widely used are Principal Components Analysis (PCA) and Detrended Correspondence Analysis (DECORANA). However, these techniques are normally used for analysis of communities, recorded at the individual species level (Grieg-Smith 1983, Kershaw & Looney 1984) and are unnecessarily sophisticated for the relatively simple task of investigating similarity between the eight study sites in terms of gross habitat composition.

The similarity coefficient of Morisita and Horn (Morisita 1959, Horn 1966) was used as a measure of ß-diversity between successive pairs of study sites. This analysis was repeated for each of the three levels of resolution of habitat classification (individual, combined, and woodland/open habitats). The index is designed to equal 1 in cases of complete similarity and 0 if the sites are dissimilar and have no species in common. At the individual habitat level of resolution, values ranged from the most similar pair of sites at 0.95 (Denny and S.Oakley) to the most dissimilar at 0.03 (Blackensford and Tollard). The complete matrix of values giving the similarity between each pair of sites at this highest level of resolution is presented in the form of a trellis diagram in Fig. 3.10a. The shading of the squares in the upper half of the diagram helps with interpretation and clearly reveals that at the individual habitat level of resolution there are two distinct clusters of sites, one comprising the five New Forest study sites and the other comprising the three agricultural sites. The same data may be presented in the form of a dendogram (Fig. 3.10b) to investigate more closely the relative similarities within the two communities. Clearly, the three New Forest sites which contain significant proportions of heathland habitats (S.Oakley, Denny, and Blackensford) are more closely related to each other in terms of similarity than to the other New Forest sites which contain relatively more woodland habitat types (Dames and Brinken). The drawback of this analytical approach is revealed by closer examination of the data for the three agricultural sites. The dendogram shows the degree of similarity between the Lockerley/Tadley group and Tollard to be 0.80, when in reality this relationship is solely due to the similarity between Tadley and Tollard. Taken in combination, however, the trellis diagram and dendogram reveal that whilst there is a fundamental division between New Forest and agricultural study sites in terms of habitat composition and abundance, there are also important differences within these groups.

These analyses were repeated at the medium level of resolution of habitat categories (Fig. 3.10c&d). The same relationships between sites were upheld, with a clear distinction between the New Forest and agricultural study sites. However, as might be expected, the decrease in resolution of habitat categories has resulted in increased similarity coefficients between all pairs of sites, values ranging from 0.13 (Blackensford & Tadley) to 0.98 (Denny & S.Oakley). A further decrease in habitat resolution to the simple distinction between woodland and open habitats has a similar effect of increasing the similarity coefficient between all pairs of sites, but also changes the structure of the dendogram, linking Lockerley more closely to the more open New Forest sites (Denny, S.Oakley, Blackensford) than to the other agricultural sites (Tadley & Tollard) (Fig 3.10e&f).

α-Diversity

Indices of α habitat diversity of the eight study sites (calculated by both the Shannon index and the Simpson index) are listed in Table 3.2. The use of the two indices is desirable because, although both are commonly used as measures of diversity and both use the same data set in their calculation, the indices measure quite different parameters of the sites. The Shannon index is a measure of the evenness of abundance of habitats in the study sites, with a high value signifying a site where there are a large number of habitat types, each with relatively large areas. The Simpson index in contrast, measures the extent of domination of the study site by a few common habitat types. Ordering the study sites in respect to increasing diversity gives the same overall result with the two different indices (Table 3.2), the agricultural sites generally being less diverse in habitat composition and abundance than the Forest sites.

Habitat Structure

Patch size of particular habitat types

The mean patch size of the individual habitat types within each study site are given in Fig 3.11. Differences in the size of patches within sites were analyzed with the Kruskal-Wallis test, as the data do not meet in full the requirements of homogeneity of variance for a parametric analysis of variance. Highly significant differences in patch size between habitat types existed in all study sites with the exception of Denny (Kruskall-Wallis tests, $p<0.001$). In the case of Denny, the patches of heathland and bog were much larger than the woodland habitats (Fig 3.11), although they were too few in number to be significantly different at $p<0.05$.

Differences between sites in the mean patch size of particular habitat types were analyzed in the same manner. All the sites were not included in every analysis, as certain habitat types were absent from some sites. There were significant differences between sites for only four habitat types: open canopy conifer, coppice deciduous, natural grassland and arable cereal (Kruskall-Wallis tests, $p<0.001$).

Cumulative woodland area

The cumulative woodland area, in hectares, for each study site is presented in Fig. 3.12. This demonstrates the increase in total woodland area with the inclusion of each additional block of woodland. Woodland no.1 is the largest block in the study site, woodland no.2 the second largest, and so on. There is a clear difference between the New Forest sites and the agricultural sites in the relative contribution to total woodland area of the first few large woodlands. This is more clearly demonstrated in Fig. 3.13 which uses the same data for each site, but expresses it in terms of % cumulative woodland area with increasing number of woodlands. In all five New Forest sites the largest woodland block contributes over 90% of the total woodland area. In contrast, in the agricultural sites, less than 50% of the total woodland area is due to the largest woodland. This method of graphical presentation, whilst not suitable for statistical analyses, gives the simplest, most revealing picture of the structural complexity of the study sites.

Grain size

The patch size data for individual habitat types were pooled within each site to give the grain size for all habitats combined (Fig 3.14a). There were highly significant differences in the overall grain size between study sites (Kruskall-Wallis test, $p<0.001$). This analysis was repeated when considering bulked woodland and open habitats within each site (Fig 3.14b & c), and again, there were highly significant differences in grain size between sites in both woodland habitats and open habitats (Kruskall-Wallis test, $p<0.001$).

Habitat change

A more animal-based approach to investigating differences in structural complexity used in this study is the calculation of the frequency of change in habitat types along a series of grid lines covering the study areas. The number of individual habitat changes per km of transect line for each site is shown in Fig. 3.15a. It is possible to rank the sites along a gradient of increasing number of habitat changes per km, reflecting a decrease in the average patch size. With the exception of Brinken, the frequency of habitat change in the agricultural sites is lower than the New Forest sites. This value is an overall estimate for the whole site, and not the average value for a number of replicated samples, and as such can not be analyzed statistically at this stage.

An interesting contrast is the replication of these analyses using a coarser level of habitat resolution. When habitat change is calculated using the distinction between open and closed habitats (Fig. 3.15b), the above relationship is reversed and change in habitats of the agricultural sites is greater than that of the New Forest sites. This is a reflection of the structure of the two environments, the agricultural areas consisting of relatively small blocks of woodland interspersed with open areas of pasture and arable farmland, with the finer structure of these woodland and open patches often relatively simple. In contrast, the New Forest sites typically consist of one or two main blocks of woodland, with adjacent areas of heathland or grassland. At a finer level of resolution, however, the large blocks are divided into a complex range of habitat patches.

Edge

The final measure of habitat structure considered in this study is the amount of woodland/open edge per ha of study area (Table 3.3). There is no distinct division between the agricultural and New Forest sites with respect to this variable. There is however, significant variation between sites (Kolmogorov Smirnov test, $D=0.24$, $p<0.001$). Clearly, sites with higher values include those with either many small habitat patches (eg. Lockerley) or an irregular boundary between open and woodland habitat types (eg. Brinken) whilst those with lower values tend to comprise a single woodland block with a regular boundary with the adjacent open habitat (eg. Denny & Dames Slough).

3.4. DISCUSSION

The stated aim of this chapter was to describe the various characteristics of the vegetational environment of the different study sites by definition of a number of essentially linear variables, which can then be used to explain some of the variation in social systems in fallow deer. These same variables can be used to demonstrate that there are significant quantitative differences in habitat composition and structure between the study sites. It will be clear to anyone having persevered this far that this objective has only been partially successful. Several potentially important variables have proven impossible to quantify or analyze statistically.

Habitat composition is a multifaceted parameter which simply can not be reduced to a single or even a series of linear variables. Essentially, at a certain level of resolution of habitat types, no two sites are exactly the same. Clearly, the relative amounts of particular habitat types differ enormously between sites, the obvious examples being arable cereal fields which account for 37-55% of total area in the agricultural sites, but are absent in all but one of the New Forest sites. The importance of these contrasts in available habitat between sites in influencing habitat use, social grouping, and mating strategies will be considered in the following chapters.

The use of ß-diversity similarity coefficients can, however, provide a single measure of the overall difference or similarity in habitat composition between sites. Whilst useful in its own right, this analysis also demonstrates the importance of the level of resolution in studies of habitat. Relationships between sites in terms of habitat composition may be reversed when the differentiation between habitat categories is altered. This is of some considerable importance, as previous studies of ungulate social grouping have largely concentrated on simple divisions between open and closed environments (Leuthold 1970; Walther 1972; Hirth 1977; Schaal 1982).

Comparisons of sites in terms of various measures of habitat or landscape diversity are frequently used in assessing differences between animal populations of various aspects of their ecology and behaviour (Magurran 1988). Tapper & Barnes (1986) found a positive correlation between the autumn density of brown hares *(Lepus europaeus)* on farmland in southern England and a measure of landscape diversity derived from a modified version of the Shannon index. However it must be stressed that, in both this and the current study, differences in the value of a diversity index simply reflect the number and equitability of habitat types within a study area, and as such are affected by the level of resolution of habitat categories. Additionally, diversity indices are not influenced by the spatial distribution of habitat types. Even under these constraints however, the calculation of a measure of α habitat diversity in the current study is useful in revealing that with the exception of Brinken, the New Forest sites contain a greater range of habitat categories, and are also less dominated by a one or two habitat types.

The constraints on statistical analysis of measures of habitat composition are largely matched by those of habitat structure. Some of the most biologically meaningful measures of structure are the most difficult to linearize. Although various measures of the spatial characteristics of juxtaposition and interspersion have been suggested (eg. Patton 1975; Porter & Church 1987), close examination of the models reveal that they are unsuitable for use in the current context. Similarly, the size of woodland blocks is a potentially important factor affecting social grouping in deer. However, the calculation of a figure comparable between study areas with different gross environmental types is more complex than initially apparent.

In the foregoing analyses, all measures of the size scale of the environment have revealed largely the same picture. The New Forest sites are typified by one large, continuous woodland block, either adjacent to, or containing within it, one or several areas of open grassland or heathland. At a finer level of habitat resolution, the open habitats, and in particular the woodland habitats, are divided into smaller blocks. Considerable variation exists both between and within sites with respect to the size of these basic habitat patches. The greatest contrast provided by the New Forest and agricultural sites is in the discontinuous nature of the woodlands in the agricultural areas. At the logical extreme it would be possible to consider Tollard Royal and Brinken as "mirror-images", Brinken typified as islands of heathland and grassland in a sea of open deciduous woodland, whilst Tollard Royal contains island woodlands surrounded by arable land and pasture.

The dominant message revealed by the analyses contained in this chapter is the importance of the level of resolution of habitat categories in all aspects of composition and structure. Very different conclusions can be obtained regarding the similarities and differences between study sites at different levels of resolution. It is essential to remember, when considering data of this type, that it is the study animal, and not the observer, which makes the decisions about what is and is not a discrete habitat type.

3.5. SUMMARY

1. The vegetational resources of the eight study sites were mapped and classified at three levels of habitat resolution. There were pronounced differences between the sites in habitat composition.
2. At the finest level of habitat resolution, the five New Forest sites and the three agricultural sites formed two distinct groupings in terms of habitat composition. At the coarsest level of habitat resolution, the distinction between the two environmental types was less pronounced.
3. Habitat diversity was higher in the Forest than in agricultural land. The New Forest sites contained a greater range of habitat categories, and were less dominated by a few habitat types.
4. The size of individual habitat patches was highly variable within and between sites.
5. Structural complexity as measured by frequency of change in individual habitat types was greater in the New Forest. In contrast, change between woodland and open habitats was more frequent in the agricultural sites.
6. Each of the New Forest sites contained a single large continuous woodland adjacent to large areas of grassland or heathland. In each site, the single largest woodland contributed over 90% of the total woodland area.
7. The agricultural sites were characterised by smaller, discontinuous woodlands interspersed with open grasslands or arable crops. In each site, the single largest woodland contributed less than 50% of the total woodland area.

Table 3.1 Habitat categories recognized at individual habitat, combined habitat, and woodland/open level of resolution. Numbers in parentheses indicate the individual habitats which comprise the combined and woodland/open categories.

Individual habitats

1. Closed canopy coniferous
2. Open canopy coniferous
3. Natural coniferous
4. Closed canopy deciduous
5. Open canopy deciduous
6. Natural deciduous
7. Coppice deciduous
8. Mixed woodland
9. Restock/Clearcut
10. Woodland rides
11. Open verges
12. Natural grassland
13. Improved grassland
14. Arable cereal
15. Arable other
16. Heathland
17. Bog/Mire
18. Bracken/Gorse
19. Not Accessible

Combined habitats

Closed canopy woodland
(1 + 4 + 7)

Open canopy woodland
(2 + 3 + 5 + 6)

Other woodland
(8 + 9)

Woodland rides
(10)

Grasslands
(11 + 12 + 13)

Arable
(14 + 15)

Other open
(16 + 17 + 18)

Not accessible
(19)

Woodland/Open

Woodland
(1 - 10)

Open
(10 -18)

Table 3.2 Study sites ranked in order of decreasing α habitat diversity as measured by the Shannon index and the Simpson index.

Study site	Shannon index	Simpson index
Denny	2.31	8.00
South Oakley	2.29	7.65
Blackensford	2.12	6.97
Dames Slough	1.78	4.82
Lockerley	1.74	4.42
Brinken	1.73	3.51
Tollard	1.48	3.15
Tadley	1.48	2.89

Table 3.3 Amount of woodland to open edge (m/ha) for each study site.

Study Site	Edge (m/ha)
Denny	17.1
Dames Slough	17.5
South Oakley	24.9
Tollard Royal	29.2
Blackensford	30.1
Tadley	39.3
Brinken	47.1
Lockerley	47.6

Fig 3.1 Habitat composition of Denny study site expressed both in terms of the area of each habitat type in hectares: A. individual habitats, C. combined habitats, E. woodland/open habitats; and in terms of the percentage of the total study site: B. individual habitats, D. combined habitats, F. woodland/open habitats.

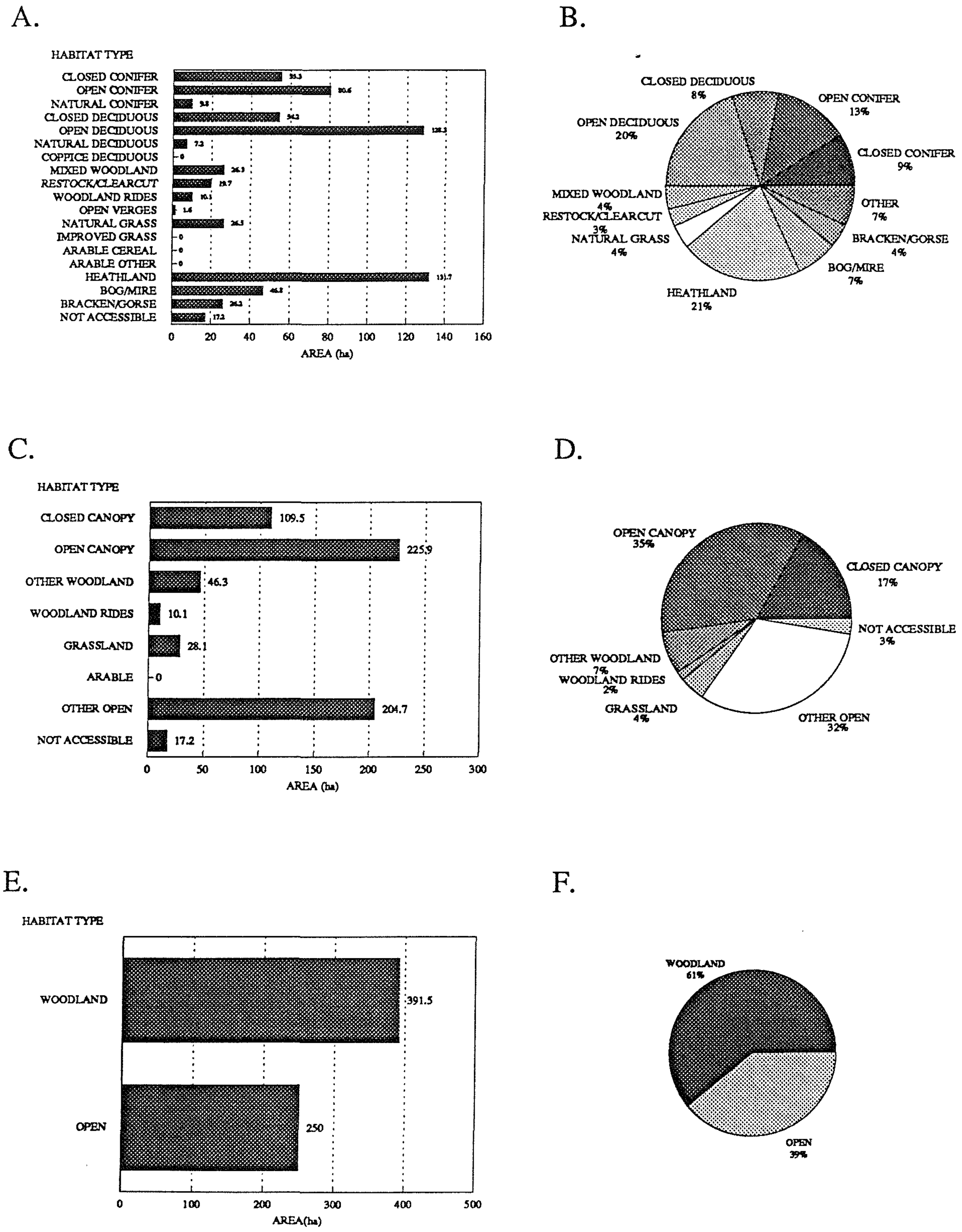


Fig 3.2 Habitat composition of the Dames Slough study site expressed both in terms of the area of each habitat type in hectares: A. individual habitats, C. combined habitats, E. woodland/open habitats; and in terms of the percentage of the total study site: B. individual habitats, D. combined habitats, F. woodland/open habitats.

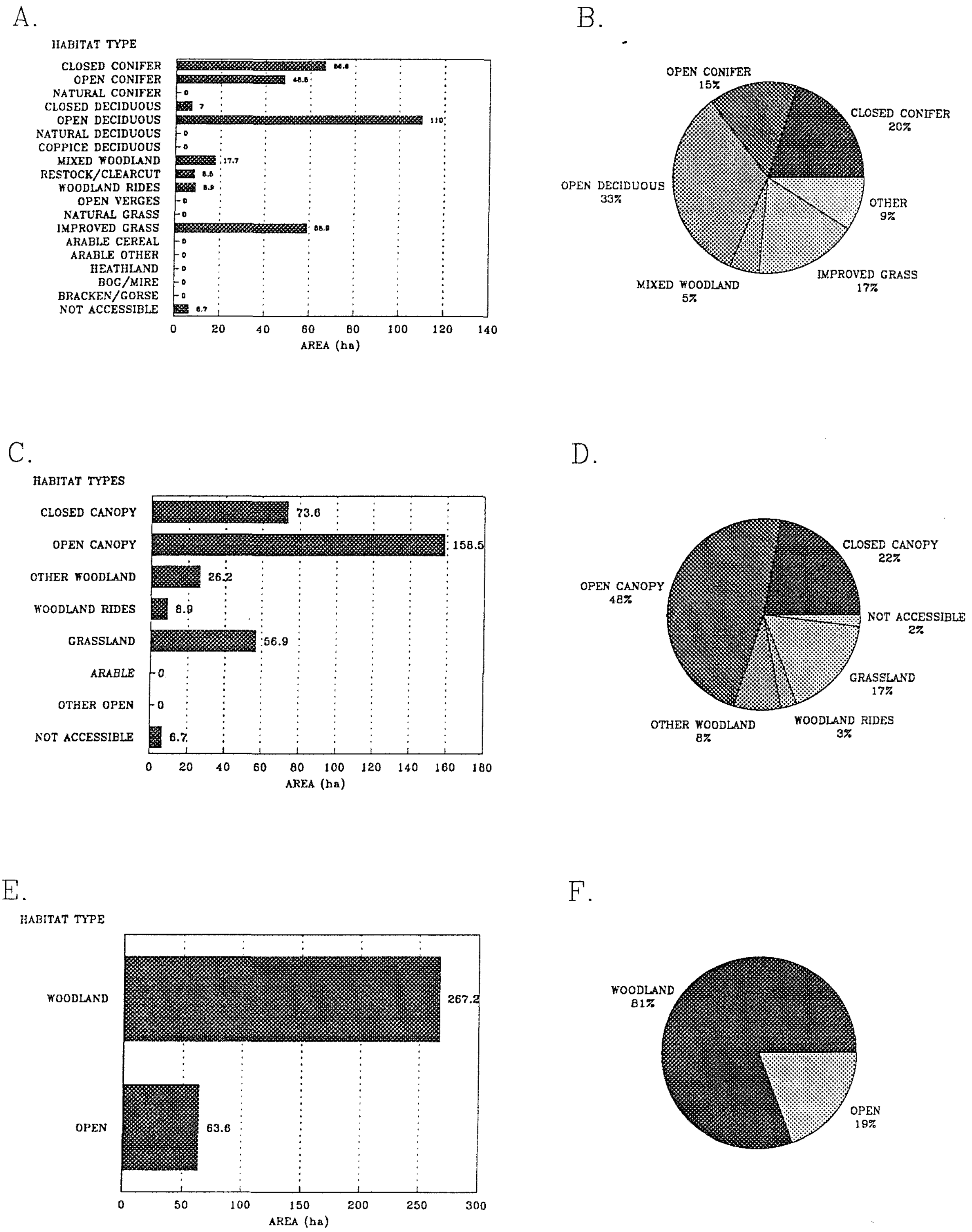


Fig 3.3 Habitat composition of South Oakley study site expressed both in terms of the area of each habitat type in hectares: A. individual habitats, C. combined habitats, E. woodland/open habitats; and in terms of the percentage of the total study site: B. individual habitats, D. combined habitats, F. woodland/open habitats.

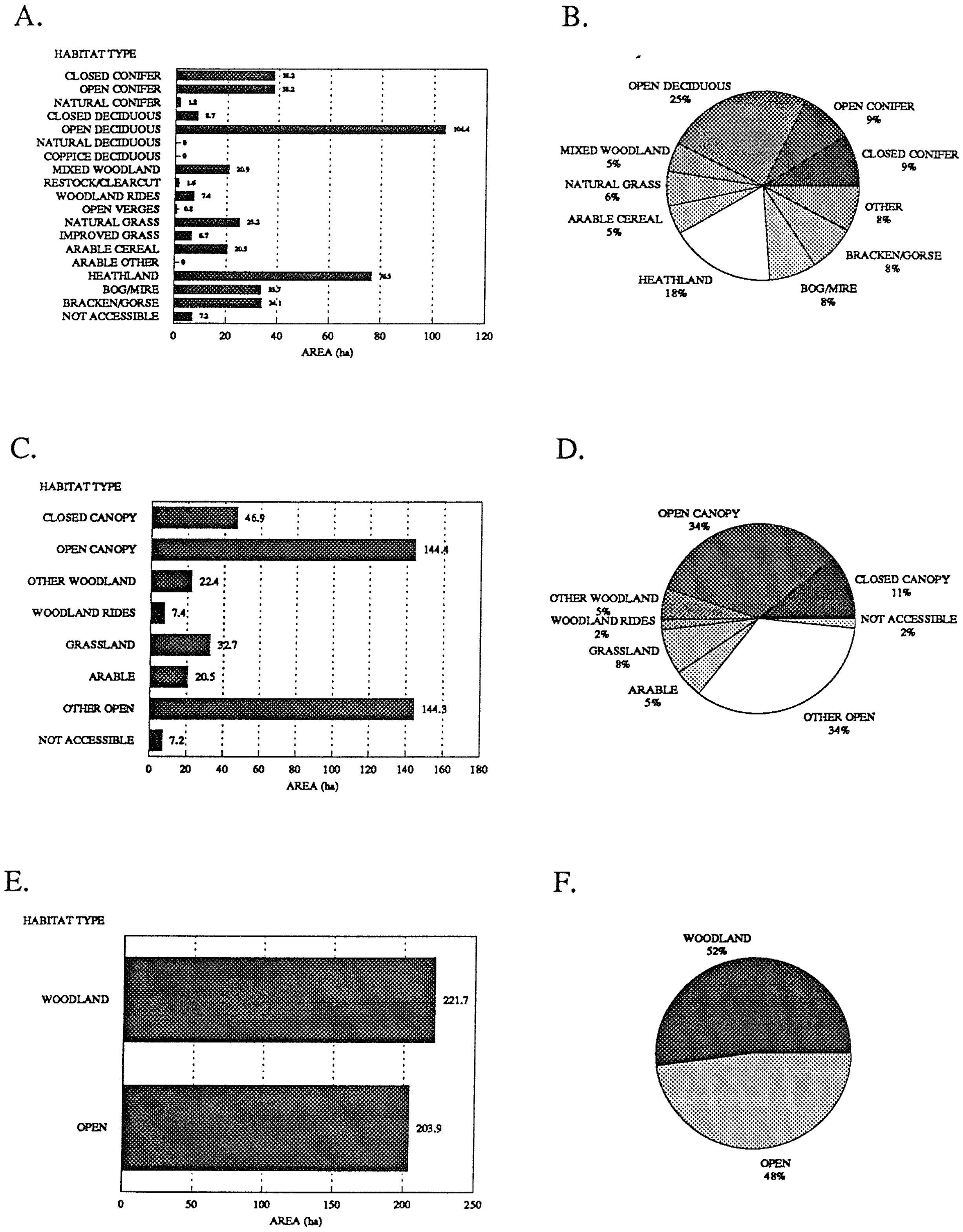


Fig 3.4 Habitat composition of the Blackensford study site expressed both in terms of the area of each habitat type in hectares: A. individual habitats, C. combined habitats, E. woodland/open habitats; and in terms of the percentage of the total study site: B. individual habitats, D. combined habitats, F. woodland/open habitats.

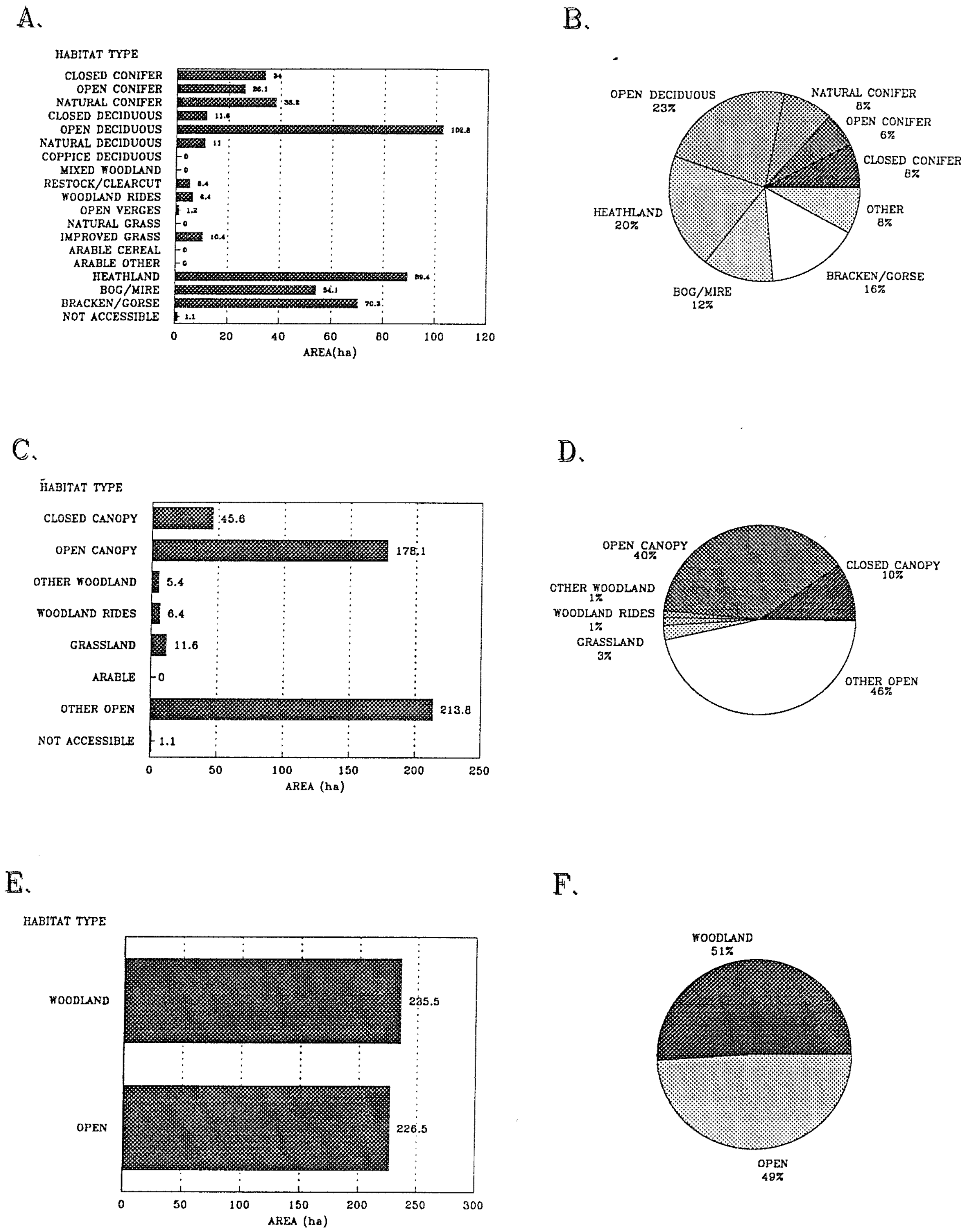


Fig 3.5 Habitat composition of the Brinken study site expressed both in terms of the area of each habitat type in hectares: A. individual habitats, C. combined habitats, E. woodland/open habitats; and in terms of the percentage of the total study site: B. individual habitats, D. combined habitats, F. woodland/open habitats.

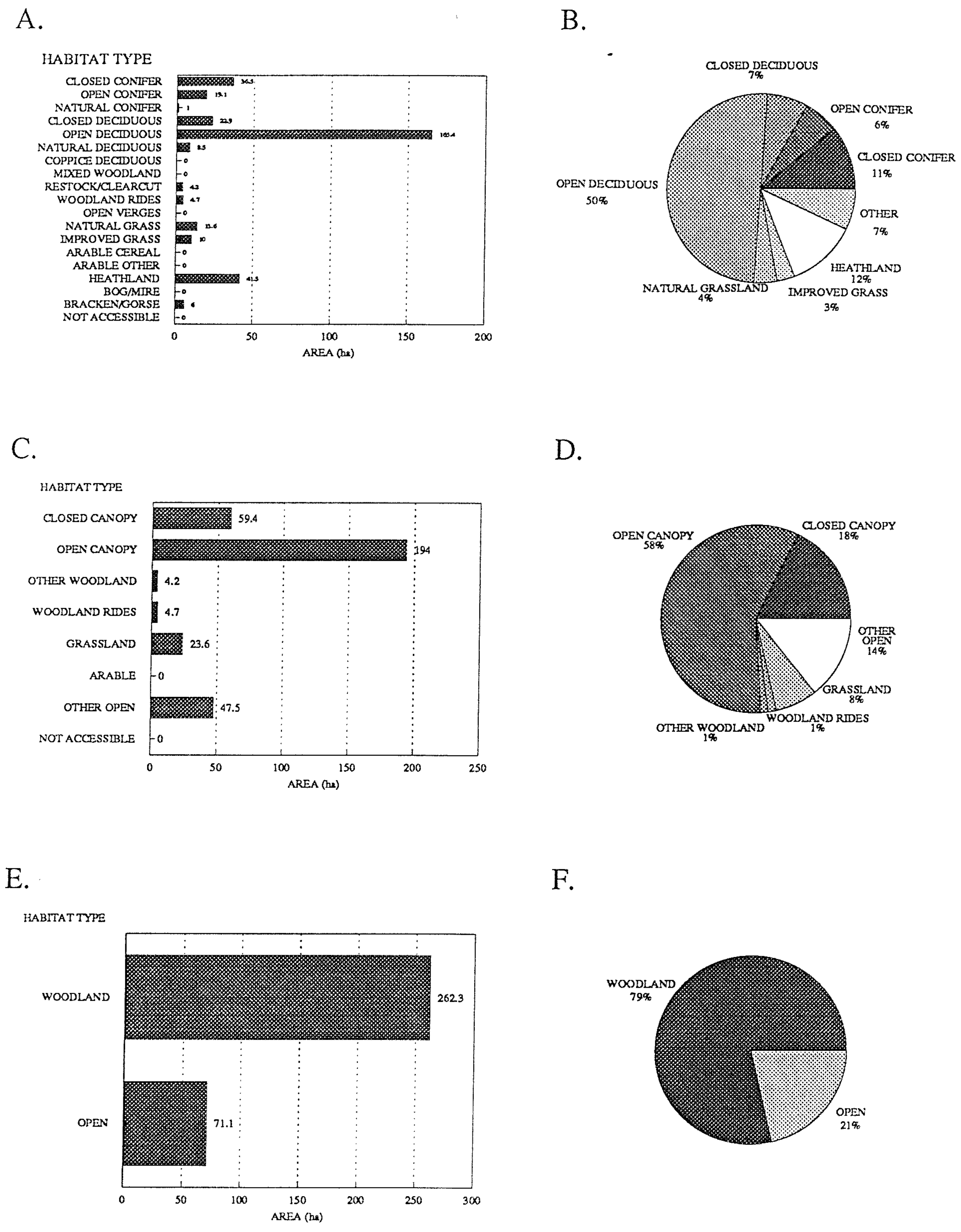


Fig 3.6 Habitat composition of the Lockerley study site expressed both in terms of the area of each habitat type in hectares: A. individual habitats, C. combined habitats, E. woodland/open habitats; and in terms of the percentage of the total study site: B. individual habitats, D. combined habitats, F. woodland/open habitats.

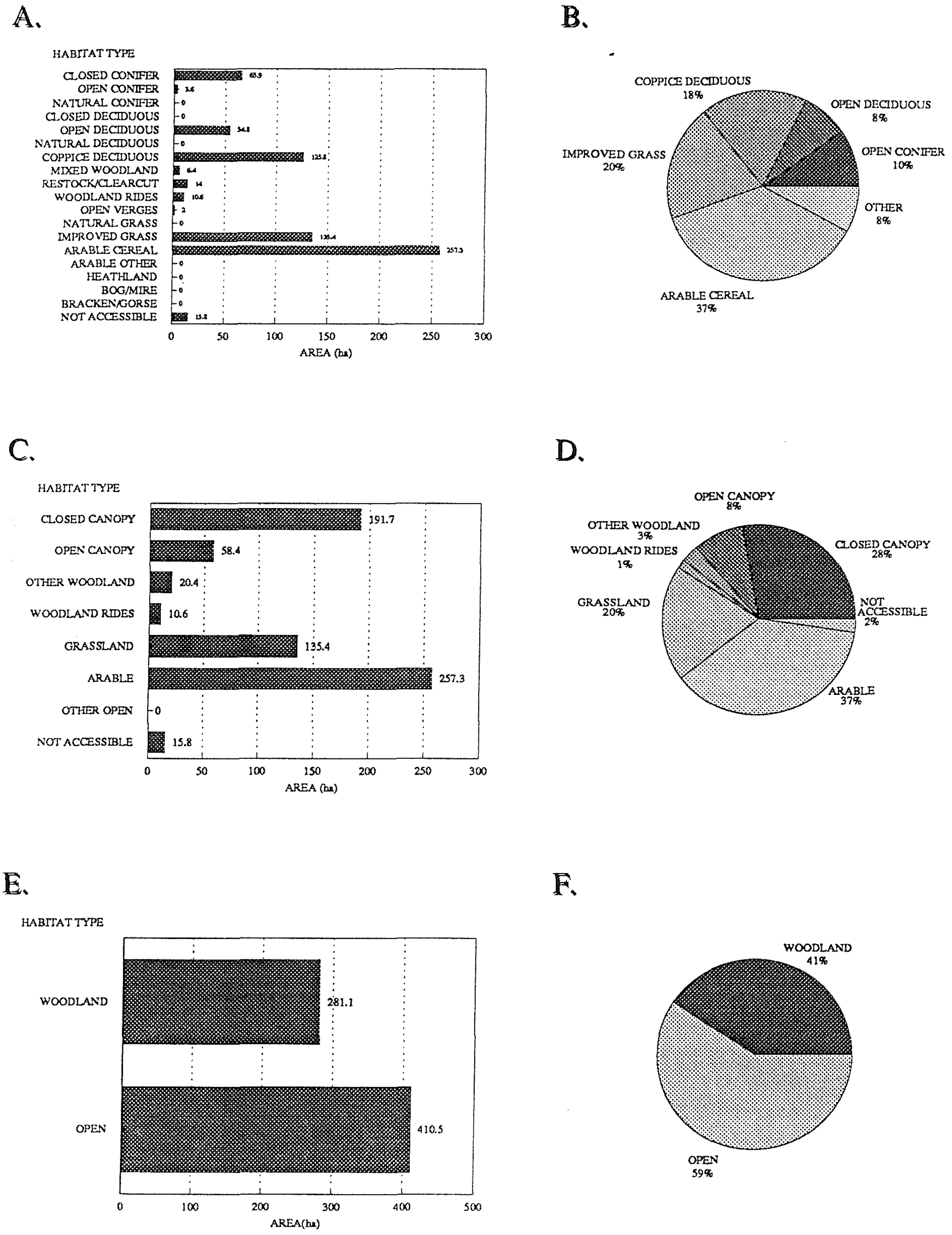


Fig 3.7 Habitat composition of the Tollard Royal study site expressed both in terms of the area of each habitat type in hectares: A. individual habitats, C. combined habitats, E. woodland/open habitats; and in terms of the percentage of the total study site: B. individual habitats, D. combined habitats, F. woodland/open habitats.

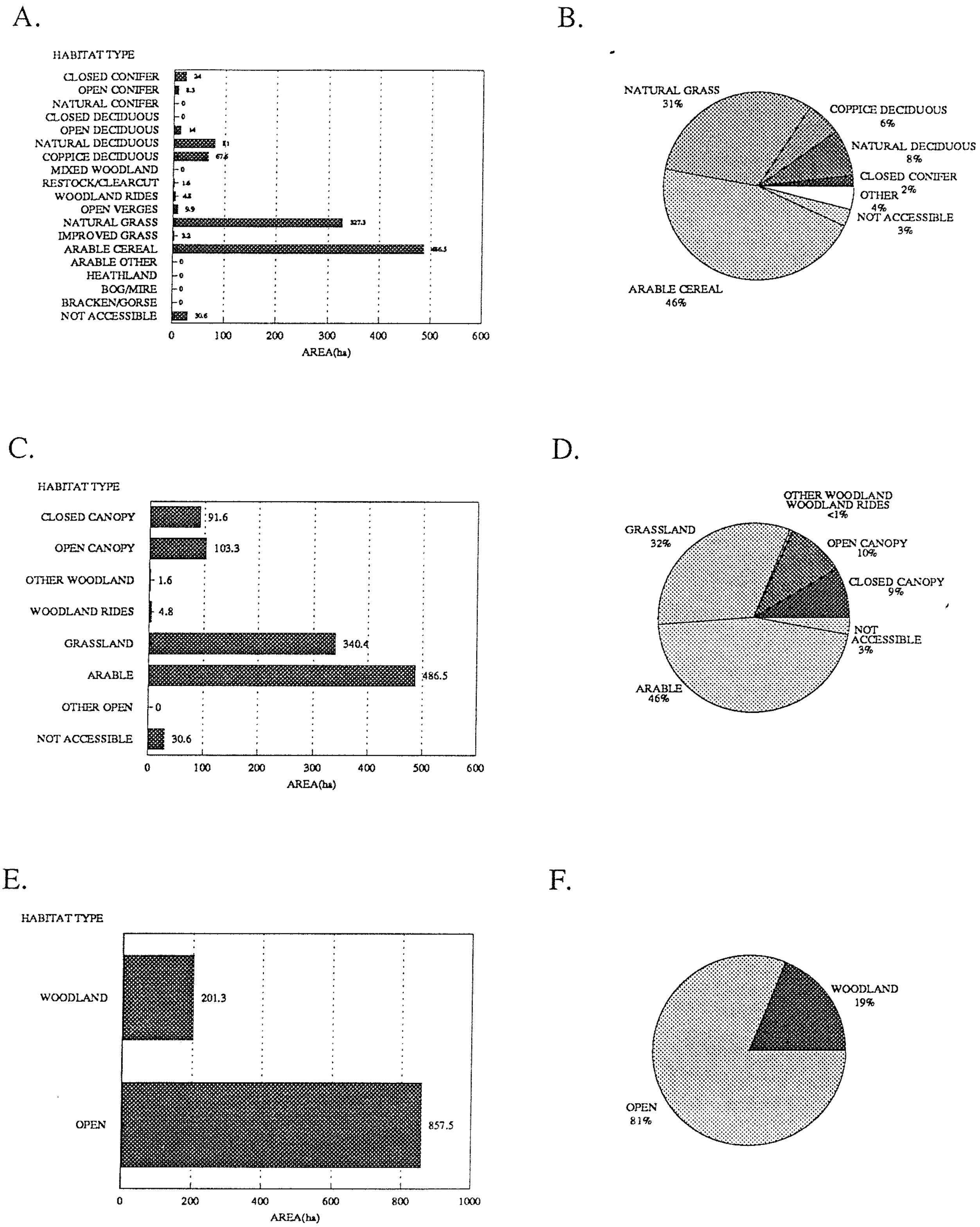


Fig 3.8 Habitat composition of the Tadley study site expressed both in terms of the area of each habitat type in hectares: A. individual habitats, C. combined habitats, E. woodland/open habitats; and in terms of the percentage of the total study site: B. individual habitats, D. combined habitats, F. woodland/open habitats.

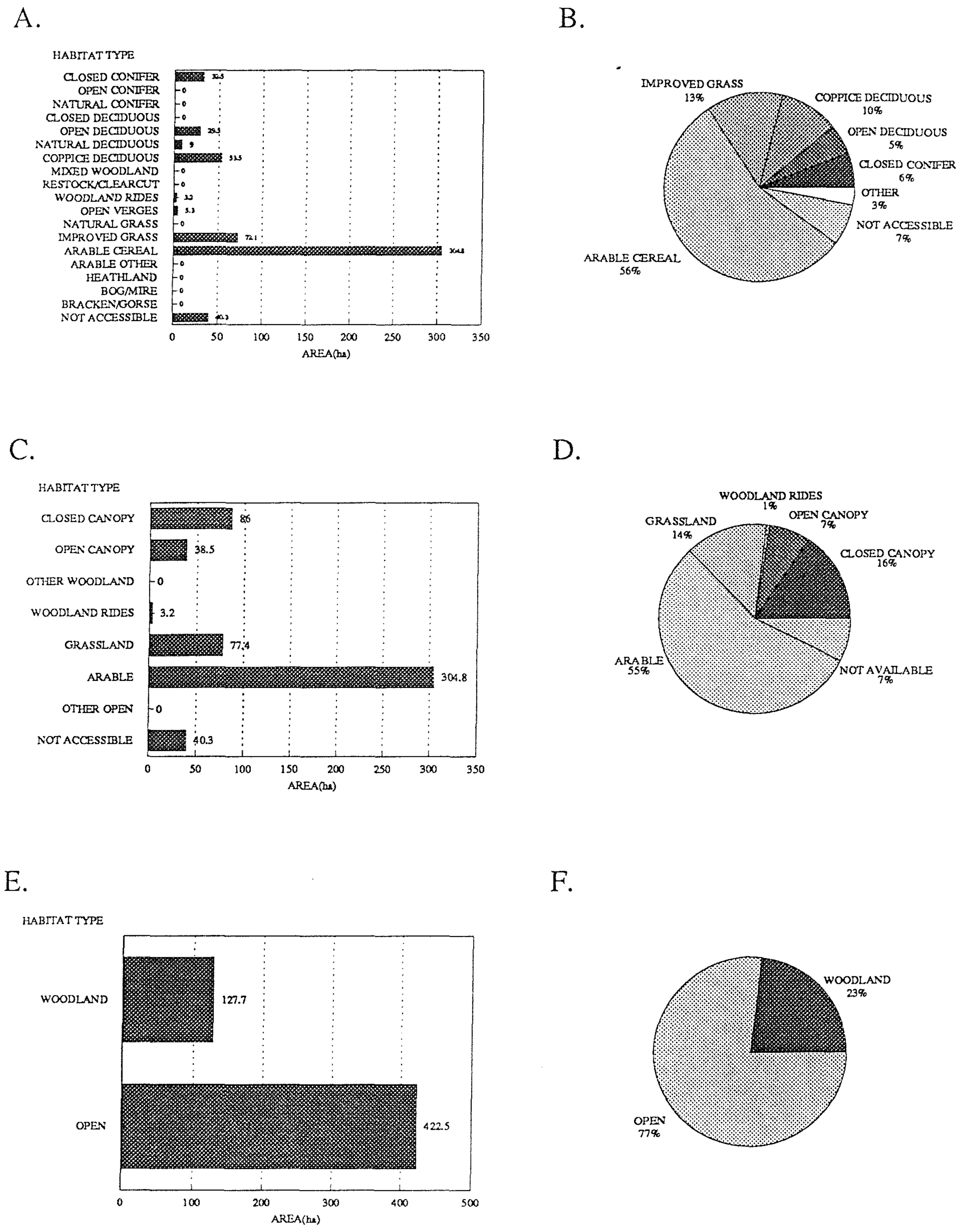
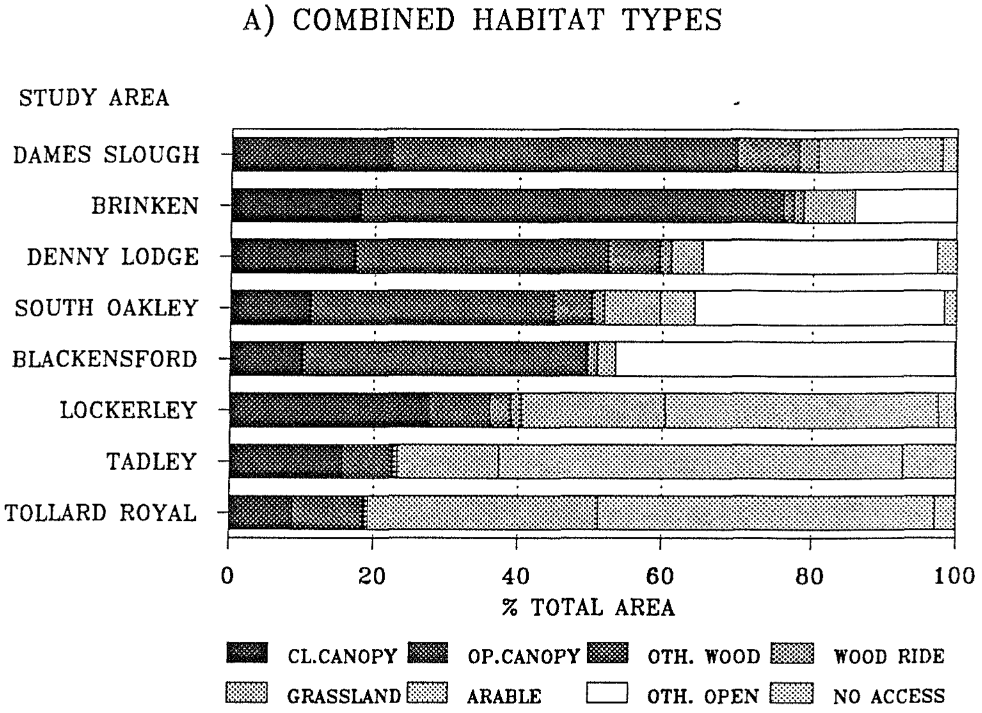
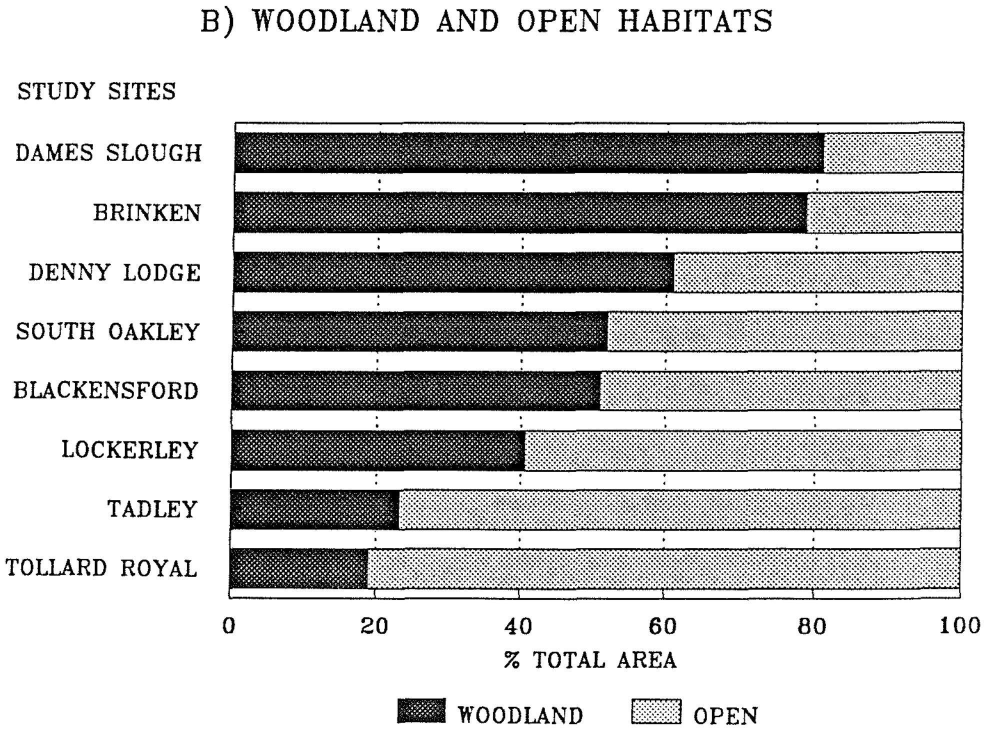
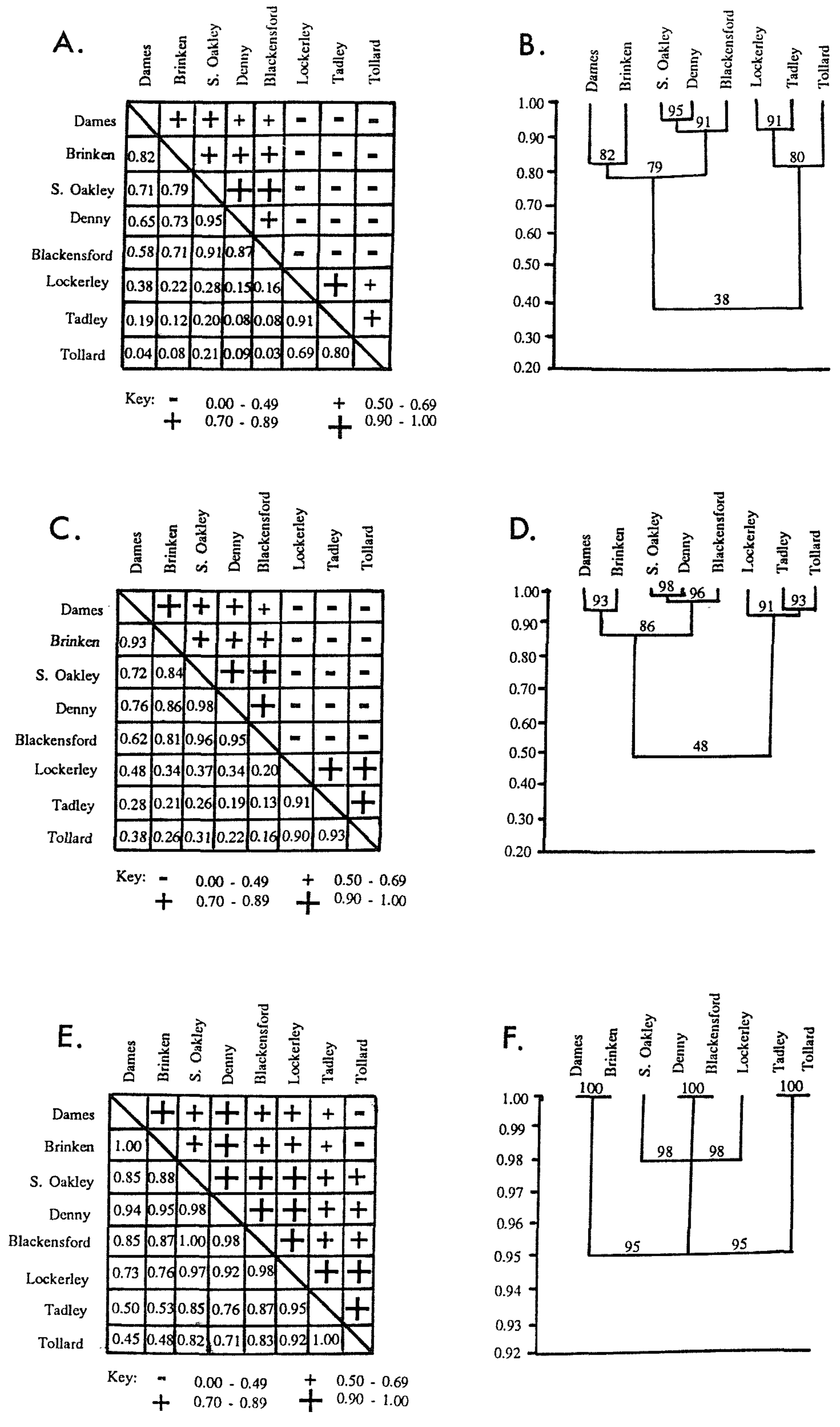


Fig 3.9 Habitat composition of the eight study sites expressed as the percentage oftotal area for: A. combined habitat types, B. woodland/open habitat types.







A.

	Dames	Brinken	S. Oakley	Denny	Blackensford	Lockerley	Tadley	Tollard
Dames		+	+	+	+	-	-	-
Brinken	0.82		+	+	+	-	-	-
S. Oakley	0.71	0.79		+	+	-	-	-
Denny	0.65	0.73	0.95		+	-	-	-
Blackensford	0.58	0.71	0.91	0.87		-	-	-
Lockerley	0.38	0.22	0.28	0.15	0.16		+	+
Tadley	0.19	0.12	0.20	0.08	0.08	0.91		+
Tollard	0.04	0.08	0.21	0.09	0.03	0.69	0.80	

Key: - 0.00 - 0.49 + 0.50 - 0.69
+ 0.70 - 0.89 + 0.90 - 1.00

C.

	Dames	Brinken	S. Oakley	Denny	Blackensford	Lockerley	Tadley	Tollard
Dames		+	+	+	+	-	-	-
Brinken	0.93		+	+	+	-	-	-
S. Oakley	0.72	0.84		+	+	-	-	-
Denny	0.76	0.86	0.98		+	-	-	-
Blackensford	0.62	0.81	0.96	0.95		-	-	-
Lockerley	0.48	0.34	0.37	0.34	0.20		+	+
Tadley	0.28	0.21	0.26	0.19	0.13	0.91		+
Tollard	0.38	0.26	0.31	0.22	0.16	0.90	0.93	

Key: - 0.00 - 0.49 + 0.50 - 0.69
+ 0.70 - 0.89 + 0.90 - 1.00

E.

	Dames	Brinken	S. Oakley	Denny	Blackensford	Lockerley	Tadley	Tollard
Dames		+	+	+	+	+	+	-
Brinken	1.00		+	+	+	+	+	-
S. Oakley	0.85	0.88		+	+	+	+	+
Denny	0.94	0.95	0.98		+	+	+	+
Blackensford	0.85	0.87	1.00	0.98		+	+	+
Lockerley	0.73	0.76	0.97	0.92	0.98		+	+
Tadley	0.50	0.53	0.85	0.76	0.87	0.95		+
Tollard	0.45	0.48	0.82	0.71	0.83	0.92	1.00	

Key: - 0.00 - 0.49 + 0.50 - 0.69
+ 0.70 - 0.89 + 0.90 - 1.00

Fig 3.10 Similarity in habitat composition between study sites expressed in terms of the Morisita-Horn Index. See text for details. Similarity indices calculated at three levels of habitat resolution: A. & B. individual habitats; C. & D. combined habitats; E. & F. woodland/open habitats.

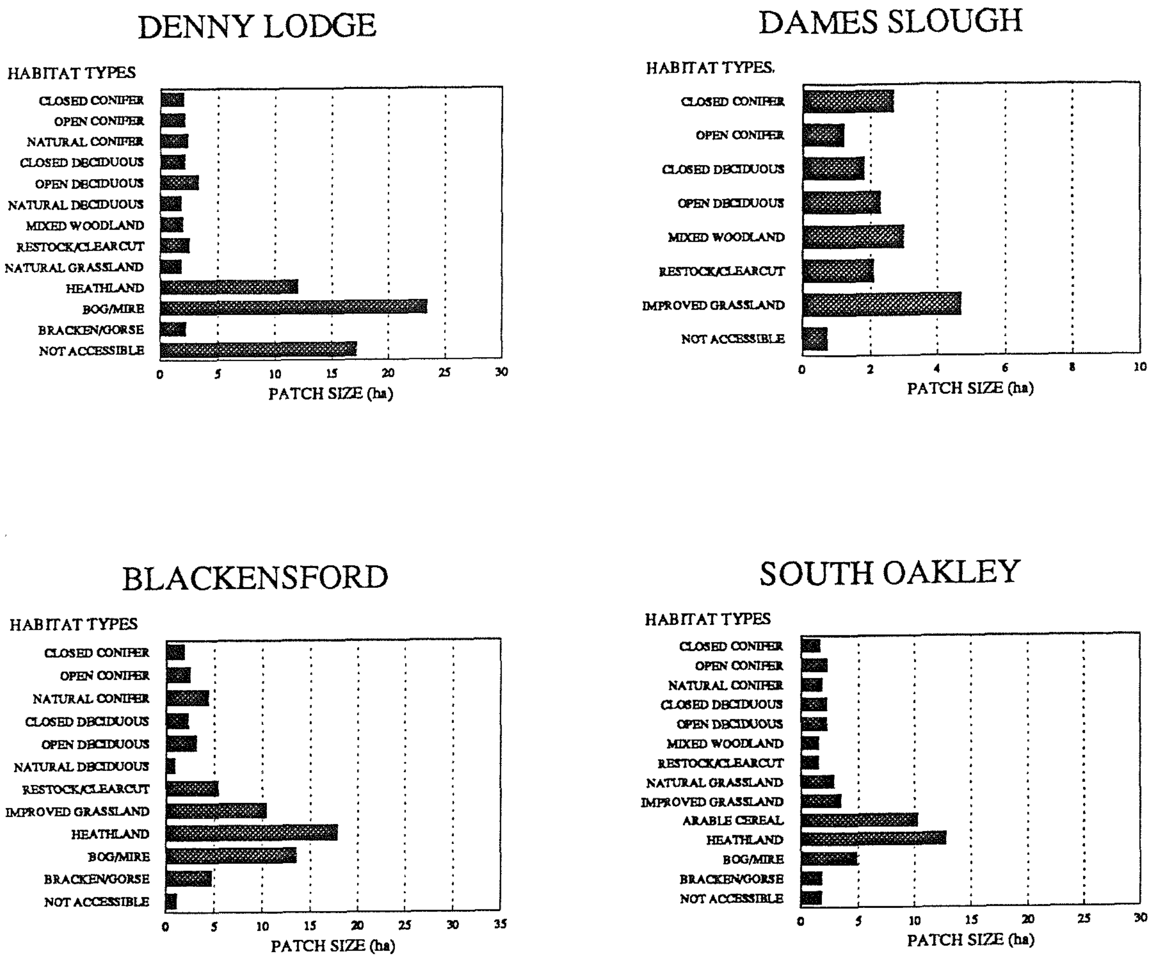


Fig 3.11 Mean patch size of individual habitat categories within each study site.

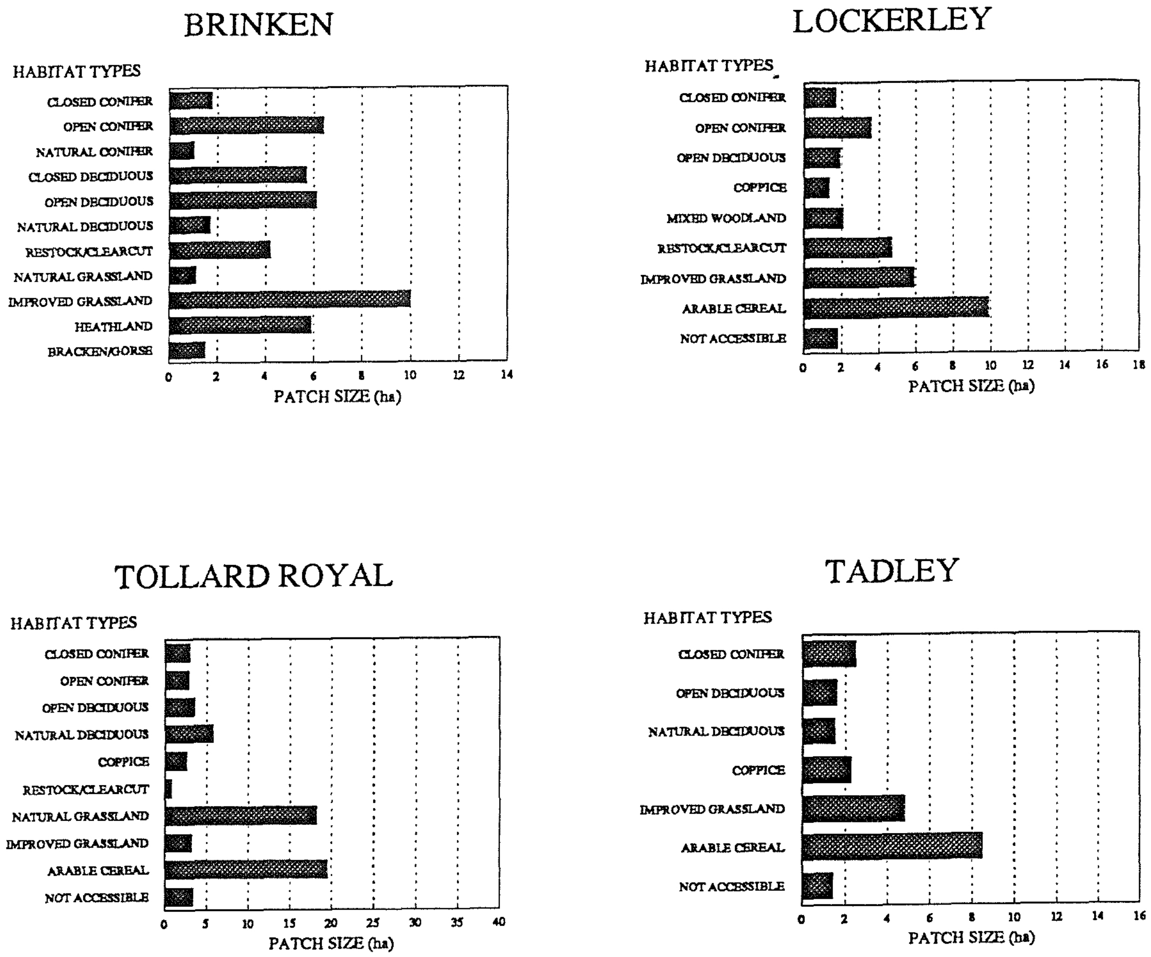
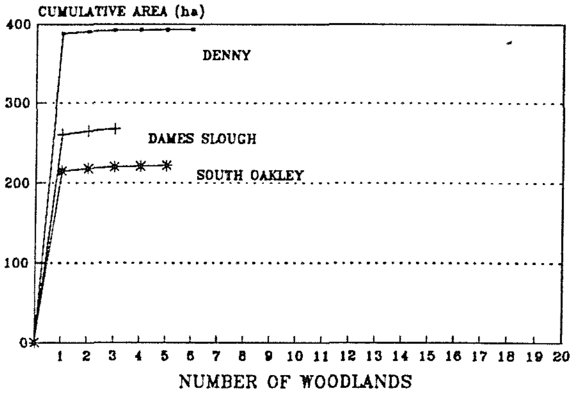


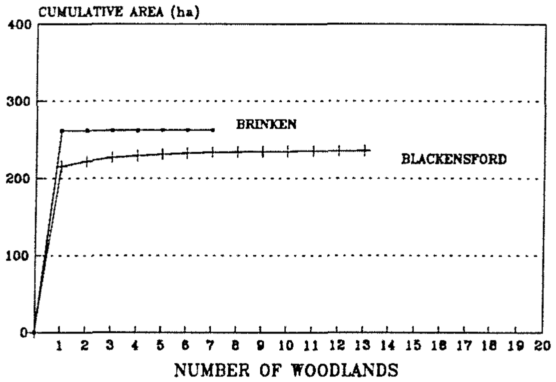
Fig 3.11 Mean patch size of individual habitat categories within each study site.

Fig 3.12 Cumulative woodland area for each study site calculated as the increase in total woodland area with the inclusion of each additional woodland block.

NEW FOREST A



NEW FOREST B



AGRICULTURAL SITES

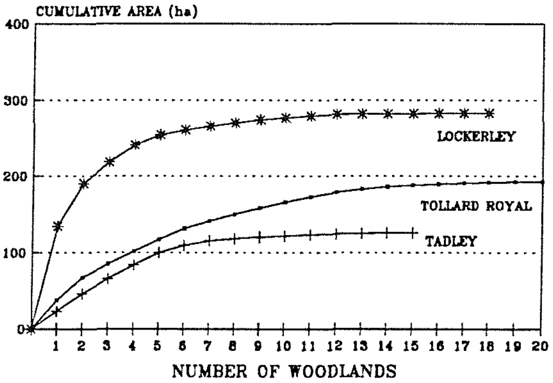


Fig 3.13 Percentage cumulative woodland area for each study site calculated as the percentage of total woodland area with the inclusion of each additional woodland block.

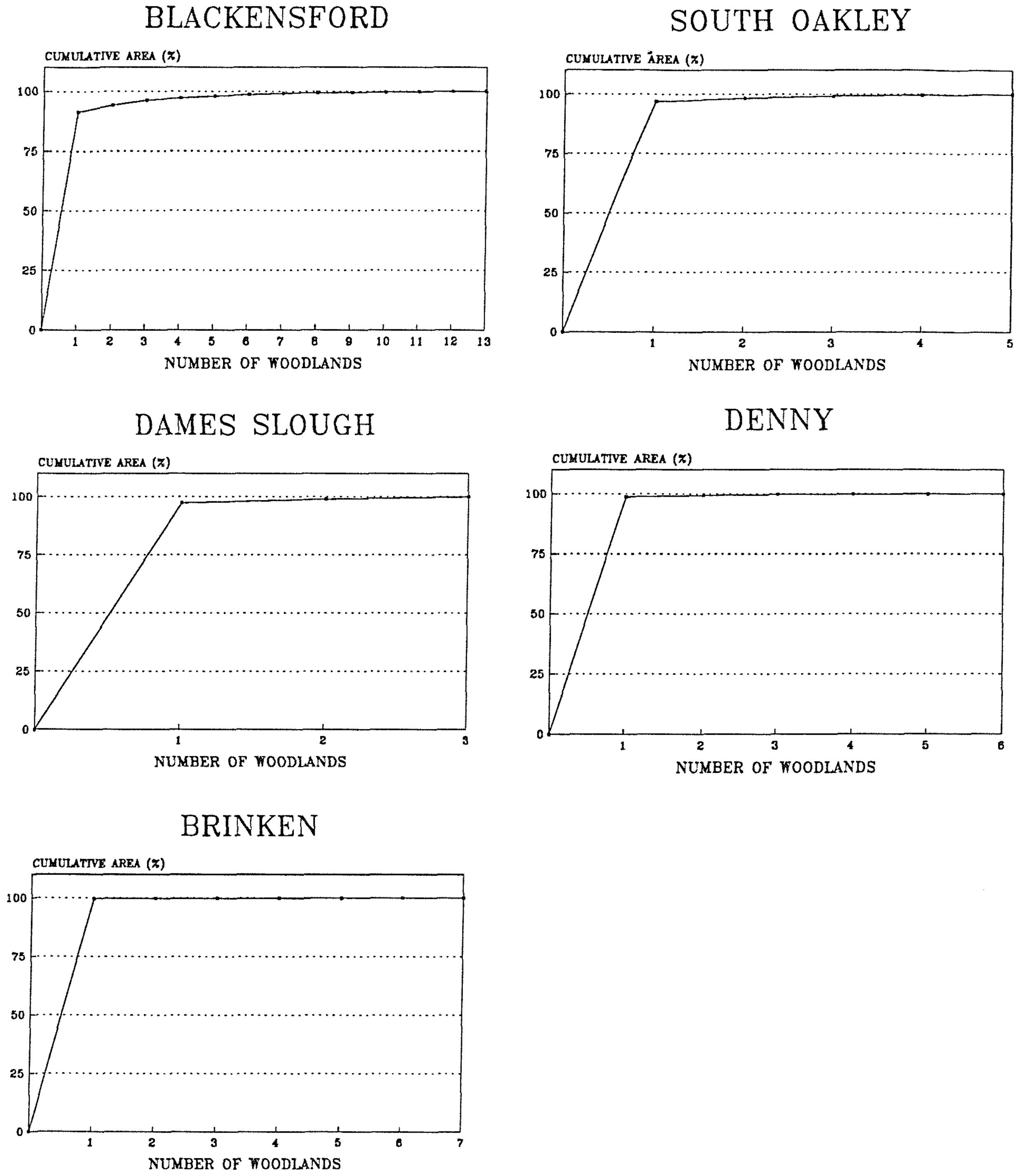
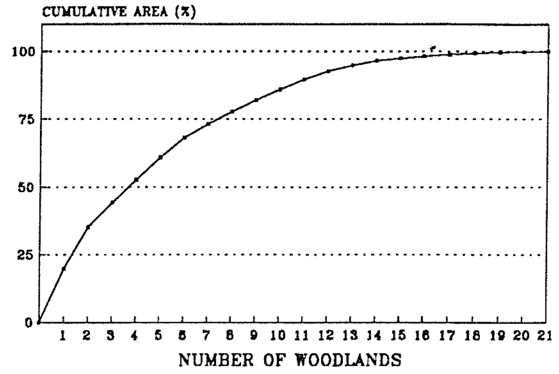
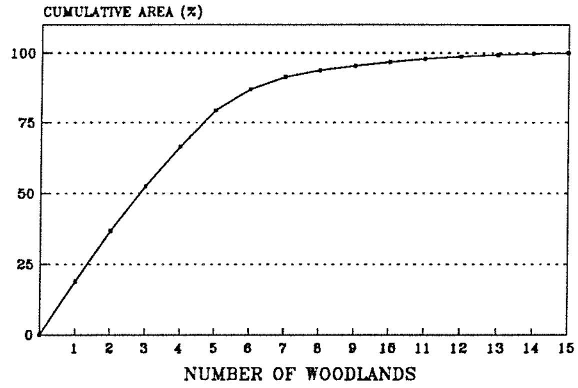


Fig 3.13 Percentage cumulative woodland area for each study site calculated as the percentage of total woodland area with the inclusion of each additional woodland block.

TOLLARD ROYAL



TADLEY



LOCKERLEY

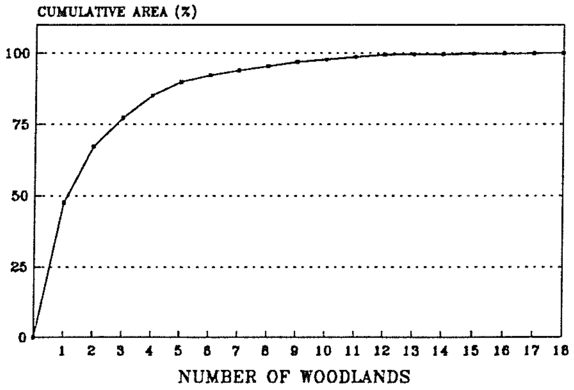
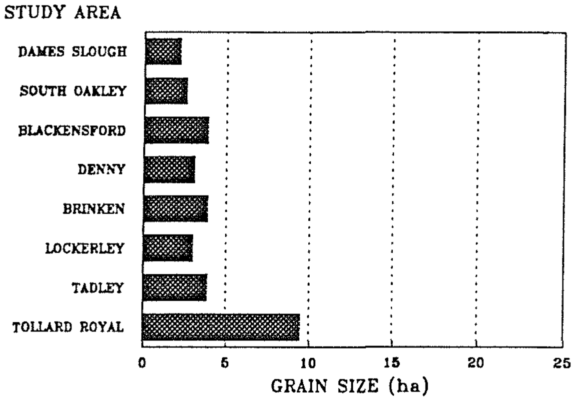
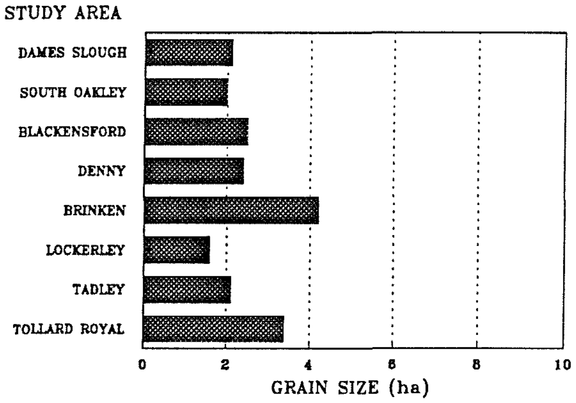


Fig 3.14 Habitat grain size of each study site calculated as the average size of each individual habitat patch for: A. all habitats combined; B. woodland habitats only; C. open habitats only.

A) ALL HABITATS COMBINED



B) WOODLAND HABITATS



C) OPEN HABITATS

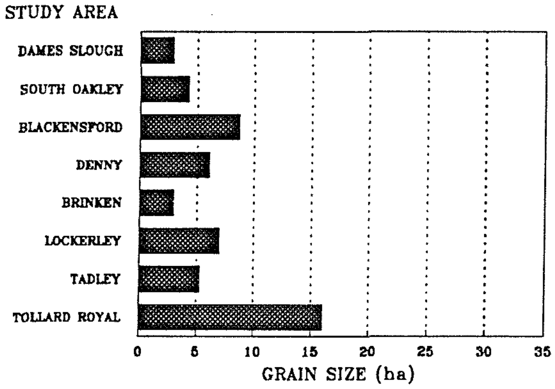
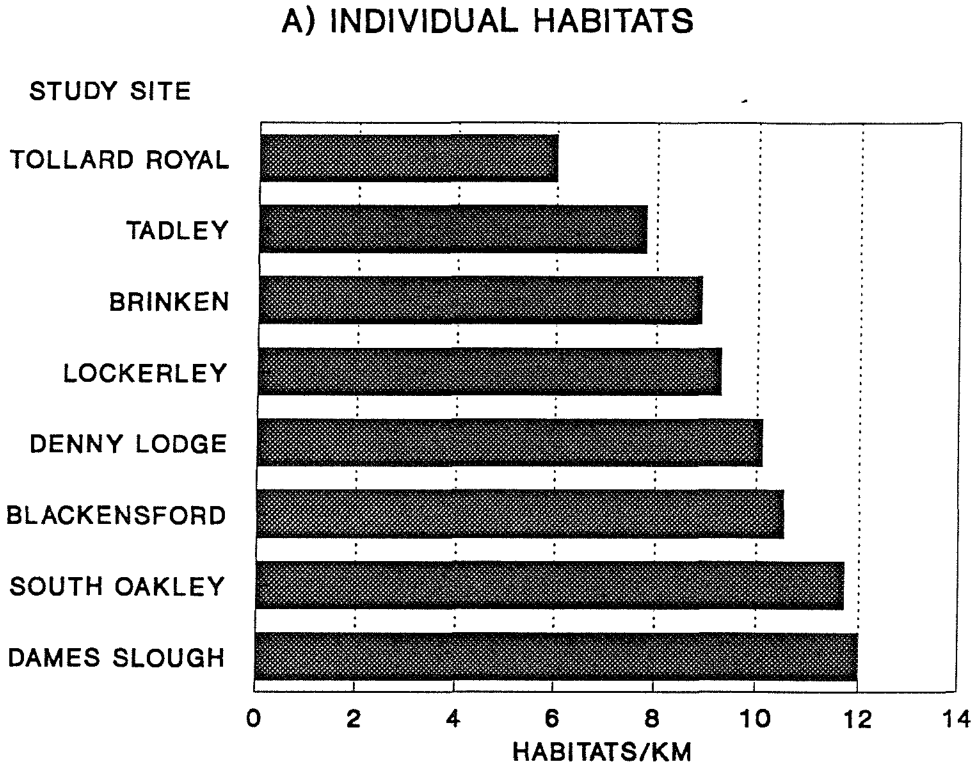
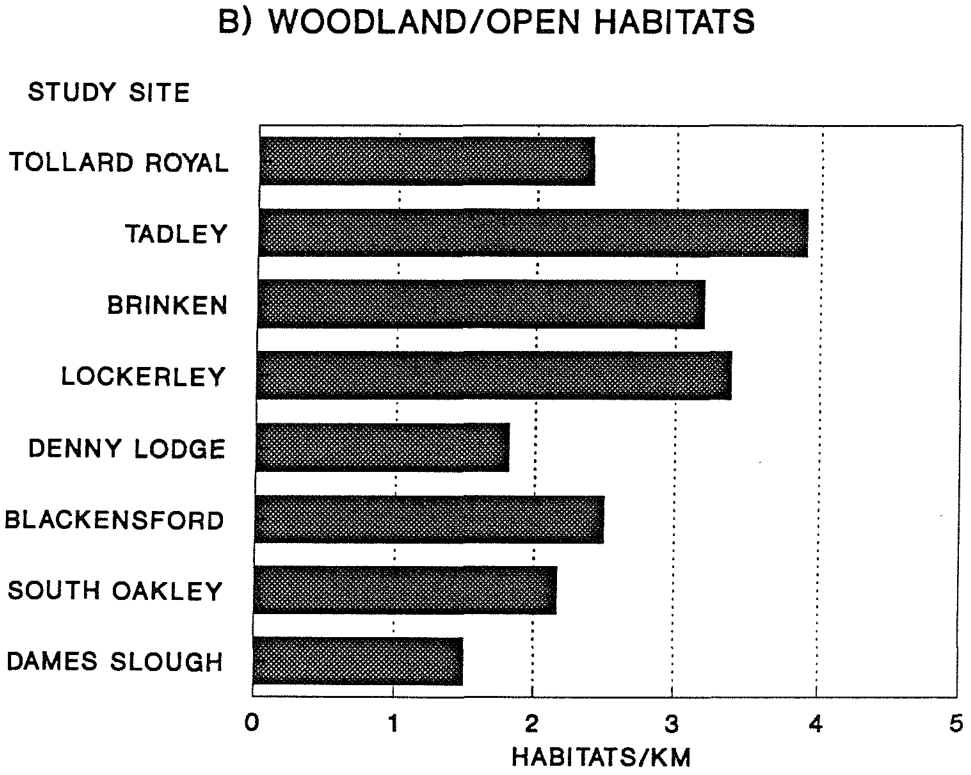


Fig 3.15 Frequency of habitat change along regularly spaced grid lines for each study site. Change between: A. individual habitats; B. woodland/open habitats.





4. PATTERNS OF HABITAT USE

4.1. INTRODUCTION

This chapter is principally concerned with the patterns of habitat use exhibited by fallow deer in the eight study sites. It is important to consider patterns of habitat occupance and selection shown by the deer because of the possible implications of habitat utilization on social systems observed. In particular, a number of studies on large herbivores have found a positive relationship between the degree of openness in the environment and the size of social group adopted by animals, eg. fallow deer (Schaal 1982), white-tailed deer *Odocoileus virginianus* (Hirth 1977; LaGory 1986), impala *Aepyceros melampus* (Leuthold 1970), Grant's gazelle *Gazella granti* (Walther 1972). If group size is related to habitat, and patterns of habitat use differ between sites, then observed differences in group size between populations may simply be a result of different patterns of habitat use. Clearly, an understanding of the adaptability of a particular size of social grouping or variation in mating system can only be gained when differences in the animals' usage of the available habitat communities between gross environmental types has been accurately quantified. In this chapter, objective comparative data on habitat use is presented, and this is set in the context of previous studies of fallow and other large herbivores. Consideration of the resulting impact on social systems will be reserved for later chapters.

How can habitat use be objectively determined?

Large herbivores rarely range randomly; more often there are certain habitats which they use preferentially and others which they avoid. A functional approach to investigating these preferences could be to choose a set of ecological parameters such as the abundance of food or availability of shelter, and study the distribution of animals in relation to variation of these parameters. In a seminal paper, Duncan (1983) pointed out the complexities of describing patterns of habitat use in such terms. In a seasonally changing environment, the values of many relevant parameters change rapidly, in particular the standing crop and nutrient content of available forage. Such an approach involves an inordinate amount of detailed field measurement which is beyond the scope or needs of many research projects. Duncan suggests that an alternative approach is to assume 'a priori' classification of the habitat into recognizable units and then observe the distribution of animals within them. This approach was adopted by Putman and colleagues for intensive studies of the grazing ecology of the assemblage of large herbivores occurring in the New Forest, southern England (summarized in Putman 1986a). As stated in the previous chapter, a modified version of Putman's habitat classification scheme has been adopted, with allowances made for the inclusion of agricultural habitat types which do not occur in the New Forest.

Wildlife studies often compare relative use of resources to their availability. When resources are used disproportionately to their availability, use is said to be selective (Johnson 1980). Although selection and preference are often used synonymously, Johnson (1980) defines the former as the process in which an animal chooses a resource and the latter as the likelihood that a resource will be chosen if offered on equal basis with others. Because of inconsistencies in the literature in the use of 'preference' (Thomas & Taylor 1990), Johnson's (1980) definition that requires equal availability has been followed; hence the work that is reported in this chapter comparing habitat use in study areas which differ in habitat composition is referred to as habitat selection.

An additional point made by Johnson (1980) is that comparing habitat use within home ranges may be misleading, because in choosing a home range, the animal has already made an important selection. For example, deer may select a home range because grazing resources are abundant; use of this resource may appear low when compared to availability within this restricted area but higher when compared to the general area from which the home range was selected. Similar concerns have subsequently been expressed by Porter & Church (1987) and Thomas & Taylor (1990). In the current study, information on the range of either individuals or populations was not available, therefore relatively arbitrary decisions were taken to delimit study area boundaries and hence could affect estimates of habitat selection.

What drives the selection of particular habitat types?

Differential use of vegetation communities by large herbivores is widely thought to be determined by the animals' need to satisfy basic requirements for food and water, shelter from the elements and from predators, rest and in the case of deer rumination, and social interactions with conspecifics (Beier & McCullough 1990). The resulting habitat use pattern may vary with age, sex, time of day, season, and weather conditions as the animals' requirements and the resources provided by the different habitats change. Most seasonal variation in habitat use by deer has been associated with seasonal changes in the availability of food and protective cover, eg. white-tailed deer (Suring & Vohs 1979; Murphy et al. 1985), black-tailed deer *Odocoileus hemionus* (Dasmann & Taber 1956; Loft et al. 1984), elk *Cervus canadensis* (Mackie 1970), and sika deer *Cervus nippon* (Mann & Putman 1989). Hanley (1984) goes further to suggest that habitat and food selection by ungulates can be predicted to a large degree on the basis of morphological features relative to nutritional constraints. Forage choice is related to four physical characteristics of ungulates (Hanley 1982). Body size and type of digestive system determine the overall time-energy constraints of foraging (Bell 1969). The ratio of rumino-reticular volume to body weight determines the type of food the ruminant is most efficient at processing (Hofmann 1973). Mouth size determines the ability of the animal to forage selectively (Jarman 1974). This hypothesis suggests that large ungulates and cecal digesters are more limited by time than are small ungulates and ruminant digesters; a high ratio of rumino-reticular volume to body weight is an adaption to exploiting graminoids; and a low ratio of rumino-reticular volume to body weight is an adaption to exploiting browse. Hanley (1984) elegantly demonstrated that the diet and habitat use of elk and black-tailed deer in the Cascades were predicted accurately by the above model. Hanley's study, however, was restricted to the summer range of his study animals (May-October), at which time the constraints of shelter are likely to be of limited importance. In contrast, Beier & McCullough (1990), working on white-tailed deer in Michegan, found that seasonal variation in habitat use was restricted to winter, when snow cover and its affect on food availabilities was the most important factor influencing habitat use.

Food and shelter have been identified as important factors influencing habitat selection in other ungulates. Duncan (1983), working on semi-wild horses *Equus caballus* in the Camargue, concluded that the primary function of selection of feeding habitat by these horses was to maximize their intake of high quality food. However, feeding activities are not the sole determinant of habitat choice in all feral horse populations. In the more temperate climate of the New Forest, whilst spring and summer horse distribution is primarily dictated by foraging, shelter from the physical elements assumes a greater priority during the winter months (Pratt et al. 1986; Putman et al. 1987).

Do species habitat use patterns change between gross environmental types?

In a number of species of deer world-wide, different populations of the same species are known to exist in environmental types contrasting greatly in habitat composition and structure (see Putman 1988 for review). In these cases, the animals are able to adapt to satisfy their requirements for food and shelter from the resources available. This can be well illustrated by a recent study of sika deer in southern England. Sika were introduced to Britain at the turn of the century and, amongst other locations, established populations in both the mixed woodlands of the New Forest and the commercial conifer plantations of Dorset, some 50km away. The habitat use and activity patterns of these populations were investigated by Mann & Putman (1989) who demonstrated that sika in the New Forest made use of a wide range of woodland habitats, showed considerable variation in habitat use in different seasons, and were active within the woodland 24 hours a day. Throughout the year, in contrast, Dorset sika were most often seen in daytime in young conifers but grazed extensively on heathland and agricultural fields beyond the forest boundary at night. Mann & Putman (1989) argued that the nocturnal habit of the Dorset sika was forced on them by the lack of adequate forage within the woodlands, and their resultant feeding in open habitats which were more prone to human disturbance. However, both populations, were able to satisfy their nutritional and shelter requirements from entirely different environmental types.

The European roe deer *Capreolus capreolus* offers another example of the ability of many cervids to adapt to different environmental circumstances. Typically a species of continuous woodland, they are also found in small coppice woodland interspersed with pasture and arable land, where they make extensive use of the more open habitats for feeding, and return to the woodlands for cover (Putman 1986b; Maublanc 1986). In the agrocenoses of central Europe, high density populations of roe deer exist entirely independent of woodlands, gaining both food and shelter from the extensive cereal crops (Zejda & Homolka 1980). Similar flexibility in patterns of habitat use are shown by Asian populations of chital *Axis axis*, sambar *Cervus unicolour*, and hog deer *Axis porcinus* (Schaller 1967; Kurt 1978; Mishra 1982).

Sex difference in habitat use

Pronounced sex differences in habitat use and diet exist in many sexually dimorphic mammals including macropods (Newsome 1980), primates (Gautier-Hion 1980), bovids (Spinage et al. 1980), caprids (Shank 1982) and cervids. They are particularly well documented in open-hill populations of Scottish red deer *Cervus elephus* where numerous studies have found that stags occupy areas of poorer quality vegetation than hinds (eg. Charles et al. 1977; Watson & Staines 1978; Staines et al. 1982; Clutton-Brock et al. 1982, 1987; Gordon 1989). In the latter two studies on the Isle of Rhum, sex differences in habitat use were less marked than in earlier studies in mainland Scotland, however there was fine-grained selection within habitat community types, particularly on short grasslands, where hinds and stags rarely used the same areas. Why do stags and hinds have different feeding habits and hence occupy different habitat types? Clutton-Brock et al. (1982) and Staines et al. (1982) suggested that because of their larger size, stags are not able to get enough digestible material from the heavily-utilized grasslands to satisfy their greater metabolic requirements and, therefore, have to feed on poorer quality swards with higher standing crops. An extension of this argument suggests that males may be excluded from mutually preferred communities by indirect competition with females, because of differential scaling of incisor breadth (and hence bite size and forage intake rate) and metabolic requirements to body weight (Clutton-Brock et al. 1987; Illius & Gordon 1987).

Alternative explanations have been suggested in long-term studies of white-tailed deer on the George Reserve in Michegan (McCullough 1979; Beier 1987; McCullough et al. 1989; Beier & McCullough 1990). Here, males make greater use of closed forest and less use of open woodlands and grasslands than do females. The grasslands and open woodlands offer improved forage conditions for females in winter and spring, with the result that females consume diets of higher quality. McCullough and colleagues suggest that allometric relationships between body size, digestive capacity and metabolic requirements allow males to subsist on lower quality but more abundant foods. However, it is clear that the supposed ability of larger animals to tolerate low quality food is not a sufficient reason for their seeking such foods, and Beier & McCullough (1990) suggest that males may yield use of higher-quality areas to reproducing females and their offspring in order to reduce competition for common resources with potential offspring. Clearly, however, such an argument is invalid as it does not explain why non-reproducing males should restrict their forage intake.

Current knowledge of patterns of habitat use in fallow deer

British populations of fallow deer are commonly regarded as essentially woodland or woodland edge animals characteristic of deciduous and mixed woodlands, although coniferous plantations may also be used. The occurrence of sizeable populations in agricultural areas with small woodland copses surrounded by arableland and pasture has long been recognized (eg. Chapman & Chapman 1975), and indeed it appears this may be far more 'typical' conditions for British fallow. Quantitative studies of habitat use by fallow in either environmental type are however limited in number.

Patterns of habitat use by fallow within the New Forest have been subject to two previous studies: from 1971-72 by Jackson (1974) and from 1979-81 by Parfitt (in Putman 1986a, 1988). These two studies shared common sites with the current project, namely Denny and Dames Slough, although differences in data collection make direct comparison difficult. Jackson's research was primarily directed towards the feeding ecology of fallow, hence his observations on habitat use were not collected in a rigorous fixed manner. Additionally, he drew a distinction between fallow inhabiting the enclosures and those on the open forest, and thus presented separate habitat use data on the basis of two separate sets of observations. Parfitt's data were collected more objectively, using similar sampling methods to the current study (regularly patrolled transect routes); however, he limited his observations to the inclosures. Both authors described a similar pattern of use. Deciduous woodland was actively selected in early spring (February-April) and autumn (August-October) and use remained high throughout the winter in good acorn and mast years. When mast was less abundant, deer made more use of forest clearings and rides; these areas were also heavily used in summer (May-July). In Jackson's data on open forest deer, use of improved grasslands was high from March to June and again in September and October (58-68% of observations), and deciduous woodland was selected throughout the rest of the year.

Limited information on habitat use by fallow in agricultural landscapes is available from the work of Heideman (1973) in East Holstein, Schaal (1982) in the Alsace and Langbein (1985) in Staffordshire. None of these studies were specifically designed to investigate habitat use and hence data was not always collected in a rigorous fashion. Taken in total they suggest that utilization of open pasture or arable crops by fallow in these environments may be extensive, for example, nearly half of all female deer, and one third of all male deer seen by Heideman throughout the year were on fields. Waterfield (1986) observed a fallow population inhabiting a mixed woodland-agricultural complex in Devon throughout the 1970's. More deer were seen on fields than any other individual habitat type in each bimonthly period of the year, rising to a peak of 72% of total observations in July and August. However when habitat selection was calculated, to make allowance for the available area of each habitat type in the environment, broadleaf woodland was selected most strongly.

Objectives of current study

In summary, the objectives of this chapter are:

1. To present a quantitative description of patterns of habitat use and habitat selection within the eight study sites.
2. To investigate seasonal variation in habitat use and selection.
3. To investigate sex differences in habitat use and selection.
4. To determine whether observed differences in habitat use between sites are due to changes in habitat availability or selectivity.

4.2. METHODS

Habitat classification

As mentioned in the introduction, the approach adopted in this study has been that of Duncan (1983) and others in recognizing 'a priori' a number of discrete habitat categories, and then determining the distribution of fallow deer within them. The individual habitat units recognized in this study are derived from a modification of the classification system of Putman and co-workers (Putman 1986a; Pratt et al. 1986; Putman et al. 1987) and have been presented in Table 3.1. The use of subjective 'a priori' classification of habitat types is justified by the analyses of Sharma (unpubl.), who demonstrated through use of rigorous ordination techniques that the vegetation categories used in this and previous New Forest studies were biologically distinct. Within-site analyses of patterns of habitat use adopt the finest level of resolution of individual habitat categories as shown in Table 3.1. The combined habitat and woodland/open level of resolution as defined in Table 3.1 are then adopted to facilitate inter-site comparisons.

Direct observations

Patterns of daytime habitat use within each site were examined by direct observation from fixed transect routes which were regularly patrolled throughout the year. The basic methodology of these transect walks has been described in detail in Chapter 2. In summary, data were collected on the number, composition, activity, and habitat of occupance of each group of deer sighted during daylight hours. Observations were aided with the use of either 9x35 binoculars or a 20x70 spotting scope. Observations were initially continued at night by spotlight, but a combination of poor visibility in woodland habitats and great disturbance of both deer and deer-rangers led to their termination. Deer had unrestricted access to all vegetation types available on the transect routes, and had ample time to move between them in the time interval between observations (usually 3 hours). Data analyzed in this chapter are based on 21021 sightings of individual deer, with a minimum of 1077 sightings for a single study site (Tadley).

Estimation of habitat use

Of necessity, survey transects could not sample all vegetation types equally, nor in perfect proportional relationship to their availability within the study sites. Therefore estimates of habitat use were obtained by weighting the numbers of animal observations (O_i) in any habitat by the relative area of that habitat surveyed (S_i) in relation to its total availability (T_i) within the study area. Habitat use (U_i) is thus presented as the proportion of total observations after weighting as:

$$U_i = [\, O_i \,/\, (\, S_i \,/\, T_i \,)\,] \,/\, \Sigma\, [\, O_i \,/\, (\, S_i \,/\, T_i \,)\,]$$

Visibility on transect routes was not constant throughout the year, being most variable in deciduous woodland or areas with a dense understorey of bracken *Pteridium aquilinum*. For this reason, estimates of the area of each habitat surveyed (S_i) on each transect were made seasonally (winter: December-February; spring: March-May; summer: June-August; autumn: September-November). Purely objective estimates of the area surveyed are difficult; experiments with stationary and moving camoflaged subjects revealed large discrepancies in visibility. For the purpose of delineating visible area a compromise was reached by taking the mid-point between the distances at which a stationary and a moving adult female deer could be seen in each habitat type.

Estimation of habitat selection

Because of differences in the area covered by the habitat types in the eight study sites the percentage use of a habitat type was compared with the percentage area occupied by that type. This was done using the electivity or selection index (E) of Jacobs (1974) calculated as:

$$E_i = (U_i - A_i) / \{ (U_i + A_i) - [2 * (U_i * A_i)] \}$$

where U_i is the estimated proportional use of habitat_i after weighting for differential visibility as defined above, and A_i is the proportion of the study area occupied by habitat_i. E is defined as the relative difference between the use and availability of a habitat type and gives an index of habitat selection by the deer. The value of E ranges from -1 to +1, values between -1 and 0 indicating avoidance, values between 0 and +1 selection.

Jacobs' index was chosen in place of Hunter's (1962) index of preference because the Hunter index compresses values for habitats which are avoided relative to those which are preferred (Duncan 1983). Several methods of normalizing Hunters index have been proposed (Duncan 1983; Pratt et al. 1986; Catt & Staines 1987), however, they were not used, either because they are difficult to interpret, or because they require assigning arbitrary values of -1 to habitats which are never used.

Statistical analyses

Because estimates of habitat use are derived from data weighted for differential sampling bias of individual habitat types and seasonal visibility, it is not possible to go back to the original data for statistical treatment. Instead analyses of differences in habitat use throughout this chapter are by G-test for goodness-of-fit or G-test for independence (with the conservative Williams correction) on percentages after conventional angular transformations (Sokal & Rohlf 1981). Although non-parametric statistical analyses of preference indices have occasionally been made (eg. Catt & Staines 1987) this approach has not been followed here and only qualitative comparisons are presented.

4.3. RESULTS

Due to the comparative nature of this study, repetition in the presentation of data sets is inevitable. For ease of comparison within and between sites transect data has been grouped into four seasons: winter (December-February); spring (March-May); summer (June-August); and autumn (September-November). The chapter is divided into three sections. An initial overview is presented of patterns of habitat use in the New Forest as a whole, based on the combined data of all five sites. For each site, data summarizing seasonal change in habitat use and selection is presented for individuals in female groups, which made up 53%-90% of all deer seen, and then contrasted to male groups and groups of mixed sex. The second section takes the same approach with the three agricultural sites, initially presenting a general overview, and then examining in detail habitat use in each site. A final section deals with comparisons between sites, both within and between the two main environmental types.

Patterns of habitat use within the New Forest: an overview

A general overview of fallow habitat use patterns in the New Forest is presented in Fig 4.1, based on the average values calculated for all deer in each of the five sites. This simplified picture demonstrates the importance of open deciduous woodland throughout the year, with estimated use never dropping below 27% in any season. Other woodland habitat types were consistently used at a lower level, with a notable increase in the utilization of closed conifer during the autumn. Woodland rides and natural and improved grasslands were important habitats throughout winter, spring, and summer, although their use declined during the autumn.

Patterns of habitat use and selection within individual New Forest sites: seasonal variation and sex differences.

Denny

Seasonal patterns of habitat use and selection at Denny by female, male, and mixed-sex groups are shown in Table 4.1. Within each group/season category, deer were never randomly dispersed across the habitat types available to them ($p<0.001$ in all cases).

Female groups showed marked seasonal variation in their patterns of habitat use. Contrasts of female distribution between seasons by G-tests demonstrated that this variation was chiefly in the winter (winter:summer $G=26.96$, $p<0.05$; winter:autumn $G=37.31$, $p<0.001$). Seasonal contrasts between spring, summer, and autumn habitat use were not significant.

Female use of the woodland habitats, including rides, was extensive throughout the year, falling to a minimum of 70% during the summer. However, considerable seasonal variation existed in the utilization of individual habitat types. Open deciduous was extensively used during winter and spring with use decreasing in summer and then increasing again in autumn. Selection for this habitat was never high due to the relative abundance of it in the study area. Open conifer was similarly heavily used in winter and spring, but did not show a corresponding increase in usage during the autumn. The comparatively small area of mixed woodlands, which at Denny were largely open canopy mixed stands of Douglas fir, Scots pine, oak, and beech were strongly selected for during this time. Woodland rides were selected throughout the year, but particularly so during summer. The closed canopy and natural woodlands, and the restocks, were never extensively utilized. Amongst the open habitat types only the natural grasslands were extensively used by female groups. This rose to 21% during the summer. Their comparatively small area resulted in a positive selection index throughout the year. Female utilization of the extensive areas of heathland and bog at Denny was minimal in all seasons.

Comparisons with male and mixed-sex groups are of limited value because of the generally small numbers of sightings of these groups at Denny. Similarly, statistical analyses of seasonal variation in habitat use within these groups must be interpreted very loosely. With these caveats in mind, all within-season comparisons between female-only and both male and mixed-sex groups gave significant results ($86.13 < G < 208.25$, $p < 0.001$ in all cases). With the exception of summer, most male groups were seen in woodland habitats, the small sample size probably showing artificially high seasonal differences at the individual habitat level. Summer use of both natural grasslands and heathland was high, the small group of young males resident in Denny were frequently observed to spend the whole day grazing on Denny Moor. An even more pronounced selection for open habitats was displayed by mixed-sex groups during summer, with estimated 75% usage at this time. Throughout the rest of the year these groups selected a mixture of open deciduous, open coniferous, and natural conifer in various combinations. Autumn habitat selection appeared little effected by the rut at Denny; mature males were very rarely seen, reproductive activity did not occur regularly within the transect area, and females tended to leave the area to rut at the nearby Stubby Copse.

Dames Slough

Seasonal habitat use and selection at Dames Slough by female, male, and mixed-sex groups are shown in Table 4.2. Within each group/season category, deer were never randomly dispersed across the habitat types available to them ($p < 0.001$ in all cases).

Patterns of utilization were less complex than at Denny, with fewer habitats represented in the site, and increased concentration on individual types.

Female groups showed marked seasonal variation in their patterns of habitat use. With the exception of summer:winter, all seasonal contrasts were significantly different (19.04 <G< 74.47, p<0.01 in all cases).

Open deciduous woodland was extensively used by female groups throughout the year. Its relative abundance in the area however, was reflected by its apparent weak avoidance in all seasons other than autumn, as shown by the selection index. Use of open and closed canopy conifer increased markedly during autumn. This appeared primarily due to the rut; the most frequented rutting stand in both years was situated in open canopy Scots pine with adjacent areas of more recent plantings (see below). Woodland rides were heavily selected throughout the year. Female use of the improved grasslands at Burley Lodge and Anderwood was very high in all seasons except autumn, nearing 50% during the spring.

A small group (10-15 individuals) of mainly young males was regularly seen in the fields and adjacent woodland at Burley Lodge throughout much of the study. These bucks made extensive use of the improved grasslands throughout winter, spring, and summer; although sample size in spring is unaccountably low. Male-group habitat use during the autumn was markedly different; open and closed conifers were used much more extensively, with a resulting decrease in the use of improved grassland. It should be noted that male deer seen within the inclosure during this period included many individuals who moved into the area before, during and after the rut. All seasonal contrasts in habitat use were significant (15.50 <G< 98.53, p<0.05 in all cases).

Mixed-sex groups were seen irregularly throughout winter, spring, and summer. These groups were predominantly on the improved grasslands at Burley Lodge. Habitat use during autumn contrasted greatly to the rest of the year, presumably due to the rut. Rutting activity in Dames Slough was concentrated in one area of open conifer (see Chapter 7) and the great majority of mixed sex groups were seen at this site. Statistical analysis of seasonal trends should be interpreted with caution because of small sample sizes. However, significant differences were found in all comparisons except winter:spring (31.39 <G< 172.63, p<0.001 in all cases).

Sex difference in habitat use between female, male, and mixed-sex groups was tested by G-test for independence within each season. With the exception of male:females in autumn, all contrasts were highly significant (28.11 <G< 117.94, p<0.001 in all cases).

South Oakley

Seasonal habitat use and selection at South Oakley by female and male groups are shown in Table 4.3. Individuals in mixed sexed groups comprised less than 4% of the total deer seen, hence habitat analysis was not undertaken. For female and male groups, within each season deer were never randomly dispersed across the habitat types ($p<0.001$ in all cases). Summer and autumn totals for females, and autumn totals for males are very low, although the intensity of sampling did not vary, and statistical analyses of these data are of dubious validity.

Female habitat use in winter was almost exclusively of open deciduous, which was largely concentrated in the northern half of the study site. During spring, both deciduous and coniferous closed canopy woodlands were increasingly used; a contrast between seasonal distributions is significant ($G=72.92$, $p<0.001$). Summer and autumn use is split between coniferous and deciduous woodlands, woodland rides, and heathland, but, as stated above, sample sizes are too small for analysis.

In contrast, male deer in winter, whilst still showing a strong selection for open deciduous, also extensively used open and closed canopy conifer and the adjacent heathland of Burley Moor. This selectivity was retained during spring, but an increasing number of males used woodland rides and the natural grasslands on the edge of Burley Moor. In summer there was a great increase in the use of woodland rides and heathland, with no males being seen in the conifers. Contrasts between winter, spring, and summer habitat use by male deer were all highly significant ($57.68 <G< 72.92$, $p<0.001$ in all cases).

There was a pronounced sex difference in habitat use in both winter and spring ($G=70.17$, $p<0.001$; $G=84.93$, $p<0.001$). Summer and autumn habitat use similarly appeared to differ between the sexes but was not analyzed statistically.

Male deer habitat use presented here is almost exclusively concerned with the various woodland habitats in South Oakley and the adjacent Burley Moor. Male deer, however, were known to make extensive use of agricultural fields on private ground to the west of the study site. One small section of this area which was included in the transect, was, however, rarely used by males. Occasional casual sightings of male groups on the fields near Burley Street and Bisterne Close, to the west and south of the village of Burley respectively, together with the keeper's cull records (W.Gulliver, pers.comm.) suggested that some male deer spent much of the spring and summer on private ground.

Brinken

Seasonal habitat use and selection at Brinken by female and mixed-sex groups are shown in Table 4.4. Male groups comprised less than 2% of the total deer seen, were almost exclusively encountered only in October, and thus were not included in this analysis. Similarly, mixed-sex groups were never seen in summer. Within each group/season category that was analyzed, deer were never randomly dispersed across the habitat types available to them (p<0.001 in all cases).

Female groups showed marked seasonal variation in their use of habitat (32.09 <G< 62.64, p<0.001 in all cases). Open deciduous was extensively used throughout the year, but particularly during autumn and winter. Its relative abundance in the area resulted in its apparent avoidance as calculated by the selection index in spring and summer. Closed deciduous showed similar seasonal trends, but of a reduced magnitude in each season. Utilization of the grassland habitats showed the converse pattern, with peak use during spring and summer. This was particularly pronounced in the high spring usage of the improved grasslands at Queens Meadow. Heathlands were consistently used at a low level throughout the year.

Mixed-sex groups were common in Brinken during spring and autumn. In the spring, these occurred exclusively on the reseeded fields at Queens Meadow, coinciding with the selection shown for this habitat by female-only groups. In reality, these often very large groups (up to a maximum 170 individuals) were feeding aggregations of female deer joined by a few young males. This theme is taken up in the discussion section of this chapter and later in sections on sexual segregation and social grouping. Mixed-sex groups in the autumn were of a very different character and showed markedly different habitat use (spring:autumn G=213.13, p<0.001). Open deciduous woodland and heathland were most extensively used, followed by closed deciduous and the improved and natural grasslands. Habitat use of mixed-sex groups in this season tended to reflect the occurrence of reproductive activity within the site.

Where contrasts were possible (spring and autumn), differences in habitat use between female and mixed-sex groups were highly significant (G=125, p<0.001; G=45.19, p<0.001).

Blackensford

Seasonal habitat use and selection at Blackensford by female, male, and mixed-sex groups is shown in Table 4.5. Within each group/season category, deer were never randomly dispersed across the habitat types available to them (p<0.001 in all cases).

Female groups showed much more limited seasonal variation in habitat use than in the other New Forest sites. Significant contrasts were only found in comparing summer distribution to other seasons (28.13 <G< 57.36, p<0.01). Open deciduous was extensively used and selected for throughout the year, falling to a minimum of still 33% during summer. No one single habitat rose to prominence in the summer, with slight increases occuring in the use of natural conifer, clearcut, heathland, and bracken. Woodland rides and the improved grasslands at Backley Holmes were increasingly used in the spring, with rides again becoming important in the autumn.

Male groups were only seen in large numbers during the autumn when they moved into the area for the rut. At this time they showed strong selection for closed conifer, followed by a continued use of open deciduous, thus reflecting the location of reproductive activity in this site (see Chapter 7). Together, these two habitat types account for almost 90% of all male-only sightings.

Mixed-sex groups during autumn showed an even higher selection for closed conifer, decrease in use of open deciduous, and increase in sightings in natural conifers. This distribution again reflects rutting activity at Blackensford. In contrast, winter and spring sightings of mixed-sex groups were concentrated on the improved grasslands and heathland at Backley. As in the other New Forest sites which showed mixed-sexing outside the rut, these groups tended to include only a few young males. Seasonal variation in habitat use by mixed-sex groups was highly significant ($157.43 < G < 213.82$, $p<0.001$). As has been described above, sex class differences in habitat use within seasons at Blackensford were pronounced ($45.57 < G < 191.17$, $p<0.001$ in all cases).

Patterns of habitat use within the agricultural sites: an overview

A general overview of fallow habitat use patterns in the agricultural sites is presented in Fig 4.2 based on the average values calculated for all deer in each of the three sites. Clearly, habitat use differs greatly from the previously described New Forest sites. Closed canopy woodlands, namely coppice deciduous and closed conifer assumed a greater importance in all seasons, with a reduction in use of open broadleaf. Improved grasslands and cereal crops were extensively used throughout the year.

Patterns of habitat use and selection within individual agricultural sites: seasonal variation and sex differences

Lockerley

Seasonal habitat use and selection at Lockerley by female, male, and mixed-sex groups are shown in Table 4.6. Male groups were rarely encountered throughout the year; the limited data are presented for comparison but statistical analyses have not been undertaken. Similarly, mixed-sex groups were rarely seen in spring and summer. Within each group/season category that was analyzed, deer were never randomly dispersed across the habitat types available to them ($p<0.001$ in all cases).

Female groups showed significant seasonal variation in their use of the available habitats, with the exception of autumn to winter (18.88 <G< 31.63, p<0.05). Throughout the year, closed canopy conifer was extensively used, dropping below 30% only in summer. Open deciduous and coppice were also widely utilized, although greater variation existed between seasons (eg. low usage of open deciduous in spring). Female deer were seen on cereal crops throughout the year, rising to a maximum 25% usage during the summer. However, the extensive area of cereals available to the deer was reflected in the low selection rating for this habitat.

As previously stated, male groups were rarely seen, and tended to be restricted to the north-eastern corner of the study site. Realistic comparisons to female habitat use can not be made due to small sample size. However, males appeared to make greater use of three large improved grassland fields than the female deer resident in this area. Mixed-sex groups were only observed in any numbers during autumn and winter at Lockerley. During the autumn, they exhibited a strong selection for closed conifer and open deciduous, thus reflecting the distribution of rutting activity on the site. With the onset of winter, selection for these two habitat types was retained, but a few groups were additionally seen on cereals (autumn:winter G=87.98, p<0.001). Contrasts between the observed habitat use of mixed-sex and female-only groups during autumn and winter were significant (G=103.03, p<0.001: G=80.04, p<0.001).

Tollard Royal

Seasonal habitat use and selection by female, male, and mixed-sex groups at Tollard Royal are shown in Table 4.7. Similar small data sets for male and mixed-sex groups as in the previous site limit statistical comparisons between the sex classes. Female deer were never dispersed randomly across the habitat types available to them (p<0.001).

Seasonal variation in female habitat use was least pronounced in this site out of all eight study sites. Winter:summer habitat use were weakly significantly different (G=20.03, p<0.05), other seasonal contrasts not so. Deciduous woodland was strongly selected by female deer throughout the year; in winter predominantly coppice, the rest of the year split between coppice and natural scrub. Closed conifer was also selected, particularly in spring and summer. Clearcuts and rides within the small woodlands regularly accounted for a small percentage of all observations, and were strongly selected for in respect to their small relative area. Use of the extensive areas of cereal and natural grasslands was consistent throughout the year at between 13-21%.

Male and mixed-sex groups were rarely encountered at Tollard Royal. Males were thought to make more extensive use of cereal crops, particularly in spring and summer; there is limited support for this theory but sample sizes are inadequate. Mixed-sex groups were increasingly encountered in spring, at which time they used coppice and natural deciduous, natural grasslands, and to a lesser extent closed conifer and cereal crops.

Tadley

Seasonal habitat use and selection by female and mixed-sex groups at Tadley are shown in Table 4.8. Male groups were encountered on only five occasions in two years, and are thus excluded from the analysis. Within each group/season category, deer were never randomly distributed across the habitat types available ($p<0.001$).

Female deer at Tadley showed marked seasonal variation in habitat use ($19.89 < G < 46.51$, $p<0.01$). Closed conifer was highly selected throughout the year, dropping to 30% usage in summer. At this time open deciduous was more extensively used. Amongst the open habitats, improved grasslands were extensively used, particularly during the spring. At no time did cereals account for more than 10% of the estimated distribution.

Mixed-sex groups were regularly encountered during the spring, at which time the improved grasslands were heavily selected. These groups typically included one or more mature males and were in direct contrast to the mixed-sex feeding aggregations found in the New Forest. Autumn and winter mixed-sex groups were of a similar nature, and tended to be found on either the reseeded pastures or adjacent deciduous woodlands. Intensive observations were not made here during the October rut for logistical reasons, but limited data suggest that female habitat selection was not affected markedly by the rut, and male deer tended to attach themselves to female groups and follow their movements (see Chapter 7).

Between-site comparison of habitat use and selection

The above sections have described, in considerable detail, seasonal patterns of habitat use for female, male, and mixed-sex groups in each of the eight study sites. In this section more rigorous analysis of differences between sites are presented. To facilitate statistical comparison of habitat use between sites, the medium level of resolution of combined habitat categories has initially been utilized. Further analyses are then undertaken at the woodland/open level of resolution. These comparisons will be restricted to female groups, for which good data sets are available for each site.

Combined habitats

The estimated percentage use and selection index for the combined habitat categories were calculated in exactly the same fashion as in the earlier within-site analysis (Table 4.9). Because of seasonal changes in habitat use patterns, analyses between sites were performed within seasons. Table 4.10 shows the results of these analyses in the form of a matrix of G-tests for independence between each possible pair of study sites. Even at this reduced level of resolution, statistically significant differences in habitat use exist between all pairs of sites, with the notable exception of the agricultural sites Lockerley and Tollard.

Within the New Forest, use of open canopy woodland was consistently high in each area. This high utilization, principally of open deciduous, occurred despite considerable variation in the availability of this resource. There are two possible interpretations of this finding. The animals in the different subpopulations may show differing degrees of selectivity for open woodland. Alternatively, and more likely, is that in some sites, eg. Brinken, there was such an abundance of open canopy woodland that genuine selection for this resource was simply not revealed by the selection index.

Use of the open communities was more variable between New Forest sites. Where improved or natural grasslands were available, they were extensively used, and their generally small relative size was reflected by their high selection index. With the exception of South Oakley females, all sites showed high usage of grasslands; the more relevant question becomes 'to what extent does grassland usage dominate spring and summer habitat use?' Heathland was available in four New Forest sites; it was used consistently at Brinken and Blackensford, and avoided consistently at Denny and South Oakley. Its usage at the first two sites may be related more to its juxtaposition with respect to other more favoured habitat types, than to any inherent attractiveness.

The agricultural sites constitute a very different environment for the deer. Extensive open canopy woodlands, typical of the New Forest, do not exist. They were replaced as the preferred cover community by closed canopy conifer, coppice deciduous, or natural deciduous woodlands, dependent upon availability. The relatively small area of these woodlands, in relation to the extensive surrounding arable or grasslands, resulted in a generally high selection index for woodland habitats in relation to the New Forest. The converse applied to utilization of the open agricultural habitats. The extensive availability of these habitats in combination with the observed patterns of deer usage resulted in artificially low selection values. Patterns of use of these open habitats also varied between agricultural sites but less so than in the case of the New Forest sites. Tollard and Lockerley showed similar patterns of habitat use throughout much of the year, whilst both were quite distinct from Tadley where improved grasslands were highly utilized.

Woodland/open

The estimated percentage use and selection index for woodland and open habitats was calculated for each site in the same fashion as above (Table 4.11). When habitat use is examined at this very coarse level of resolution, a final very important point emerges. Despite the eight sites providing very different combinations of woodland and open habitat types (see Fig 3.9), fallow remain very much a woodland-inhabiting species. With the exception of the high spring and summer use of improved grasslands at Dames Slough and Brinken in the New Forest, use of woodlands does not fall below 60% at any time. Table 4.12 shows a matrix of G-tests for independence between each possible pair of sites. Differences in habitat use between sites do remain, albeit at a reduced level of statistical significance.

The relationship between habitat availability and habitat use is clearly revealed by analysis at this coarse level of resolution. The New Forest and agricultural study sites greatly differ in the relative amounts of woodland and open habitat, however, as described above, use of woodland is high in all sites. Table 4.11 lists the selection index for woodland in each site; whilst considerable variation exists in the selection of woodland in the Forest sites, woodland selection is consistently high in the agricultural sites. Conversely, selection for open habitats is consistently low in these agricultural sites, whilst being more variable in the New Forest.

4.4. DISCUSSION

Patterns of habitat use of fallow deer observed in the present study differ quite markedly from earlier reports in the literature. Some exploration of this difference is perhaps appropriate before we turn to answer the more specific questions posed in the introduction.

Within the New Forest sites, selection of woodland habitats tends to follow the patterns previously described by Jackson (1974) and Parfitt (in Putman 1986a), with open deciduous being widely used through autumn, winter, and spring. Other woodland types may also be extensively used, but are more dependent upon local abundance. The earlier studies concentrated on the enclosures, setting artificial geographical limits which were not relevant to the deer populations, and tended not to recognize the importance of the open forest communities, in particular the extensive use made of natural and improved grasslands. These grasslands need not be large; use of the Burley Lodge fields in Dames Slough is generally restricted to a narrow strip within 100m of the adjoining woods. The finding in this study of extensive grassland utilization has other implications; the large groups typical of fallow on New Forest grasslands may well have been under-sampled by Jackson and Parfitt, thus their figures for average group size may not be representative of deer in the Forest as a whole. There is no doubt that the same individuals move from enclosure to open forest; regular sightings, often within the same day, of two individually recognizable does at Denny and one at Dames Slough, in both habitat categories, suggest that this may be quite typical behaviour.

The patterns of habitat use described in the agricultural populations suggest that earlier studies may have gone to the other extreme and over-emphasized the importance of fields. Cereal crops and improved pasture were widely exploited by fallow, however the estimates of 50-70% usage by Heideman (1973) and Waterfield (1986) are more likely to be due to sampling bias than to any real differences in the populations. Putman (1986b) has described patterns of habitat use by roe deer in similar agricultural environments in southern England. Here too, roe make extensive seasonal use of arable land and pasture. However, wooded areas and rides and glades within woodland remained extremely important habitats at all times of year, rarely falling below 40% of habitat use overall.

The current study was not without its own limitations, and results must be interpreted with these in mind. Habitat use was estimated purely from direct observations, and only during daylight hours. Nocturnal patterns of habitat use may well be quite different, and may notably affect overall differences in habitat use between New Forest and agricultural sites. Limited amounts of spotlighting on fields and other open areas in two New Forest (Dames Slough & South Oakley) and two agricultural (Lockerley & Tollard Royal) sites indicated that nocturnal use of fields may be very high. Spotlighting, however, can rarely give an accurate estimate of overall patterns of habitat use; dense cover communities are invariably undersampled (McCullough 1982).

Seasonal patterns of habitat use

In common with many grazing herbivores (see reviews in Putman 1986a, 1988) fallow deer populations in the present study showed pronounced seasonal variation in utilization of vegetation communities. Although there was some variation between sites, in general New Forest fallow showed increased use of grasslands and woodland rides during spring and summer, and relied more on the various woodland communities during autumn and winter. This is in keeping with known seasonal variation in diet of fallow in the New Forest. Fallow are preferentially grazers; grasses form nearly 60% of the diet of New Forest fallow during the growing season, from March to September (Jackson 1974, 1977; Parfitt in Putman 1986a). During autumn and winter however, the deer rely more heavily on fruit crops and broadleaf browse, and habitat use reflects this change. Similar seasonal variation in habitat use in relation to available forage has been reported for other temperate woodland species of deer, including white-tailed (Murphy et al. 1985) and black-tailed (Loft et al. 1984) deer populations in North America, as well as tropical species such as chital in Nepal (Mishra 1982) and Sri Lanka (Balasubramaniam et al. 1980) where use of grasslands is greatest during the monsoon season.

Patterns of habitat use in the agricultural sites appeared more complex, and a universal explanation based on food availability more difficult to find. Existing knowledge of seasonal change in the diet of agricultural populations of fallow is limited to the studies of Waterfield (1986) in South Devon, who found that grasses formed the bulk of the diet throughout spring and summer, with bramble *Rubus fruticosus*, fruits, and broadleaf browse taken more in autumn and winter. Waterfield was unable to distinguish between grasses taken from fields or woodland, although he does state that barley *Hordeum sp.* was rarely eaten. In direct contrast, Heideman (1973), whilst not attempting dietary analysis, states that the bulk of food taken in his German study site was from cultivated agricultural crops.

In this study, improved and natural grasslands and agricultural crops were used throughout the year, with no common seasonal patterns emerging for the three sites. Modern intensive farming methods resulted in arable crops being available for much of the year; additionally, deer were often observed feeding on weeds and natural grasses within cereal fields. Feeding resources within the woodlands appeared limited; rides and tracks were typically less grassy than in the New Forest, and extensive areas of open canopy woodland with accompanying ground flora less common. This circumstantial evidence suggests that fallow in these sites may satisfy most of their foraging requirements from agricultural land, with woodlands being used primarily for shelter. Studies of roe deer in similar agricultural environments in southern England (Johnson 1984; Putman 1986b) and northern France (Maublanc 1986; Cibien et al. 1989) also suggest that deer make extensive use of agricultural land; importantly however, woodland resources remain extremely important for forage throughout the year.

Patterns of habitat use in contrasting environments

The New Forest and agricultural study sites offered environments greatly differing in habitat composition and structure. The Forest sites typically comprised one or two large expanses of continuous open canopy woodland, with adjacent, often quite large areas of grassland or heathland. In contrast, the agricultural sites were characterised by a number of much smaller woodlands, of varying structure and composition, interspersed with pasture and arable land. How different were the populations' responses in utilizing these resources?

When examining patterns of habitat use at the finest level of resolution of individual habitat types, it does appear that overall patterns between the two environmental types were very different. For example, use of open canopy deciduous woodland predominated throughout the year in the New Forest, whereas it was of much more limited importance in the agricultural sites. This difference was related to contrasting habitat availabilities in the two environment types, an issue discussed in more detail below. However, when habitats are viewed in terms of the resources they offer to the deer, much greater similarities between the sites are apparent.

In the New Forest as a whole, an estimated 60-80% use was made of woodland habitats, with the various grassland and heathland communities comprising the remainder. Obviously, these figures are based on day-time observations only, and it was likely that use of open habitats increased at night. In the agricultural sites, patterns of utilization of woodland appeared similar, ranging from 70-80% of total observations, after weighting for differential visibility. In these latter sites, use of open areas was split between improved or natural grasslands and the available cereal crops. Clearly, the main differences between the two environmental types were in the types of woodland that were used, predominantly open canopy deciduous in the New Forest and a mixture of closed canopy conifer, coppice and natural deciduous in the agricultural sites, and in the exploitation of cereal crops by the agricultural populations.

Habitat availability and selection

Were these apparent differences in habitat use due to differences in the availability of particular resources, or did they reflect genuine changes in habitat selection by deer in the different sites? This question is first considered with respect to habitat use and selection at the individual level of habitat resolution.

In the New Forest, use of open canopy deciduous was uniformly high in all sites, despite considerable variation in its relative availability. This was reflected by the great range of the selection index, implying total avoidance to intense selection. In this case, however, it was more likely that the selection index gave a false impression of avoidance; more plausibly, in these sites there was simply too much open deciduous for its selection to be recorded. Variation in the use of other habitats appeared to be straightforward cases of availability, for example where improved or natural grasslands were available, they were heavily utilized by deer.

In the agricultural sites, habitat availability contrasted greatly with the New Forest sites. The extensive open deciduous woodlands typical of the latter sites did not exist. Instead, deer utilized whatever woodland communities were available in the site. The relative area of these woodlands was small with respect to the surrounding arableland and pasture, and thus was apparently highly selected by the deer. In contrast, the open habitats, the grasslands and cereals, were very abundant, and the level of use suggested avoidance by the deer. This is somewhat misleading, however, as grasslands and cereals were extensively used. However, they comprised an over abundant resource whose selection could not be detected.

This question introduces a major problem with the interpretation of selection indices. When resources are overabundant, genuine selection for a particular category of resource may be understated. Conversely, the occasional use of a very scarce resource may imply intense selection. There is no simple solution; interpretation of indices must be based upon detailed knowledge of the species behaviour and ecology before conclusions are drawn.

This issue may be simplified by examining habitat use, availability, and selection at the woodland/open level of habitat resolution. The New Forest sites present relatively large amounts of woodland, and relatively small amounts of open habitat. The agricultural sites present the exact opposite. At this level of resolution, differences between environmental types in habitat use are reduced. This suggests that habitat selection changes; the New Forest deer are selecting open habitats, whilst the agricultural deer are selecting woodland. The essence of the preceding argument is that the New Forest deer are still selecting woodland, but it is so abundant that the selection index can not record it. Similarly, the agricultural deer do not avoid open habitat; it is an overabundant resource and hence under-emphasized in the selection index.

Sex differences in habitat use

One of the main problems experienced in this study has been the difficulty of collecting adequate data on male habitat use. Male deer were rarely seen in the agricultural sites, probably reflecting a genuinely biased sex ratio typical of these areas due in part to a tendency among stalkers to shoot male deer. Within the New Forest, male deer were regularly encountered in only two sites, Dames Slough and South Oakley. Even here, males were not seen throughout the year, and certainly their entire ranges were not sampled by the transect routes. There was a suggestion that male deer spent more time on agricultural land and improved pasture. Certainly, throughout the Forest, buck groups tend to be associated with areas of improved grazing. Whether or not males select better quality range in the New Forest than females is debatable. Where differences in range quality have been demonstrated in large herbivores, it is typically the males who occupy the poorer quality range or select the less nutritious forage, eg. red deer (Clutton-Brock et al. 1982; Staines et al. 1982), white-tailed deer (Beier & McCullough 1990), black-tailed deer (Bowyer 1984) and bighorn sheep (Geist & Petocz 1977). However Shank (1982), working on Rocky Mountain bighorn sheep, demonstrated that rams overwintered on range of superior quality to ewes and juvenile sheep, and suggested that factors other than dietary requirements or pressures led to sexual segregation. This suggestion gains some limited support from the earlier fallow deer dietary studies of Jackson (1974), who states (from an admittedly limited sample of males) that 'the types of food taken by male and small-deer are the same and show similar seasonal trends but that bucks tend to take graminids from maintained pastureland to a greater extent'. Plans to investigate sex difference in feeding ecology in the current study were unfortunately put into abeyance due to limits of time.

Patterns of habitat use by groups of mixed sex also appeared to differ between sites. In the New Forest, non-reproductive mixed-sex groups (eg. those occurring over winter and spring) were seen almost exclusively on natural or improved grasslands and appeared to be the result of males, typically sub-adult, joining female groups on favoured feeding resources. Similar behaviour has been reported for white-tailed deer by Hirth (1977) in more open brushy savanna habitat in Texas. In the agricultural sites in this study, mixed-sex groups, when they did occur, were not solely restricted to feeding areas, and appeared, though with admittedly little direct evidence, to be of a less transient nature than in the New Forest. There is some supporting evidence for this change from other fallow studies; Schaal (1982) saw more mixed-sex groups in open habitats than in woodlands in his Alsace study area, and suggests that they were of a more permanent nature than simple feeding aggregations.

4.5. SUMMARY

1. Seasonal patterns of habitat use and selection were examined in the eight study sites at each of the three levels of habitat resolution.
2. Female deer in the New Forest sites made extensive use of open canopy deciduous woodland, particularly during autumn and winter. Other woodland types were utilized to a lesser extent. Natural and improved grasslands were used more frequently during spring and summer.
3. Seasonal variation in female habitat use in the agricultural sites was more complex, with no consistent patterns emerging. Amongst the woodland habitats, use of coppiced deciduous and closed coniferous was high throughout the year. Utilization of improved grasslands and cereal crops was also consistently high.
4. At this finest level of resolution, differences between sites in female habitat use were due more to varying availability than selection.
5. Differences between the New Forest and agricultural sites in patterns of female habitat use were markedly reduced when examined at the coarsest level of resolution of woodland and open habitats. On average, 60-80% use was made of woodland habitats in the New Forest, and 70-80% use made of woodland habitats in agricultural land.
6. At this coarse level of resolution, the similarity in female habitat use between sites suggests that habitat selection changes from New Forest to agricultural environments. Overabundant habitat resources in both environments - woodland in

the New Forest, open habitat in the agricultural sites - can underemphasize the values of selection indices.

7. Male deer in the New Forest appeared to spend more time on arable land and improved grassland than female deer. In contrast, male deer in agricultural land showed similar patterns of habitat use to females.
8. Non-reproductive mixed-sex groups in the New Forest occured almost exclusively on natural and improved grasslands. Similar such groups in agricultural land occured in a range of habitat types and were not limited to feeding areas.

Table 4.1 Estimated percentage habitat use (U) and selection index (E) for deer in the Denny study area 1987-88. Both measures were calculated after weighting for differential sampling bias. See text for details. A) female groups B) male groups C) mixed sex groups.

HABITAT	WINTER		SPRING		SUMMER		AUTUMN	
	U	E	U	E	U	E	U	E
A)								
CLOSED CONIFER	2.3	-0.59	2.9	-0.51	3.2	-0.48	1.6	-0.71
OPEN CONIFER	22.1	0.33	15.9	0.13	12.3	-0.01	10.6	-0.09
NATURAL CONIFER	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
CLOSED DECIDUOUS	5.9	-0.19	6.8	-0.12	1.8	-0.66	0.9	-0.82
OPEN DECIDUOUS	32.8	0.32	33.8	0.34	15.8	-0.14	23.5	0.10
NATURAL DECIDUOUS	1.6	0.17	2.5	0.39	5.3	0.66	0.5	-0.37
MIXED WOODLAND	7.1	0.28	17.3	0.66	14.6	0.61	45.0	0.90
RESTOCK/CLEARCUT	0.3	-0.85	2.4	-0.13	3.0	-0.02	1.5	-0.36
WOODLAND RIDES	7.5	0.67	7.2	0.66	20.6	0.88	9.9	0.75
OPEN VERGES	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
NATURAL GRASS	14.3	0.59	8.1	0.34	21.2	0.72	6.0	0.19
HEATHLAND	4.3	-0.70	3.2	-0.77	2.3	-0.83	0.5	-0.96
BOG	1.8	-0.63	0.0	-1.00	0.0	-1.00	0.0	-1.00
BRACKEN/GORSE	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
SAMPLE SIZE (N)	681		897		484		308	
B)								
CLOSED CONIFER	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
OPEN CONIFER	5.5	-0.42	29.2	0.48	0.0	-1.00	16.0	0.14
NATURAL CONIFER	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
CLOSED DECIDUOUS	0.0	-1.00	0.0	-1.00	9.3	0.05	0.0	-1.00
OPEN DECIDUOUS	94.5	0.97	11.6	-0.31	40.2	0.46	67.1	0.78
NATURAL DECIDUOUS	0.0	-1.00	2.6	0.40	1.8	0.23	0.0	-1.00
MIXED WOODLAND	0.0	-1.00	37.7	0.87	0.0	-1.00	0.0	-1.00
RESTOCK/CLEARCUT	0.0	-1.00	0.0	-1.00	1.1	-0.49	0.0	-1.00
WOODLAND RIDES	0.0	-1.00	6.0	0.60	8.4	0.70	1.8	0.08
OPEN VERGES	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
NATURAL GRASS	0.0	-1.00	12.9	0.55	21.0	0.72	9.9	0.44
HEATHLAND	0.0	-1.00	0.0	-1.00	18.3	-0.07	5.2	-0.65
BOG	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
BRACKEN/GORSE	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
SAMPLE SIZE (N)	27		21		52		31	
C)								
CLOSED CONIFER	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
OPEN CONIFER	32.8	0.54	0.0	-1.00	0.0	-1.00	11.4	-0.06
NATURAL CONIFER	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
CLOSED DECIDUOUS	0.0	-1.00	16.3	0.36	0.0	-1.00	0.0	-1.00
OPEN DECIDUOUS	47.0	0.56	55.1	0.66	0.0	-1.00	37.6	0.41
NATURAL DECIDUOUS	0.0	-1.00	0.0	-1.00	21.6	0.92	20.1	0.91
MIXED WOODLAND	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
RESTOCK/CLEARCUT	0.0	-1.00	0.0	-1.00	0.0	-1.00	3.0	-0.01
WOODLAND RIDES	0.0	-1.00	20.1	0.88	3.4	0.37	19.6	0.88
OPEN VERGES	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
NATURAL GRASS	20.2	0.71	8.5	0.37	48.9	0.91	8.4	0.36
HEATHLAND	0.0	-1.00	0.0	-1.00	26.1	0.16	0.0	-1.00
BOG	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
BRACKEN/GORSE	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
SAMPLE SIZE (N)	58		97		111		36	

Table 4.2 Estimated percentage habitat use (U) and selection index (E) for deer in the Dames Slough study area 1987-88. Both measures were calculated after weighting for differential sampling bias. See text for details. A) female groups B) male groups C) mixed sex groups

HABITAT	WINTER		SPRING		SUMMER		AUTUMN	
	U	E	U	E	U	E	U	E
A)								
CLOSED CONIFER	7.9	-0.49	0.0	-1.00	5.5	-0.62	15.5	-0.15
OPEN CONIFER	2.9	-0.71	6.5	-0.42	7.0	-0.39	14.1	-0.02
CLOSED DECIDUOUS	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
OPEN DECIDUOUS	29.8	-0.08	22.1	0.27	25.0	-0.19	35.3	0.05
MIXED WOODLAND	1.5	-0.58	10.9	0.37	4.7	-0.06	0.0	-1.00
RESTOCK/CLEARCUT	2.5	0.00	0.0	-1.00	2.2	-0.07	1.0	-0.43
WOODLAND RIDES	19.3	0.79	11.8	0.66	17.4	0.77	15.7	0.74
IMPROVED GRASS	36.2	0.45	48.7	0.63	38.2	0.48	18.3	0.02
SAMPLE SIZE (N)	392		447		555		366	
B)								
CLOSED CONIFER	0.0	-1.00	0.0	-1.00	0.0	-1.00	15.9	-0.14
OPEN CONIFER	0.0	-1.00	0.0	-1.00	9.0	-0.26	24.5	0.31
CLOSED DECIDUOUS	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
OPEN DECIDUOUS	34.9	0.04	25.1	-0.19	34.7	0.04	32.7	-0.01
MIXED WOODLAND	0.0	-1.00	0.0	-1.00	4.1	-0.14	0.0	-1.00
RESTOCK/CLEARCUT	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
WOODLAND RIDES	3.4	0.13	0.0	-1.00	3.7	0.17	5.7	0.37
IMPROVED GRASS	61.6	0.76	74.9	0.87	48.5	0.63	21.2	0.11
SAMPLE SIZE (N)	145		32		214		133	
C)								
CLOSED CONIFER	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
OPEN CONIFER	19.8	0.18	11.9	-0.12	0.0	-1.00	71.7	0.87
CLOSED DECIDUOUS	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
OPEN DECIDUOUS	11.8	-0.57	23.6	-0.23	0.0	-1.00	16.0	-0.44
MIXED WOODLAND	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
RESTOCK/CLEARCUT	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
WOODLAND RIDES	13.0	0.69	6.3	0.42	0.0	-1.00	1.9	-0.17
IMPROVED GRASS	55.3	0.70	58.3	0.73	100.0	1.00	10.5	-0.30
SAMPLE SIZE (N)	62		77		85		406	

Table 4.3. Estimated percentage habitat use (U) and selection index (E) for deer in the South Oakley study area 1987-88. Both measures were calculated after weighting for differential sampling bias. See text for details. A) female groups B) male groups

HABITAT	WINTER		SPRING		SUMMER		AUTUMN	
	U	E	U	E	U	E	U	E
A)								
CLOSED CONIFER	0.0	-1.00	5.1	-0.29	0.0	-1.00	14.7	0.27
OPEN CONIFER	3.5	-0.46	2.5	-0.58	39.3	0.74	0.0	-1.00
NATURAL CONIFER	0.0	-1.00	0.3	-0.12	0.0	-1.00	0.0	-1.00
CLOSED DECIDUOUS	0.0	-1.00	13.2	0.76	12.4	0.74	0.0	-1.00
OPEN DECIDUOUS	93.1	0.95	70.4	0.76	41.1	0.36	57.2	0.61
MIXED WOODLAND	0.0	-1.00	0.2	-0.94	0.0	-1.00	0.0	-1.00
RESTOCK/CLEARCUT	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
WOODLAND RIDES	1.5	-0.07	1.8	0.02	6.2	0.58	20.1	0.87
OPEN VERGES	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
NATURAL GRASS	0.0	-1.00	0.6	-0.83	0.0	-1.00	0.0	-1.00
IMPROVED GRASS	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
CEREAL	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
HEATHLAND	1.9	-0.84	2.6	-0.78	0.9	-0.92	8.0	-0.43
BOG	0.0	-1.00	3.3	-0.44	0.0	-1.00	0.0	-1.00
BRACKEN/GORSE	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
SAMPLE SIZE (N)	105		392		33		41	
B)								
CLOSED CONIFER	17.2	0.36	10.6	0.09	0.0	-1.00	52.6	0.84
OPEN CONIFER	27.0	0.60	29.1	0.61	0.0	-1.00	11.1	0.12
NATURAL CONIFER	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
CLOSED DECIDUOUS	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
OPEN DECIDUOUS	46.1	0.45	40.1	0.35	27.5	0.08	18.4	-0.18
MIXED WOODLAND	0.0	-1.00	3.2	-0.22	11.6	0.44	0.0	-1.00
RESTOCK/CLEARCUT	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
WOODLAND RIDES	0.0	-1.00	6.9	0.61	25.3	0.90	0.0	-1.00
OPEN VERGES	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
NATURAL GRASS	0.0	-1.00	3.5	-0.27	4.5	-0.15	1.6	-0.60
IMPROVED GRASS	0.4	-0.60	0.8	-0.31	1.4	-0.06	0.0	-1.00
CEREAL	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
HEATHLAND	9.3	-0.36	5.8	-0.56	29.7	0.32	16.3	-0.06
BOG	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
BRACKEN/GORSE	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
SAMPLE SIZE (N)	227		282		99		31	

Table 4.4. Estimated percentage habitat use (U) and selection index (E) for deer in the Brinken study area 1988-89. Both measures were calculated after weighting for differential sampling bias. See text for details. A) female groups B) mixed sex groups

HABITAT	WINTER		SPRING		SUMMER		AUTUMN	
	U	E	U	E	U	E	U	E
A)								
CLOSED CONIFER	0.0	-1.00	0.0	-1.00	0.0	-1.00	7.7	-0.19
OPEN CONIFER	1.4	-0.62	0.0	-1.00	0.0	-1.00	4.0	-0.18
NATURAL CONIFER	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
CLOSED DECIDUOUS	20.0	0.54	5.3	-0.14	8.7	0.13	15.7	0.43
OPEN DECIDUOUS	50.5	0.02	31.6	-0.36	28.6	-0.42	50.9	0.03
NATURAL DECIDUOUS	0.0	-1.00	0.4	-0.74	6.5	0.45	1.8	-0.18
RESTOCK/CLEARCUT	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
WOODLAND RIDES	1.6	0.06	2.7	0.32	4.5	0.53	4.3	0.52
NATURAL GRASS	6.5	0.24	4.4	0.05	14.8	0.61	5.3	0.14
IMPROVED GRASS	11.4	0.61	50.9	0.94	29.9	0.86	4.6	0.22
HEATHLAND	8.7	-0.20	4.7	-0.48	7.2	-0.30	5.7	-0.40
BRACKEN/GORSE	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
SAMPLE SIZE (N)	592		1386		694		457	
B)								
CLOSED CONIFER	0.0	-1.00	0.0	-1.00	-	-	0.0	-1.00
OPEN CONIFER	0.0	-1.00	0.0	-1.0	-	-	0.0	-1.00
NATURAL CONIFER	0.0	-1.00	0.0	-1.00	-	-	0.0	-1.00
CLOSED DECIDUOUS	45.1	0.84	0.0	-1.00	-	-	9.2	0.16
OPEN DECIDUOUS	39.5	-0.20	0.0	-1.00	-	-	51.3	0.03
NATURAL DECIDUOUS	0.0	-1.00	0.0	-1.00	-	-	5.7	0.40
RESTOCK/CLEARCUT	0.0	-1.00	0.0	-1.00	-	-	0.0	-1.00
WOODLAND RIDES	0.0	-1.00	0.0	-1.00	-	-	1.6	0.06
NATURAL GRASS	0.0	-1.00	0.0	-1.00	-	-	6.0	0.20
IMPROVED GRASS	0.0	-1.00	100.0	1.00	-	-	9.0	0.52
HEATHLAND	15.5	0.13	0.0	-1.00	-	-	17.2	0.19
BRACKEN/GORSE	0.0	-1.00	0.0	-1.00	-	-	0.0	-1.00
SAMPLE SIZE (N)	18		531		0		253	

Table 4.5. Estimated percentage habitat use (U) and selection index (E) for deer in the Blackensford study area 1988-89. Both measures were calculated after weighting for differential sampling bias. See text for details. A) female groups B) male groups C) mixed sex groups

HABITAT	WINTER		SPRING		SUMMER		AUTUMN	
	U	E	U	E	U	E	U	E
A)								
CLOSED CONIFER	4.5	-0.26	3.2	-0.41	7.6	0.02	10.8	0.21
OPEN CONIFER	1.9	-0.51	1.8	-0.54	1.5	-0.60	1.5	-0.59
NATURAL CONIFER	16.0	0.36	7.4	-0.06	19.3	0.45	12.5	0.23
CLOSED DECIDUOUS	8.4	0.56	7.1	0.50	5.6	0.40	6.2	0.44
OPEN DECIDUOUS	40.2	0.40	45.3	0.49	33.2	0.27	45.2	0.49
NATURAL DECIDUOUS	5.9	0.44	3.7	0.23	0.0	-1.00	1.3	-0.30
RESTOCK/CLEARCUT	0.3	-0.56	0.2	-0.75	3.2	0.48	0.6	-0.36
WOODLAND RIDES	7.6	0.71	11.6	0.81	5.5	0.61	14.2	0.84
OPEN VERGES	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
IMPROVED GRASS	3.8	0.27	9.0	0.62	4.8	0.37	1.6	-0.18
HEATHLAND	7.0	-0.52	9.8	-0.38	10.9	-0.32	3.2	-0.76
BOG	2.4	-0.69	0.8	-0.88	0.0	-1.00	0.6	-0.91
BRACKEN/GORSE	1.9	-0.81	0.0	-1.00	8.4	0.32	2.3	-0.77
SAMPLE SIZE (N)	706		875		251		800	
B)								
CLOSED CONIFER	0.0	-1.00	0.0	-1.00	0.0	-1.00	59.5	0.90
OPEN CONIFER	0.0	-1.00	0.0	-1.00	0.0	-1.00	2.0	-0.49
NATURAL CONIFER	0.0	-1.00	0.0	-1.00	8.1	-0.01	1.7	-0.67
CLOSED DECIDUOUS	0.0	-1.00	0.0	-1.00	0.0	-1.00	2.2	-0.07
OPEN DECIDUOUS	62.2	0.70	94.4	0.97	53.0	0.60	30.3	0.21
NATURAL DECIDUOUS	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.1	-0.89
RESTOCK/CLEARCUT	0.0	-1.00	0.0	-1.00	9.5	0.80	0.2	-0.68
WOODLAND RIDES	37.8	0.95	0.0	-1.00	9.7	0.77	3.2	0.41
OPEN VERGES	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
IMPROVED GRASS	0.0	-1.00	5.6	0.44	14.8	0.77	0.0	-1.00
HEATHLAND	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.3	-0.97
BOG	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.1	-0.98
BRACKEN/GORSE	0.0	-1.00	0.0	-1.00	5.0	-0.55	0.2	-0.98
SAMPLE SIZE (N)	14		13		39		344	
C)								
CLOSED CONIFER	0.0	-1.00	0.0	-1.00	0.0	-1.00	65.0	0.92
OPEN CONIFER	0.0	-1.00	0.0	-1.00	0.0	-1.00	1.1	-0.70
NATURAL CONIFER	0.0	-1.00	21.4	0.50	0.0	-1.00	9.9	0.10
CLOSED DECIDUOUS	8.7	0.57	0.0	-1.00	0.0	-1.00	3.7	0.19
OPEN DECIDUOUS	8.1	-0.53	0.0	-1.00	0.0	-1.00	17.8	-0.14
NATURAL DECIDUOUS	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.3	-0.78
RESTOCK/CLEARCUT	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-0.89
WOODLAND RIDES	10.8	0.79	0.0	-1.00	0.0	-1.00	0.3	-0.66
OPEN VERGES	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
IMPROVED GRASS	41.1	0.94	78.6	0.99	100.0	90.00	0.4	-0.69
HEATHLAND	31.3	0.31	0.0	-1.00	0.0	-1.00	0.7	-0.95
BOG	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.2	-0.98
BRACKEN/GORSE	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.6	-0.94
SAMPLE SIZE (N)	175		210		29		1121	

Table 4.6. Estimated percentage habitat use (U) and selection index (E) for deer in the Lockerley study area 1987-88. Both measures were calculated after weighting for differential sampling bias. See text for details. A) female groups B) male groups C) mixed sex groups

HABITAT	WINTER		SPRING		SUMMER		AUTUMN	
	U	E	U	E	U	E	U	E
A)								
CLOSED CONIFER	31.3	0.62	32.1	0.64	25.8	0.54	36.1	0.69
OPEN CONIFER	6.2	0.85	5.9	0.85	0.0	-1.00	1.9	0.57
OPEN DECIDUOUS	22.0	0.53	4.9	-0.25	18.9	0.46	16.7	0.40
COPPICE DECIDUOUS	17.1	-0.04	34.8	0.41	19.0	0.03	21.6	0.11
MIXED WOODLAND	0.7	-0.14	0.0	-1.00	0.0	-1.00	2.6	0.48
RESTOCK/CLEARCUT	3.5	0.27	0.4	-0.68	0.8	-0.45	0.4	-0.70
WOODLAND RIDES	7.5	0.68	12.1	0.80	7.6	0.68	1.9	0.11
OPEN VERGES	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
IMPROVED GRASS	1.1	-0.91	1.7	-0.87	2.7	-0.80	5.6	-0.61
CEREAL	10.6	-0.67	8.0	-0.75	25.2	-0.28	13.4	-0.59
SAMPLE SIZE (N)	440		354		204		426	
B)								
CLOSED CONIFER	55.1	0.84	13.1	0.18	36.4	0.69	31.0	0.62
OPEN CONIFER	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
OPEN DECIDUOUS	37.2	0.75	0.0	-1.00	0.0	-1.00	6.6	-0.10
COPPICE DECIDUOUS	0.0	-1.00	0.0	-1.00	0.0	-1.00	54.7	0.69
MIXED WOODLAND	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
RESTOCK/CLEARCUT	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
WOODLAND RIDES	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
OPEN VERGES	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
IMPROVED GRASS	0.0	-1.00	86.9	0.84	63.6	0.76	1.7	-0.87
CEREAL	7.7	-0.75	0.0	-1.00	0.0	-1.00	6.0	-0.80
SAMPLE SIZE (N)	35		15		12		36	
C)								
CLOSED CONIFER	55.5	0.84	36.2	0.69	0.0	-1.00	62.6	0.88
OPEN CONIFER	0.0	-1.00	0.0	-1.00	0.0	-1.00	5.6	0.84
OPEN DECIDUOUS	21.3	0.52	0.0	-1.00	0.0	-1.00	28.9	0.65
COPPICE DECIDUOUS	0.0	-1.00	63.8	0.78	0.0	-1.00	0.0	-1.00
MIXED WOODLAND	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
RESTOCK/CLEARCUT	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
WOODLAND RIDES	7.5	0.68	0.0	-1.00	68.8	0.99	2.8	0.30
OPEN VERGES	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
IMPROVED GRASS	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
CEREAL	15.7	-0.52	0.0	-1.00	31.2	-0.13	0.0	-1.00
SAMPLE SIZE (N)	90		18		19		198	

Table 4.7. Estimated percentage habitat use (U) and selection index (E) for deer in the Tollard Royal study area 1987-88. Both measures were calculated after weighting for differential sampling bias. See text for details. A) female groups B) male groups C) mixed sex groups

HABITAT	WINTER		SPRING		SUMMER		AUTUMN	
	U	E	U	E	U	E	U	E
A)								
CLOSED CONIFER	7.1	0.53	16.3	0.79	15.2	0.77	7.2	0.54
OPEN CONIFER	1.2	0.23	0.8	0.03	0.1	-0.72	0.2	-0.54
OPEN DECIDUOUS	2.8	0.36	2.2	0.26	1.2	-0.04	1.9	0.18
NATURAL DECIDUOUS	2.9	-0.47	21.1	0.53	21.8	0.54	26.3	0.62
COPPICE DECIDUOUS	57.7	0.90	40.6	0.82	41.1	0.82	42.4	0.83
RESTOCK/CLEARCUT	0.7	0.63	1.4	0.81	1.2	0.78	2.6	0.89
WOODLAND RIDES	6.8	0.88	4.1	0.81	3.0	0.74	4.3	0.82
OPEN VERGES	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
NATURAL GRASS	9.4	-0.62	7.0	-0.71	5.3	-0.78	8.3	-0.66
IMPROVED GRASS	0.0	-1.00	0.0	-1.00	0.2	-0.27	0.0	-1.00
CEREAL	11.4	-0.74	6.4	-0.85	10.9	-0.75	6.7	-0.84
SAMPLE SIZE (N)	558		938		445		468	
B)								
CLOSED CONIFER	26.5	0.88	16.7	0.79	53.5	0.96	9.1	0.63
OPEN CONIFER	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
OPEN DECIDUOUS	0.0	-1.00	3.8	0.50	0.0	-1.00	0.0	-1.00
NATURAL DECIDUOUS	0.0	-1.00	0.0	-1.00	14.8	0.35	30.4	0.68
COPPICE DECIDUOUS	0.0	-1.00	53.0	0.89	0.0	-1.00	31.1	0.74
RESTOCK/CLEARCUT	14.4	0.98	0.0	-1.00	0.0	-1.00	1.2	0.78
WOODLAND RIDES	11.5	0.93	7.2	0.89	2.9	0.74	0.0	-1.00
OPEN VERGES	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
NATURAL GRASS	0.0	-1.00	4.8	-0.80	0.0	-1.00	23.2	-0.19
IMPROVED GRASS	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
CEREAL	47.6	0.03	14.4	-0.67	28.8	-0.35	4.9	-0.89
SAMPLE SIZE (N)	9		33		22		19	
C)								
CLOSED CONIFER	0.0	-1.00	9.1	0.62	0.0	-1.00	29.2	0.89
OPEN CONIFER	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
OPEN DECIDUOUS	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
NATURAL DECIDUOUS	84.5	0.97	26.2	0.62	0.0	-1.00	0.0	-1.00
COPPICE DECIDUOUS	0.0	-1.00	37.1	0.79	90.4	0.99	33.0	0.76
RESTOCK/CLEARCUT	15.5	0.98	0.0	-1.00	0.0	-1.00	0.0	-1.00
WOODLAND RIDES	0.0	-1.00	3.9	0.80	0.0	-1.00	0.0	-1.00
OPEN VERGES	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
NATURAL GRASS	0.0	-1.00	15.8	-0.41	0.0	-1.00	0.0	-1.00
IMPROVED GRASS	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
CEREAL	0.0	-1.00	7.8	-0.82	9.6	-0.78	37.8	-0.17
SAMPLE SIZE (N)	10		99		10		51	

Table 4.8 Estimated percentage habitat use (U) and selection index (E) for deer in the Tadley study area 1987-88. Both measures were calculated after weighting for differential sampling bias. See text for details. A) female groups B) mixed sex groups

HABITAT	WINTER		SPRING		SUMMER		AUTUMN	
	U	E	U	E	U	E	U	E
A)								
CLOSED CONIFER	58.8	0.92	46.4	0.86	30.9	0.75	63.3	0.93
OPEN DECIDUOUS	2.7	-0.35	3.0	-0.29	28.6	0.75	19.4	0.62
NATURAL DECIDUOUS	9.6	0.73	10.9	0.76	7.4	0.66	1.6	-0.02
COPPICE DECIDUOUS	3.1	-0.54	0.0	-1.00	12.5	0.14	0.0	-1.00
WOODLAND RIDES	4.8	0.79	6.8	0.85	2.1	0.58	1.6	0.47
OPEN VERGES	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
IMPROVED GRASS	11.9	-0.05	29.8	0.48	13.6	0.02	11.5	-0.07
CEREAL	9.0	-0.85	3.0	-0.95	4.8	-0.92	2.7	-0.96
SAMPLESIZE (N)	194		262		120		128	
B)								
CLOSED CONIFER	0.0	-1.00	0.0	-1.00	-	-	0.0	-1.00
OPEN DECIDUOUS	32.9	0.79	16.2	0.55	-	-	0.0	-1.00
NATURAL DECIDUOUS	0.0	-1.00	0.0	-1.00	-	-	0.0	-1.00
COPPICE DECIDUOUS	0.0	-1.00	13.5	0.18	-	-	0.0	-1.00
WOODLAND RIDES	0.0	-1.00	0.0	-1.00	-	-	0.0	-1.00
OPEN VERGES	0.0	-1.00	0.0	-1.00	-	-	0.0	-1.00
IMPROVED GRASS	58.8	0.81	70.3	0.88	-	-	100.0	1.00
CEREAL	8.3	-0.86	0.0	-1.00	-	-	0.0	-1.00
SAMPLE SIZE (N)	84		222		0		67	

Table 4.9 Estimated percentage habitat use (U) and selection index (E) of the combined habitat categories for female deer in each study area. Both measures were calculated after weighting for differential sampling bias. See text for details. (na = not available).

HABITAT	WINTER		SPRING		SUMMER		AUTUMN	
	U	E	U	E	U	E	U	E
DENNY								
CLOSED WOODLAND	8.3	-0.39	9.7	-0.31	5.0	-0.59	2.5	-0.78
OPEN WOODLAND	56.5	0.41	52.2	0.33	33.4	-0.04	34.7	-0.01
OTHER WOODLAND	7.3	0.01	19.6	0.52	17.5	0.47	46.5	0.84
WOODLAND RIDES	7.5	0.67	7.2	0.66	20.6	0.88	9.9	0.75
GRASSLANDS	14.3	0.57	8.1	0.32	21.2	0.71	6.0	0.16
ARABLE	na	na	na	na	na	na	na	na
OTHER OPEN	31.9	-0.76	3.2	-0.87	2.3	-0.90	0.5	-0.98
DAMES SLOUGH								
CLOSEDWOODLAND	7.9	-0.54	0.0	-1.00	5.5	-0.66	15.5	-0.21
OPEN WOODLAND	32.6	-0.31	28.6	-0.39	32.0	-0.32	49.4	0.03
OTHER WOODLAND	4.0	-0.34	10.9	0.18	6.9	-0.07	1.0	-0.78
WOODLAND RIDES	19.3	0.79	11.8	0.66	17.4	0.77	15.7	0.74
GRASSLANDS	36.2	0.45	48.7	0.63	38.2	0.48	18.3	0.02
ARABLE	na	na	na	na	na	na	na	na
OTHER OPEN	na	na	na	na	na	na	na	na
SOUTH OAKLEY								
CLOSED WOODLAND	0.0	-1.00	18.3	0.29	12.4	0.07	14.7	0.16
OPEN WOODLAND	96.6	0.96	73.2	0.68	80.4	0.78	57.2	0.44
OTHER WOODLAND	0.0	-1.00	0.2	-0.94	0.0	-1.00	0.0	-1.00
WOODLAND RIDES	1.5	-0.07	1.8	0.02	6.2	0.58	20.1	0.87
GRASSLANDS	0.0	-1.00	0.6	-0.87	0.0	-1.00	0.0	-1.00
ARABLE	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
OTHER OPEN	1.9	-0.93	6.0	-0.78	0.9	-0.96	8.0	-0.71
BLACKENSFORD								
CLOSED WOODLAND	12.9	0.15	10.4	0.03	13.3	0.17	17.0	0.30
OPEN WOODLAND	64.0	0.48	58.2	0.38	53.9	0.30	60.5	0.42
OTHER WOODLAND	0.3	-0.56	0.2	-0.75	3.2	0.48	0.6	-0.36
WOODLAND RIDES	7.6	0.71	11.6	0.81	5.5	0.61	14.2	0.84
GRASSLANDS	3.8	0.22	9.0	0.59	4.8	0.33	1.6	-0.23
ARABLE	na	na	na	na	na	na	na	na
OTHER OPEN	11.3	-0.74	10.6	-0.76	19.3	-0.56	6.1	-0.86
BRINKEN								
CLOSED WOODLAND	21.2	0.11	4.2	-0.66	8.5	-0.40	18.3	0.02
OPEN WOODLAND	51.5	-0.13	25.7	-0.60	34.3	-0.45	57.8	-0.01
OTHER WOODLAND	0.0	-1.00	0.0	-1.00	0.0	-1.00	0.0	-1.00
WOODLAND RIDES	1.5	0.03	2.2	0.22	4.4	0.53	3.6	0.44
GRASSLANDS	16.9	0.45	64.1	0.92	43.8	0.82	11.9	0.28
ARABLE	na	na	na	na	na	na	na	na
OTHER OPEN	9.0	-0.25	3.8	-0.62	8.9	-0.26	8.5	-0.28

Table 4.9 (cont.)

HABITAT	WINTER		SPRING		SUMMER		AUTUMN	
	U	E	U	E	U	E	U	E
LOCKERLEY								
CLOSED WOODLAND	48.3	0.42	67.0	0.68	44.8	0.36	57.7	0.56
OPEN WOODLAND	28.3	0.62	10.8	0.14	18.9	0.43	18.5	0.42
OTHER WOODLAND	4.1	0.18	0.4	-0.78	0.8	-0.59	3.0	0.00
WOODLAND RIDES	7.5	0.68	12.1	0.80	7.6	0.68	1.9	0.11
GRASSLANDS	1.1	-0.91	1.7	-0.87	2.7	-0.80	5.6	-0.62
ARABLE	10.6	-0.67	8.0	-0.75	25.2	-0.28	13.4	-0.58
OTHER OPEN	na	na	na	na	na	na	na	na
TOLLARD								
CLOSED WOODLAND	63.2	0.90	56.1	0.86	57.3	0.87	50.0	0.83
OPEN WOODLAND	8.3	-0.09	23.8	0.49	22.2	0.45	26.8	0.55
OTHER WOODLAND	1.0	0.75	1.3	0.79	1.1	0.77	2.4	0.88
WOODLAND RIDES	6.8	0.88	4.2	0.81	2.9	0.73	3.9	0.80
GRASSLANDS	9.2	-0.65	7.8	-0.70	5.1	-0.80	8.4	-0.68
ARABLE	11.4	-0.74	6.8	-0.84	11.4	-0.74	8.5	-0.80
OTHER OPEN	na	na	na	na	na	na	na	na
TADLEY								
CLOSED WOODLAND	50.9	0.70	34.6	0.48	43.4	0.61	53.3	0.72
OPEN WOODLAND	15.9	0.43	14.8	0.39	36.0	0.76	17.6	0.48
OTHER WOODLAND	na	na	na	na	na	na	na	na
WOODLAND RIDES	4.0	0.75	4.4	0.77	2.1	0.58	1.3	0.40
GRASSLANDS	20.3	0.22	44.3	0.66	13.6	-0.02	25.5	0.35
ARABLE	8.9	-0.85	2.0	-0.97	4.8	-0.92	2.2	-0.96
OTHER OPEN	na	na	na	na	na	na	na	na

Table 4.10 Results of G-test for independence between seasonal use of combined habitat categories by female deer in each site. *** p<0.001, ** p<0.01, * p<0.05, ns not significant

		DEN	DAM	OAK	BLA	BRI	LOC	TOL
DAM	WINTER	***						
	SPRING	***						
	SUMMER	*						
	AUTUMN	***						
OAK	WINTER	***	***					
	SPRING	***	***					
	SUMMER	***	***					
	AUTUMN	***	***					
BLA	WINTER	*	***	***				
	SPRING	***	***	*				
	SUMMER	***	***	***				
	AUTUMN	***	***	*				
BRI	WINTER	***	***	***	*			
	SPRING	***	***	***	***			
	SUMMER	***	***	***	***			
	AUTUMN	***	***	***	*			
LOC	WINTER	***	***	***	***	***		
	SPRING	***	***	***	***	***		
	SUMMER	***	***	***	***	***		
	AUTUMN	***	***	***	***	***		
TOL	WINTER	***	***	***	***	***	*	
	SPRING	***	***	***	***	***	ns	
	SUMMER	***	***	***	***	***	ns	
	AUTUMN	***	***	***	***	***	ns	
TAD	WINTER	***	***	***	***	***	***	**
	SPRING	***	***	***	***	***	***	***
	SUMMER	***	***	***	***	***	***	*
	AUTUMN	***	***	***	***	***	***	**

Table 4.11 Estimated percentage habitat use (U) and selection index (E) of the woodland/open habitat categories for female deer in each study area. Both measures were calculated after weighting for differential sampling bias. See text for details. (na = not available)

SITE	HABITAT	WINTER		SPRING		SUMMER		AUTUMN	
		U	E	U	E	U	E	U	E
DENNY	WOOD	79.6	0.43	88.7	0.67	72.5	0.26	93.5	0.80
	OPEN	20.4	-0.43	11.3	-0.67	27.5	-0.26	6.5	-0.80
DAMES	WOOD	63.8	-0.42	51.3	-0.60	61.8	-0.45	81.7	0.02
	OPEN	36.2	0.42	48.7	0.60	38.2	0.45	18.3	-0.02
OAKLEY	WOOD	98.1	0.96	94.1	0.87	99.1	0.98	92.0	0.83
	OPEN	1.9	-0.96	5.9	-0.87	0.9	-0.98	8.0	-0.83
BLACK	WOOD	84.9	0.69	80.4	0.60	75.9	0.50	92.3	0.84
	OPEN	15.1	-0.69	19.6	-0.60	24.1	-0.50	7.7	-0.84
BRINKEN	WOOD	73.4	-0.15	40.0	-0.70	48.1	-0.60	84.6	0.19
	OPEN	26.6	0.15	60.0	0.70	51.9	0.60	15.4	-0.19
LOCKERLEY	WOOD	88.3	0.83	90.3	0.86	72.1	0.58	81.0	0.72
	OPEN	11.7	-0.83	9.7	-0.86	27.9	-0.58	19.0	-0.72
TOLLARD	WOOD	79.2	0.88	86.6	0.93	83.6	0.91	75.0	0.85
	OPEN	20.8	-0.88	13.4	-0.93	16.4	-0.91	25.0	-0.85
TADLEY	WOOD	79.1	0.85	67.2	0.75	81.6	0.87	85.8	0.91
	OPEN	20.9	-0.85	32.8	-0.75	18.4	-0.87	14.2	-0.91

Table 4.12 Results of G-test for independence between seasonal use of woodland/open habitat categories by female deer in each site. *** p<0.001, ** p<0.01, * p<0.05, ns not significant

		DEN	DAM	OAK	BLA	BRI	LOC	TOL
DAM	WINTER	ns						
	SPRING	***						
	SUMMER	ns						
	AUTUMN	ns						
OAK	WINTER	***	***					
	SPRING	ns	***					
	SUMMER	***	***					
	AUTUMN	ns	ns					
BLA	WINTER	ns	*	**				
	SPRING	ns	**	*				
	SUMMER	ns	ns	***				
	AUTUMN	ns	ns	ns				
BRI	WINTER	ns	ns	***	ns			
	SPRING	***	ns	***	***			
	SUMMER	**	*	***	***			
	AUTUMN	ns	ns	ns	ns			
LOC	WINTER	ns	**	*	ns	ns		
	SPRING	ns	***	ns	ns	***		
	SUMMER	ns	ns	***	ns	**		
	AUTUMN	*	ns	ns	ns	ns		
TOL	WINTER	ns	ns	***	ns	ns	ns	
	SPRING	ns	***	ns	ns	***	ns	
	SUMMER	ns	*	***	ns	***	ns	
	AUTUMN	**	ns	*	*	ns	ns	
TAD	WINTER	ns	ns	***	ns	ns	ns	ns
	SPRING	*	ns	***	ns	*	**	*
	SUMMER	ns	ns	***	ns	***	ns	ns
	AUTUMN	*	ns	ns	ns	ns	ns	ns

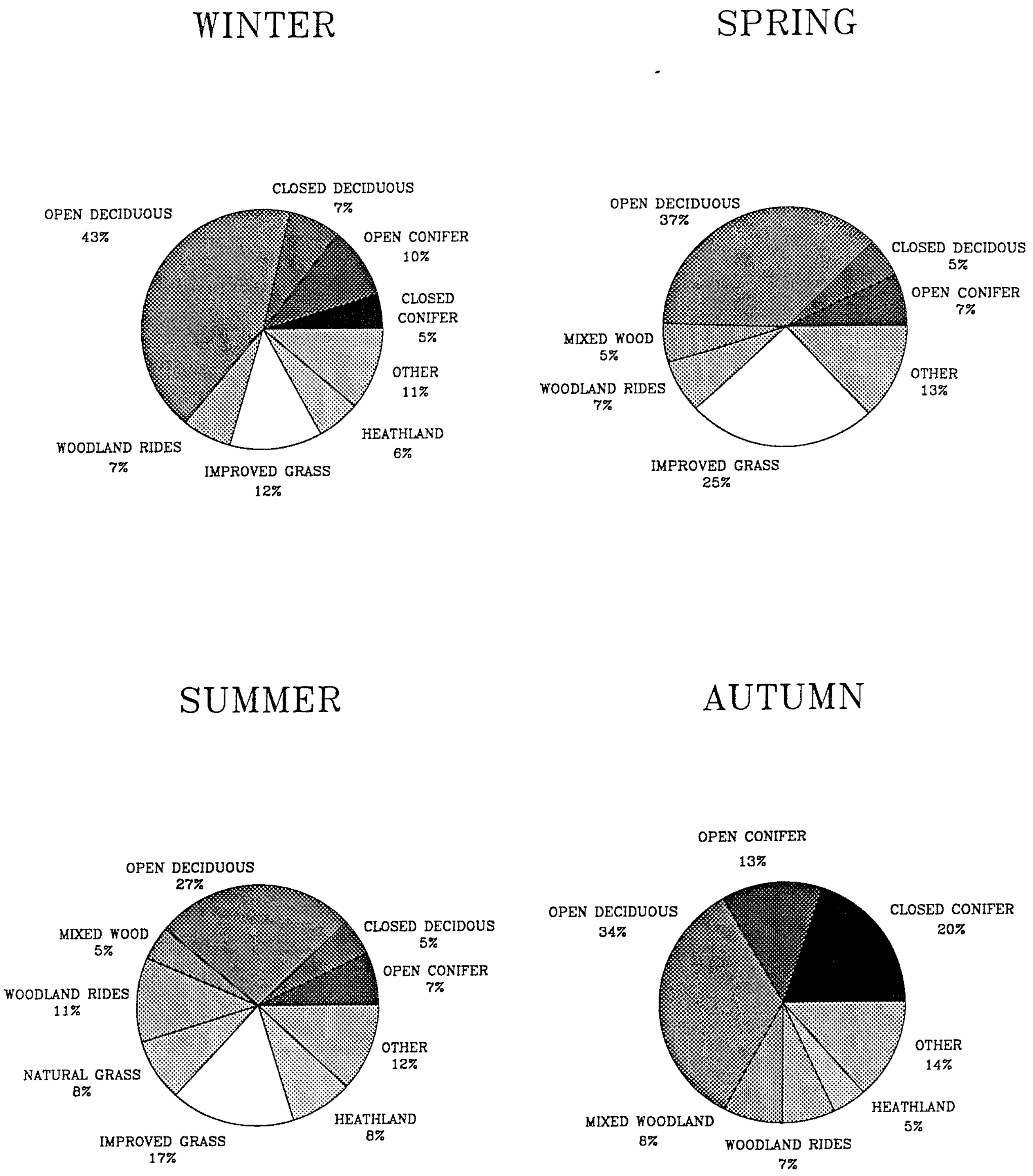
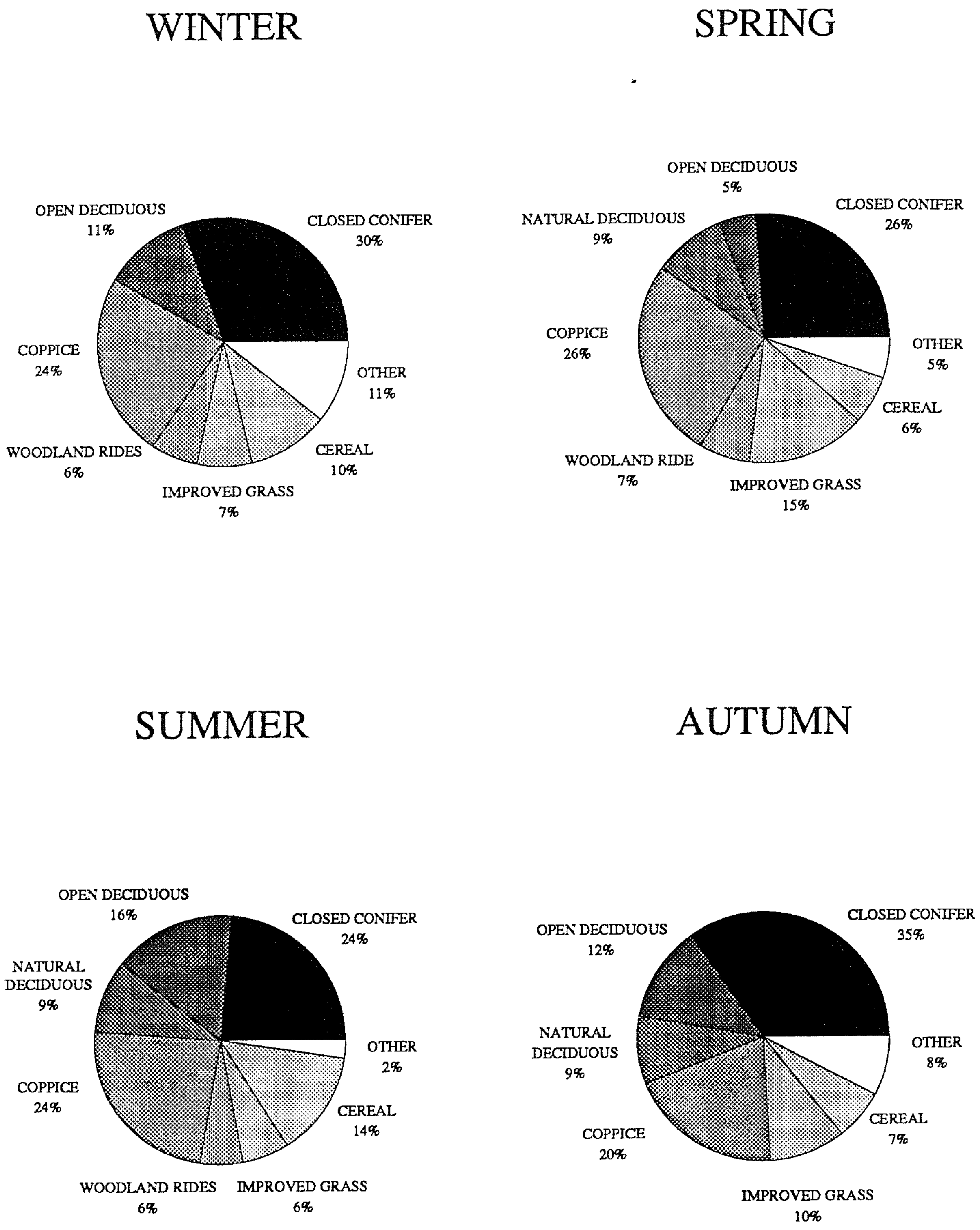


Fig 4.1 Estimated percentage use of individual habitat categories by deer in the New Forest expressed as an average value of five study sites.

Fig 4.2 Estimated percentage use of individual habitat categories by deer in agricultural areas expressed as an average value of three study sites.



5. POPULATION STRUCTURE AND SEXUAL SEGREGATION

5.1. INTRODUCTION

The previous two chapters have concentrated on the vegetational environment experienced by the deer, initially contrasting the study sites in terms of habitat composition and structure, and then going on to describe patterns of habitat use and preference. The focus now shifts to the deer populations themselves, and in this chapter some of the population parameters that may have an influence upon social systems will be examined. First of these is the density of deer in each site, which might be expected to affect considerably all aspects of fallow social systems. A related parameter is dispersion, a measure of the tendency of animals to cluster together or not. The third population parameter considered here is sex-ratio, the relative numbers of males and females in each population or subpopulation. Finally, the levels of sexual segregation exhibited by the deer in each study site will be examined, an attempt made to explain the observed variation in the degree of segregation observed in these and other fallow populations in terms of the population parameters already described.

Density and deer populations

The literature on estimating population densities of large-mammals is extensive but Caughley (1977) and Seber (1982) cover the main procedures and their statistical backgrounds, whilst Mitchell et al. (1977) and more recently Staines & Ratcliffe (1987) discuss these methods in the context of woodland deer. As Mitchell et al. (1977) state 'the difficulties lie in applying these techniques to specific situations and assessing the reliability of estimates thus obtained'.

In the current context, density is of great interest with reference to its possible effects on social systems. Quantitative, comparative studies of intraspecific variation in social organisation in large mammals are limited in number, and the role of population density unclear. For example, group size has been found to be positively related to population density in eastern grey kangaroos *Macropus giganteus* (Southwell 1984), but Hirth (1977) was unable to show a relationship between these two parameters in white-tailed deer *Odocoileus virginianus*. Similarly, population density has often been invoked to explain intraspecific differences in mating strategy, as, very relevantly, in fallow deer by Schaal (1987) and Clutton-Brock et al. (1988). Until recently however, little data has been available to substantiate these claims (Langbein & Thirgood 1989).

Dispersion and deer populations

Dispersion is a term used to describe the distribution of a population in space over a given period of time. In the current context, dispersion reflects the extent to which the deer use certain parts of their range more than others, and thus possibly inflate the local density experienced by individuals in relation to the overall density over the entire site. The theory has been developed primarily in relation to studies of dispersion in invertebrates, as an understanding of dispersion is vital in the analysis of predator-prey and host-parasite relationships (Southwood 1978). To my knowledge, no formal studies of dispersion as defined above have been undertaken on cervids or other ungulates.

Sex-ratio variation in mammals

Many populations of mammals have been shown to have sex-ratios biased towards females. There is considerable debate as to whether females can manipulate the sex-ratio of their progeny so as to maximize their own fitness (Trivers & Willard 1973; Silk 1983), with current opinion suggesting that the observed trends do not support any particular adaptive theory (Clutton-Brock et al. 1984, 1986). There is more evidence, however, that males are much less viable than females as both adults and juveniles, with increased mortality and shorter life-spans being documented in a wide range of species (Clutton-Brock, Albon et al. 1985). Increased male mortality may be a consequence of injuries resulting from competition for mating rights; for example, in bighorn sheep *Ovis canadensis* (Geist 1971), caribou *Rangifer tarandus* (Bergerud 1974) and red deer *Cervus elaphus* (Clutton-Brock et al. 1979), between 5-10% of breeding males may be injured or killed each year. Males in dimorphic ungulate species are also more likely to die than females during periods of food shortage, eg. mule deer *Odocoileus hemionus* (Robinette et al. 1957), caribou (Klein 1968), elk *Cervus canadensis* (Houston 1982) and red deer (Clutton-Brock, Major et al. 1985), probably because they are unable to satisfy their greater nutritional requirements on poorer quality swards from which the smaller females can collect adequate food. Sex differences in survival are also found among juvenile mammals. In most social mammals, juvenile or adolescent males disperse from their natal group and consequently show higher rates of mortality (Greenwood 1980). Sex differences in juvenile mortality are most pronounced in strongly dimorphic species (Clutton-Brock et al. 1985) and increase during periods of bad weather or food shortage, eg. Soay sheep (Grubb 1974) and caribou (Bergerud 1971).

Ungulate sexual segregation

In most species of sexually dimorphic, seasonally breeding cervids, the sexes live separately throughout the year, coming together for only a brief period during the rut.

Exceptions to this general rule certainly do exist; for example, some populations of chital *Axis axis* and barasingha *Cervus duvauceli* in India form mixed-sex herds throughout the year (Schaller 1967), as do taruca *Hippocamelus antisensis* in southern Peru (Merkt 1987). Sexual segregation is also shown in some of the mountain and savannah dwelling bovids (Geist 1971; Schaller 1977; Jarman 1979) and several alternative theories have been suggested in explanation.

Geist (1971), working with bighorn sheep, noted that breeding age males tended to leave female ranges after the rut, and spend much of the remainder of the year segregated from females and juveniles. He later hypothesized that males avoid the better quality habitat occupied by females in order to avoid competing for scarce resources with females which might carry their offspring or directly with offspring which they might have fathered (Geist & Petocz 1977). A similar idea has been suggested to explain sexual segregation in white-tailed deer (McCullough 1979; Beier & McCullough 1990). This could only be the case if group selection was operating, since it cannot otherwise explain why males not successful in the rut occupy different ranges from females.

An alternative, also due to Geist (Geist & Bromley 1978), suggested that through possession of antlers, male deer were less vulnerable to predation, hence moving away from antlerless and defenceless female deer would further reduce these risks. However, this theory would not explain observed segregation in reindeer and caribou, in which antlers are carried by both sexes.

Jarman (1983) suggests that a more general explanation might arise from the needs of males of polygynous, heteromorphic species to monitor their individual ranks within the local male population. A male most safely achieves breeding status only by continuous self-assessment relative to other males; the risk he commits himself to in challenging for breeding status may be less than if he had matured in isolation. Jarman (1979) presents some supporting evidence for impala *Aepyceros melampus*. This theory may well hold for some antelope where male dominance may last for long periods of time. However, it is difficult to accept in fallow deer, as the dominance hierarchy changes frequently throughout the rut, and status at the beginning of the rut does not necessarily guarantee reproductive success (see Chapter 8).

Most recent explanations of ungulate sexual segregation are based on differences in the feeding strategies of the two sexes imposed upon them by their relative size and metabolic requirements. The increased tendency towards polygynous mating systems in social ungulates is accompanied by increased sexual dimorphism, which is in turn accompanied by greater nutritional requirements of males (Clutton-Brock et al. 1982; Staines et al. 1982). Because of differential scaling of incisor breadth and metabolic requirements to bodyweight, male ungulates may simply be outcompeted by conspecific females, and forced to graze on poorer quality swards with a higher standing crop (Illius & Gordon 1987; Clutton-Brock et al. 1987). Differences in feeding strategies may require the sexes to forage in different areas and thus result in the sexual segregation observed. Whether this explanation accounts for sexual segregation in fallow deer is debatable; if anything males may occupy the better quality grazing (see Chapter 4), thus alternative explanations may be required.

Sexual segregation has been widely reported among fallow deer (eg. Jackson 1974; Chapman & Chapman 1975; Putman 1986a) such that in most populations studied, males and females occur in single-sexed groups, and indeed occupy distinct geographical ranges, except for the brief period of the rut. However, studies in more open agricultural environments suggest that this may not always be the case, with adult males associating with females throughout the winter and into the spring (Heideman 1973; Schaal 1982; Langbein 1985; Waterfield 1986). These studies have simply presented data on the occurrence of non-reproductive mixed-sex groups and have not offered a functional explanation for such intra-specific variation.

Objectives of the current study

In summary the objectives of this chapter are:

1. To obtain quantitative estimates of density, dispersion, and sex ratio in each population.
2. To investigate the extent of sexual segregation in each population.
3. To determine the relationship between observed levels of sexual segregation and the population parameters listed above.

5.2. METHODS

Direct Observation

The population parameters described in this chapter are based on direct observation from fixed transect routes which were regularly patrolled throughout the year. The basic methodology of these transect walks has been described in detail in Chapter 2. In summary data were collected on the number, composition, activity, habitat of occupance, and location of all groups of deer observed. The calendar year was partitioned into the same seasons as in the previous habitat use analysis (Winter: December-February; Spring: March-May; Summer: June-August; Autumn: September-November).

Density

Density estimates were based on dawn transects only, being the period in which deer were most active and hence readily observable. For each such transect, the number of deer seen of each sex and age class and the habitat of occupance was recorded. Density was estimated separately for females (does, yearlings of both sexes, fawns of both sexes) and males (bucks and yobs). The inclusion of male fawns and yearlings in the female category was necessitated by the tendency of these two age classes to remain in female groups.

Density was estimated by two separate methods. In method A, the total number of females and males observed on each transect (N) was related to the area visible on the transect irrespective of habitat type (V), and density calculated as:

$$D_a = N / V$$

In method B, the number of females and males seen in each individual habitat type_i on each transect was recorded (N_i). This value was then weighted by the relative area of that habitat surveyed on the transect in relation to its total availability in the site (S_i). Density was then calculated as the sum of all weighted habitats divided by the total area (T) of the site as:

$$D_b = [\ \Sigma\ (\ N_i / S_i\ )\ ] / T$$

Visibility in each site and hence the area surveyed of each habitat type on the transects varied seasonally; adjustments were made for such variation. Dawn transects were replicated six times per site in each season in both years of the study. Seasonal density estimates from 1987 and 1988 (or in the case of Blackensford, 1988 and 1989) were not significantly different (Mann-Whitney U-tests $p>0.05$). Data from the two years were therefore combined for all further analysis, giving a total of twelve replicate dawn transects per season per site, excluding Brinken for which only one year's data (1989) was available.

In each site, seasonal density estimates were derived from approximately normally distributed replicates, justifying presenting a parametric mean and standard error. However, the data did not fulfil the requirements of homogeneity of variance for ANOVA and were thus analyzed by Kruskal-Wallis test and Mann-Whitney U-tests (Sokal & Rohlf 1981).

Dispersion

The dispersion of the deer in each site was calculated using Morisita's index (Morisita 1962, 1964). A 4 ha grid based on Ordinance Survey coordinates was superimposed onto a 1:10000 map of each study site, and the grid cell of all individual deer sightings recorded. For each study site, the total number of deer seen in each cell on a seasonal and annual basis was calculated. Morisita's index is given by the formula:

$$I_\delta = N \, [\, \Sigma \, n_i \, (n_i - 1) \, / \, \Sigma \, x \, (\Sigma \, x - 1 \,)$$

where N = total number of grid cells sampled on the transect
n_i = numbers in the $_i$th grid cell
Σx = the sum of the numbers of individuals in all cells

When the distribution is random the index gives a value of unity; when the distribution is regular the index will be less than one, and when the distribution is contagious or clumped the index will be greater than one. The significance of the departure from a random distribution shown by the index may be tested by comparing F_o calculated:

$$F_o = [\, I_\delta \, (\Sigma \, x - 1 \,) + N - \Sigma \, x \,] \, / \, (N\text{-}1)$$

with the value of F in statistical tables (Rohlf & Sokal 1981), the appropriate value being that for F where N_1 = N-1 and $N_2 = \infty$. Increased clustering of the deer population will be reflected by an increase in the value of the index. Morisita's index is particularly useful in the current context because of its relative independence of the type of distribution, the number of grid cells sampled, and the size of the sampling unit (Southwood 1966).

Sex Ratio

A seasonal sex ratio was estimated for each population by simply calculating the total number of individuals of each sex and age class observed on all transects. The categories recognized were: bucks (5 yr+ males), yobs (2-4 yr. males), prickets (yearling males), does, fawns, and small deer (all non-antlered deer which could not be identified to precise age classes). The first three categories were grouped together as males and the latter three as females. In contrast to the density estimates, this division includes prickets as male deer. It was not possible to accurately determine the sex of all fawns observed in the field, hence these were all included as females, and therefore will slightly distort the estimated sex ratio. A similar consideration is applied to individuals categorized as small-deer; this class will inevitably include a certain percentage of male fawns and yearlings. Analysis of seasonal changes in sex ratio within sites and comparisons between sites were made by G-test for independence on the original transect data (Sokal and Rohlf 1981).

Sexual Segregation

Analysis of sexual segregation was initially performed at the group level by considering the proportion of groups observed in each study site of single sex, either males only (bucks, yobs, yearling males), or females only (does, and yearlings and fawns of both sexes), compared to the proportion of groups containing adults of both sex (bucks, yobs, and does). Such an approach is identical to that adopted in earlier fallow studies (eg. Heideman 1973; Jackson 1974; Waterfield 1986). The principal drawback of this method of analysis is that it attaches equal weight to all groups, regardless of size. Hence a female group of two does and two fawns is equated to a mixed-sex group of 100 deer. To an extent this may be resolved by focusing at the level of the individual animal. Segregation is then expressed as the proportion of individuals occurring in single-sex groups and in mixed-sex groups, following the methodology of Schaal (1982). The drawback of this second approach is that because females greatly outnumber males in the majority of sites, it is difficult to isolate the level of segregation exhibited by males in the populations. For example, if only ten males are observed out of a total sample of 1000 deer, and all of these males are in mixed-sex groups which in total comprise 100 deer, then the estimate of population segregation of 90% certainly does not reflect the experience of the typical male. In this chapter data has been presented utilizing both the above approaches principally for comparison to the earlier studies.

Formal statistical analysis of sexual segregation in this study attempts to isolate levels of segregation exhibited by males and by females. The first analysis investigates the distribution of individual female deer into groups containing females only (does, and yearlings and fawns of both sexes) and groups containing males (bucks and yobs). A seasonal frequency distribution of individuals in the two group types was calculated for each site, and seasonal and inter-site comparisons of the extent of segregation made by G-test for independence. This analysis is then replicated for males; the numbers of two-year plus male deer observed on all transects in male only and in mixed-sex groups is presented as a frequency distribution and analyzed in identical fashion. The male analysis is then taken further to investigate site differences in patterns of sexual association between age classes of males by distinguishing between bucks (5+ years old) and yobs (2-4 years old).

Finally, the relationship between the extent of sexual segregation in each study site and the population parameters described above were investigated through non-parametric Spearman rank correlation (Seigel 1956).

5.3. RESULTS

Density

Female deer

Seasonal and annual estimates of female density as calculated by both methods 'A' and 'B' for each site are given in Table 5.1. There are considerable differences in the values of the estimates obtained by the two analytical approaches and it is appropriate to consider here the merits and demerits of each approach before pursuing formal statistical analyses. Method 'A' simply presents the number of deer seen in the area surveyed, and is thus making the implicit assumption that densities outside of this very limited area are similar to those within it. Method 'B' essentially calculates an estimate of total theoretical population size and derives a density estimate from this value. This second approach makes the assumption that use of particular habitat types is uniform across the site; for example the high utilization of grasslands visible on the transect is reflected by high utilization of grasslands elsewhere in the study site. Clearly, both approaches have considerable drawbacks. Examination of the estimates of density given by each method (Table 5.1) suggests that values derived by method 'B' are highly variable within sites; the variance of the replicated samples within each season as reflected by the standard error of the mean are much higher than for method 'A'. Given the relatively small home range of female fallow deer (estimated at 70 ha in the New Forest by Rand, in Putman 1986a) it seems unlikely that large changes in density would occur within seasons. Thus the estimates derived from method 'A' were used for all further analysis of density in this and the following chapters.

The extent of seasonal variation in female density varied between sites. In the New Forest sites, density varied little throughout the year at Denny, Dames Slough, and Brinken (Kruskall-Wallis tests, $P>0.05$, not significant). At South Oakley, seasonal variation was pronounced (Kruskall-Wallis test, $p<0.01$), with summer and autumn densities lower than the peak in winter and spring (Mann-Whitney U-tests, $p<0.001$). Significant seasonal variation was also shown at Blackensford (Kruskall-Wallis test, $p<0.001$). However at this site peak densities were attained in autumn and spring (Mann-Whitney U-tests: autumn>summer, $p<0.01$; autumn>winter, $p<0.05$; spring>summer, $p<0.01$; spring>winter, $p<0.05$).

Seasonal variation in estimated density in the three agricultural populations showed similar trends, with a decrease in density during the summer, although this was only statistically significant in the case of Tollard and Tadley (Kruskall-Wallis tests, $p<0.01$). In these two sites, densities in both winter and spring were higher than in summer (Mann-Whitney U-tests, $p<0.01$).

Because of the pronounced seasonal density variation in four of the sites, comparisons between sites were made at the seasonal level. These data are presented in the form of a matrix of Mann-Whitney U-tests between each possible pair of seasonal densities; for example, Denny is compared to Dames Slough in each of the winter, spring, summer, and autumn seasons (Table 5.2). This table simply lists the statistical significance of the analyses, and it is necessary to refer back to Table 5.1 to see the magnitude and direction of the difference. While such a complex table is obviously difficult to interpret, it is possible to point out several clear trends in the data.

Amongst the New Forest sites, the Brinken population clearly existed at the highest density, ranging from 70-87 deer/100ha, some two to ten times greater than the other sites, excluding the exceedingly low autumn densities at South Oakley. An intermediate level of density was represented by the three sites of Denny, Dames Slough and Blackensford, with seasonal densities ranging from 16-41 deer/100ha. South Oakley was consistently the lowest density Forest site studied, particularly during autumn when very few females were seen, and formed a distinct third tier on the scale of relative density.

The agricultural populations recorded female densities equivalent to those of South Oakley in the New Forest, with estimates ranging from 4-13 deer/100 ha. Differences in density between the three sites were not great, with Tadley at marginally higher annual and seasonal densities than Tollard Royal and Lockerley. Comparison of the minimum and maximum in the range of female density estimates between the three agricultural populations and the New Forest sites, excluding South Oakley, suggests a minimum threefold difference in density between the two environmental types.

Male deer

Seasonal and annual estimates of densities of male deer of two years or older in each site as assessed by both method 'A' and method 'B' are presented in Table 5.3. In contrast to the estimates for female density, male density estimates within single seasons were highly variable using both methods of analysis, a reflection of the tendency on individual transects to encounter males in groups or not at all. For consistency and comparison to female densities, the method 'A' estimate is used throughout.

The density of males varied greatly between seasons in all New Forest sites with the exception of Denny (Kruskall-Wallis tests: Dames Slough $p<0.05$; South Oakley $p<0.01$; Blackensford and Brinken $p<0.001$). At Dames Slough, summer and autumn densities were higher than spring (Mann-Whitney U-tests, $p<0.05$), the reasons for which are unknown. Seasonal changes at the remaining three sites appear directly linked to the autumn rut. At South Oakley, a relatively high density of males remained in the area throughout winter, spring and summer, and then virtually disappeared in the autumn

(Mann-Whitney U-tests: winter, spring, summer > autumn, $p<0.01$). The exact opposite occurred at Blackensford and Brinken, with very low densities of male deer throughout the year until autumn, when an increase of males in late September was associated with the rut (Mann-Whitney U-tests, Blackensford and Brinken: autumn > winter, spring, and summer, $p<0.001$).

In the three agricultural sites, seasonal variation in male density was much less pronounced (Kruskall-Wallis tests, $p>0.05$). This is in part a reflection of the overall low densities of adult male deer in these populations, the tendency of males to use the same range as females, and also the discontinuous nature of deer distribution in these environments, possibly inhibiting large scale male migrations between areas as seen in the New Forest.

Contrasts of male densities between sites are shown in the form of a seasonal matrix of Mann-Whitney U-tests in Table 5.4. Within the New Forest sites, relatively high densities of adult males occur throughout the winter, spring, and summer only at South Oakley and Dames Slough, within the ranges of two of the well-established buck groups. However, autumn male densities at Blackensford and Brinken attain very high levels, reflecting the movement of males to these areas before, during, and after the October rut. The levels of male density indicated for these two areas at this time (10.4 and 9.0 males/100ha respectively) are almost certainly a underestimate of true male density during the peak two weeks of the rut in late October (see Chapter 7).

The estimated seasonal and annual male densities in the agricultural populations were exceedingly low, an approximate tenfold decrease in relation to estimates from the New Forest sites. This difference is in contrast to the threefold decrease in small-deer density.

Dispersion

Deer were distributed non-randomly in all seasons in all study sites ($p<0.001$) (Table 5.5). In other words, they made more extensive use of certain areas visible on the transect routes than others. The tests of significance of the departure from a random distribution indicated that the deer in all study sites were significantly clustered; further comparisons between sites can not be made statistically.

There was no clear distinction between New Forest and agricultural sites in dispersion. Tadley and Brinken, and then Tollard and Dames Slough, attained the highest annual values of the index, with the group comprising Lockerley, South Oakley, Denny, and Blackensford at the bottom of the scale. Amongst the highly clustered sites, the agricultural populations showed less seasonal variation in dispersion, in direct contrast to the highly variable Brinken population in the New Forest.

Sex ratio

The seasonal distribution of individual deer encountered on transect routes between the different age/sex classes for each site are shown in Table 5.6. These data are summarised in this table as the estimated percentage of males and females in each population.

In each site, there was significant seasonal variation in the contribution of males and females to the total number of observations within that season. This analysis is summarised in Table 5.7, which presents a seasonal matrix of G-tests within each site. Reference must be made back to Table 5.6 to see the magnitude and direction of the difference. In most sites fairly simple trends in the data can be seen. At Denny, the percentage of males in winter and spring was significantly lower than in summer and autumn. In the Dames Slough subpopulation, the principle cause of seasonal variation was the sharp decrease in the number of males during the spring. The trends at Brinken were similarly very simple; the subpopulation contained almost exclusively females throughout winter, spring, and summer, then an influx of males occurred during the autumn rut. At Blackensford, seasonal changes in sex ratio were more gradual; a predominantly female subpopulation in spring gained more males during summer to peak levels during autumn, and then declined again during winter. Changes in sex ratio at South Oakley were more complex, and the value of the data are limited by the very small sample sizes during summer and autumn.

Seasonal variation in sex ratio in the agricultural sites, whilst still statistically significant (Table 5.7), was generally more limited than in the forest sites. All three sites were highly skewed to females throughout the year. In each population, a decrease in male numbers during a single season was responsible for the variation which existed annually. At Lockerley this was in spring, Tadley in summer, and at Tollard Royal in winter. Overall, however, there were not the large seasonal changes in sex ratio typical of several of the New Forest sites.

Comparison of sex ratios between study sites was performed at a seasonal level on the distribution of observations of male and female deer. These results are presented in the now familiar matrix of G-tests in Table 5.8. Throughout the winter, spring and summer, Brinken had consistently the highest percentage of females of all the New Forest populations. Tollard Royal and Tadley came close to this level of skew in the sex ratio, however in these two agricultural populations, there was no sudden increase in the numbers of males in autumn. Denny, Blackensford and Lockerley showed an intermediate sex ratio, with considerable variation throughout the year. The populations at South Oakley and Dames Slough were the only ones in which male deer formed a large proportion of the observed animals throughout much of the year.

In summary Fig 5.1 expresses sex ratio as the number of females per male encountered in the population on a seasonal basis. The enormously skewed winter, spring and summer sex ratios at Brinken are clearly contrasted to the nearly 1:1 ratio between males and females at South Oakley. Similarly, the differences between sites in the extent of seasonal sex ratio variation are very apparent.

Sexual segregation

Population focused: groups or individuals?

One approach to examining sexual segregation is to simply determine the occurrence of "mixed sexing" in the population as a whole. This may be expressed either in terms of the percentage of groups that contain adults of both sexes, or as the percentage of individuals occurring in mixed-sex groups. Both approaches are shown for each site in Figure 5.2. Reservations regarding each approach have been stated in the Methods section of this chapter and statistical analyses of the data expressed in this form have not been carried out. Closer examination of Figure 5.2 reveals an important difference between these two approaches in examining the same data set, notably that the "group" method emphasises the contribution of the smaller single-sex groups in relation to the typically larger mixed-sex groups. In terms of comparative studies of the extent of mixed-sex grouping in different deer populations, these two methods can give notably different results. Clearly, in most sites, a group based analysis suggests higher levels of sexual segregation.

Female focused

The seasonal distribution of female deer into female groups (does, yearlings and fawns of both sexes) and groups containing males (bucks and yobs) in each study site is shown in Figure 5.3. Within each site there was significant seasonal variation in the distribution of individuals in the two group types, summarised in Table 5.9 in a seasonal matrix of G-tests. Within the New Forest, the highest levels of mixed-sexing occurred during the autumn in the Dames Slough, Blackensford, and Brinken populations. At this time, up to 51% of females occurred in groups containing male deer, and we should remember that it was in these three sites in which there was intense rutting activity over this period (Chapter 7). However, even outside the period of the rut, during winter and spring, up to 27% of females were encountered in mixed sex groups in these three sites. Within site seasonal variation was even more pronounced in the Tadley population where high levels of autumn, winter, and spring mixed-sexing decreased to total segregation in summer.

Comparisons between sites were performed at a seasonal level on the distribution of observations of females between female groups and mixed-sex groups (Table 5.10). Significantly different distributions existed between all sites in at least one, or more typically three or four seasons. High levels of mixed-sexing in the autumn (before, during and after the rut) are easiest to explain, and, as previously stated, those New Forest sites with high levels of autumn reproductive activity showed a correspondingly high incidence of females in mixed-sex groups. Similarly, in the agricultural populations, autumn mixed-sexing was common at Lockerley and Tadley. Together with Blackensford, mixed-sexing continued throughout the winter in these two populations. In the spring Tadley and Brinken showed an increases in mixed-sexing, with particularly Tadley attaining levels nearing half of all female observations. Segregation of female deer in summer was relatively high in all sites, with only Denny and Dames showing more than 10% mixed-sexing.

Male focused

The seasonal distribution of two-year plus male deer into male-only and mixed-sex groups is shown in Figure 5.4. Before any conclusions are drawn from these data is worth pointing out the great variation in the total numbers of males seen in any one season in each site, ranging from 550 in autumn at Blackensford to only two in summer at Tadley. A second point is that, in general, males showed lower levels of segregation than females, particularly in winter and spring.

The extent of seasonal variation in male segregation differed between sites (Table 5.11). Lockerley and Tollard showed least significant variation, male single-sexing ranging from 50-80% of observations, but with small sample size reducing the resolution of the statistical tests. Similarly, the extreme seasonal variation shown at Tadley, from 100% mixed sex in winter to 100% segregated in summer, is based on a total of only 10 male deer. Within the New Forest, all sites showed some significant seasonal variation. This was more pronounced in Brinken (0-40% segregated) and Blackensford (29-72%) than in Denny (41-69%), Dames Slough (50-79%) and Oakley (86-100%). Of particular interest are the high levels of mixed-sexing shown in winter and spring at Blackensford and Brinken, and in summer at Brinken.

Between site comparisons of male segregation were made at a seasonal level, contrasting the distribution of males into male groups and groups of mixed-sex (Table 5.12). Males at South Oakley consistently showed the highest levels of segregation throughout the year, falling below 96% only during autumn, when sample size at this site was very low. The 100% segregation shown by Tadley males in summer is of dubious validity, being based on only a single observation of two bucks. During winter and spring, an intermediate level of segregation, ranging from 57-79%, was shown by male deer at Denny, Dames Slough, Lockerley, and Tollard. Very significantly lower levels of segregation were shown by Blackensford and Brinken males in this period. Summer provides a reversal of the above trends, with the majority of males at Denny (59%) and Brinken (100%) occurring in mixed sex groups, but sexual segregation increasing in its extent at all other sites.

Age differences in male segregation

The preceding analyses of sexual segregation, whether from a population, female, or male focus, have included all males above two years of age in the 'male' category. The reasons for this distinction are twofold; it coincides with the age categorization of male deer by previous fallow deer workers (eg. Jackson 1974; Schaal 1982; Waterfield 1986), and, more importantly, it is the only division that can be made with total accuracy as male antler development beyond two years of age can be highly variable. With this limitation in mind, it is however desirable to investigate whether there are age differences in male segregation from the female population, and further, to examine whether such differences are constant across the eight study sites.

The occurrence of bucks (males of 5+ years) and yobs (males of 2-4 years) in male and mixed-sex groups is shown in Table 5.13, expressed as the percentage of two year-plus males observed in each site. Because of the complexity of the table, the details for each site will be described in turn.

Few bucks were seen at Denny at any time of year; of these most were in male groups. The great majority of Denny males were yobs and were evenly split between male groups and mixed-sex groups. In this population, mixed-sex groups were primarily due to yobs associating with females. Segregation in the South Oakley population was equally simple. Bucks and yobs were seen throughout the year, although numbers of both age classes greatly declined through summer and autumn in both years. Segregation of both bucks and yobs was almost total, with only a few mixed-sex groups occurring in autumn.

A complicating factor in the Dames Slough, Blackensford, and Brinken populations was the autumn rut. At this time, both bucks and yobs were found in equal proportions in male groups and mixed-sex groups. Throughout the remainder of the year at Dames Slough, approximately 80% of all males, both bucks and yobs, were segregated from females. At Blackensford, very few bucks were seen in winter, spring, and summer; of those that were, they were almost invariably in male groups. The majority of yobs, however, were seen with females. Brinken was almost exclusively a female area from winter to summer. The mixed-sex groups that did occur in winter and spring were, however, were largely due to yobs, in this case joining large female groups grazing on reseeded fields.

Male deer of any age above yearling were rarely seen in the agricultural populations. At Lockerley, bucks were evenly split between male groups and mixed-sex groups throughout the year, only decreasing slightly in summer. Yobs were predominantly seen in male groups. At Tollard, a similar pattern occurred during the spring, with bucks and yobs equally found in male and mixed-sex groups. During summer, however the majority of males of both ages were segregated from the females. The only season in which large numbers of males were observed at Tadley was during spring, at which time both bucks and yobs were typically in mixed sex groups.

Correlates of Sexual Segregation

The relationships between the population parameters introduced earlier in this chapter (female density, male density, dispersion and sex ratio) and the extent of mixed-sex grouping by both females and males were investigated through non-parametric Spearman rank correlation (Table 5.14). The percentage of females in mixed sex groups was not correlated to any of the parameters listed above.

The percentage of males of more than two years of age in mixed-sex groups during winter and spring was positively correlated to sex ratio (winter: $rs=0.76$, $N=8$, $p<0.05$; spring: $rs=0.86$, $N=8$, $p<0.01$). Thus the fewer males of any age there were in the population in respect to the number of females, the greater the likelihood that adult males would be in mixed-sex groups. Population dispersion in spring was also positively correlated to the percentage of males in mixed-sex groups, suggesting that segregation of males was lowest when populations were highly clustered. In contrast to sex ratio, neither male nor female density was correlated to the segregation of males.

5.4. DISCUSSION

In this chapter comparative data on population structure for each of the eight study sites has been presented, the extent of seasonal segregation between the sexes has been described; and then site differences in the latter related in terms of the population parameters described. In this discussion estimates of population density, dispersion, sex ratio, and the occurrence of mixed-sex groups shall first be contrasted to published accounts of fallow deer and other ungulates in the literature, and then an attempt made to give a functional explanation for the observed variation in sexual segregation across a range of wild fallow populations.

Density, Aggregation, and Sex Ratio

Assessing the density of woodland deer is notoriously difficult (see reviews by Mitchell et al. 1977; Staines & Ratcliffe 1987) and some consideration of the accuracy of the density estimates in the current study is necessary before discussing their implications. The single method used throughout the analyses in this chapter makes the assumption that density in the sampling area is typical of density elsewhere in the study site. This is rather a large assumption given that it has also been shown that deer are neither randomly nor evenly distributed across the site, but are highly clustered in given areas. The second method adopted (and subsequently dropped from the analyses) attempts to calculate a total theoretical population size based on the assumption that use of particular habitat types is uniform across the study site. This is also a very large assumption, as it is likely that the juxtaposition of habitat types influences their utilization. Clearly, neither method can be absolutely relied on to give accurate measures of density. However, as methodology was consistent across sites, the available estimates at the very least provide a useful index of density suitable for comparison within and between sites.

Female density in this study, both within sites between seasons and within seasons between sites, showed great variation; even within the New Forest estimates ranged from as little as 2.2 to 86.8 deer/100ha. The range of densities in the five New Forest sites reflected the non-uniform distribution of fallow deer in this population noted by previous workers (Jackson 1974; Putman 1986a). Seasonal variation not withstanding, there were three quite distinct levels of female density in the eight sites. The Brinken subpopulation in the New Forest existed at extremely high densities throughout the year; at an average 78.5 deer/100ha it was more than twice the density of any published figures for wild fallow populations (reviewed in Chapman & Chapman 1975; Apollonio 1989). The middle density tier was occupied by the three New Forest sites of Denny, Dames Slough, and Blackensford. Densities in these areas ranged from 16-40 deer/100ha, comparable to wild fallow populations in Essex (Chapman & Chapman 1975) and South Devon (Waterfield 1986) in England, Coto Donana, S. Spain (Braza 1975) and San Rossore, Italy (Apollonio 1989). The final New Forest subpopulation at South Oakley, and the three agricultural sites at Lockerley, Tollard, and Tadley, formed a distinctive third density level, ranging from 2-16 deer/100 ha. These densities are similar to those recorded in mixed-woodland and agricultural complexes in Staffordshire, England (Langbein 1985), Salzau, W. Germany (Heideman 1973), and Selestat, N.E. France (Schaal 1982, 1987).

Male densities also varied widely between and within sites. Males above the age of yearling were very uncommon in the agricultural study sites, the possible reasons for this biased sex ratio are discussed below. Within the New Forest, male densities were highly variable, reflecting the patchy distribution of male deer throughout the Forest for much of the year. The majority of New Forest adult male fallow congregate into relatively large (10-20 individuals) male groups which are associated with traditional 'buck-areas', of which ten are known to the author. Two of these 'buck-areas', South Oakley and Dames Slough, were included in the sample used in this study.

Within this general framework, fallow densities varied greatly between seasons. In the agricultural populations, seasonal lows in female density were all in summer; whether this reflects the inadequacies of the visibility correction factor or a genuine decrease in deer numbers at this time is unclear. A possibility is that the populations increased their ranges in summer with a resulting decrease in density, and such a suggestion gains some limited support from the observed increased dispersion in summer in two of the sites. Home range studies on fallow deer are limited; the little data available from the New Forest suggests that in fact individual summer ranges are smaller than winter (Rand, in Putman 1986a). Seasonal changes in range size in cervids appear highly variable. Summer ranges in female white-tailed deer have been reported as being both smaller than (Beier & McCullough 1990) and larger than (Tierson et al. 1985) winter ranges. Similarly, female red deer on open hill ground decreased their range size in winter on Rhum (Clutton-Brock et al. 1982) and in the Western (Darling 1937) and Eastern (Mitchell et al. 1977) Highlands; whilst in forest-dwelling populations in Western Scotland no seasonal changes in range size were apparent (Hinge 1986; Catt & Staines 1987). In the current study, male densities varied little between seasons in the agricultural sites. There was little evidence of large-scale movements of male deer in and out of the study areas, either during the rut or at any other time.

Significant seasonal changes in female and male density in the New Forest were limited to Brinken, Blackensford and South Oakley. Here, changes were due in part to movements of deer before, during, and after the autumn rut. Densities in the latter two sites were possibly linked; individually recognized bucks who spent the winter and spring at South Oakley and on neighbouring private farmland were subsequently seen rutting at Blackensford. Movement of females from South Oakley to Blackensford is less likely; the sharp decline in female density at South Oakley occurred during the summer, at the same time at which Blackensford densities were also low. This summer decrease in female density parallels that observed in the agricultural populations and it may have a similar cause. As stated earlier, studies of ranging behaviour of individually known fallow deer are limited, and little information is available on seasonal movement patterns of either sex. It is known that males may move very large distances (up to 20km) for the rut (Chapman & Chapman 1975; Putman 1986a), however most authors have assumed that female ranges change little at this time.

Deer in all populations were unevenly dispersed; not surprisingly certain areas in each site were more heavily used than others. This was particularly true in the case of Brinken in spring when 50% of all deer seen were on a 10ha reseeded field, which was fenced to stop public access. The rationale behind calculating an index of dispersion was to determine whether the low density agricultural populations were less evenly dispersed, due to their use of small woodlands, than the deer of the New Forest; thus the actual density experienced within the woodlands would be higher than overall levels previously indicated. In reality this was not the case, however 'clustering' in the two environmental types appeared to be a response to different pressures. In the agricultural sites it was, as stated, the increased use of small woodlands; in the New Forest however, the principal cause was the persistent large aggregations on preferred feeding areas.

Sex ratios in all sites bar South Oakley were skewed towards females; this was particularly pronounced in the three agricultural populations and at Brinken. Taking the five New Forest sites as a representative sample of sex ratio in the population as a whole results in a distribution of approximately 1 male : 3 females, somewhat less skewed than in the agricultural populations. A recent review of wild fallow population statistics by Apollonio (1989), whilst largely based on unverified data, indicates that many populations exist at near to 1:1 sex ratio. Two related questions are now apparent. Are the estimates of biased sex ratios, particularly in the agricultural populations, accurate reflections of the numbers of males and females present? If so, why are sex ratios so skewed?

Within the New Forest, the possibility exists that "buck-areas" were underepresented in my sample of five sites. For example, the largest known New Forest buck-group, based for much of the year on improved grasslands 1km to the south-east of Brinken, was not included in the sample for logistic reasons. Additionally, many male deer are thought to over-winter on private ground off the Forest, remain there throughout spring and summer, and only return to rut in the autumn. The Forestry Commission's own estimates of total population size suggest a sex ratio of approximately 1 male: 2 females (M.Noble pers.comm.). However, this census is more likely to underestimate females than males; most rangers have a very good idea of the numbers of bucks on their beats. In the agricultural sites it appears unlikely that large numbers of male deer lived adjacent to the study areas; contact with neighbouring game-keepers was good and no large buck groups were reported.

So why were sex ratios so skewed in favour of females? A major explanation given for increased male mortality is that males, either juvenile or adult, are more likely to die than females during periods of food shortage due to their greater metabolic requirements (Clutton-Brock, Albon et al. 1985 and references therein). It appears unlikely that food limitation is a major factor regulating wild deer populations in southern England.

There is little direct evidence for this, however the rapid increase in many southern deer populations following a curtailment of an annual cull suggests that human control is the principal factor determining population levels.

As stated in the introduction to this chapter, male cervids suffer much higher mortality than females throughout life (Clutton-Brock & Albon 1985). Examples were given of increased male mortality due to rutting injuries in red deer, caribou, and bighorn sheep. During the three years of the current study, at least one male was killed at Blackensford as a direct result of a fight, and during the 1989 rut 7/31 males present were observed to receive injuries, including one case of blinding in one eye. Additionally, increased male movement during the rut probably results in increased mortality due to road accidents (Langbein 1985).

A final consideration is the extent of selective culling of the deer populations. In the New Forest, the deer cull is strictly controlled, with the aim of maintaining a constant population. In contrast, in the agricultural populations, little coordination in deer management occurs between neighbouring estates, with the result that stalkers rarely know exactly how many deer have been killed on adjoining ground. Additionally, the increasing popularity of private deer stalking has resulted in a largely uncontrolled cull, with particular emphasis on adult male deer as trophies.

Sexual Segregation

The introduction to this chapter briefly summarized various hypotheses which attempt to explain the common occurrence, for at least part of the year, of segregation of the sexes in most ungulates. It appears unlikely that any of these models can explain the segregation exhibited by fallow deer. The most plausible theory, which explains the use of inferior grazing resources by male deer as a result of 'scramble' competition with females (Clutton-Brock et al. 1987; Illius & Gordon 1987), does not fit the limited data available for New Forest fallow, where male deer typically occupy good quality range and have access to food of similar quality to females (Jackson 1974). In this respect, fallow deer are unusual for ungulates; where sex difference in habitat use has been demonstrated, it is typically the males who occupy the poorer quality range or select the less nutritious forage, eg. red deer (Clutton-Brock et al. 1982) and black-tailed deer (Beier & McCullough 1990) (see Chapter 4 for full discussion). It may be that food is not a limiting resource for fallow populations in the New Forest, and males are able to remain on top quality range. There is clearly a need for a intensive study of sex difference in feeding ecology and habitat use of fallow in the New Forest and elsewhere.

Whatever its cause, sexual segregation outside the rut is widely believed to be typical for fallow deer (eg. Chapman & Chapman 1975) and the remainder of this chapter will be concerned with discussing the significance of deviation from that supposed norm.

In the current study, mixed-sex groupings outside of the autumn reproductive season occurred in all sites with the exception of South Oakley. The observation of winter and spring mixed-sex groups in the New Forest is in contrast to the earlier studies of Jackson (1974) who suggested fairly strict segregation, with the sexes operating largely independently outside the rut. This difference may be a result of Jackson's study concentrating largely within the Inclosures; non-reproductive mixed-sex groups tend to occur on improved or natural grasslands on the open forest (see Chapter 4 and below). The extent to which the sexes remained in segregated groups in the New Forest differed between males and females; in each site during winter, spring and summer a clear majority of female deer were found in single-sex groups. Where mixed-sex groups did occur they almost invariably contained only a few males. For example, large mixed-sex groups on the improved grasslands at Brinken in spring were composed of up to 170 does and fawns accompanied by two or three young bucks. In contrast, male deer were but rarely seen outside the 'buck-areas' such as South Oakley or Dames Slough in winter, spring and summer; however when they were seen, they were frequently accompanying female deer. This trend was most clearly shown in Blackensford and Brinken, where, significantly, non-reproductive mixed-sexed groups were invariably due to young males (yobs) joining female groups. This distinction between the age of males is important, as it appears that 'mixed-sexing' in the Forest is largely a result of young males joining female feeding aggregations.

Levels of sexual segregation in the agricultural sites differed in two important aspects from the New Forest. First, whereas non-reproductive mixed-sex groups in the latter population were largely due to young males associating with females on favoured feeding areas, agricultural mixed-sex groups contained mature bucks throughout the year. Secondly, whilst sample sizes are admittedly small, mixed-sex groups in two of the three agricultural populations, Lockerley and Tollard, were not exclusively based on vegetation communities used for feeding. These two results suggest that mixed-sex groups in the agricultural populations may be more than simple feeding aggregations or associations of deer on favoured areas. Unfortunately, the limited data available from the agricultural populations does not allow this last issue to be resolved. Detailed observations are required on the daily associations of individually known male deer in the agricultural environment, which will only be obtained by intensive radio-telemetry.

Levels of mixed-sexing in the agricultural sites were generally not as high as those recorded elsewhere in fallow populations inhabiting similar "mosaic" environments where woodlands and fields or other open areas are closely interspersed. Mixed-sex groups formed from 25-60% of all groups observed during winter by Heideman (1973) and Schaal (1982), with mixed-sexing particularly common in more open habitats in Schaal's Alsace study site. Levels of mixed-sexing approaching those of the current study were recorded by Langbein (1985) and Waterfield (1986) in Staffordshire and Devon respectively, where from 10-20% of all groups encountered from November to March contained adults of both sexes.

Population differences in the extent of sexual segregation have also been recorded in other ungulate species. In most Scottish red deer populations the sexes are segregated for over 80% of the year (Mitchell et al. 1977; Clutton-Brock et al. 1982); in the Crimea however, only 18-29% of stags were in all-male groups (Yanushko 1957). North American elk are similarly sexually segregated in most populations (eg. Houston 1982) but Altmann (1956) found more mixing of the sexes on winter range when animals were found in fairly restricted areas near artificial feeding sites. Perhaps the best parallel of the current study is that of Hirth (1977) who investigated the comparative social organisation of two populations of white-tailed deer contrasting markedly in the environments that they occupied. In a woodland population in Michigan adult males and females had no social contact outside of the rut. In a more open savannah habitat in Texas, mixed-sex feeding groups occurred throughout the year in open habitats; these groups were intermediate between simple aggregations and stable social groups, grazing over wide areas whilst maintaining a cohesive structure, but then breaking up when animals returned to cover communities.

Contrasting the levels of sexual segregation in each of the sites in the current study with the parameters generated on the transects suggests a positive relationship between the extent of winter and spring male segregation and the relative numbers of males in the population. It appears that when male numbers were high, there was a tendency for males to stay in male-only groups (eg. South Oakley). Conversely, when male numbers were low, either because there were few males in the population (agricultural sites), or because the population was principally a "doe-area" (New Forest sites), males often joined female groups. This relationship was significant in terms of sex ratio, but just below significance in terms of male densities. The percentage of females in mixed-sex groups was not correlated to any of the population parameters measured. However, if low male numbers were the principle cause of mixed-sexing amongst males, by definition this parameter would not be related to female segregation.

The idea that the degree of sex separation may depend on population density was originally suggested by Putman (1986a), who speculated that small populations divided into component sexes might produce 'herds' too small to be separately viable. This idea appears to gain some support from the data collected in the current study, however it is desirable to test it against fallow populations elsewhere. Unfortunately, comparable data which distinguishes between male and female components of sexual segregation are not available, and comparison of overall levels of mixed-sexing provide contradictory results. The low density populations studied by Heideman (1973) and Schaal (1982) both showed high levels of mixed-sexing, however the sex ratios in these populations were much closer to unity than those in the current study (male:females; Salzau 1:1; Selestat 1:2). Similarly, a 1:2 sex ratio was recorded in the moderately segregated population studied by Langbein (1985). In each case, overall density may have been low, but there should have been enough males in each population to form male-only groups. Clearly, whilst Putman's hypothesis might account for much of the mixed-sexing in the current study, an alternative explanation is required for these other sites.

5.5. SUMMARY

1. Female and male densities varied greatly, both within seasons between study sites, and within study sites between seasons.
2. Seasonal variation not withstanding, there were three levels of female density. The highest densities were recorded at Brinken in the New Forest (78.5 deer/100ha), medium densities recorded at Denny, Dames Slough and Blackensford in the New Forest (16-40 deer/100ha), and lowest densities at the Forest site South Oakley and the three agricultural sites (2-16 deer/100ha).
3. Female densities in the three agricultural sites were lowest in summer. Seasonal variation in female density was less pronounced in the New Forest sites, however where variation did occur, seasonal lows were also in summer.
4. Excluding the autumn rutting period, high male densities were found in only two sites: South Oakley and Dames Slough in the New Forest.
5. Seasonal variation in male density was largely due to the autumn rut. Male density decreased at this time at South Oakley, and increased at Blackensford and Brinken.
6. Deer in all populations were unevenly dispersed.
7. Sex ratios in all study sites bar South Oakley were skewed towards females.
8. Mixed-sex groups outside the autumn reproductive season occured in all study sites with the exception of South Oakley.
9. In each study site, the majority of female deer occurred in single-sex groups.
10. Mixed-sex groups in the New Forest sites were largely a result of young males joining feeding aggregations. Mixed-sex groups in the agricultural sites often contained mature males and were not exclusively based on vegetation communities used for feeding.
11. Levels of sexual segregation appeared linked to the relative numbers of males in the population. Where male numbers were high, males remained in single-sex groups. Where male numbers were low, mixed-sex groups occurred.

Table 5.1 Estimates of female density (deer per 100 ha) at each season and study site by methods A and B (see text for detail of calculation). Values are means ± standard error, from twelve replicated dawn transects in each season.

	Study Site	Winter	Spring	Summer	Autumn	Annual
Method A	Denny	23.8±1.6	23.7±2.7	18.3±2.5	18.1±1.9	21.0±1.1
	Dames Slough	27.2±4.1	31.1±5.3	37.7±3.5	34.6±4.4	32.6±2.2
	South Oakley	10.8±3.2	16.0±3.2	2.5±1.9	2.2±1.1	7.9±1.3
	Blackensford	23.3±3.4	36.3±4.8	16.2±1.7	35.1±4.2	27.7±1.9
	Brinken	86.8±18.2	70.5±4.7	73.8±11.0	83.0±20.0	78.5±7.4
	Lockerley	6.1±0.8	6.4±0.9	4.8±0.8	7.7±1.0	6.3±0.5
	Tollard Royal	5.9±0.7	6.4±0.7	3.5±0.6	4.8±0.7	5.2±0.3
	Tadley	8.9±1.5	12.9±2.1	5.2±1.4	8.9±1.9	9.0±0.9
Method B	Denny	19.6±4.6	24.7±6.2	12.7±3.4	14.2±5.2	17.8±2.3
	Dames Slough	18.1±6.2	16.2±7.1	19.6±5.8	28.2±6.3	20.5±3.3
	South Oakley	8.9±3.4	9.1±2.7	6.2±2.2	5.7±2.6	7.5±2.1
	Blackensford	24.6±5.1	31.7±5.7	12.1±3.2	42.6±4.9	27.8±4.6
	Brinken	60.6±21.1	51.9±14.2	59.7±12.6	78.4±15.7	62.7±9.6
	Lockerley	6.8±1.6	7.9±2.7	6.1±1.2	8.4±2.3	7.3±1.1
	Tollard Royal	5.2±1.9	5.2±1.4	2.1±1.0	3.9±0.9	4.1±0.7
	Tadley	8.0±2.2	9.2±1.9	3.2±1.5	6.9±2.8	6.8±0.9

Table 5.2 Results of Mann-Whitney U-tests between female density estimates for each site. *** $p<0.001$, ** $p<0.01$, * $p<0.05$, ns not significant

		DEN	DAM	OAK	BLA	BRI	LOC	TOL
DAM	ANNUAL	***						
	WINTER	ns						
	SPRING	ns						
	SUMMER	***						
	AUTUMN	**						
OAK	ANNUAL	***	***					
	WINTER	**	**					
	SPRING	*	*					
	SUMMER	***	***					
	AUTUMN	***	***					
BLA	ANNUAL	***	ns	***				
	WINTER	ns	ns	**				
	SPRING	ns	ns	**				
	SUMMER	ns	***	***				
	AUTUMN	***	ns	***				
BRI	ANNUAL	***	***	***	***			
	WINTER	***	**	***	***			
	SPRING	***	**	***	**			
	SUMMER	***	*	***	***			
	AUTUMN	***	*	***	*			
LOC	ANNUAL	***	***	ns	***	***		
	WINTER	***	***	ns	***	***		
	SPRING	***	***	**	***	***		
	SUMMER	***	***	ns	***	***		
	AUTUMN	***	***	***	***	***		
TOL	ANNUAL	***	***	ns	***	***	ns	
	WINTER	***	***	ns	***	***	ns	
	SPRING	***	***	**	***	***	ns	
	SUMMER	***	***	ns	***	***	ns	
	AUTUMN	***	***	**	***	***	ns	
TAD	ANNUAL	***	***	ns	***	***	ns	**
	WINTER	***	***	ns	**	***	ns	ns
	SPRING	**	**	ns	***	***	*	**
	SUMMER	***	***	ns	***	***	ns	ns
	AUTUMN	***	***	**	***	***	ns	ns

Table 5.3 Estimates of male density (deer per 100 ha) at each season and study site by methods A and B (see text for detail of calculation). Values are means ± standard error, from twelve replicated dawn transects in each season.

	Study Site	Winter	Spring	Summer	Autumn	Annual
Method A	Denny	1.3±1.6	1.1±1.2	2.2±1.1	2.2±1.9	1.6±0.9
	Dames Slough	3.6±1.0	1.6±2.1	7.1±2.6	6.8±3.2	4.8±2.1
	South Oakley	6.1±2.7	5.9±3.1	5.4±2.4	0.7±0.3	4.5±1.8
	Blackensford	1.0±1.6	0.8±1.1	1.3±1.6	10.4±6.9	3.4±1.4
	Brinken	0.5±0.2	0.7±0.6	1.0±0.7	9.0±7.8	2.7±1.8
	Lockerley	0.3±0.1	0.1±0.1	0.3±0.2	0.8±0.4	0.4±0.2
	Tollard Royal	0.1±0.1	0.2±0.1	0.2±0.1	0.2±0.1	0.2±0.1
	Tadley	0.4±0.1	0.7±0.2	0.1±0.1	0.5±0.4	0.4±0.2
Method B	Denny	0.9±0.6	1.2±1.2	1.6±0.8	1.8±1.2	1.4±0.5
	Dames Slough	2.6±1.1	1.7±0.8	4.2±1.7	6.9±2.1	3.9±0.7
	South Oakley	8.1±2.3	7.9±2.7	6.2±1.4	0.9±0.3	5.0±1.3
	Blackensford	0.6±0.2	0.4±0.2	0.9±0.3	8.4±1.2	2.6±0.9
	Brinken	0.3±0.1	0.6±0.2	0.9±0.2	11.2±4.3	3.3±2.1
	Lockerley	0.1±0.1	0.1±0.1	0.2±0.1	0.4±0.2	0.2±0.1
	Tollard Royal	0.1±0.1	0.1±0.1	0.1±0.1	0.2±0.1	0.1±0.1
	Tadley	0.2±0.1	0.5±0.2	0.1±0.1	0.2±0.1	0.2±0.1

Table 5.4 Results of Mann-Whitney U-tests between male density estimates for each site. *** $p<0.001$, ** $p<0.01$, * $p<0.05$, ns not significant

		DEN	DAM	OAK	BLA	BRI	LOC	TOL
DAM	ANNUAL	*						
	WINTER	ns						
	SPRING	ns						
	SUMMER	**						
	AUTUMN	*						
OAK	ANNUAL	*	ns					
	WINTER	*	ns					
	SPRING	*	*					
	SUMMER	ns	ns					
	AUTUMN	ns	**					
BLA	ANNUAL	ns	ns	ns				
	WINTER	ns	ns	**				
	SPRING	ns	ns	**				
	SUMMER	ns	*	*				
	AUTUMN	**	ns	***				
BRI	ANNUAL	ns	ns	ns	ns			
	WINTER	ns	**	***	ns			
	SPRING	ns	ns	**	ns			
	SUMMER	ns	**	**	ns			
	AUTUMN	*	ns	***	ns			
LOC	ANNUAL	*	***	***	*	**		
	WINTER	ns	**	***	ns	ns		
	SPRING	*	*	***	ns	ns		
	SUMMER	*	***	***	ns	ns		
	AUTUMN	ns	***	ns	***	***		
TOL	ANNUAL	*	***	***	**	**	ns	
	WINTER	*	***	***	ns	ns	ns	
	SPRING	*	*	***	ns	ns	ns	
	SUMMER	*	***	***	ns	ns	ns	
	AUTUMN	*	***	ns	***	***	ns	
TAD	ANNUAL	*	**	***	*	**	ns	ns
	WINTER	ns	**	***	ns	ns	ns	ns
	SPRING	ns	ns	***	ns	ns	ns	ns
	SUMMER	*	***	***	*	ns	ns	ns
	AUTUMN	ns	**	ns	***	***	ns	ns

Table 5.5 Seasonal and annual values of Morisita's dispersion index for each study site.

	Winter	Spring	Summer	Autumn	Annual
Denny	4.4	2.9	6.0	3.2	3.1
Dames Slough	12.2	8.9	6.7	10.6	6.0
South Oakley	6.7	3.6	5.8	8.3	3.1
Blackensford	3.1	4.8	3.3	5.1	2.7
Brinken	4.3	23.8	10.9	4.1	9.7
Lockerley	6.4	5.4	3.7	5.4	4.3
Tollard Royal	10.0	9.2	9.7	7.4	7.1
Tadley	12.1	10.3	9.2	13.0	9.0

Table 5.6 Distribution of observations of different age/sex classes expressed as the percentage of total observations for each site. Definition of age/sex classes given in text.

	Total	Bucks	Yobs	Prick	Does	Fawns	SD	Male	Female
Denny									
Annual	2801	0.9	6.9	3.9	38.1	17.7	32.5	11.6	88.4
Winter	766	1.3	4.3	3.8	27.8	13.7	49.1	9.4	90.6
Spring	1026	0.0	4.7	3.8	31.8	22.5	37.2	8.5	91.5
Summer	638	0.0	12.4	3.9	54.2	13.5	16.0	16.3	83.7
Autumn	371	3.8	8.6	4.6	49.1	20.2	13.7	17.0	83.0
Dames									
Annual	2922	6.9	8.4	14.5	25.1	8.2	36.9	29.8	70.2
Winter	605	5.6	7.8	17.0	23.6	9.9	36.0	30.4	69.6
Spring	557	1.3	3.9	3.4	14.0	7.0	70.4	8.6	91.4
Summer	854	5.4	13.3	22.5	35.0	7.8	15.9	41.2	58.8
Autumn	906	12.7	6.7	12.3	23.5	8.3	36.5	31.7	68.3
Oakley									
Annual	1265	31.2	13.8	9.6	16.8	7.0	21.5	54.7	45.3
Winter	341	40.2	15.0	13.5	11.4	5.0	15.0	68.6	31.4
Spring	704	25.6	11.2	7.4	19.3	8.9	27.6	44.2	55.8
Summer	137	44.5	24.1	7.3	13.1	2.2	8.8	75.9	24.1
Autumn	83	20.5	14.5	16.9	24.1	6.0	18.1	51.8	48.2
Blackensford									
Annual	4492	8.6	5.7	8.3	23.9	9.4	44.0	22.6	77.4
Winter	890	0.9	3.4	5.3	23.7	14.3	52.5	9.6	90.4
Spring	1098	0.3	2.0	2.7	16.3	9.1	69.6	5.0	95.0
Summer	314	1.6	6.4	12.1	43.9	12.4	23.6	20.1	79.9
Autumn	2190	17.0	8.4	11.8	24.9	7.2	30.7	37.2	62.8
Brinken									
Annual	3998	1.7	1.3	2.2	18.7	8.3	68.0	5.1	94.9
Winter	613	0.3	0.3	1.0	26.9	13.9	57.6	1.6	98.4
Spring	1917	0.0	1.0	0.9	3.7	1.7	92.7	1.9	98.1
Summer	707	1.0	0.4	0.7	41.6	16.3	40.0	2.1	97.9
Autumn	761	7.5	3.3	7.8	28.6	12.7	40.1	18.5	81.5
Lockerley									
Annual	1840	3.6	2.7	8.0	24.6	8.2	52.8	14.3	85.7
Winter	565	3.0	2.3	9.2	16.6	5.0	63.9	14.5	85.5
Spring	390	1.5	1.5	6.7	17.9	3.8	68.5	9.7	90.3
Summer	235	2.6	3.0	11.1	49.4	11.9	22.1	16.6	83.4
Autumn	650	5.8	3.7	6.6	26.6	12.3	44.9	16.2	83.8
Tollard Royal									
Annual	2657	1.8	2.1	2.7	24.7	7.9	60.8	6.6	93.4
Winter	571	0.9	0.5	0.9	13.0	5.4	79.3	2.3	97.7
Spring	1069	2.0	2.0	3.4	20.1	4.5	68.1	7.3	92.7
Summer	477	2.1	3.4	2.9	43.4	14.3	34.0	8.4	91.6
Autumn	540	2.2	3.1	3.0	29.8	11.5	50.4	8.3	91.7
Tadley									
Annual	1058	1.3	3.0	3.6	29.9	6.7	55.5	7.9	92.1
Winter	268	1.1	3.0	3.4	26.5	6.3	59.7	7.5	92.5
Spring	465	1.3	4.1	3.9	25.6	4.3	60.9	9.2	90.8
Summer	123	0.8	0.8	2.4	37.4	8.1	50.4	4.1	95.9
Autumn	202	2.0	2.0	4.0	39.6	11.9	40.6	7.9	92.1

Table 5.7 Results of G-test for independence between seasonal sex ratios within study sites. *** p<0.001, ** p<0.01, * p<0.05, ns not significant

		Winter	Spring	Summer
Denny	Spring	ns		
	Summer	***	***	
	Autumn	***	***	ns
Dames	Spring	***		
	Summer	***	***	
	Autumn	ns	***	***
Oakley	Spring	***		
	Summer	ns	***	
	Autumn	**	ns	***
Black	Spring	***		
	Summer	***	***	
	Autumn	***	***	***
Brink	Spring	ns		
	Summer	ns	ns	
	Autumn	***	***	***
Lock	Spring	*		
	Summer	ns	*	
	Autumn	ns	**	ns
Tollard	Spring	***		
	Summer	ns	ns	
	Autumn	***	ns	ns
Tadley	Spring	ns		
	Summer	ns	*	
	Autumn	ns	ns	ns

Table 5.8 Results of G-test for independence between seasonal sex ratios.
*** p<0.001, ** p<0.01, * p<0.05, ns not significant

		DEN	DAM	OAK	BLA	BRI	LOC	TOL
DAM	ANNUAL	***						
	WINTER	***						
	SPRING	ns						
	SUMMER	***						
	AUTUMN	***						
OAK	ANNUAL	***	***					
	WINTER	***	***					
	SPRING	***	***					
	SUMMER	***	***					
	AUTUMN	***	***					
BLA	ANNUAL	***	***	***				
	WINTER	ns	***	***				
	SPRING	**	**	***				
	SUMMER	ns	***	***				
	AUTUMN	***	***	**				
BRI	ANNUAL	***	***	***	***			
	WINTER	***	***	***	***			
	SPRING	***	***	***	***			
	SUMMER	***	***	***	***			
	AUTUMN	ns	***	***	***			
LOC	ANNUAL	**	***	***	***	***		
	WINTER	**	***	**	**	***		
	SPRING	ns	ns	***	**	***		
	SUMMER	ns	***	***	ns	***		
	AUTUMN	ns	***	***	***	ns		
TOL	ANNUAL	***	***	***	***	**	***	
	WINTER	***	***	***	***	ns	***	
	SPRING	ns	ns	***	*	***	ns	
	SUMMER	***	***	***	***	***	**	
	AUTUMN	***	***	***	***	***	***	
TAD	ANNUAL	***	***	***	***	***	***	ns
	WINTER	ns	***	***	ns	***	**	***
	SPRING	ns	ns	***	**	***	ns	ns
	SUMMER	***	***	***	***	ns	***	ns
	AUTUMN	**	***	***	***	***	**	ns

Table 5.9 Results of G-test for independence between seasonal distribution of female deer into female groups and mixed-sex groups within study sites. *** <0.001, ** p<0.01, * p<0.05, ns not significant

		Winter	Spring	Summer
Denny	Spring	ns		
	Summer	***	*	
	Autumn	ns	ns	**
Dames	Spring	ns		
	Summer	ns	ns	
	Autumn	***	***	***
Oakley	Spring	ns		
	Summer	ns	ns	
	Autumn	ns	*	**
Black	Spring	ns		
	Summer	***	***	
	Autumn	***	***	***
Brink	Spring	***		
	Summer	***	***	
	Autumn	***	ns	***
Lock	Spring	***		
	Summer	**	ns	
	Autumn	***	***	***
Tollard	Spring	***		
	Summer	ns	***	
	Autumn	***	ns	***
Tadley	Spring	***		
	Summer	***	***	
	Autumn	ns	**	***

Table 5.10 Results of G-test for independence between seasonal distribution of female deer into female groups and mixed-sex groups.
*** p<0.001, ** p<0.01, * p<0.05, ns not significant

		DEN	DAM	OAK	BLA	BRI	LOC	TOL
DAM	ANNUAL	***						
	WINTER	***						
	SPRING	***						
	SUMMER	ns						
	AUTUMN	***						
OAK	ANNUAL	**	***					
	WINTER	ns	*					
	SPRING	**	***					
	SUMMER	**	**					
	AUTUMN	ns	***					
BLA	ANNUAL	***	***	***				
	WINTER	***	***	***				
	SPRING	***	*	***				
	SUMMER	ns	ns	*				
	AUTUMN	***	**	***				
BRI	ANNUAL	***	**	***	***			
	WINTER	**	***	ns	***			
	SPRING	***	***	***	***			
	SUMMER	***	***	ns	***			
	AUTUMN	***	***	**	***			
LOC	ANNUAL	***	***	***	***	*		
	WINTER	***	*	**	ns	***		
	SPRING	**	***	ns	***	***		
	SUMMER	*	ns	*	ns	***		
	AUTUMN	***	***	*	***	ns		
TOL	ANNUAL	***	***	ns	***	***	***	
	WINTER	***	***	**	***	**	***	
	SPRING	ns	***	**	***	***	**	
	SUMMER	***	***	ns	***	***	***	
	AUTUMN	ns	***	ns	***	***	***	
TAD	ANNUAL	***	***	***	ns	***	***	***
	WINTER	***	***	***	***	***	***	***
	SPRING	***	***	***	***	***	***	***
	SUMMER	***	***	ns	***	ns	***	ns
	AUTUMN	***	***	**	***	ns	ns	***

Table 5.11 Results of G-test for independence between seasonal distribution of male deer into male groups and mixed-sex groups within study sites. *** <0.001, ** p<0.01, * p<0.05, ns not significant

		Winter	Spring	Summer
Denny	Spring	ns		
	Summer	*	**	
	Autumn	ns	ns	*
Dames	Spring	ns		
	Summer	ns	ns	
	Autumn	***	*	***
Oakley	Spring	ns		
	Summer	ns	ns	
	Autumn	**	ns	***
Black	Spring	ns		
	Summer	***	**	
	Autumn	***	**	ns
Brink	Spring	ns		
	Summer	ns	ns	
	Autumn	ns	***	**
Lock	Spring	ns		
	Summer	ns	ns	
	Autumn	ns	ns	ns
Tollard	Spring	ns		
	Summer	ns	*	
	Autumn	ns	ns	*
Tadley	Spring	ns		
	Summer	**	**	
	Autumn	ns	ns	*

Table 5.12 Results of G-test for independence between seasonal distribution of male deer into male groups and mixed-sex groups.
*** p<0.001, ** p<0.01, * p<0.05, ns not significant

		DEN	DAM	OAK	BLA	BRI	LOC	TOL
DAM	ANNUAL	***						
	WINTER	*						
	SPRING	ns						
	SUMMER	***						
	AUTUMN	ns						
OAK	ANNUAL	***	***					
	WINTER	***	***					
	SPRING	***	***					
	SUMMER	***	***					
	AUTUMN	*	***					
BLA	ANNUAL	*	***	***				
	WINTER	**	***	***				
	SPRING	**	**	***				
	SUMMER	ns	ns	***				
	AUTUMN	ns	*	**				
BRI	ANNUAL	**	***	***	ns			
	WINTER	ns	*	***	ns			
	SPRING	***	***	***	**			
	SUMMER	**	***	***	***			
	AUTUMN	**	ns	***	***			
LOC	ANNUAL	ns	*	***	ns	**		
	WINTER	ns	*	***	*	ns		
	SPRING	ns	ns	*	*	***		
	SUMMER	*	ns	***	ns	***		
	AUTUMN	ns	ns	***	ns	ns		
TOL	ANNUAL	ns	ns	***	***	***	ns	
	WINTER	ns	ns	*	**	ns	ns	
	SPRING	ns	ns	***	**	***	ns	
	SUMMER	***	ns	***	ns	***	ns	
	AUTUMN	ns	ns	*	ns	ns	ns	
TAD	ANNUAL	***	***	***	***	**	***	***
	WINTER	***	***	***	*	ns	***	***
	SPRING	***	***	***	**	ns	***	***
	SUMMER	ns	ns	ns	ns	ns	ns	ns
	AUTUMN	*	ns	***	*	ns	ns	ns

Table 5.13 Seasonal distribution of bucks and yobs in male groups and mixed-sex groups expressed as the percentage of all males (2 yrs.+) observed for each site.

	Total	Male groups		Mixed-sex groups	
		Bucks	Yobs	Bucks	Yobs
Denny					
Annual	212	8.5	47.6	2.8	41.0
Winter	45	15.6	44.4	6.7	33.3
Spring	48	0.0	68.8	0.0	31.3
Summer	73	0.0	41.1	0.0	58.9
Autumn	46	23.9	39.1	6.5	30.4
Dames Slough					
Annual	442	29.6	40.7	15.4	14.3
Winter	81	33.3	45.7	8.6	12.3
Spring	29	20.7	55.2	3.4	20.7
Summer	159	24.5	62.9	3.8	8.8
Autumn	173	34.1	15.6	31.2	19.1
South Oakley					
Annual	568	68.1	28.7	1.4	1.8
Winter	188	72.9	25.5	0.0	1.6
Spring	257	67.7	28.0	2.3	1.9
Summer	94	64.9	35.1	0.0	0.0
Autumn	29	51.7	34.5	6.9	6.9
Blackensford					
Annual	637	32.5	15.7	27.8	24.2
Winter	38	13.2	15.8	7.9	63.2
Spring	24	12.5	20.8	0.0	70.8
Summer	25	20.0	52.0	0.0	28.0
Autumn	550	35.3	13.8	31.6	19.3
Brinken					
Annual	112	29.5	9.8	30.4	30.4
Winter	4	25.0	0.0	25.0	50.0
Spring	15	0.0	0.0	0.0	100.0
Summer	10	70.0	30.0	0.0	0.0
Autumn	83	30.1	9.6	39.8	20.5
Lockerley					
Annual	117	27.4	29.9	29.9	12.8
Winter	30	26.7	30.0	30.0	13.3
Spring	12	25.0	50.0	25.0	0.0
Summer	13	30.8	46.2	15.4	7.7
Autumn	62	27.4	22.6	33.9	16.1
Tollard					
Annual	106	30.2	35.8	17.0	17.0
Winter	8	37.5	37.5	25.0	0.0
Spring	43	32.6	25.6	20.9	20.9
Summer	26	38.5	46.2	0.0	15.4
Autumn	29	17.2	41.4	24.1	17.2
Tadley					
Annual	43	7.0	7.0	23.3	62.8
Winter	8	0.0	0.0	25.0	75.0
Spring	25	4.0	4.0	20.0	72.0
Summer	2	50.0	50.0	0.0	0.0
Autumn	8	12.5	12.5	37.5	37.5

Table 5.14 Spearman rank correlation coefficients between population parameters and the percentage of females in mixed-sex groups and the percentage of males in mixed-sex groups. ** p<0.01, * p<0.05, ns not significant

Population	Season	Percentage in mixed-sex groups	
		Females	Males
Female density (N=8)	Annual	0.52 ns	0.36 ns
	Winter	-0.07 ns	0.05 ns
	Spring	0.58 ns	0.31 ns
	Summer	0.34 ns	0.07 ns
	Autumn	0.57 ns	0.59 ns
Male density (N=8)	Annual	0.10 ns	-0.36 ns
	Winter	0.02 ns	-0.50 ns
	Spring	0.06 ns	-0.49 ns
	Summer	0.46 ns	0.12 ns
	Autumn	0.55 ns	0.31 ns
Dispersion (N=8)	Annual	0.22 ns	0.36 ns
	Winter	0.05 ns	-0.36 ns
	Spring	0.55 ns	0.64 *
	Summer	-0.42 ns	-0.54 ns
	Autumn	0.33 ns	0.19 ns
Sex ratio	Annual	0.12 ns	0.64 *
	Winter	-0.29 ns	0.76 *
	Spring	0.52 ns	0.86 **
	Summer	-0.34 ns	-0.10 ns
	Autumn	-0.26 ns	0.19 ns

Fig 5.1 Sex ratio in each study site expressed as the number of females encountered per male on all transects.

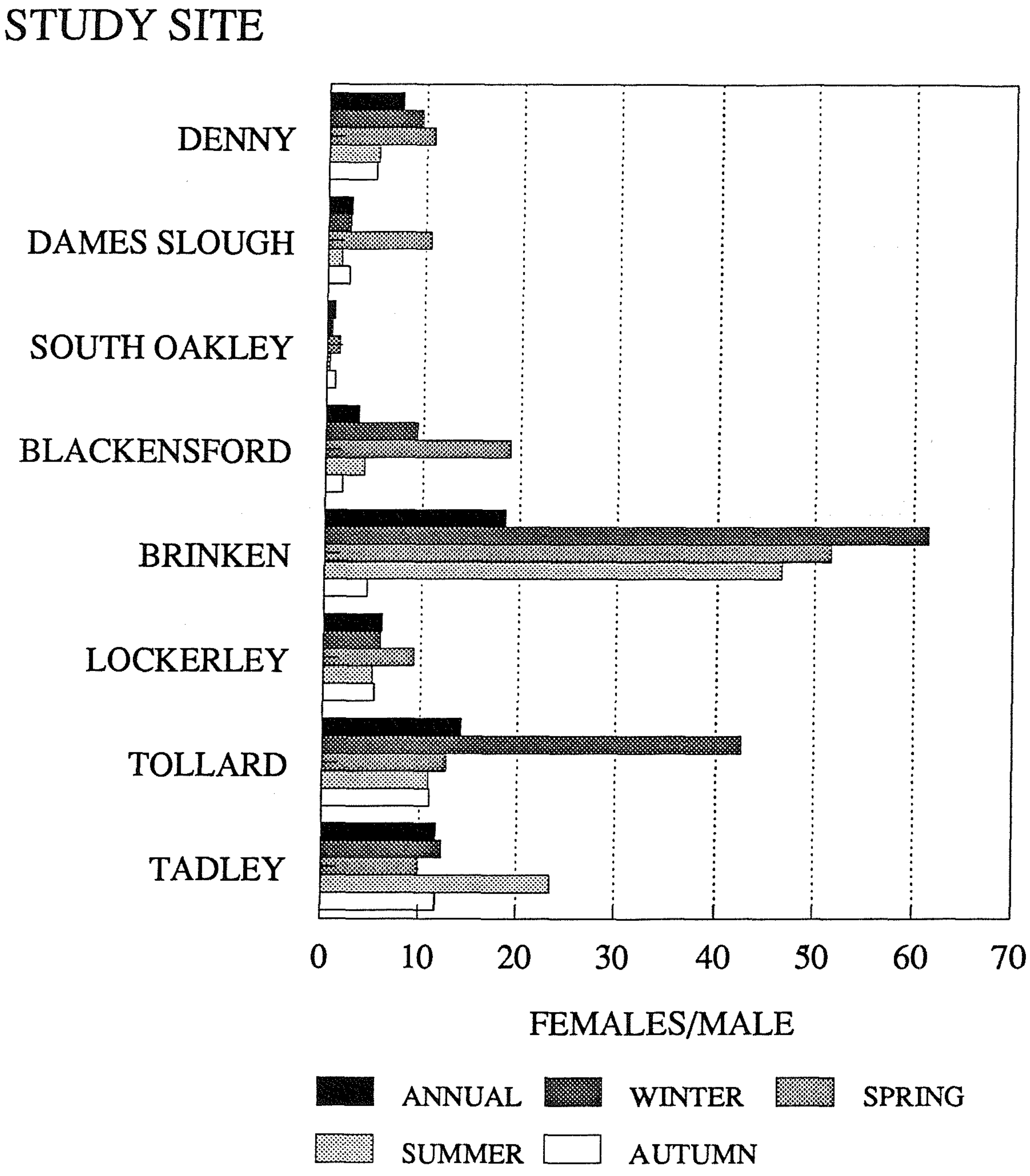


Fig 5.2 Sexual segregation in each study site expressed both as the percentage of all groups observed which are of mixed-sex, and as the percentage of all individuals observed in mixed-sex groups.

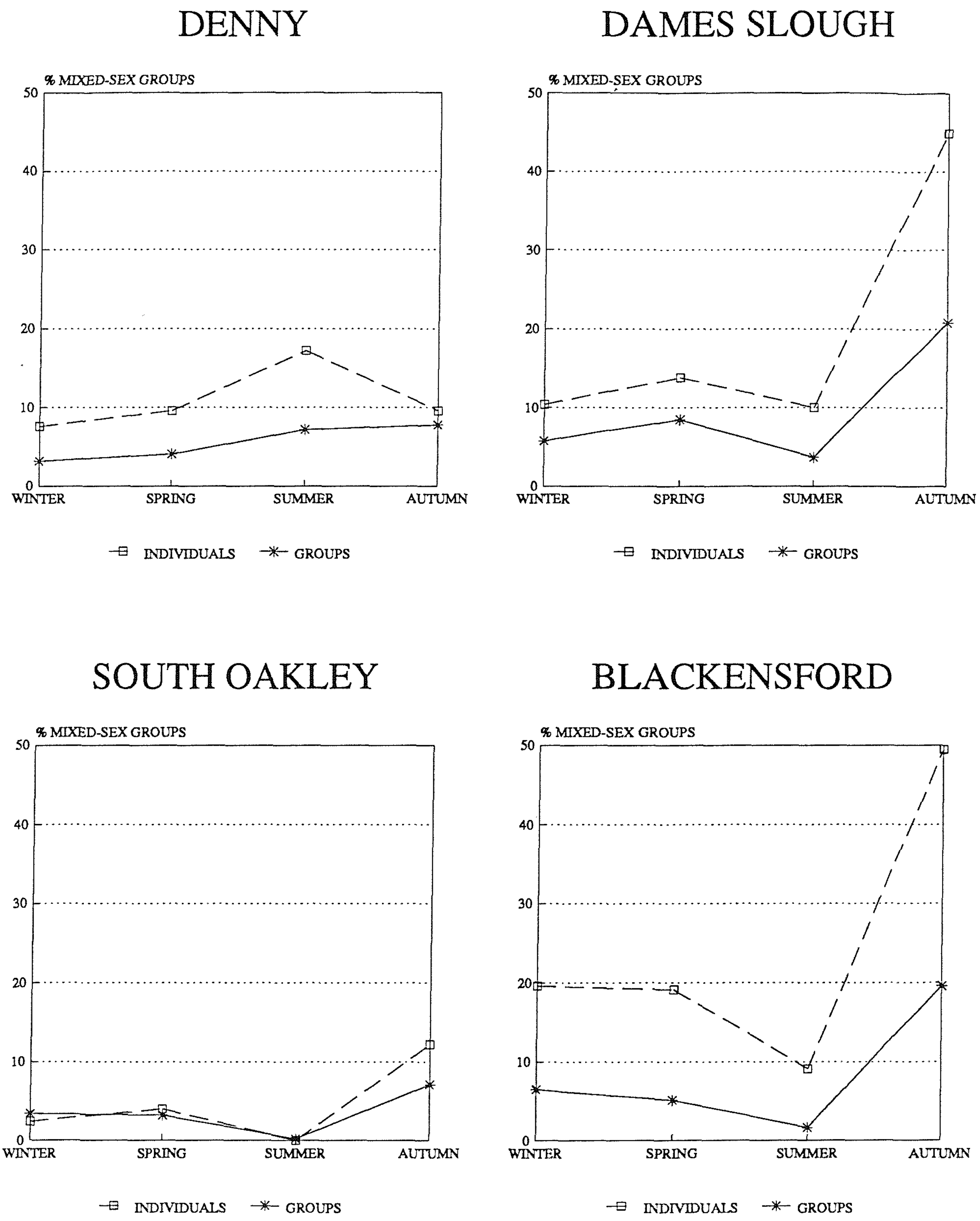
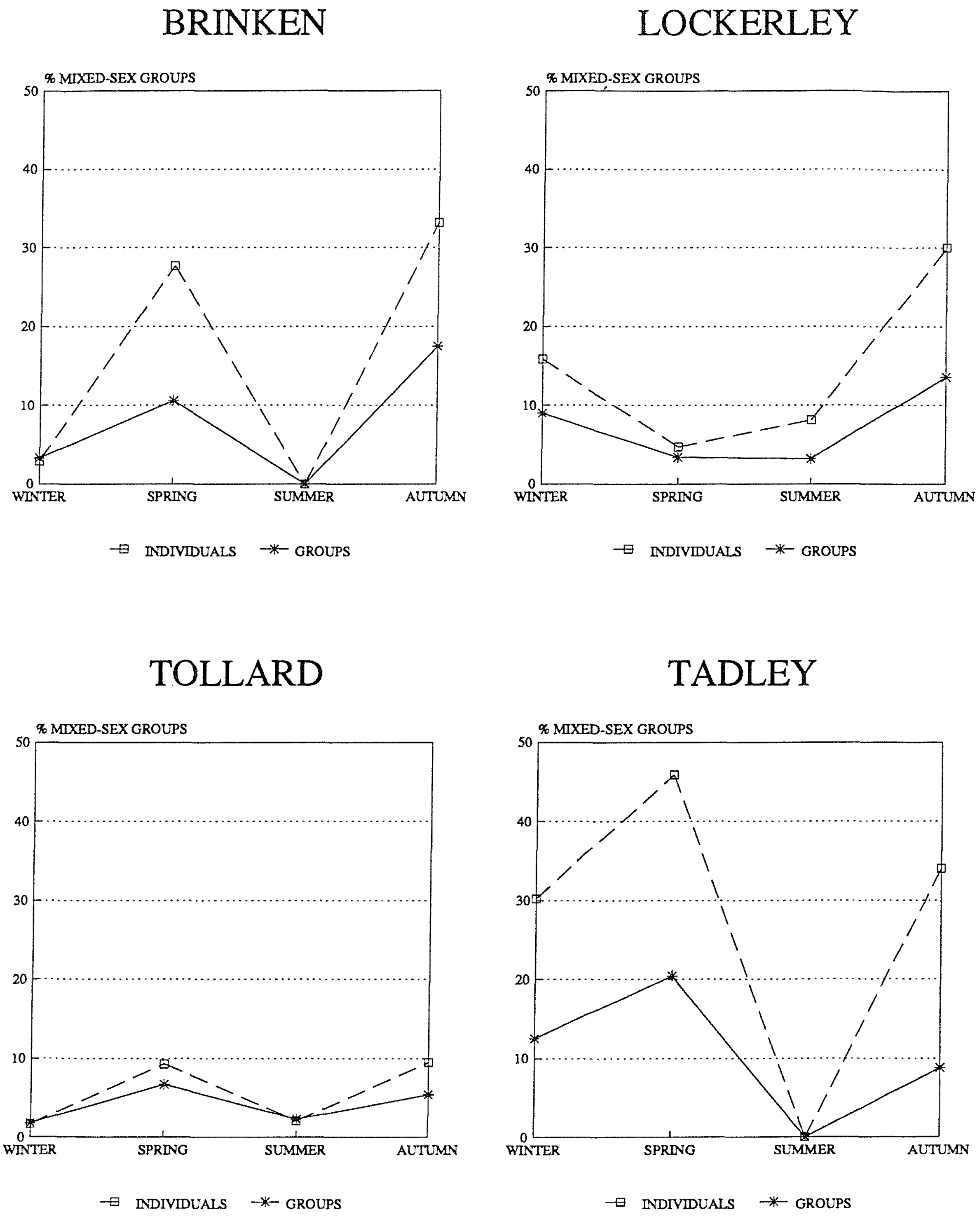


Fig 5.2 (continued)


BRINKEN

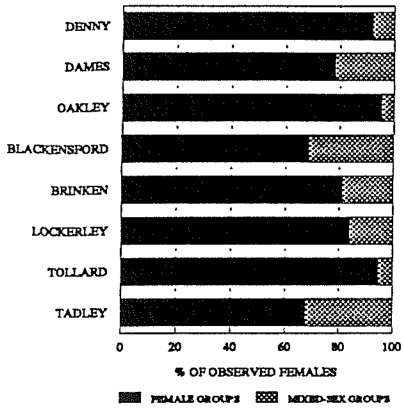
LOCKERLEY

TOLLARD

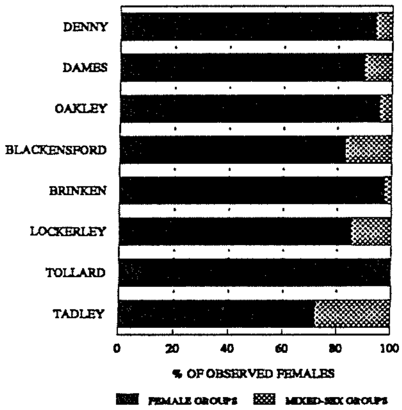
TADLEY

Fig 5.3 Annual and seasonal distribution of female deer into female groups and mixed-sex groups expressed as the percentage of all females observed in each site in each season.

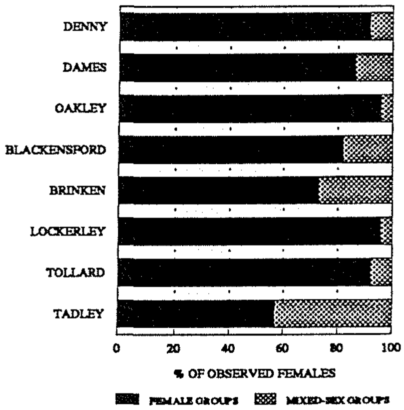
ANNUAL



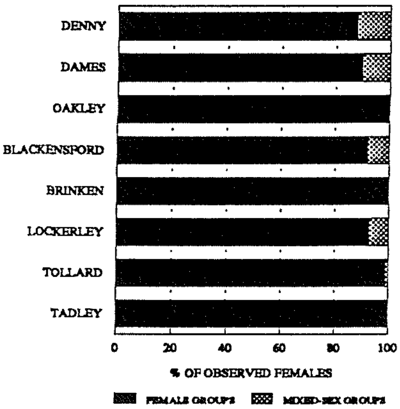
WINTER



SPRING



SUMMER



AUTUMN

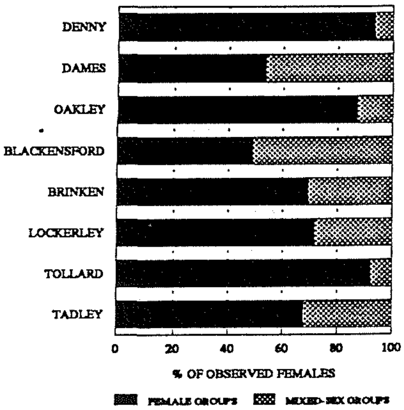
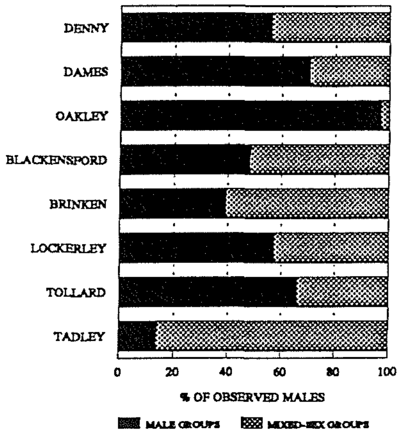


Fig 5.4 Annual and seasonal distribution of male deer into male groups and mixed-sex groups expressed as the percentage of all males observed in each site in each season.

ANNUAL



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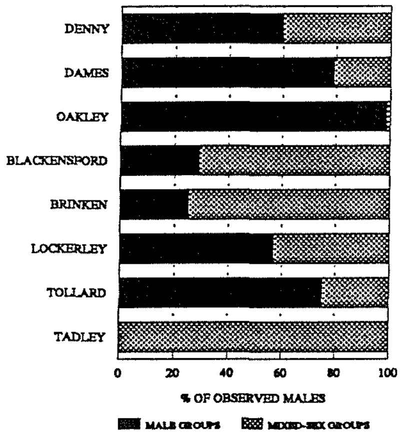

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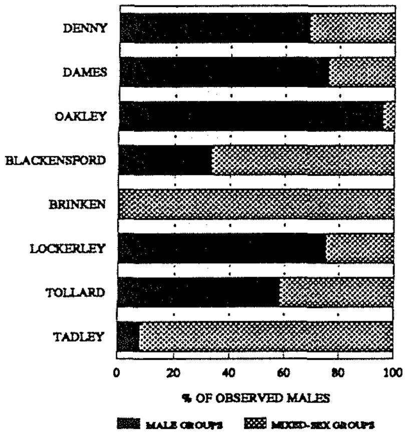
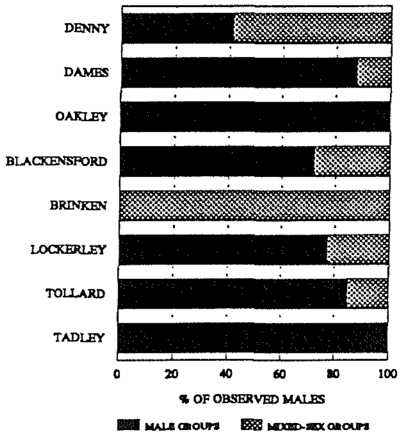
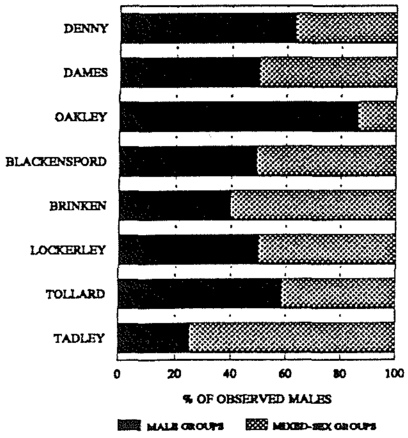


SUMMER



AUTUMN



6. PATTERNS OF SOCIAL GROUPING

6.1. INTRODUCTION

This chapter is principally concerned with variation in patterns of social grouping in populations of fallow deer living at different densities in environments contrasting markedly in habitat composition and structure. Earlier studies have demonstrated that fallow group size varies seasonally (eg. Jackson 1974) and in response to habitat (eg. Schaal 1982); however we have little understanding of how these two factors interact within populations. Additionally, previous workers have concentrated on single populations, and therefore very limited data are available on the influence upon grouping patterns of parameters such as population density and dispersion. In this chapter, grouping patterns within the eight study sites are initially examined, and the effects of season and habitat upon the size of female, male, and mixed-sex groups investigated. Comparisons are then drawn between sites, contrasting group size overall and within seasons and habitats, to determine the extent to which environmental influences on group size act to the same degree in different populations. Finally, having established that the study populations differ in grouping characteristics, the relationship between group size and the ecological parameters introduced in the three preceding chapters is investigated.

Interspecific variation in ungulate group size

The general introduction to this thesis considered in detail the ecological factors leading towards group living in mammals and birds. With few exceptions, these factors could be divided into three categories: escaping predators, acquiring resources, and interactions between conspecifics. The relationships between these parameters were clearly identified by the pioneering studies of Jarman (1974) and Estes (1974) on African antelope. Jarman's hypothesis, which related group size and social behaviour to body size and feeding style, was reviewed in Chapter 1. To summarise, Jarman demonstrated that small species have a high metabolic requirement per unit body weight and need to select high quality food. These food items often occur in closed habitats and are scarce and scattered in distribution, so small species are forced to lead a solitary territorial existence. In contrast, the large species eat poor quality food in bulk and graze unselectively on the open savannah. It is not economical to defend food supplies and these species aggregate in large herds for defence against predators. Antelope of intermediate size show aspects of the ecology and social organisation in between these two extremes.

The parallels between the socioecology of antelope and deer have long been recognized (eg. Jarman 1974; Geist 1974; Putman 1981) and differences between the 'typical' social systems of deer species can largely be explained on the same basis. Thus the small brocket deer *Mazama* spp. and pudu *Pudu* spp. of South American rainforests feed solitarily on highly nutritious, dispersed food items, whilst the large bodied open grassland barasingha *Cervus duvauceli* and rusa deer *Cervus timorensis* of Asia are bulk grazers foraging in large groups of up to several hundred (Putman 1988). Between these two extremes are deer of open woodland and forest edge, typified perhaps by the chital *Axis axis* of India, and the familiar European fallow deer. These species are intermediary in their foraging requirements, taking a mixture of browse and grasses, and may be found in groups varying greatly in size. Putman reviews the interaction of habitat type and feeding ecology in the evolution of social group size in deer and provides a useful summary table for a range of different species (Putman 1988, Table 4.1).

Intraspecific variation in ungulate group size

The previous section has implied that there are species-specific patterns of social grouping in many ungulates, largely driven by the requirements of feeding ecology. However it is now clear that the social organisation of many mammals and birds can be highly variable, with group size and social behaviour closely related to environmental variables such as habitat composition and structure and characteristics of the populations themselves. Amongst the ungulates, this variability was originally demonstrated in some of the better studied species of African antelope. Grants gazelles *Gazella granti* occur in open plains and scrub areas in the Serengeti and show a pronounced shift towards smaller groups in scrub and larger groups in the open (Walther 1972). Similar variability in relation to habitat openness was reported for impala *Aepyceros melampus* and hartebeest *Alcelaphus buselaphus cokei* at Tsavo and Nairobi National Parks in Kenya (Leuthold 1970; Leuthold & Leuthold 1975). More detailed analysis of impala and topi *Damiliscus lunatus* social grouping in the Serengeti suggested that intraspecific variation in group size was due to the quality, abundance and distribution of the food supply, the same factors influencing differences between species. (Duncan 1975; Jarman & Jarman 1979).

It is now very clear that similar intraspecific variation in grouping patterns occur in many cervids. Some deer species are more flexible in their habitat requirements and may be found in a range of environmental types; in these instances, typical group size has been shown to be high flexible and adaptable to ecological circumstance. An extreme example of this is shown by the European roe deer *Capreolus capreolus* which demonstrates great flexibility in adapting its sociality to different environments. Roe are relatively small, selective browsers and typically found in dense woodlands with deep cover. In these circumstances they are solitary and seasonally territorial (Cumming 1966; Hosey 1974). However, they are frequently found in small woodlands in agricultural areas where they remain solitary whilst in woods but form temporary associations of up to ten individuals when foraging on fields (Maublanc et al. 1985, 1987; Putman 1988). In the agrocenosis conditions of Central Europe, with no woodland cover, roe may form permanent social groups during winter and spring of up to 70 individuals (Bresinski 1982; Kaluzinski 1982).

Similar grouping patterns are shown by many other deer species which occur in a range of environmental types. Group size typical of populations in more open habitats are larger than those in woodland habitats as, for example, hog deer *Axis porcinus* and chital (Kurt 1978; Mishra 1982), red deer *Cervus elaphus* (Mitchell et al. 1977), black-tailed deer *Odocoileus hemionus* (Dasman & Taber 1956), moose *Alces alces* (Peek et al. 1974), and reindeer *Rangifer tarandus* (Skogland 1989).

Furthermore, it is clear that the adaptiveness of group size is not limited to differences between populations; in those areas where populations live in heterogeneous environments containing habitats differing in the extent of cover and distribution of food, group size may change with utilization of different habitats. For example, group size of sika deer *Cervus nippon* on Kinkazan Island, Japan, was larger in grassland than in woodland (Takatsuki 1983). Similar results were found in the two sika populations in Southern England studied by Putman & Mann (1990), with larger groups encountered in more open vegetation types than in dense forest. In these latter populations, group sizes within given habitats (eg. deciduous woodland, fields) were not different between the two sites; therefore overall differences between the populations in mean group size were due to different patterns of habitat use in the two areas (Mann & Putman 1989).

Similar increases in group size in response to habitat openness are not shown in all populations, however. White-tailed deer *Odocoileus virginianus* are widespread across much of North and Central America. Hirth (1977) made detailed studies of two populations; one inhabiting deciduous woodland in Michigan and the other scrub savannah habitat in Texas. Open grasslands were available to each population, but were much larger and more continuous in the Texas site. Group size in woodland was similar in both populations. In the Texas site, there was a very marked tendency for deer to form larger groups as the habitat became more open. In the Michigan site, however, deer did not alter their group size or composition in response to habitat. Hirth speculates that the lack of response to open areas in Michigan was due to the small size of those fields and the proximity of forest cover.

Hirth (1977) suggested that the large group size adopted by white-tailed deer in open habitat in the Texas population was an anti-predator response, invoking both the increased vigilance and dilution effect of groups. This idea was subsequently rejected by LaGory (1986) who did not find a habitat difference in vigilance behaviour in white-tails in a population on Ossabaw Island, Georgia. Group membership resulted in individual decreases in vigilance time and increases in foraging time in all habitats. LaGory suggested the observed smaller group size in woodland may simply occur because deer had difficulty maintaining contact with others when visibility was restricted.

Fallow deer group size: Current knowledge and outstanding questions

The original descriptive studies of social organisation of fallow, largely on populations living in or near extensive areas of woodland (eg. Cadman 1966; Chapman & Chapman 1975), suggested that fallow were a 'herding species', typically found in large groups. With hindsight, such an assessment can now clearly be seen as an oversimplification; fallow social organisation is complex and influenced by a number of factors including season, habitat, and population density.

The first quantitative studies by Jackson (1974) in the New Forest established that group size showed clear seasonal changes; groups were larger over the winter and spring, breaking up in early summer as females became more solitary during the fawning season, and reforming during the autumn. These seasonal patterns were confirmed by subsequent work by Parfitt (in Putman 1986a) in the same area. In both of these studies, the majority of groups encountered contained five or less individuals. Jackson (1974), and later Putman (1981, 1986a), suggested that fallow group size in the New Forest also varied with habitat openness, as small groups of deer typical of woodland came together to graze on open lawns and other favoured feeding areas, although neither author presented supporting data.

Quantitative descriptions of the effect of habitat on group size in fallow are available for some agricultural populations, where deer live in small woodlands surrounded by extensive areas of cereal crops and open pasture. Heideman (1973) working at Salzau, W. Germany, recorded larger groups on open fields than in woodland, and observed small groups aggregating on fields. A more detailed study by Schaal (1982) on a fallow population in the Alsace, contrasted animals living in a forest environment to those in a more open habitat, as well as deer inhabiting intermediate, semi-closed scrub. Solitary animals were seen most often in woodland, and mean group size was largest in the open. Identical group size variation in response to habitat openness has now been reported in British populations of fallow inhabiting similar mixed woodland-agricultural complexes (Waterfield 1986).

The studies described above suggest that, in common with many ungulates, group size in fallow deer is very variable and adaptable to environmental circumstance. However, because of differences in methodology and interpretation, comparisons between existing studies are difficult. We do not know if the response to habitat openness is universal and, if not, which characteristics of the environment are responsible. Habitat use has been shown to vary seasonally, therefore if group size is influenced by habitat, seasonal variation in group size may be explained by seasonal patterns of habitat use. Similarly, overall differences in group size between populations may be due to different patterns of habitat availability and utilization or, alternatively, due to differences between populations in group size adopted in particular habitats. If group size within similar habitats does vary between populations, we need to know why. Is this due to structural parameters of the environment such as the size of individual habitat patches, or are characteristics of the populations themselves important, such as density and dispersion?

Objectives of current study

In summary the objectives of this chapter are:

1. To investigate the effects of season and habitat on group size in the eight study sites.
2. To compare group size between study sites, both overall and within individual habitats and seasons.
3. To determine which environmental and population parameters are correlated to group size and its variability within sites.

6.2. METHODS

Direct Observation

Grouping characteristics of each population were examined by direct observation from fixed transect routes which were regularly patrolled throughout the year. The basic methodology of these transect walks has been described in detail in Chapter 2. In summary, data were collected on the number, composition, activity, and habitat of occupance of each group of deer sighted during daylight hours. Groups were categorized as either female, male, or mixed-sex, and were subsequently treated separately in the analysis. Data analysed in this chapter are based on observations of 4609 groups totalling 21034 individual deer. The calendar year was divided into the same four seasons as in earlier analyses (Winter: December-February; Spring: March-May; Summer: June-August; Autumn: September-November). Investigation of the influence of habitat type on group size was made initially at the simplest level of resolution of woodland/open habitats; additional analyses were undertaken in some cases utilizing the medium level of combined habitats (Table 3.1).

Definitions: Groups, Aggregations and Associations

Following Jarman & Coulson (1989) a group was defined as 'a number of animals observed in substantially closer proximity to one another than to other members of the population, and potentially able to communicate and interact cohesively with, and respond to the actions of, other members of the group'. This definition has spatial and behavioural components but does not imply that a group persists through time. In some studies of group-living animals, arbitrary maximal separations have been used to delimit groups, as for example by Underwood (1982b), working on a range of African savannah-dwelling ungulates, who considers 50m distance to separate members of different social groups. Clutton-Brock et al. (1982) undertook a more rigorous approach by determining the discontinuity in the bimodal distribution of nearest-neighbour distances, and setting that as a distance criteria to define groups of red deer. This approach may be applicable in the relatively homogeneous savannah or heathland environments of the two aforementioned studies, however in the current context, a 50m distance separating individuals in a conifer thicket may be of considerably different biological significance than the same distance separating individuals on a stubble field. Other studies have emphasized behavioural criteria, as for example LaGory (1986) who defines a group of white-tailed deer as those individuals who are moving together or escaping together. In practice there is usually less difficulty in deciding in the field what constitutes a group than there is in constructing a rigid set of criteria for its definition.

The behavioural component of the definition distinguishes a group from an aggregation (Jarman & Coulson 1989). The latter arises when animals are drawn to a spatially concentrated resource, are brought into proximity, but do not interact cohesively with each other. Putman (1981, 1986a, 1988) has suggested that there are two levels of social organisation in fallow deer (and other cervids): the strict fundamental social unit, identified here as the group, and casual aggregations of a number of these units, occurring together merely because they are using the same area simultaneously. However, in the current study, where individuals were brought together by common attraction to a spatially limited resource, as for example the good quality grazing available on New Forest improved grasslands, individuals often did act cohesively, in that they would respond to an alarm signal given by a single animal, and as such appeared to be aware of the behaviour of conspecifics. In the present study such units are termed associations, with the implicit recognition that they contained more than one social group, and might be only of a temporary nature. However, based on current behaviour at the time of observation, associations and groups were virtually indistinguishable in the field and, as such, were treated as a single entity for quantitative comparisons of grouping patterns within and between sites. It is acknowledged that this is a very difficult issue to resolve to everyone's satisfaction. Clearly, an association of 100 does, fawns and followers grazing on a field constitutes a very different, and easily recognizable, social unit to a single doe and fawn. However, between these two extremes lie a range of apparent social groupings which could arguably be assigned to either category.

Measures of group size - frequency distribution

Variation in group size within a population is most completely displayed as a frequency distribution, showing the frequency (or % frequency) of occurance of groups of particular sizes. Such an approach has been adopted by several of the earlier studies of fallow deer (eg. Jackson 1974; Schaal 1982; Waterfield 1986) and numerous other studies of social ungulates. An alternative is to determine the distribution of individuals into groups of each size class, thus placing the emphasis more upon the individual than the group, as has been suggested in the analysis of earlier chapters. These distributions can be tested by G-test for goodness-of-fit to a theoretical distribution such as a Poisson series or G-test for independence between different seasons or sites (Sokal & Rohlf 1981). In practice, however, these distributions are unwieldy tools for comparison, particularly when as in the current study complex questions are being asked of the data set. In this chapter both individual and group based frequency distributions are presented only as an overall measure for each site, and further comparisons are restricted to one of two measures of central tendency.

Measures of group size - central tendency

The most frequently used measure of central tendency of the group size frequency distribution is the arithmetic mean (eg. Schaal 1982; Parfitt in Putman 1986a [fallow deer]; Hirth 1977; LaGory 1986 [white-tailed deer]). However, mean group size reflects the perception of the external observer, not the social or ecological experience of the average animal being studied. Jarman (1974, 1982) introduced typical group size as a measure of the group in which the average individual occurs, intending it to reflect the social experience of the individual. The method of calculation of typical group size may be compared with mean group size by examination of the formulae below.

Mean group size $X = \Sigma x_i / n$
with standard error $S_x = \surd \{ [\Sigma x_i^2 - (\Sigma x_i)^2 / n] / n-1 \} / n$

Typical group size $G = \Sigma x_i^2 / \Sigma x$
with standard error $S_g = \surd \{ [\Sigma x_i^3 - (\Sigma x^2)^2 / \Sigma x] / (\Sigma x-1) \} / \Sigma x$

where x_i is the number of individuals in the $_i$th group and n is the number of groups.

Typical group size is more sensitive to variations in the group size frequency distribution than is mean group size, and in practice is approximately equal to mean group size plus one standard deviation. Although several subsequent authors have voiced concerns regarding the biological interpretation of the mean group size measure (eg. Underwood 1982b; Wirtz & Lorscher 1983), no published data are available for ungulate typical group sizes since Jarman's original 1974 paper. In contrast, typical group size has been widely used to describe the grouping characteristics of macropods (reviewed in Jarman & Coulson 1989). In this chapter both mean group size and typical group size are presented in parallel for all data sets. This is done both to facilitate comparison with previous studies of fallow and other ungulates, and also because mean group size may provide a useful currency for certain biological questions. For example, a possible factor influencing male mating strategy may be the size of female groups during the rut; males perceive female groups as external observers, hence mean group size is a more relevant measurement (see Chapter 7).

Two alternative measures of grouping tendency not utilized in this study are those of modal and median group size. Modal group size is simply the group size class in which the highest frequency was observed. The concept of modal group size is inherent in many non-statistical treatments of sociality that are expressed in such terms as 'mostly found alone'. Modal group size may be considered both in terms of the group size in which most individuals are found, or as the group size which occurs most frequently in the population. The limitation of either measure is that it conveys no information about the less frequent size classes in the frequency distribution.

Median group size was used by Wirtz & Lorscher (1983) to characterise the distribution of group sizes of eight antelope species. Clutton-Brock et al. (1982), influenced by Jarman (1982), used the group size of the median individual red deer, calculated by ranking the group size of all individuals seen and taking the median figure. However, neither of these methods utilizing median values fully exploit the data; the actual numeric value of all observations other than the median are not utilized in the calculation.

Woodland to open group size ratio

The group size of numerous social ungulates have been observed to change when animals move from closed to open habitats. As shall be shown in this chapter fallow deer also display this tendency, however there is considerable variation between study populations in the magnitude of the difference between habitats. This relationship can be quantified by calculating the woodland to open group size ratio as:

Group size in open habitat / Group size in woodland habitat

Statistical analysis

Analyses of differences between sites in the frequency distribution of individuals into groups of different sizes were made by G-test for independence with the Williams correction on the original data (Sokal & Rohlf 1981).

Frequency distributions of group size were not normally distributed, nor were conditions of homogeneity of variance met for ANOVA. Logarithmic transformation of the data did not resolve these problems for all sites, thus further analysis was by non-parametric Kruskall-Wallis and Mann-Whitney U tests (Siegel 1956). These non-parametric significance tests of differences in group size based on ranks almost certainly give a conservative estimate of the significance of the corresponding typical group size comparison (Underwood 1982b).

The relationship between group size and the ecological parameters of the previous three chapters was assessed by non-parametric Spearman rank correlation (Siegel 1956).

6.3. RESULTS

The results of this chapter are presented in four sections. The first provides an initial overview of female, male and mixed-sex group sizes in each study site, expressed as frequency distributions of particular size classes. The second section concentrates on within-site comparisons, exploring the influence of season and habitat, in both isolation and conjunction, upon group size. Section three investigates site differences in group size, both overall and within particular seasons and habitats. The final section examines group size in the eight study sites in terms of different patterns of habitat use and habitat composition and structure, and in respect to the population parameters previously described.

An overview of group size

The size of groups recorded in the eight study sites ranged from solitary animals to associations of 160 individuals. One approach to describing group size is to determine the frequency of occurrence of discrete size classes in each population. Groups of females, males, and mixed sex animals were categorized as containing 1-3, 4-6, 7-9, or 10+ individuals. The occurrence of groups of the four size classes is expressed as a percentage of total groups observed (Table 6.1). Thus, for example, 66.5% of all female-only groups seen at Denny were of the 1-3 category, 22.0% contained 4-6 individuals, 6.1% 7-9 individuals, and 5.4% 10+ individuals. Examination of Table 6.1 reveals that largely similar trends were shown by female groups in the other sites; in each case approximately

60-70% of all groups encountered were of the smallest size category, with limited variation in the frequency of occurrence of the larger group sizes in the different sites. Sample sizes for male-only and mixed-sex groups were much smaller and more variable trends were shown in the data. With the exception of South Oakley, more than 60% of all male groups observed contained from 1-3 individuals. Whilst groups of mixed-sex were relatively uncommon in most sites (see Chapter 5), their group-size distribution was more uniform than in the previous two cases, with the larger size classes occurring relatively more frequently.

Such an approach suggests that, for at least female-only and arguably male-only groups, fallow deer tend to be found in predominantly small groups. Is this however an accurate interpretation of the data? An alternative is to view the group size frequency distribution from an individual perspective, determining the percentage of individuals observed in groups of the four size classes. Reinterpretation of the data set utilizing this approach is presented in parallel to the group-based analysis in Table 6.1. Drawing upon the same example as above, that of female groups at Denny, it is clear that quite different conclusions could be drawn from the re-analysis. The smallest group-size category, that of 1-3 individuals, which occurs by far the most frequently in the site, in fact only accounts for some 34.6% of the individuals observed. A very similar percentage of the population (31.1%) occur in groups of 4-6 individuals, with the remaining 34.3% split between the two larger size classes. Examination of Table 6.1 reveals that a similar shift in emphasis from smaller to larger groups occurs in each site when the data are reanalysed in terms of individual distribution. This shift is particularly pronounced for the Brinken subpopulation where groups of 10+ animals account for 65.5% of the individuals sampled, but make up only 14.1% of total groups observed.

Used in conjunction, these two approaches can accurately portray overall grouping characteristics within individual sites. However, comparisons between sites, or between different seasons or habitats, are often difficult to interpret. Analysis by G-test of between-site comparisons of frequency distributions for both groups of different sizes and individuals into different size groups is shown in Table 6.2. Contrasting the statistical analyses of the two approaches to investigating group size suggests that differences between sites are amplified using the individual distribution. To a certain extent this is a reflection of the increased sample size of individual-based analyses; the significance of the statistical test increases as sample size increases even when the proportions of the distribution remain the same. This is not the only weakness of such analyses, however; group distributions and individual distributions are not directly comparable between sites. For example, groups of 10+ animals were observed at similar frequencies at Brinken and Tollard (14.1% and 11.0% of groups seen respectively). However, the number of individual deer seen in such groups varies greatly between the sites (65.5% and 33.1% respectively).

In summary, the two frequency distribution analyses in this section provide a useful descriptive overview of grouping characteristics in the eight study sites. In each site, groups of the smallest category of 1-3 individuals were encountered most frequently; however, individual deer were distributed more evenly between the group size classes. Frequency distributions are restricted in their usefulness for comparative studies, either between or within sites, and as such will not be presented in any further analyses.

Within-site comparisons of group size

Variation in response to season

Seasonal estimates of mean group size and typical group size for female, male and mixed sex groups in each study site are given in Tables 6.3 - 6.10.

Female groups

Restricting the analyses to female-only groups, significant seasonal variation in group size was shown in all eight study sites (Kruskall-Wallis tests, $p<0.001$; except Tadley $p<0.01$). In each site, excluding Tadley (see below), winter and spring group sizes were larger than in summer and autumn (Mann-Whitney U-tests, $p<0.01$). In the five New Forest sites, the largest groups as measured by the mean group size were recorded in spring; trends in typical group size were identical except in the case of Denny, where winter typical group size was marginally higher than spring. The smallest group sizes in the Forest sites, by either measure, occurred during the autumn, excluding the summer minimum at South Oakley, in any case based on a very small sample size. In contrast, at Lockerley and Tollard, the largest group sizes were recorded during the winter, and the smallest during the summer. These trends were identical with either mean or typical group size. In the agricultural site Tadley (Table 6.9), maximum and minimum group sizes were recorded in spring and summer respectively; group sizes in these seasons were significantly different (Mann-Whitney U-test, $p<0.001$), however other seasonal comparisons were not.

Male groups

Male deer were encountered less frequently in all sites excluding South Oakley (see Chapter 5), hence sample sizes are greatly reduced. Significant seasonal variation in group size was shown at Dames Slough (Kruskall-Wallis test, $p<0.001$), South Oakley, Blackensford, Lockerley (Kruskall-Wallis tests, $p<0.01$) and Tollard (Kruskall-Wallis test,

$p<0.05$). Male group size varied little at Denny, whilst at Brinken and Tadley male groups were observed only twice outside the autumn reproductive season. In those New Forest sites in which significant seasonal variation was shown, the largest male group sizes were observed during the spring and smallest during the autumn (spring:autumn, Mann-Whitney U-tests, $p<0.01$). At Lockerley and Tollard, the smallest group sizes were also seen in the autumn, but no consistent patterns in the other seasons emerged.

Mixed-sex groups

Mixed-sex groups were encountered irregularly outside of the autumn reproductive season in all sites (see Chapter 5), hence sample sizes were often too small for statistical analysis. This was the case in the three agricultural sites, however some general qualitative comments on the data can be made. Mixed-sex groups were often much larger than the corresponding female or male groups; this was true in all seasons at Lockerley and Tadley, but only during the autumn at Tollard. There was no common direction to any apparent seasonal changes in mixed sex group size in the three sites.

Larger samples were available from some New Forest sites which allow formal statistical analysis. At Denny and Blackensford, winter, spring, and summer mixed sex groups were all significantly larger than in autumn (Mann-Whitney U-tests, $p<0.01$). In contrast, at Dames Slough there was no seasonal variation in group size; this lack of variation exists despite mixed groups occurring chiefly in woodland during the autumn, whilst at other times of year they were almost exclusively on open grassland. Mixed-sex groups were only seen in any numbers at Brinken during spring and autumn; however the contrast between these two seasons was marked, with the occurrence of very large associations of up to 160 individuals during spring, and much smaller rutting groups during autumn (spring:autumn, Mann-Whitney U-test, $p<0.001$).

Variation in response to habitat

Variation in estimates of mean group size and typical group size for each study site and sex class in relation to changes in habitat are given in Tables 6.3 - 6.10. This analysis was performed at two levels of resolution; initially habitats were categorized as either woodland or open, and subsequently a more detailed investigation utilized the medium level of combined habitats (see Table 3.1).

Female groups

Female groups in the New Forest showed pronounced and highly significant differences in both mean and typical group sizes between woodland and open habitats in all sites excluding South Oakley (Mann-Whitney U-tests, $p<0.001$). In these four sites, mean group sizes were approximately 2-4 times larger in the open than in woodland; the same trends were found using the typical group size measure with differences between the habitats even more pronounced. Analysis at the medium level of habitat resolution demonstrates that there was little variation within the four woodland categories in any of the four sites. However, when significant woodland group size variation did occur it was not as might have been predicted; groups on woodland rides were smaller than in open canopy woodland at Denny (Mann-Whitney U-test, $p<0.001$), and closed canopy woodland group sizes were highest of all woodland categories at Blackensford (Mann-Whitney U-tests, $p<0.01$). Variation within the open habitat categories was more pronounced. At Blackensford and Brinken group sizes on grassland were markedly higher than on heathland (Mann-Whitney U-tests, $p<0.01$), likely a reflection of aggregation in the former habitat. Grassland group sizes at Dames Slough were similarly high, however there were no other open habitats for comparison. In contrast at Denny, there was little difference between grassland and heathland groups; at this site, however, these two open habitats are closely interspersed. At South Oakley, sample size in open habitat was very limited (total 11 groups observed), but the little data that is available suggests that habitat effects were minimal. Similar results were obtained at the medium level of habitat resolution.

Tollard and Tadley female group sizes were also larger in open habitat than in woodland (Mann-Whitney U-tests; $p<0.001$, $p<0.05$); similar trends were shown as in the four Forest sites. Here too, group size varied little within the woodland habitat types. At Tadley, groups were larger on grasslands than arable crops (Mann-Whitney U-test, $p<0.01$); opposite trends were shown at Tollard but were not significant. In direct contrast, female group size at Lockerley did not vary significantly when analyzed at the woodland/open level of habitat resolution. This was not due to sampling limitations, as adequate numbers of groups were seen in both woodland and open habitats. Closer examination at a finer level of habitat resolution indicates that some limited variation in group size does exist (Kruskall-Wallis test, $p<0.05$); groups on grassland, although occurring relatively infrequently, were significantly larger than all other habitat categories (Mann-Whitney U-tests, $p<0.01$). Group size on arable land, which was used much more intensively at Lockerley (see Chapter 4), was no larger than in any of the woodland habitats.

Male groups

Male group size in the New Forest showed more limited variation in response to change in habitat openness; significant increases in open habitat group size were shown only at Dames Slough (Mann-Whitney U-test, $p<0.001$). The lack of significant variation in other sites was in part due to small sample size in one or both of the habitats. However even at South Oakley, where male groups were frequently seen in both open and woodland, group size did not markedly change. At Dames Slough, the variation was entirely due to the big male groups found on the grasslands at Burley Lodge; these groups were significantly larger than in all other habitats (Mann-Whitney U-tests, $p<0.01$).

Amongst the agricultural sites, adequate male samples for statistical analysis existed only at Lockerley and Tollard; in these sites male group sizes were larger in open than woodland (Mann-Whitney U-tests, $p<0.05$). In both sites, male group size did not vary between the woodland habitat types. Significant variation overall (Kruskall-Wallis test, $p<0.05$), was a result of the relatively large male groups on arable fields (arable:all woodland habitats, Mann-Whitney U-tests, $p<0.05$).

Mixed-sex groups

Group size variation in response to woodland/open habitat was shown in three New Forest sites; Dames, Blackensford, and Brinken. In each site, open habitat group sizes were markedly larger than in woodland (Mann-Whitney U-tests, $p<0.001$). In common with female groups, group size variation within woodland habitats was not pronounced; significant overall variation at this level of habitat resolution in each of the three sites (Kruskall-Wallis test, $p<0.001$) was due to very large mixed-sex groups on improved grasslands (grassland: all other habitats, Mann-Whitney U-tests, $p<0.01$). Mixed-sex groups at Denny did not vary significantly in size at either level of habitat resolution.

Analysis of mixed-sex group-size variation in response to habitat in the agricultural sites was limited by small sample size. Group size appeared to follow the same trends as with females in these sites; Lockerley groups showed little change between habitats, and Tollard and Tadley groups increased in size in the open, but statistical analyses were inconclusive.

Seasonal and habitat influences isolated

The data presented suggest, with some limitations, that both season and habitat may have an effect on the grouping patterns of female, male and mixed-sex groups. However, these two separate influences have not yet been isolated; if group size is affected by habitat, and patterns of habitat use change seasonally (see Chapter 4), then observed seasonal patterns in group size may merely reflect changes in habitat use. Conversely, apparent changes in group size in relation to habitat could result from the combined effects of seasonal changes in grouping patterns and habitat use. In the analysis of this section the effects of these two factors are isolated for each study site; initially seasonal group size variation within habitats is examined, and then group size variation between habitats within seasons. Data are presented as in the previous section; initially at the woodland/open level of habitat resolution, and then at the level of combined habitats

(Tables 6.11 - 6.18). For simplicity, statistical analysis is restricted to the former approach.

Female groups

Within woodland, highly significant seasonal variation was shown in all sites excluding Tadley (Kruskall-Wallis tests, $p<0.001$). In each of the seven sites, winter and spring group sizes were larger than in summer and autumn (Mann-Whitney U-tests, $p<0.01$). At the agricultural site Tadley, similar trends were shown but were well below significance.

Seasonal variation in open habitat was very similar. Within the New Forest, Denny, Dames Slough, Blackensford and Brinken showed similar patterns to woodland seasonal variation; winter and spring groups were larger than in summer and autumn (Kruskall-Wallis test, $p<0.01$; Mann-Whitney U-tests, $p<0.01$). Sample size at South Oakley was too small for analysis. Seasonal group size variation in open habitat in the agricultural sites was also pronounced (Kruskall-Wallis test, $p<0.01$) but no consistent patterns emerged for the three sites. At Lockerley, summer group size in open habitat was smaller than for all other seasons (Mann-Whitney U-tests, $p<0.05$); similar patterns emerged at Tollard but additionally winter group size was significantly larger than at other times of year (Mann-Whitney U-tests, $p<0.01$). At Tadley, groups in open habitat in spring were larger than in other seasons (Mann-Whitney U-tests, $p<0.05$).

The alternative approach to investigating this data is to examine differences in woodland and open group sizes within single seasons. Within the New Forest, during winter and spring, there were significant increases in group size in open as compared to woodland habitat at Denny, Dames Slough, Brinken and Blackensford (Mann-Whitney U-tests, $p<0.01$). This difference between habitats was maintained in summer in the former three sites (Mann-Whitney U-tests, $p<0.001$) but not at Blackensford where summer groups were only marginally smaller in woodland than in open habitat. During the autumn, the woodland/open difference broke down at Denny and Brinken; to a certain extent at Denny this reflected the decreased use of open habitat at this time (see Chapter 4). However at Brinken there was a marked decrease in female group size on grassland and heathland during the autumn rut. At South Oakley, few female groups were seen in the open, and comparisons between habitats in any season were not significant.

Amongst the agricultural sites, only Tollard showed clear group size differences between woodland and open habitats in all seasons (Mann-Whitney U-tests; winter, summer, autumn, $p<0.01$; spring, $p<0.05$). Group size at Tadley was highly variable; open habitat groups were significantly larger than woodland groups in spring (Mann-Whitney U-test, $p<0.01$), but not in other seasons. In contrast to all other sites, group size variation in relation to habitat at Lockerley was significant only during the autumn, at which time open habitat groups were larger than in woodland (Mann-Whitney U-test, $p<0.001$); during the rest of the year groups in each habitat were of approximately equal size.

In summary, seasonal change in female group size is confirmed; essentially similar variation in grouping patterns occurs in both woodland and open habitats, with groups relatively larger in winter and spring and smaller in summer and autumn. It appears that the effect of habitat upon female group size may not be uniform throughout the year. Similarly, the habitat/group size relationship is not universal; considerable variation exists, particularly in the agricultural study sites.

Male groups

Within woodland, seasonal variation in male group size was shown in the same five sites (Dames Slough, South Oakley, Blackensford, Lockerley and Tollard) that showed overall seasonal change (Kruskall-Wallis tests, $p<0.05$). Where the data set was large enough for formal analysis, male group size in woodland was significantly smaller in autumn than other seasons (Mann-Whitney U-tests, $p<0.05$). This relationship was particularly clear at Dames Slough and Blackensford where autumn reproductive activity was pronounced. Seasonal group size variation in open habitat was shown only at Dames Slough (Kruskall-Wallis test, $p<0.001$), where winter group size was larger than all other seasons (Mann-Whitney U-tests, $p<0.01$). Dames Slough was also the only site at which significant male group size variation in relation to habitat occurred within seasons. Male groups on the open fields at Burley Lodge were larger than in the adjacent woodland in all seasons but spring (Mann-Whitney U-tests, $p<0.01$).

Mixed-sex groups

Significant seasonal variation in mixed-sex group size within habitats was shown in the same three sites that showed overall seasonal change. At Denny, this was restricted to woodland habitats (Kruskall-Wallis test, $p<0.01$) where winter and spring groups were larger than summer and autumn (Mann-Whitney U-tests, $p<0.05$). Seasonal variation at Blackensford and Brinken was limited to open habitat (Kruskall-Wallis tests, $p<0.01$) where autumn group size was smaller than group size in spring (both sites, Mann-Whitney U-tests, $p<0.01$) and winter (Blackensford, Mann-Whitney U-test, $p<0.05$). Group size variation between woodland and open habitats occurred in autumn at Dames Slough and Brinken (Mann-Whitney U-tests, $p<0.05$, $p<0.01$); here mixed-sex groups on grassland were larger than in woodland. Similar variation was shown during winter at Blackensford and spring at Tollard (Mann-Whitney U-tests, $p<0.05$).

Within-site comparisons of group size: a summary

There was a pronounced seasonal change in female group size in all sites, with larger groups in winter and spring and smaller groups in summer and autumn. This shift was not simply in response to changing patterns of habitat use; group size decreased in summer and autumn in both woodland and open environments. Seasonal variation in the size of male groups and groups of mixed-sex was less clear cut, in part due to small sample size in some study sites. Generally, male and mixed-sex groups were smallest during the rut, with little seasonal variation shown throughout the rest of the year.

In conjunction with the effect of season, the habitat type also strongly influenced female group size in most sites. This was most pronounced in the New Forest, where female groups were larger in open habitat than in woodland during much of the year. Group size varied little between woodland habitats; however female groups on New Forest grasslands were larger than on heathland. Similar habitat effects were shown at Tollard and Tadley; female groups in the open were larger than in woodland, group size varied little within woodlands, and there was some limited variation in group size between the open habitats. Habitat influences on female group size at Lockerley were much reduced in relation to the other sites. Woodland and open groups differed little in size throughout much of the year.

Habitat effects on male group size were varied. Within the New Forest, clear decreases in woodland group size were shown in one site but little change in another. When mixed-sex groups occurred, they largely followed the pattern of female group size; open habitat groups were larger than similar groups in woodland.

Between-site comparisons of group size

Overall differences

Group size overall, presented here as both mean and typical group size (Fig 6.1), varied significantly between the sites for all three group types (Kruskall-Wallis tests, $p<0.001$). Analysis at this very simplistic level will investigate all group types; more detailed subsequent analysis will largely concentrate on females for which good data sets exist for all sites.

Contrary to initial expectations, there were no obvious divisions between the New Forest and agricultural study sites in overall female group size. Group size at Brinken seems clearly larger than elsewhere; 2 times the mean group size and 5 times the typical group size of other sites. However, the values of these measures were greatly inflated by the occasional occurrence, particularly in spring, of very large associations of female groups on the fields at Queen's Meadow. The non-parametric tests of significance used in this analysis do not utilize the magnitude of differences between groups; thus what appears to be a difference of biological importance between Brinken and the other seven sites, is of reduced statistical validity. Overall group size at Brinken was significantly larger than at Denny and Blackensford (Mann-Whitney U-test, $p<0.001$), but not in any other sites. Reanalysis of female group size variation excluding Brinken also gave a highly significant result (Kruskall-Wallis test, $p<0.001$). Which sites were responsible for this variation? Female group sizes at Denny and Blackensford were significantly smaller than at all other sites (Mann-Whitney U-tests: Dames Slough and South Oakley, $p<0.05$; Lockerley, Tollard and Tadley, $p<0.001$). Overall female group size was not significantly differentamongst these latter five sites, two Forest and three agricultural.

Male group size variation between sites was much simpler (Fig 6.1). The largest male groups were at South Oakley and Dames Slough (Mann-Whitney U-tests, Dames Slough and South Oakley: all other sites, $p<0.01$), the only sites at which males were consistently seen outside of the rut. The mean size of groups encountered in these two sites was approximately six, whilst the average male was in a group of eleven or twelve. Elsewhere in the Forest and in the three agricultural sites mean group size was approximately two, with typical group size ranging from two to five individuals. This group size variation is probably more a reflection of the number of males available in the population to form a larger group than any environmental influence.

Between-site comparisons of mixed-sex group size (Fig 6.1) suffer the same problems as the earlier female group size analysis; the Brinken distribution was highly skewed and a few very large associations (150 individuals) exaggerate both measures of central tendency. Based on ranks, Brinken mixed-sex groups were no larger (or smaller) than any other site. When group size data was reanalysed excluding Brinken, significant variation between the sites (Kruskall-Wallis test, $P<0.001$) was a result of the large mixed-sex groups at Tadley (Tadley:all other sites, Mann-Whitney U-tests, $p<0.01$); variation between other sites was not significant.

Female group size : a recap

The data and analyses presented above suggest that overall differences in female group size between sites were less than had been predicted; significant variation was limited to smaller groups being observed in two New Forest sites. However, in the previous section of this chapter, it was shown that there was considerable variation in group size within sites in relation to both season and habitat. The next stage of the analysis of this section is to contrast female group size between sites within seasons and habitats.

Variation within seasons

Female group size varied significantly within each season (Fig 6.2), however this variation was less pronounced during winter (Kruskall-Wallis test, $p<0.05$) than at other times of year (spring, summer, autumn: Kruskall-Wallis test, $p<0.001$). Winter group size was relatively uniform, with only South Oakley females in significantly smaller groups than the other sites (Mann-Whitney U-test, $p<0.05$).

During the spring, Brinken females were found in very much larger groups than elsewhere (Mann-Whitney U-tests, $p<0.01$). However, variation between the remaining sites was more limited. Groups at Denny were smaller than the other sites, excluding Lockerley and South Oakley (Mann-Whitney U-tests, $p<0.05$).

Summer variation between the sites was more pronounced, but still there were no clear divisions between Forest and agricultural populations. Brinken females were again in the biggest groups, significantly larger than all but Dames Slough (Mann-Whitney U-tests, $p<0.01$). Dames Slough groups were larger than all other Forest sites and Lockerley (Mann-Whitney U-tests, $p<0.05$), but not Tollard and Tadley. The smallest female groups were at South Oakley, significantly smaller than all other sites (Mann-Whitney U-tests, $p<0.01$).

Between-site comparisons in autumn showed slightly clearer differences between the two main environmental types in female group size. Excluding for the moment Dames Slough and Brinken, the three remaining Forest sites were all significantly smaller than the three agricultural sites (Mann-Whitney U-tests, $p<0.05$). Variation in female group size within the three Forest sites was not significant, nor was variation within the three agricultural sites. Female group size at Dames Slough and Brinken was larger than at Blackensford (Mann-Whitney U-test, $p<0.001$), but not different to any other site.

Variation within habitats

Group size has been shown to relate to habitat - but is the relationship with habitat the same in all sites ? For simplicity of interpretation, within-habitat female group size variation between sites was examined at the resolution of woodland and open (Fig 6.3). Earlier analyses demonstrated that, for most sites, there was little variation in group size within different components of these two categories, and the study sites differed significantly in female group size in both habitat types (Kruskall-Wallis tests, $p<0.001$).

Examination of woodland group size suggests that there were differences between agricultural and Forest sites, however these differences were not clear cut, and there was overlap between the two environmental types. Woodland group size at Lockerley, Tollard, and Tadley was significantly larger than at Denny, Dames Slough and Blackensford (Mann-Whitney U-test, $p<0.01$). Group size in woodland at Brinken was intermediate between the two clusters of sites; larger than the other Forest sites (Mann-Whitney U-tests, $p<0.01$), but with a tendency to be smaller than the agricultural populations. Woodland group size at South Oakley does not fit neatly into the pattern of the other New Forest populations. Female deer were present in this site principally during winter and spring (see Chapter 5) when group sizes are large; it is thus likely that yearly figures of group size are exaggerated because of over-sampling in these seasons.

There was a suggestion that open habitat group size also differed between the two environmental types, however in this case the trend was in the opposite direction. Open group size was largest at Brinken and Dames Slough (Mann-Whitney U-tests, $p<0.01$), the two Forest sites which contained considerable areas of improved grassland that were extensively utilized by deer. Open group size in the remaining three Forest sites was larger than at Lockerley (Mann-Whitney U-tests, $p<0.05$) but not at Tollard and Tadley.

Variation within seasons and habitats

The preceding analyses suggest that there were differences between the two environmental types in patterns of female grouping; woodland group size tended to be larger in the agricultural populations, whilst open group size was largest in some New Forest sites. Earlier analysis shows that the extent of variation between sites in female group size changes seasonally. This section looks at between-site variation in group size in both woodland and open habitats in each of the four seasons (Table 6.19).

Winter group size varied between study sites in both woodland and open habitats, (Kruskall-Wallis tests; $p<0.01$, $p<0.05$). Woodland groups in the Forest sites Denny, Dames Slough and South Oakley were smaller than in all other sites (Mann-Whitney U-tests, $p<0.05$), however group size in these remaining five sites did not vary significantly. Variation between sites in open habitat group size was as great within as between environmental types.

Spring group size also varied between sites in both habitats, although variation at this time was more pronounced in open than in woodland (Kruskall-Wallis tests; $p<0.01$, $p<0.05$). Woodland groups at Denny were significantly smaller than all other sites excluding Dames Slough (Mann-Whitney U-tests, $p<0.05$). Variation between other sites in woodland group size was not significant. Group sizes in the open at this time can be divided into two classes, with significant differences between but not within the classes (Mann-Whitney U-tests, $p<0.05$). Larger groups were found at Brinken, Tadley, Blackensford, and Dames Slough; smaller groups at South Oakley, Denny, Tollard and Lockerley.

Between-site female group size variation in summer was again more pronounced in open habitat than woodland (Kruskall-Wallis tests; $p<0.001$, $p<0.05$). Woodland group sizes in the agricultural sites were slightly larger than in the Forest, however this was only significant in the case of Lockerley (Mann-Whitney U-tests, $p<0.05$). Open habitat group size at Brinken and Dames Slough was clearly larger than at all other sites (Mann-Whitney U-test, $p<0.01$), a reflection of the continuing tendency of deer in these two sites to aggregate onto improved grasslands.

Female group size in autumn is of considerable interest because of its possible influence on male mating strategies during the rut. Differences between the agricultural and Forest sites were most pronounced in woodland at this time (Kruskall-Wallis test, $p<0.001$); group sizes in the three agricultural populations were larger than in all the Forest populations (Mann-Whitney U-test, $p<0.05$). Within the Forest sites, female groups at Blackensford were smaller than at Brinken (Mann-Whitney U-test, $p<0.001$), with the remaining three sites intermediary between the two. Autumn group size in open habitat also varied between the sites (Kruskall-Wallis test, $p<0.05$), but less so than in woodland. Open group size at Denny was smaller than all other sites excluding South Oakley (Mann-Whitney U-tests, $p<0.05$) but differences between other sites were not significant.

Woodland to open group size ratio

Data presented in the second section of this chapter suggested that female group size was strongly affected by habitat openness; in most sites group size was larger in open habitats than in woodland. However the magnitude of this change varied both between sites within seasons and between seasons within sites. For comparison between sites this is best presented as a ratio calculated as woodland group size / open group size. This ratio may be expressed in either the currency of mean group size or typical group size. The sites were then ranked in order of increased value of the woodland open ratio (Table 6.20). Use of either mean or typical group size had little effect on rankings, resulting in only minor changes in the order of sites. Lockerley and South Oakley consistently showed the least change in group size between habitats, Dames Slough and Brinken the greatest change.

Between-site comparisons of group size : a summary

Overall female group size varied between sites, however variation was as pronounced within the two environmental categories as between them. Group size was affected by season and habitat to varying degrees in each site and analysis concentrated on contrasting the sites with these factors isolated. There was a suggestion that female deer in the agricultural sites occurred in larger groups than in the New Forest when in woodland, but in smaller groups when in open habitat. Group size differences between female deer in the two environments were not clear cut; there was considerable overlap between Forest and agricultural sites. Environmental class differences in woodland group size were pronounced in autumn, with possible implications for mating system variation.

Male group size variation between sites was pronounced. Large male groups were regularly seen only at South Oakley and Dames Slough in the New Forest, likely more a reflection of total male numbers in the different populations than environmental factors. Very large mixed-sex groups were limited to Brinken and Tadley; elsewhere mixed-sex group size variation was not significant.

Ecological correlates of group size

In this final section patterns of social grouping described in the different study sites and differences between them will be related to the ecological parameters of earlier chapters: habitat composition, diversity, and structure (Chapter 3); patterns of habitat use (Chapter 4); and population density and dispersion (Chapter 5). All data have been previously presented and are not replicated here; reference is made to the relevant tables and figures. Analysis is restricted to female-only groups for which good data sets are available for each site; all subsequent references to group size thus refer only to females.

Habitat composition

In the third section of this chapter it was shown that whilst group size in most sites varied between woodland and open habitats, there was little variation within these categories; hence the effect of habitat composition upon group size can be examined at the simplest level of resolution of percentage woodland and open habitat (Fig 3.9).

Female group sizes overall, in woodland, and in open habitat, for each site are given in Figure 6.1 and Tables 6.3 - 6.10. There was no relationship between percentage woodland in each site and overall group size. However, as the relative area of woodland increased in the study site, there was a decrease in woodland mean group size ($rs=-0.7381$, $n=8$, $p<0.05$). Group size in open habitat was not related to percentage woodland directly, however the ratio of woodland to open mean group size (Table 6.20) increased as percentage woodland increased ($rs=0.7186$, $n=8$, $p<0.05$).

In summary, increased percentage woodland was accompanied by a decrease in woodland group size and a corresponding increase in the difference between woodland and open group size. There was no simple relationship between group size overall and the relative amounts of woodland and open habitat in the sites.

Habitat diversity

Measures of habitat diversity of the eight study sites were presented in Table 3.2. Two indices were used to calculate diversity, however both resulted in the same ranking and thus give identical results in non-parametric correlation analysis. Habitat diversity was negatively correlated to overall mean group size (rs=-0.7545, n=8, $p<0.05$), but not to group size in either woodland or open. There was no relationship between habitat diversity and the woodland to open group size ratio. It is important to remember that the diversity indices are not measures of the spatial distribution of habitat types, but simply reflect the number and relative abundance of habitat types within each site.

Habitat structure

Female group size, both overall and separately in woodland and open habitats, and the woodland to open group size ratio were examined in respect to three habitat structure parameters that could be converted into linear measures: grain size of all individual habitats, all woodland habitats, and all open habitats (Fig 3.14); amount of woodland to open edge (Table 3.3); and the occurrence of habitat change, both at an individual habitat level and at woodland to open level (Fig 3.15). There was no relationship between any of the above habitat structure parameters and the two measures of grouping characteristics.

Habitat use

Habitat use patterns were earlier examined at the combined level of habitat resolution and differences between sites shown to be highly significant (Tables 4.9 & 4.10). Are group size differences between sites thus simply a reflection of different patterns of habitat use?

Analyses in this chapter have shown that differences in group size in most sites were largely between woodland and open habitats; group size varied little within these two categories. Investigation of the effect of habitat use upon group size between sites should therefore be based at this level of resolution. The analyses of this chapter have also revealed that group size within woodland and open habitats is not fixed between sites, therefore similar patterns of habitat use may not necessarily be reflected by similar patterns of group size. In contrast to the previous habitat composition and structure parameters, habitat use varies with season, therefore analysis of the relationship between patterns of habitat use and group size was performed on a seasonal basis. Seasonal estimates of mean and typical group size overall, and in woodland and open habitat were presented in Fig 6.11 and Tables 6.11 - 6.18.

The estimated seasonal percentage use of all woodland habitats by female groups in each site was presented in Table 4.11. Use of woodland was analysed in relation to mean and typical female group size overall, in woodland habitat, in open habitat, and to the woodland open group size ratio. Each correlation analysis was repeated for winter, spring, summer, and autumn. Group size was independent of habitat use in all seasons except spring, when there was a significant negative correlation between overall mean group size and use of woodlands (rs=-0.6667, n=8, p<0.05). Spring use of woodlands was also negatively correlated to typical group size in open habitats (rs=-0.7619, n=8, p<0.05), suggesting that high utilization of open habitat at this time was accompanied by large open habitat group size. The spring mean and typical woodland open group size ratios were also negatively correlated to use of woodland (rs=-0.6429, n=8, p<0.05; rs=-0.7186, n=8, p<0.05), reflecting the same pattern as the previous two relationships.

In summary, group size and the woodland to open group size ratio were largely independent of patterns of habitat use. Only in spring was the increased use of open habitat in some populations reflected by increased group size both in open habitat and as an overall measure. Similarly, in this season, the increased use of open habitat and subsequent large group sizes, resulted in a larger woodland to open group size ratio.

Population density

Population density varied greatly between the study sites, both annually and within individual seasons (Table 5.1). Were annual and seasonal grouping patterns simply a reflection of the density experienced by the deer?

There was no simple relationship between estimates of annual density and overall group size; large group size occurred in both high density populations such as Brinken and low density populations such as Tadley. However, when group size was analyzed separately for woodland and open habitats, significant correlations with population density emerge. Density was negatively correlated to woodland group size (mean: rs=-0.8571, n=8, p<0.01; typical: rs=-0.7857, n=8, p<0.05). Conversely, density was positively correlated to open group size (mean: rs=0.8571, n=8, p<0.01; typical: rs=0.7143, n=8, p<0.05). Thus in high density populations open habitat group size was bigger and woodland habitat group size was smaller than in low density populations. From this result it is clear that the woodland open group size ratio should also be related to density; there was a positive correlation between the ratio of group size between the two habitats and population density (mean: rs=0.7143, n=8, p<0.05; typical: rs=0.8743, n=8, p<0.01).

The above relationships are significant for data summarised over the whole year, however both group size and population density vary seasonally. Are these relationships retained in each season?

Group size overall was independent of seasonal density throughout the year, however there was considerable variation in the relationship between density, and woodland and open group size in different seasons. Woodland group size was negatively correlated to density in winter (mean: $rs=-0.6667$, $n=8$, $p<0.05$; typical: $rs=-0.7619$, $n=8$, $p<0.05$) and in autumn (mean: $rs=-0.3333$, $n=8$, ns: typical: $rs=-0.7381$, $n=8$, $p<0.05$) but independent of density in spring and summer. Open group size was positively correlated to density in spring (mean: $rs=0.7306$, $n=8$, $p<0.05$; typical: $rs=0.6108$, $n=8$, $p<0.01$) and summer (mean and typical: $rs=0.8333$, $n=8$, $p<0.01$) but independent of density in winter and autumn.

Since woodland group size was related to density in autumn and winter and open group size was related to density in spring and summer, it would be expected that the woodland to open group size ratio would be significantly correlated to density throughout the year. This is in fact true; high density populations had a more pronounced difference between woodland and open group sizes in each season (Spearman rank correlations, $rs>0.6429$, $n=8$, $p<0.05$).

Population dispersion

Population dispersion as measured by Morisita's index was presented on an annual and seasonal basis in Table 5.5. Essentially a high value of the dispersion index suggests that the deer made non-random use of space; some areas of the study sites were used more extensively than others. Was group size related to population dispersion?

Overall mean and typical group size were positively correlated to the annual value of the dispersion index (mean: $rs=0.9581$, $n=8$, $p<0.01$; typical: $rs=0.7904$, $n=8$, $p<0.05$), but woodland and open habitat group sizes were independent. The magnitude of the woodland to open group size ratio was not related to population dispersion.

Population dispersion varied seasonally in most study sites and it is worth investigating whether the annual trends described above were replicated in each season. This was not the case; significant correlations between dispersion and overall group size were restricted to spring and summer (mean: $rs=0.8333$, $n=8$, $p<0.01$; typical: $rs=0.7143$, $n=8$, $p<0.05$). Open habitat group size was also positively correlated to dispersion in these two seasons (Spearman rank correlations: $rs>0.6905$, $n=8$, $p<0.05$).

Ecological correlates of group size : a summary

Changes in group size within and between sites were examined with respect to the ecological parameters presented in the previous three chapters.

Overall group size was independent of habitat composition, however an increase in the percentage woodland was reflected by a decrease in the woodland group size. Habitat diversity was negatively correlated to overall group size. Habitat structure, in terms of grain size, amount of edge, and frequency of habitat change, was not related to any of the grouping parameters.

Group size and the extent of change in group size between woodland and open habitats were largely independent of patterns of habitat use. Only in spring was the increased use of open habitat in some populations reflected by an increased group size and woodland to open group size ratio.

Group size overall was independent of population density, but in high density populations open habitat group size was larger and woodland group size smaller than in low density populations. Density was positively correlated to the woodland open group size ratio.

Group size was positively correlated to population dispersion; not surprisingly those sites in which deer were highly aggregated in space had larger group sizes.

6.4. DISCUSSION

How should group size be described?

Two approaches to describing group size have been emphasized throughout this chapter - which one provides the more biologically meaningful description of grouping tendencies? The traditional 'observer-centred' measures (eg. mean group size and frequency of groups of certain sizes) reflect the perception of the external observer; whether he or she be the field worker or other individual deer in the population. The 'animal-centred' measures of Jarman (1974) and others (eg. typical group size and frequency of individuals in groups of certain sizes) are intended to reflect the social perception of the individual deer. To a certain extent, the validity of either approach depends upon the question to be answered. When that question concerns the adaptiveness of particular group sizes to individuals in certain habitats, in my view the latter approach is more appropriate. When the response of individual animals to the group size of others in the population is of interest, as in the case of male mating strategies, the 'observer-centred' measures may be more suitable.

Much of the above makes the assumption that the exact distribution of group sizes in the population is known and, as such, both 'observer-centred' and 'animal-centred' measures simply present different biological perspectives, and neither is in any way 'wrong'. However in practice, field sampling is rarely that perfect, and it is worth briefly considering the extent to which the two approaches are open to bias by the inclusion of atypical groups. In most fallow populations, visibility is a limiting factor in the accuracy of group size assessments; under these circumstances, it is likely that large groups are more visible than small groups or solitary individuals, and as such will be overepresented in the sample. The 'animal-centred' measures are more influenced by the occasional observation of large groups, as shown by the very large values for typical group size during spring at Brinken. However this bias is a problem of sampling methodology, and not an inherent flaw in the analytical approach. 'Observer-centred' measures, on the other hand, do not reflect the individual deer's experience of its social environment.

The preceding issues are fundamental to the interpetation of group size data and largely account for differences between the conclusions of the current study, and those of earlier New Forest fallow deer workers (Jackson 1974; Parfitt in Putman 1986a) which are summarized by Putman (1986a) as 'groups larger than five [deer] are infrequent'. In the current study, groups of seven or more deer accounted for less than 20% of all groups encountered in each of the five Forest sites, in close agreement with Jackson and Parfitt's data. However, the number of individuals in these groups are in fact much greater than the preceding analysis implies; from 35% to 75% of all individuals seen were in groups of seven or more deer. Therefore I suggest that the size of group in which the typical fallow deer finds itself in the New Forest, disregarding habitat type, is larger than that which has been previously stated.

What is the true social unit?

In two thought-provoking reviews of cervid social organisation, Putman (1981, 1988) stressed the distinction between strict fundamental social groupings, the 'social unit', and casual aggregations of more than one of these units to form larger groups. Using fallow deer as his principal example, he suggested that the social unit in this species (and perhaps in all cervids) was the individual, or possibly the immediate family group. The large groups of fallow commonly seen on favoured feeding grounds were temporary aggregations, as revealed by their fragmentation into smaller groups when the deer return to woodland. Putman suggests that these smaller groups, of seven or eight individuals, are in themselves not much more permanent than the large aggregations. These groups vary in individual composition from day to day and their size simply reflects a response to habitat, and not the cohesiveness of a social unit. This idea is of considerable significance to the questions being asked in this chapter, as it offers a mechanism by which fallow deer might adaptively manipulate their group size to reflect the habitat of current occupance. There are, however, only limited data supporting the 'group flux' theory. Waterfield (1986), in Devon, and Rand (unpublished) in the New Forest, working with fallow deer recognisable by natural markings, have suggested that social groups vary in individual composition on a daily basis; however their data are inevitably limited. More rigorous evidence for the turnover of social groups has been presented for individually marked sika deer (Horwood & Masters 1970) and further investigation of this question in a similarly marked fallow deer population would be very worthwhile.

The influence of season

Female group size varied seasonally in all sites, attaining maximum values in winter or spring and minimum values in summer or autumn. This was not a simple reflection of changing patterns of habitat use; group size varied in a similar fashion in both woodland and open habitats. Additionally, observed seasonal patterns of habitat use, particularly in the New Forest, suggest that deer make more extensive use of woodlands during the winter (Chapter 4), the very season during which maximum group size is often attained. Similar seasonal changes in female group size have been reported in other wild fallow populations; eg. Jackson (1974) and Parfitt (in Putman 1986a) for the New Forest, Heideman (1973), Langbein (1985) and Waterfleld (1986) for agricultural populations in W.Germany, Staffordshire and Devon respectively. Which factors are likely to be causing such seasonal variation?

Seasonal change in group size of most other ungulates seems linked to food supply. Buffalo *Syncerus caffer*, wildebeest *Connochaetus taurinus*, and impala group sizes are smaller during the dry season when food is scarce, than during the wet season when food is most abundant (Sinclair 1974; Jarman & Jarman 1974, 1979; Rodgers 1977). Lower food supply in winter limits the size of reindeer groups in alpine Norway and increases their dispersion (Skogland 1989). Group size of red deer *Cervus elaphus* on Rhum is larger in summer than winter, possibly reflecting reduced foraging competition (Clutton-Brock et al. 1982). Is food supply likely to be similarly affecting fallow group size?

Fallow deer are preferentially grazers, particularly during spring and summer when grass forms nearly 60% of their total food intake (Jackson 1974, 1977). In a temperate European climate, forage production is limited mainly to this fairly well-defined period, therefore if group size reflected food availability, the largest groups should occur during spring and summer. This was obviously not the case; groups increased in size after the autumn rut, remained high during winter and spring, and decreased in early summer. There is a possibility that winter group size is influenced by food availability within woodlands; fruit and mast crops are often highly localized and may cause feeding aggregations. However, good mast crops did not occur in every autumn, and in any case would not cause the winter increase in group size in open habitats.

The early summer decrease in female group size coincided with the birth of fawns in June, and it was likely that this contributed significantly to the reduction in group size at this time. Solitary females were seen more frequently in June than any other month by Jackson (1974) in the New Forest. In the weeks immediately following birth, females often left their young fawns concealed in thick cover whilst they moved to more open areas of good grazing. The large foraging groups of spring did not reform, however, and group size remained low throughout summer and autumn. The increase in female group size in woodland during early winter may be a response to the opening of woodland habitat due to leaf-fall and dieback of ground flora, however such an explanation does not account for the winter increase in open habitat group size.

Seasonal change in white-tailed deer grouping patterns as reported by Hirth (1977) show the greatest similarity to those observed in fallow. Here too, female group size was lowest in June during parturition, then steadily increased throughout summer and autumn to reach a maximum during winter and early spring. Maximum group sizes were attained well before the spring flush of new plant growth, hence as in fallow deer, it seems unlikely that seasonal grouping patterns were driven by food availability.

Seasonal variation in male grouping patterns were largely limited to the autumn, where male group size was greatly reduced in all sites in which they were regularly observed. The autumn reduction was associated with the rut, as male intolerance and aggression increased at this time. Group size did not vary significantly throughout the rest of the year. Fallow bucks cast their antlers during April and May, and at this time may be more solitary as they are vulnerable to attack by younger, still antlered, males. Such movements away from the buckherds are only temporary, however, and are not reflected in reduced male group sizes. Broadly similar conclusions were reached by Jackson (1974) in the New Forest, and Langbein (1985) and Waterfield (1986) in agricultural populations. Variation in the size of mixed-sex groups was more limited, and if any seasonal trends were shown generally groups were smallest during the autumn. This was clearest in some New Forest sites, where non-reproductive mixed-sex groups were principally large aggregations on favoured feeding areas (Chapter 5).

The influence of habitat

Habitat appeared to have a pronounced effect on female group size in all sites excluding South Oakley and Lockerley. Group size in open habitats such as grasslands or fields was larger than in woodland, particularly so during winter and spring, and as Putman (1986a, 1988) suggests, was almost certainly caused by animals aggregating on favoured feeding resources. On numerous occasions, small groups of deer were observed moving onto fields and more or less immediately joining existing large foraging groups. Conversely, when feeding groups left fields undisturbed, smaller subgroups often split from the main party. When these large groups were disturbed however, they would often flee as a single unit into nearby woodland cover, but how long these groups remained together in woodland is unknown.

The contrast between open and woodland habitats was not shown at South Oakley and Lockerley and it is worth briefly considering why these populations differed. At South Oakley, very few female groups were ever seen on the open heathland and grasslands, and it is quite possible that was a reason why large groups did not form. This was not the case at Lockerley, where use of fields was no less intense than at the other two agricultural sites, and alternative explanations will be suggested below.

Within individual sites group size did not appear to vary much within woodland habitats; there were no consistent differences between female group size in closed or open canopy woodland, nor any evidence that females aggregated on woodland rides. This is not to suggest that deer do not distinguish between woodland types; clear selection for particular woodland communities has earlier been demonstrated (Chapter 4). Grassland groups were larger than those on heathland in the New Forest, probably a reflection of aggregation in the former habitat. Male group size varied less in response to habitat openness, although to a certain extent this was a reflection of small sample size. Additionally, male groups in woodland were rarely very far from adjacent open habitat, and it may be that these groups simply did not have time to split up.

An earlier study of fallow social grouping in the New Forest concluded that habitat had little effect on group size (Parfitt in Putman 1986a). These results are now explicable in the light of the recognition that group size varies only between woodland and open habitats; Parfitt restricted his studies to the enclosed woodlands where group size varies little. The suggestion by Jackson (1974) and Putman (1981) that fallow deer aggregate in open habitat in the New Forest is confirmed by the results of the current study. Elsewhere in fallow populations that inhabit heterogeneous environments, group size has been shown to show similar variation (Heideman 1973; Schaal 1982; Waterfield 1986), thus reflecting a general trend amongst ungulates to aggregate in open environments (eg. Leuthold 1970; Walther 1972; Hirth 1977; Jarman & Jarman 1979; Takatsuki 1983; LaGory 1986; Putman & Mann 1990).

With the exception of Lockerley and possibly South Oakley, female deer occur in larger groups in open habitat than woodland. What causes this aggregation? Female deer clearly used open habitat mainly for foraging; it is quite plausible, therefore, that large groups simply occurred because individuals concentrated on favoured feeding areas. The decrease in individual vigilance time in large foraging groups is often quoted as a force promoting sociality in large herbivores (eg. Berger 1978; Lipetz & Bekoff 1982; Jarman 1987) however its relationship with habitat type is obscure. Schaal (1985b) demonstrated that fallow deer in large groups spent less time vigilant than those in small groups, but was unable to show any significant change in vigilance with habitat. LaGory (1986) reached similar conclusions with white-tailed deer and suggested that smaller groups in woodland may arise simply because deer have difficulty maintaining contact with other group members in denser cover. Data on vigilance in relation to group size and habitat was collected from January to September 1989, however has yet to be properly analysed, and thus at this stage it is impossible to say which of the above factors is most important.

Site differences in grouping

Differences between the study sites in the size of male groups were pronounced; large groups were seen only at South Oakley and Dames Slough in the New Forest. The explanation for this seems quite simple, as these were the only two sites in which males occurred in any numbers (Chapter 5). The size of mixed-sex groups also showed simple variation between the sites; these groups were much larger at Brinken and Tadley than elsewhere. This was probably a result of aggregation on good feeding areas, although the Tadley groups appeared to be of a more permanent nature.

Female group size, irrespective of season and habitat, varied only slightly between areas, and no clear cut division was apparent between Forest and agricultural sites. This was surprising, as previous work in agricultural populations (Heideman 1973; Schaal 1982; Langbein 1985; Waterfield 1986) had suggested that groups were typically much larger than those recorded by Jackson (1974) and Parfitt (in Putman 1986a) in the New Forest. Investigation of site differences of these studies is difficult, however, as workers often used different methods of data collection and analysis.

Grouping differences between the two environmental types in the current study proved more complex. Although there was some overlap between sites, female groups in the agricultural sites occurred in larger groups than in the New Forest when in woodland, but in smaller groups when in open habitats. These two trends counteracted, thus resulting in the apparent overall similarity in group size between Forest and agricultural sites. These two relationships between group size and habitat resulted in the New Forest sites also showing the most extreme variation in group size when moving from a woodland to open habitat (eg. very small groups in woodland and very large groups in open). The agricultural sites showed less variation between habitats, particularly so at Lockerley where woodland and open group sizes were more or less identical.

Between-site differences in female group size in both woodland and open habitats did not remain constant throughout the year and were particularly pronounced in woodland during the autumn. Female groups at this time were larger in each agricultural population than in all Forest sites. This is of considerable interest for its possible implications for mating systems, as the size and distribution of female groups is likely to have a large influence on male mating strategies (Gosling 1986; Clutton-Brock 1989).

Ecological correlates of population variation in social grouping

The preceding sections have established the basic patterns of social grouping of fallow deer in the eight study populations. Certain similarities run through all sites; in particular the overriding influence of seasonal variation on female group size. However populations differ in the group size adopted in different habitats and in the extent of grouping flexibility. Can variation can be related to the ecological environment in which the animals live; the habitat available in terms of its composition and structure, the utilisation of those habitats, and finally the characteristics of the deer population themselves?

There was no simple relationship between the habitat composition of the sites, in terms of the relative amounts of woodland and open habitat, and group size of the population. In other words, the openness of the environment as a whole did not effect group size. This is in marked contrast to other ungulate species reported in the literature, in which populations in open environments characteristically form larger groups than in closed environments. Although there was great variation between the sites in the proportions of woodland and open habitats, there were no sites which were exclusively woodland or open. Additionally, patterns of habitat use, when examined at the level of resolution of woodland and open habitat, did not differ greatly between sites; deer in 'open' environments selected woodlands, deer in 'closed' environments selected open habitats (Chapter 4). Therefore genuine site differences in habitat composition were nullified by differential habitat selection.

Increased woodland area was, however, reflected by decreased woodland group size. How is this relationship best interpreted? I believe that woodland area is best viewed as an 'indirect' measure of habitat structure. To appreciate this argument it is necessary to think laterally and to consider what exactly the 'direct' measures of habitat structure are measuring. Grain size and habitat change are reflections of the size scale of the environment at the level of the individual habitat patch. It has been demonstrated that group size does not vary at this level of habitat resolution, hence the independence of group size from these two measures of habitat structure is not surprising. In Chapter 3 the suggestion was made that the average size of woodlands in a study site would be important determinants of social grouping, however a linear measure was impossible to attain. It is now suggested that the total woodland area (expressed as a percentage) is a good substitute for average woodland size. High percentage woodland sites contain one large woodland (New Forest sites), low percentage woodland sites contain several smaller woodlands (agricultural sites). How is all this related to group size? Woodland group size is small when woodlands are big. It is possible that female groups may lose their cohesion in large woodlands, resulting in smaller group sizes. This idea has been previously suggested by LaGory (1986) to explain white-tailed deer grouping patterns. In the agricultural sites in the current study, woodlands are smaller, and female groups in woodland do not split up before moving onto open habitat. The above ideas are largely speculation, however they do offer a partial explanation for observed grouping patterns particularly at Lockerley.

Group size and the extent of change in group size between open and woodland habitats was largely independent of patterns of habitat use in the eight study sites. There were two good reasons for predicting this lack of a relationship. Firstly, as mentioned above, when habitat use is compared at the woodland to open habitat level of resolution, differences between sites are limited. This level of resolution is appropriate because, as has been shown, group size changes within sites are largely limited to increased group size in open habitat. Secondly, there were differences between sites in the group size adopted in particular habitat types. For example, woodland group size was larger in the three agricultural sites than in most of the New Forest sites.

Finally, did the population parameters of density and dispersion have an influence on group size? Density affects are rarely mentioned in the literature on ungulate sociality, and Hirth (1977) states that high densities alone are insufficient to produce large groups of white-tailed deer. However, density is closely linked to group size in several medium to large macropod species eg. eastern grey kangaroo *Macropus giganteus* (Southwell 1984), common wallaroo *M. robustus* (Taylor 1982) and red kangaroo *M. rufus* (Johnson 1983), with large groups forming in high density populations.

Group size overall was not related to density, however group sizes within woodland and open habitats were. In high density populations, open habitat group size was larger and woodland group size smaller than in low density populations. It necessarily follows that high density was associated with increased flexibility in woodland to open group sizes. It is easy to see how density might affect open habitat group size; if large open habitat groups form by the aggregation of several smaller units as seems likely (see above and Putman 1988), then this is more likely to happen in a high density population because more social units are available. Clearly, the maximum size attained is also likely to be affected by density. It is more difficult to suggest why woodland group size in high density populations should be low. The possibility remains that both this relationship and the previous one are merely artifacts of a relationship between woodland structure and group size; high density populations occur in large woodlands in which the typical group size is small, low density populations occur in small woodlands in which the typical group size is large.

Group size was correlated to population dispersion; not surprisingly those sites in which deer were concentrated in space also had larger group sizes. This was in some ways a measure of the extent of aggregation in the population; very large groups on fields occurred in populations that were less dispersed (eg. Brinken, Dames Slough, and Tadley).

The flexible fallow: group size reconsidered

Fallow deer show marked flexibility in patterns of social grouping both within and between populations. A common seasonal pattern, apparently driven by the annual reproductive cycle, is shown in all populations; group size is large during winter and spring, decreases during parturition, and increases again after the autumn rut. In common with most large herbivores, fallow groups increase in size in open habitat in most populations. Differences between populations, however, are not explicable by habitat openness alone. Utilisation of woodland and open habitats is similar between sites, despite the great differences in habitat availability. Additionally, the group size adopted within a single habitat type differs between sites, with 'closed' environment (eg. New Forest) populations having smaller groups in woodland but larger groups in open habitats than 'open' environment (eg. agricultural) populations. Structural characteristics of the environment, such as woodland patch size, may influence group size in woodland, whilst population density and dispersion may similarly influence group size in open habitat; untangling the effect of the two is difficult.

6.5. SUMMARY

1. Groups were divided into four categories on the basis of size: 1-3 individuals, 4-6 individuals, 7-9 individuals and 10+ individuals. In each site, groups of 1-3 individuals were encountered most frequently, however individual deer were more evenly distributed evenly between the group size classes.
2. Female groups in all sites were largest in winter and spring and smallest in summer and autumn. Seasonal effects on group size were similar in woodland and open habitats.
3. Seasonal variation in group size of male groups and mixed-sex groups was more variable. In general, male groups and mixed-sex groups were smallest during autumn.
4. Female groups in the New Forest sites were larger in open habitat than in woodland throughout the year. Group size varied little between woodland habitats, however groups were larger on grassland than heathland.
5. Female groups at two of the agricultural sites showed similar trends. In the third site however, habitat influences were reduced and woodland and open groups differed little in size throughout the year.
6. Habitat effects on male group size varied between sites.
7. Mixed-sex groups showed similar variation in responce to habitat as female groups. In most sites, groups were larger in open habitat than in woodland.

8. Female group size overall varied between sites, however variation was as pronounced within the New Forest and agricultural sites as between them.
9. Females in the agricultural sites tended to occur in larger groups than in the New Forest sites when in woodland, but in smaller groups when in open habitat. Environmental class differences in woodland group size were most pronounced in autumn.
10. Large male groups occured in only two New Forest sites, more likely a reflection of total male numbers than environmental factors.
11. Female group size overall in each site was independent of habitat composition, however an increase in the percentage woodland area was reflected by smaller woodland group size.
12. Female group size overall was negatively correlated to habitat diversity.
13. Female group size was independent of all measures of habitat structure, however woodland group size was smaller in sites containing large woodlands than in sites containing small woodlands.
14. Female group size was largely independent of patterns of habitat use.
15. Female group size overall was largely independent of female density, however in high density populations open habitat group size was larger and woodland group size smaller than in low density populations.
16. Female group size overall was positively correlated to population dispersion.

Table 6.1 A. Frequency distribution of individuals into groups of different sizes expressed as percentage of total observations.
B. Frequency distribution of groups of different sizes expressed as percentage of total groups observed.

		A. Individual distribution					B. Group distribution				
Site	Group	Total	1-3	4-6	7-9	10+	Total	1-3	4-6	7-9	10+
Denny	Female	2370	34.6	31.1	14.1	20.2	701	66.5	22.0	6.1	5.4
	Male	125	70.4	29.6	0.0	0.0	56	85.7	14.3	0.0	0.0
	Mixed	302	8.9	18.9	18.5	53.6	43	27.9	27.9	16.3	27.9
Dames	Female	1761	26.0	27.5	16.2	30.3	429	60.4	22.4	8.6	8.6
	Male	524	17.7	6.7	13.5	62.0	96	60.4	7.3	9.4	22.9
	Mixed	630	6.8	8.7	9.5	74.9	65	27.7	16.9	10.8	44.6
S.Oakley	Female	574	31.0	27.9	14.1	27.0	152	63.8	21.7	7.2	7.2
	Male	641	11.2	11.2	21.2	56.3	97	41.2	15.5	18.6	24.7
	Mixed	46	17.4	26.1	32.6	23.9	8	37.5	25.0	25.0	12.5
Blackensford	Female	2636	37.1	27.4	14.1	21.4	803	70.9	18.6	6.0	4.6
	Male	402	60.0	20.6	13.9	5.5	216	87.5	8.3	3.2	0.1
	Mixed	1430	9.0	14.7	16.1	60.3	160	28.8	26.3	18.8	26.3
Brinken	Female	3129	13.7	13.2	7.7	65.5	411	57.2	21.2	7.5	14.1
	Male	67	53.7	13.4	30.6	0.0	40	70.0	5.0	2.5	2.5
	Mixed	802	4.6	4.7	8.4	82.3	46	30.4	17.4	19.6	32.6
Lockerley	Female	1426	28.7	35.3	18.7	17.3	384	59.1	26.3	8.9	5.7
	Male	98	56.1	13.3	30.6	0.0	43	83.7	7.0	9.3	0.0
	Mixed	325	4.3	14.8	25.8	55.1	40	12.5	25.0	27.5	35.0
Tollard	Female	2399	26.6	27.5	12.8	33.1	571	57.6	24.0	7.4	11.0
	Male	83	47.0	53.0	0.0	0.0	40	75.0	25.0	0.0	0.0
	Mixed	176	11.9	30.7	13.6	43.8	28	32.1	39.3	10.7	17.9
Tadley	Female	709	23.7	24.0	15.5	36.8	157	57.3	22.3	9.6	10.8
	Male	6	100.0	0.0	0.0	0.0	3	100.0	0.0	0.0	0.0
	Mixed	373	0.0	2.9	8.6	88.5	20	0.0	10.0	20.0	70.0

Table 6.2 Results of G-tests for independance between group size distributions between sites. Female, male, and mixed-sex groups were examined separately. A. Frequency distribution of individuals into groups of different sizes. B. Frequency distribution of groups of different sizes.
* p<0.05, ** p<0.01, *** p<0.001, ns not significant

		A.							B.						
		Denny	Dames	Oakley	Black	Brinken	Locker	Tollard	Denny	Dames	Oakley	Black	Brinken	Locker	Tollard
Dames	Female	***							*						
	Male	***							***						
	Mixed	***							ns						
Oakley	Female	**	ns						ns	ns					
	Male	***	***						***	*					
	Mixed	**	***						ns	ns					
Black	Female	*	***	**					ns	***	ns				
	Male	***	***	***					ns	***	***				
	Mixed	ns	***	***					ns	*	ns				
Brinken	Female	***	***	***	***				***	ns	ns	***			
	Male	***	***	***	**				ns	*	***	***			
	Mixed	***	**	***	***				ns	*	ns	ns			
Locker	Female	***	***	***	***	***			ns	ns	ns	**	***		
	Male	***	***	***	***	***			*	***	***	ns	ns		
	Mixed	*	***	***	***	***			ns	*	ns	ns	ns		
Tollard	Female	***	*	*	***	***	***		***	ns	ns	***	ns	*	
	Male	**	***	***	***	***	***		ns	***	***	*	ns	*	
	Mixed	***	***	**	***	***	***		ns	*	ns	ns	ns	*	
Tadley	Female	***	*	***	***	***	***	*	*	ns	ns	**	ns	ns	ns
	Male	ns	***	***	*	ns	ns	*	ns	ns	ns	*	ns	ns	ns
	Mixed	***	***	***	***	***	***	***	**	*	*	***	*	ns	***

Table 6.3 Seasonal variation and habitat variation in estimates of mean group size ± standard error and typical group size ± standard error for female, male and mixed sex groups at Denny. Values without standard errors represent a single observation.

Sex	Season	Mean group size	Typical group size
Female	Winter	4.01±0.27	7.02±0.19
	Spring	4.13±0.21	6.53±0.13
	Summer	2.56±0.19	5.14±0.20
	Autumn	2.46±0.16	3.70±0.12
Male	Winter	3.00±0.54	3.89±0.28
	Spring	2.20±0.21	2.52±0.12
	Summer	2.13±0.38	3.24±0.30
	Autumn	1.94±0.22	2.35±0.17
Mixed Sex	Winter	11.60±2.51	14.31±0.64
	Spring	9.70±1.04	10.81±0.33
	Summer	6.94±1.12	9.85±0.50
	Autumn	3.00±0.39	3.61±0.26

Sex	Habitat	Mean group size	Typical group size
Female	Closed canopy	2.36±0.32	3.35±0.26
	Open canopy	3.47±0.16	5.69±0.12
	Other woodland	2.82±0.12	4.21±0.15
	Woodland rides	2.30±0.13	3.74±0.13
	Grassland	5.25±0.44	8.70±0.25
	Arable	-	-
	Other open	7.24±0.98	10.01±0.34
	Closed	2.95±0.10	4.92±0.08
	Open	5.62±0.41	9.02±0.20
Male	Closed canopy	1.00	1.00
	Open canopy	2.11±0.21	2.84±0.16
	Other woodland	2.00±0.71	2.50±0.50
	Woodland rides	2.50±0.83	3.60±0.52
	Grassland	2.38±0.30	2.68±0.15
	Arable	-	-
	Other open	2.83±0.64	3.71±0.39
	Closed	2.12±0.20	2.89±0.15
	Open	2.57±0.33	3.17±0.22
Mixed sex	Closed canopy	4.00	4.00
	Open canopy	6.58±0.89	8.86±0.32
	Other woodland	2.00	2.00
	Woodland rides	6.71±1.70	9.72±0.74
	Grassland	10.11±2.23	14.54±0.54
	Arable	-	-
	Other open	5.50±0.61	5.91±0.26
	Closed	6.36±0.76	8.90±0.31
	Open	8.27±1.48	12.24±0.53

Table 6.4 Seasonal variation and habitat variation in estimates of mean group size ± standard error and typical group size ± standard error for female, male and mixed sex groups at Dames Slough. Values without standard errors represent a single observation.

Sex	Season	Mean group size	Typical group size
Female	Winter	4.78±0.42	7.82±0.27
	Spring	6.39±0.62	10.57±0.31
	Summer	3.56±0.34	8.63±0.38
	Autumn	3.03±0.25	5.12±0.18
Male	Winter	11.15±2.30	17.34±0.41
	Spring	6.40±1.95	9.38±0.95
	Summer	7.64±1.01	11.41±0.28
	Autumn	2.66±0.38	5.36±0.32
Mixed Sex	Winter	10.33±3.61	17.90±0.99
	Spring	11.00±3.25	17.73±0.93
	Summer	12.14±3.06	17.54±0.90
	Autumn	9.02±0.96	13.65±0.33

Sex	Habitat	Mean group size	Typical group size
Female	Closed canopy	2.20±0.37	2.82±0.24
	Open canopy	2.80±0.18	4.36±0.14
	Other woodland	2.88±0.41	3.86±0.26
	Woodland rides	2.75±0.22	5.34±0.28
	Grassland	7.41±0.49	11.37±0.24
	Arable	-	-
	Other open	-	-
	Closed	2.76±0.13	4.76±0.15
	Open	7.41±0.49	11.37±0.24
Male	Closed canopy	1.67±0.54	2.20±0.49
	Open canopy	3.54±0.66	8.30±0.44
	Other woodland	3.00	3.00
	Woodland rides	1.78±0.26	2.44±0.24
	Grassland	9.89±1.03	13.66±0.29
	Arable	-	-
	Other open	-	-
	Closed	2.92±0.44	6.99±0.39
	Open	9.89±1.03	13.66±0.29
Mixed Sex	Closed canopy	-	-
	Open canopy	8.14±1.09	13.43±0.43
	Other woodland	-	-
	Woodland rides	4.50±0.85	5.78±0.48
	Grassland	14.33±1.54	17.82±0.38
	Arable	-	-
	Other open	-	-
	Closed	7.48±0.93	12.59±0.41
	Open	14.33±1.54	17.82±0.38

Table 6.5 Seasonal variation and habitat variation in estimates of mean group size ± standard error and typical group size ± standard error for female, male and mixed sex groups at South Oakley. Values without standard errors represent a single observation.

Sex	Season	Mean group size	Typical group size
Female	Winter	3.18±0.40	4.83±0.26
	Spring	4.96±0.49	8.80±0.32
	Summer	1.50±0.14	1.83±0.14
	Autumn	2.56±0.48	3.98±0.36
Male	Winter	9.91±1.68	16.50±0.52
	Spring	6.74±0.81	10.84±0.38
	Summer	4.50±0.79	7.53±0.38
	Autumn	3.10±0.77	5.00±0.43
Mixed Sex	Winter	4.00±1.41	5.00±0.65
	Spring	7.00±1.46	8.21±0.51
	Summer	-	-
	Autumn	5.00±1.41	5.80±0.61

Sex	Habitat	Mean group size	Typical group size
Female	Closed canopy	2.56±0.61	3.87±0.48
	Open canopy	3.91±0.36	7.78±0.30
	Other woodland	1.00	1.00
	Woodland rides	2.40±0.47	3.78±0.38
	Grassland	10.00	10.00
	Arable	-	-
	Other open	5.00±0.87	6.52±0.27
	Closed	3.65±0.31	7.32±0.27
	Open	5.45±0.90	7.10±0.28
Male	Closed canopy	4.00±0.93	5.94±0.60
	Open canopy	7.20±1.03	13.74±0.43
	Other woodland	9.50±1.06	9.74±0.35
	Woodland rides	4.21±0.97	7.34±0.51
	Grassland	7.25±2.53	14.31±1.26
	Arable	-	-
	Other open	7.60±1.18	11.26±0.54
	Closed	6.25±0.72	12.04±0.36
	Open	7.50±1.11	12.10±0.53
Mixed Sex	Closed canopy	8.00	8.00
	Open canopy	4.50±0.77	5.30±0.34
	Other woodland	-	-
	Woodland rides	-	-
	Grassland	-	-
	Arable	-	-
	Other open	11.00	11.00
	Closed	5.00±0.81	5.91±0.32
	Open	11.00	11.00

Table 6.6 Seasonal variation and habitat variation in estimates of mean group size ± standard error and typical group size ± standard error for female, male and mixed sex groups at Blackensford. Values without standard errors represent a single observation.

Sex	Season	Mean group size	Typical group size
Female	Winter	4.64±0.32	8.05±0.25
	Spring	5.57±0.41	10.35±0.26
	Summer	2.20±0.18	3.92±0.22
	Autumn	2.12±0.08	3.27±0.09
Male	Winter	2.33±0.51	3.00±0.33
	Spring	4.33±0.72	4.69±0.36
	Summer	2.82±0.96	6.42±0.72
	Autumn	1.76±0.12	3.39±0.16
Mixed Sex	Winter	15.73±3.23	23.02±0.71
	Spring	26.25±3.14	29.25±0.60
	Summer	14.50±1.77	14.93±0.47
	Autumn	7.28±0.66	15.54±0.56

Sex	Habitat	Mean group size	Typical group size
Female	Closed canopy	3.87±0.46	7.20±0.37
	Open canopy	2.81±0.10	4.64±0.09
	Other woodland	2.00±0.19	2.58±0.18
	Woodland rides	2.55±0.18	4.30±0.15
	Grassland	10.39±1.24	16.94±0.40
	Arable	-	-
	Other open	3.31±0.29	5.21±0.21
	Closed	2.82±0.09	4.83±0.08
	Open	5.95±0.59	12.85±0.34
Male	Closed canopy	1.60±0.36	2.00±0.33
	Open canopy	1.80±0.17	3.57±0.21
	Other woodland	1.33±0.19	1.50±0.19
	Woodland rides	1.41±0.17	1.95±0.20
	Grassland	3.20±1.34	6.00±0.89
	Arable	-	-
	Other open	1.00±0.00	1.00±0.00
	Closed	1.85±0.12	3.59±0.15
	Open	2.10±0.75	4.81±0.82
Mixed Sex	Closed canopy	8.81±1.39	21.33±1.02
	Open canopy	6.17±0.56	10.03±0.34
	Other woodland	3.00±0.00	3.00±0.00
	Woodland rides	6.33±1.96	8.16±0.80
	Grassland	21.67±2.42	26.52±0.46
	Arable	-	-
	Other open	8.50±1.61	10.33±0.61
	Closed	7.22±0.67	15.68±0.57
	Open	18.38±2.19	24.65±0.48

Table 6.7 Seasonal variation and habitat variation in estimates of mean group size ± standard error and typical group size ± standard error for female, male and mixed sex groups at Brinken. Values without standard errors represent a single observation.

Sex	Season	Mean group size	Typical group size
Female	Winter	6.80±0.88	16.65±0.57
	Spring	23.49±5.24	92.43±1.53
	Summer	5.55±1.19	37.28±1.69
	Autumn	3.26±0.44	11.41±0.89
Male	Winter	2.00	2.00
	Spring	-	-
	Summer	13.00	13.00
	Autumn	1.79±0.32	3.40±0.42
Mixed Sex	Winter	6.00±1.63	7.33±0.46
	Spring	75.86±22.85	124.05±2.04
	Summer	-	-
	Autumn	7.03±1.00	12.12±0.55

Sex	Habitat	Mean group size	Typical group size
Female	Closed canopy	3.58±0.55	4.58±0.27
	Open canopy	3.31±0.18	5.13±0.13
	Other woodland	-	-
	Woodland rides	3.25±0.74	5.26±0.50
	Grassland	14.10±2.33	74.10±1.21
	Arable	-	-
	Other open	5.13±0.82	11.11±0.55
	Closed	3.33±0.17	5.11±0.12
	Open	12.05±1.83	67.99±1.15
Male	Closed canopy	-	-
	Open canopy	1.39±0.22	2.04±0.31
	Other woodland	-	-
	Woodland rides	1.00	1.00
	Grassland	2.45±0.68	4.56±0.64
	Arable	-	-
	Other open	7.00±4.24	12.14±0.86
	Closed	1.37±0.21	2.00±0.30
	Open	3.15±0.98	7.15±0.76
Mixed Sex	Closed canopy	2.50±0.35	2.60±0.24
	Open canopy	4.94±0.68	6.64±0.39
	Other woodland	-	-
	Woodland rides	-	-
	Grassland	42.20±13.51	107.10±2.31
	Arable	-	-
	Other open	7.30±1.18	9.19±0.47
	Closed	4.57±0.62	8.33±0.14
	Open	28.24±8.81	96.97±2.35

Table 6.8 Seasonal variation and habitat variation in estimates of mean group size ± standard error and typical group size ± standard error for female, male and mixed sex groups at Lockerley. Values without standard errors represent a single observation.

Sex	Season	Mean group size	Typical group size
Female	Winter	4.84±0.34	6.97±0.16
	Spring	4.51±0.37	6.85±0.18
	Summer	2.34±0.19	3.62±0.14
	Autumn	3.35±0.21	5.03±0.14
Male	Winter	3.50±0.83	5.46±0.44
	Spring	3.00±1.17	5.27±0.80
	Summer	4.00±0.47	4.17±0.24
	Autumn	1.44±0.16	1.89±0.18
Mixed Sex	Winter	9.00±1.44	11.31±0.53
	Spring	6.00±2.04	8.11±0.88
	Summer	6.33±0.72	6.58±0.30
	Autumn	8.25±0.83	10.24±0.28

Sex	Habitat	Mean group size	Typical group size
Female	Closed canopy	3.71±0.20	5.68±0.13
	Open canopy	3.84±0.37	6.31±0.22
	Other woodland	2.44±0.69	4.18±0.52
	Woodland rides	3.45±0.48	6.04±0.31
	Grassland	6.00±0.75	7.40±0.30
	Arable	3.41±0.32	5.49±0.20
	Other open	-	-
	Closed	3.67±0.16	5.84±0.10
	Open	3.86±0.31	6.01±0.17
Male	Closed canopy	1.80±0.28	3.15±0.33
	Open canopy	2.60±1.22	5.46±0.93
	Other woodland	-	-
	Woodland rides	-	-
	Grassland	3.67±0.72	4.09±0.34
	Arable	4.00±0.94	5.10±0.56
	Other open	-	-
	Closed	1.91±0.30	3.60±0.34
	Open	3.88±0.65	4.74±0.39
Mixed Sex	Closed canopy	8.08±0.85	10.43±0.31
	Open canopy	8.50±1.33	10.18±0.48
	Other woodland	-	-
	Woodland rides	6.50±0.56	6.69±0.22
	Grassland	-	-
	Arable	10.50±3.18	12.43±0.91
	Other open	-	-
	Closed	8.00±0.66	10.05±0.25
	Open	10.50±3.18	12.43±0.91

Table 6.9 Seasonal variation and habitat variation in estimates of mean group size ± standard error and typical group size ± standard error for female, male and mixed sex groups at Tollard. Values without standard errors represent a single observation.

Sex	Season	Mean group size	Typical group size
Female	Winter	5.38±0.47	9.65±0.26
	Spring	5.15±0.31	8.65±0.21
	Summer	2.76±0.18	4.67±0.16
	Autumn	3.70±0.24	5.65±0.15
Male	Winter	1.80±0.72	3.22±0.70
	Spring	2.75±0.38	3.36±0.19
	Summer	2.75±0.66	4.00±0.34
	Autumn	1.27±0.15	1.53±0.18
Mixed Sex	Winter	5.00±0.71	5.20±0.33
	Spring	7.00±1.16	9.67±0.49
	Summer	2.50±0.43	2.80±0.33
	Autumn	7.25±2.52	14.28±1.27

Sex	Habitat	Mean group size	Typical group size
Female	Closed conifer	3.73±0.24	6.97±0.20
	Open conifer	3.30±0.26	5.31±0.18
	Other woodland	4.06±0.36	5.13±0.18
	Woodland rides	4.16±0.41	6.70±0.27
	Grassland	4.57±0.49	7.57±0.40
	Arable	6.05±0.53	10.62±0.26
	Other open	-	-
	Closed	3.78±0.15	6.40±0.12
	Open	5.50±0.38	9.67±0.22
Male	Closed conifer	2.00±0.39	3.00±0.31
	Open conifer	1.20±0.18	1.33±0.21
	Other woodland	1.00±0.00	1.00±0.00
	Woodland rides	1.75±0.65	2.71±0.61
	Grassland	1.50±0.20	1.67±0.17
	Arable	3.56±0.50	4.19±0.19
	Other open	-	-
	Closed	1.68±0.24	2.57±0.24
	Open	2.73±0.41	3.63±0.22
Mixed Sex	Closed conifer	4.85±0.74	6.33±0.36
	Open conifer	4.25±0.41	4.41±0.19
	Other woodland	6.00	6.00
	Woodland rides	5.00±2.12	6.80±0.80
	Grassland	11.00±3.54	13.27±0.97
	Arable	9.67±3.44	17.00±1.07
	Other open	-	-
	Closed	4.80±0.54	6.02±0.27
	Open	10.00±2.73	15.98±0.84

Table 6.10 Seasonal variation and habitat variation in estimates of mean group size ± standard error and typical group size ± standard error for female, male and mixed sex groups at Tadley. Values without standard errors represent a single observation.

Sex	Season	Mean group size	Typical group size
Female	Winter	4.38±0.54	7.20±0.37
	Spring	6.45±0.98	12.65±0.48
	Summer	2.81±0.34	4.57±0.26
	Autumn	4.43±0.78	8.55±0.49
Male	Winter	-	-
	Spring	2.00	2.00
	Summer	2.00	2.00
	Autumn	2.00	2.00
Mixed Sex	Winter	14.00±3.94	20.64±1.06
	Spring	20.18±4.01	28.94±0.85
	Summer	-	-
	Autumn	22.33±5.97	27.12±0.91

Sex	Habitat	Mean group size	Typical group size
Female	Closed canopy	4.59±0.59	7.05±0.31
	Open canopy	3.08±0.37	4.80±0.24
	Other woodland	-	-
	Woodland rides	3.14±0.39	4.50±0.22
	Grassland	8.42±1.26	14.62±0.44
	Arable	3.04±0.47	4.84±0.37
	Other open	-	-
	Closed	3.59±0.27	5.66±0.17
	Open	6.10±0.82	12.52±0.41
Male	Closed canopy	-	-
	Open canopy	2.00	2.00
	Other woodland	-	-
	Woodland rides	-	-
	Grasslands	2.00±0.00	2.00±0.00
	Arable	-	-
	Other open	-	-
	Closed	2.00	2.00
	Open	2.00±0.00	2.00±0.00
Mixed Sex	Closed canopy	10.00	10.00
	Open canopy	9.25±0.64	9.43±0.22
	Other woodland	-	-
	Woodland rides	-	-
	Grasslands	22.71±3.38	29.75±0.56
	Arable	8.00	8.00
	Other open	-	-
	Closed	9.40±0.54	9.55±0.17
	Open	21.73±3.29	29.22±0.58

Table 6.11 Estimates of mean group size ± standard error and typical group size ± standard error for female, male and mixed sex groups at Denny in each season and habitat type. Values without standard errors represent a single observation.

		Mean group size				Typical group size			
	Habitat	Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn
Female	Closed canopy	2.67±0.61	3.00±0.54	1.20±0.18	1.50±0.35	3.50±0.35	3.89±0.39	1.33±0.21	1.67±0.33
	Open canopy	3.44±0.25	4.04±0.30	3.03±0.49	2.55±0.27	5.07±0.16	6.49±0.20	6.21±0.42	3.85±0.21
	Other woodland	3.00±0.78	3.59±0.39	1.96±0.37	2.68±0.34	4.22±0.43	4.79±0.24	3.53±0.40	3.75±0.23
	Woodland rides	2.91±0.37	3.20±0.41	1.76±0.11	2.03±0.24	4.38±0.25	5.27±0.30	2.39±0.12	3.05±0.23
	Grassland	6.31±1.01	6.09±0.84	4.50±0.68	3.42±0.61	10.50±0.50	8.66±0.36	7.83±0.44	4.71±0.36
	Arable	-	-	-	-	-	-	-	-
	Other open	10.00±2.00	8.57±0.70	4.50±0.25	1.33±0.27	12.80±0.46	8.97±0.21	4.56±0.12	1.50±0.29
	Closed	3.26±0.19	3.74±0.21	2.10±0.16	2.39±0.16	4.83±0.13	5.91±0.14	3.96±0.20	3.58±0.13
	Open	7.09±0.94	6.69±0.69	4.50±0.61	3.00±0.53	11.19±0.38	8.75±0.26	7.47±0.40	4.42±0.36
Male	Closed canopy	-	-	1.00	-	-	-	1.00	-
	Open canopy	3.00±0.54	1.91±0.24	1.00±0.00	2.00±0.29	3.89±0.28	2.24±0.17	1.00±0.00	2.45±0.22
	Other woodland	-	3.00	1.00	-	-	3.00	1.00	-
	Woodland rides	-	3.00	3.00±1.41	1.00	-	3.00	4.33±0.67	1.00
	Grassland	-	3.00	2.00±0.50	2.50±0.35	-	3.00	2.50±0.33	2.60±0.24
	Arable	-	-	-	-	-	-	-	-
	Other open	-	-	3.50±0.75	1.50±0.35	-	-	4.14±0.38	1.67±0.33
	Closed	3.00±0.54	2.08±0.23	1.50±0.47	1.92±0.28	3.89±0.28	2.41±0.14	2.67±0.59	2.39±0.22
	Open	-	3.00	2.75±0.52	2.00±0.35	-	3.00	3.55±0.31	2.25±0.25
Mixed Sex	Closed canopy	-	4.00	-	-	-	4.00	-	-
	Open canopy	9.50±2.08	9.40±0.83	5.00±1.50	3.33±0.65	11.32±0.51	9.77±0.27	6.80±0.75	4.10±0.38
	Other woodland	-	-	-	2.00	-	-	-	2.00
	Woodland rides	-	11.00±2.16	4.00	3.33±0.54	-	12.27±0.67	4.00	3.60±0.27
	Grassland	20.00	13.00	10.80±2.55	2.00±0.00	20.00	13.00	13.81±0.63	2.00±0.00
	Arable	-	-	-	-	-	-	-	-
	Other open	-	-	5.50±0.61	-	-	-	5.91±0.26	-
	Closed	9.50±2.08	9.33±1.09	4.80±1.21	3.20±0.44	11.32±0.51	10.48±0.36	6.33±0.66	3.81±0.27
	Open	20.00	13.00	7.91±1.45	2.00±0.00	20.00	13.00	10.82±0.58	2.00±0.00

Table 6.12 Estimates of mean group size ± standard error and typical group size ± standard error for female, male and mixed sex groups at Dames Slough in each season and habitat type. Values without standard errors represent a single observation.

		Mean group size				Typical group size			
	Habitat	Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn
Female	Closed canopy	2.50±1.06	-	1.25±0.22	3.00±0.35	3.40±0.60	-	1.40±0.24	3.17±0.21
	Open canopy	3.36±0.43	3.35±0.48	2.58±0.37	2.50±0.26	4.57±0.26	4.70±0.31	4.59±0.32	3.86±0.25
	Other woodland	3.33±1.09	5.33±0.54	2.11±0.33	2.00±0.00	4.40±0.65	5.50±0.22	2.58±0.23	2.00±0.00
	Woodland rides	3.22±0.35	4.93±1.59	2.28±0.26	2.34±0.24	4.42±0.20	12.10±1.20	4.06±0.28	3.39±0.18
	Grassland	8.70±0.95	8.94±0.88	6.40±0.91	6.32±0.81	11.06±0.40	11.82±0.31	12.45±0.59	8.30±0.26
	Arable	-	-	-	-	-	-	-	-
	Other open	-	-	-	-	-	-	-	-
	Closed	3.25±0.26	4.11±0.67	2.33±0.19	2.44±0.17	4.45±0.15	8.14±0.63	4.10±0.19	3.60±0.15
	Open	8.70±0.95	8.94±0.88	6.40±0.91	6.32±0.81	11.06±0.40	11.82±0.31	12.45±0.59	8.30±0.26
Male	Closed canopy	-	-	-	1.67±0.54	-	-	-	2.20±0.49
	Open canopy	9.00±3.30	4.00	6.50±1.85	2.03±0.41	12.63±0.49	4.00	10.69±0.59	4.24±0.50
	Other woodland	-	-	3.00	-	-	-	3.00	-
	Woodland rides	1.50±0.43	-	2.20±0.66	1.67±0.27	2.00±0.45	-	3.18±0.54	2.07±0.23
	Grassland	18.67±1.41	7.00±2.35	10.57±1.19	5.27±1.05	19.30±0.26	10.14±1.01	12.45±0.25	7.55±0.40
	Arable	-	-	-	-	-	-	-	-
	Other open	-	-	-	-	-	-	-	-
	Closed	4.71±2.01	4.00	4.71±1.21	1.92±0.29	10.70±0.83	4.00	9.09±0.61	3.67±0.39
	Open	18.67±1.41	7.00±2.35	10.57±1.19	5.27±1.05	19.30±0.26	10.14±1.01	12.45±0.25	7.55±0.40
Mixed Sex	Closed canopy	-	-	-	-	-	-	-	-
	Open canopy	2.67±0.54	6.50±2.47	-	8.55±1.95	3.00±0.38	8.38±0.85	-	13.98±0.44
	Other woodland	-	-	-	-	-	-	-	-
	Woodland rides	-	3.00±0.00	-	4.00±0.63	-	3.00±0.00	-	4.50±0.30
	Grassland	22.00±2.12	19.33±3.60	12.14±3.06	12.67±1.59	22.41±0.45	21.34±0.73	17.54±0.90	14.46±0.41
	Arable	-	-	-	-	-	-	-	-
	Other open	-	-	-	-	-	-	-	-
	Closed	4.50±1.64	4.75±1.52	-	8.11±1.08	6.89±0.86	6.68±0.82	-	13.33±0.43
	Open	22.00±2.12	19.33±3.60	12.14±3.06	12.67±1.59	22.41±0.45	21.34±0.73	17.54±0.90	14.46±0.41

Table 6.13 Estimates of mean group size ± standard error and typical group size ± standard error for female, male and mixed sex groups at South Oakley in each season and habitat type. Values without standard errors represent a single observation.

		Mean group size				Typical group size			
	Habitat	Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn
Female	Closed canopy	-	2.86±0.74	1.00	2.00	-	4.20±0.51	1.00	2.00
	Open canopy	3.34±0.44	5.07±0.60	1.61±0.18	2.38±0.53	5.04±0.27	9.47±0.39	1.97±0.15	3.32±0.45
	Other woodland	-	1.00	-	-	-	1.00	-	-
	Woodland rides	1.50±0.35	3.75±0.74	1.25±0.22	2.60±1.00	1.67±0.33	4.33±0.40	1.40±0.24	4.54±0.77
	Grassland	-	10.00	-	-	-	10.00	-	-
	Arable	-	-	-	-	-	-	-	-
	Other open	2.50±0.35	7.40±0.22	1.00	3.50±1.77	2.60±0.24	7.43±0.08	1.00	5.29±0.71
	Closed	3.23±0.42	4.73±0.52	1.52±0.15	2.43±0.47	4.94±0.27	8.91±0.36	1.86±0.14	3.71±0.40
	Open	2.50±0.35	7.83±0.44	1.00	3.50±1.77	2.60±0.24	7.98±0.17	1.00	5.29±0.71
Male	Closed canopy	5.67±2.18	3.00±0.35	-	3.50±1.77	8.18±0.96	3.17±0.21	-	5.29±0.71
	Open canopy	10.13±2.26	7.15±1.17	3.50±1.44	1.60±0.36	17.71±0.62	10.96±0.46	5.86±0.73	2.00±0.33
	Other woodland	-	11.00	8.00	-	-	11.00	8.00	-
	Woodland rides	-	4.25±1.00	4.17±1.83	-	-	4.25±1.00	9.00±0.94	-
	Grassland	-	11.00±4.18	4.00±1.25	2.00	-	17.36±1.35	5.17±0.66	2.00
	Arable	-	-	-	-	-	-	-	-
	Other open	11.80±3.06	7.80±1.63	5.00±1.32	7.00±0.00	15.78±1.06	9.51±0.31	7.80±0.61	7.00±0.00
	Closed	9.39±1.96	6.06±0.81	4.27±1.19	2.14±0.65	16.75±0.60	9.67±0.38	7.89±0.57	3.53±0.57
	Open	11.80±3.06	9.22±2.14	4.73±1.03	5.33±1.36	15.78±1.06	13.67±0.85	7.19±0.52	6.38±0.43
Mixed Sex	Closed canopy	-	8.00	-	-	-	8.00	-	-
	Open canopy	4.00±1.42	4.50±1.06	-	5.00±1.41	5.00±0.65	5.00±0.50	-	5.80±0.61
	Other woodland	-	-	-	-	-	-	-	-
	Woodland rides	-	-	-	-	-	-	-	-
	Grassland	-	-	-	-	-	-	-	-
	Arable	-	-	-	-	-	-	-	-
	Other open	-	11.00	-	-	-	11.00	-	-
	Closed	4.00±1.41	5.67±1.19	-	5.00±1.41	5.00±0.65	6.41±0.45	-	5.80±0.61
	Open	-	11.00	-	-	-	11.00	-	-

Table 6.14 Estimates of mean group size ± standard error and typical group size ± standard error for female, male and mixed sex groups at Blackensford in each season and habitat type. Values without standard errors represent a single observation.

		Mean group size				Typical group size			
	Habitat	Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn
Female	Closed canopy	6.80±1.78	6.10±1.31	4.14±0.77	2.34±0.22	11.47±0.84	8.93±0.59	5.14±0.38	3.10±0.17
	Open canopy	3.92±0.23	4.51±0.34	1.98±0.23	1.95±0.09	5.21±0.12	6.53±0.17	3.34±0.23	2.90±0.11
	Other woodland	3.00±1.25	2.50±0.35	2.07±0.21	1.58±0.22	4.56±0.73	2.60±0.24	2.38±0.16	1.95±0.19
	Woodland rides	4.25±0.78	4.00±0.49	1.23±0.12	1.94±0.13	6.53±0.35	5.71±0.24	1.38±0.13	2.64±0.11
	Grassland	14.86±2.99	13.15±1.98	5.14±1.63	5.40±1.12	19.06±0.78	19.11±0.49	8.78±0.91	7.74±0.38
	Arable	-	-	-	-	-	-	-	-
	Other open	4.05±0.64	4.33±0.72	1.82±0.20	3.33±0.48	5.99±0.36	6.49±0.44	2.30±0.17	4.36±0.27
	Closed	4.17±0.26	4.49±0.28	2.06±0.17	1.97±0.07	6.18±0.17	6.60±0.15	3.30±0.17	2.84±0.08
	Open	6.96±1.32	8.97±1.31	2.62±0.50	4.16±0.57	13.50±0.67	16.22±0.49	5.37±0.57	6.12±0.29
Male	Closed canopy	-	-	-	2.20±0.28	-	-	-	4.23±0.29
	Open canopy	2.33±0.72	5.00±0.71	4.00±2.45	1.66±0.15	3.00±0.49	5.20±0.32	8.50±1.01	3.16±0.21
	Other woodland	-	-	2.00±0.00	1.20±0.18	-	-	2.00±0.00	1.33±0.21
	Woodland rides	2.33±0.72	-	1.50±0.35	1.27±0.16	3.00±0.49	-	1.67±0.33	1.71±0.22
	Grassland	-	3.00±0.00	3.25±1.67	-	-	3.00±0.00	6.69±1.00	-
	Arable	-	-	-	-	-	-	-	-
	Other open	-	-	1.00±0.00	1.00±0.00	-	-	1.00±0.00	1.00±0.00
	Closed	2.33±0.51	5.00±0.71	2.83±1.32	1.77±0.12	3.00±0.33	5.20±0.32	6.53±1.04	3.42±0.16
	Open	-	3.00±0.00	2.80±1.40	1.00±0.00	-	3.00±0.00	6.29±1.01	1.00±0.00
Mixed Sex	Closed canopy	3.00	-	-	8.84±1.42	3.00	-	-	21.53±1.03
	Open canopy	2.50±0.35	3.00	-	6.17±0.57	2.60±0.24	3.00	-	9.99±0.35
	Other woodland	-	-	-	3.00±0.00	-	-	-	3.00±0.00
	Woodland rides	9.00	-	-	4.00±0.71	9.00	-	-	4.25±0.37
	Grassland	25.60±3.04	28.00±3.06	14.50±1.77	9.25±2.68	27.41±0.53	30.34±0.56	14.93±0.47	12.35±0.95
	Arable	-	-	-	-	-	-	-	-
	Other open	11.00±3.54	-	-	7.25±1.24	13.27±0.97	-	-	8.10±0.47
	Closed	5.75±1.78	3.00	-	7.22±0.69	7.96±0.71	3.00	-	15.89±0.59
	Open	21.43±3.46	28.00±3.06	14.50±1.77	8.25±1.52	25.33±0.63	30.34±0.56	14.93±0.47	10.48±0.62

Table 6.15 Estimates of mean group size ± standard error and typical group size ± standard error for female, male and mixed sex groups at Brinken in each season and habitat type. Values without standard errors represent a single observation.

		Mean group size				Typical group size			
	Habitat	Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn
Female	Closed canopy	5.33±0.98	5.00	5.00	2.43±0.49	5.88±0.38	5.00	5.00	3.12±0.34
	Open canopy	3.98±0.40	5.52±0.70	2.07±0.23	2.82±0.17	5.84±0.25	7.72±0.33	3.09±0.21	3.57±0.11
	Other woodland	-	-	-	-	-	-	-	-
	Woodland rides	5.00	10.00	2.50±0.83	2.33±0.56	5.00	10.00	3.60±0.52	3.14±0.42
	Grassland	13.17±2.54	43.74±10.11	8.27±2.18	4.20±1.45	24.41±0.80	106.82±1.42	46.25±1.99	24.21±2.07
	Arable	-	-	-	-	-	-	-	-
	Other open	6.23±2.09	10.40±2.97	3.69±0.82	3.66±.73	15.37±1.20	14.65±0.81	6.08±0.51	5.87±0.46
	Closed	4.08±0.37	5.67±0.67	2.17±0.22	2.75±0.16	5.83±0.22	7.78±0.30	3.24±0.19	3.51±0.10
	Open	10.67±1.87	38.53±8.81	7.52±1.84	4.05±1.07	22.51±0.71	102.94±1.46	43.01±1.88	19.69±1.65
Male	Closed canopy	-	-	-	-	-	-	-	-
	Open canopy	2.00	-	-	1.35±0.23	2.00	-	-	2.04±0.34
	Other woodland	-	-	-	-	-	-	-	-
	Woodland rides	-	-	-	1.00	-	-	-	1.00
	Grassland	-	-	-	2.45±0.68	-	-	-	4.56±0.64
	Arable	-	-	-	-	-	-	-	-
	Other open	-	-	13.00	1.00	-	-	13.00	1.00
	Closed	2.00	-	-	1.33±0.22	2.00	-	-	2.00±0.33
	Open	-	-	13.00	2.33±0.64	-	-	13.00	4.43±0.63
Mixed Sex	Closed canopy	2.00	-	-	3.00	2.00	-	-	3.00
	Open canopy	8.00	-	-	4.76±0.70	8.00	-	-	6.51±0.43
	Other woodland	-	-	-	-	-	-	-	-
	Woodland rides	-	-	-	2.00	-	-	-	2.00
	Grassland	-	75.86±22.85	-	12.75±3.11	-	124.05±2.04	-	18.82±0.92
	Arable	-	-	-	-	-	-	-	-
	Other open	8.00	-	-	7.22±1.30	8.00	-	-	9.34±0.53
	Closed	5.00±2.12	-	-	4.53±0.65	6.80±0.80	-	-	6.28±0.41
	Open	8.00	75.86±22.85	-	9.82±1.75	8.00	124.05±2.04	-	15.13±0.70

Table 6.16 Estimates of mean group size ± standard error and typical group size ± standard error for female, male and mixed sex groups at Lockerley in each season and habitat type. Values without standard errors represent a single observation.

		Mean group size				Typical group size			
	Habitat	Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn
Female	Closed canopy	4.48±0.45	4.36±0.47	2.78±0.31	3.16±0.27	6.44±0.23	6.66±0.26	3.69±0.20	4.78±0.20
	Open canopy	5.13±0.81	4.89±0.95	2.06±0.37	3.33±0.46	8.07±0.37	6.55±0.38	3.12±0.33	4.69±0.29
	Other woodland	4.00±1.25	1.00	1.00	2.00±0.87	5.17±0.66	1.00	1.00	3.50±0.73
	Woodland rides	5.25±0.81	5.00±1.09	1.73±0.26	1.43±0.19	6.24±0.36	7.87±0.46	2.16±0.21	1.60±0.16
	Grassland	11.00	7.50±2.47	4.00±1.25	5.78±0.75	11.00	9.13±0.83	5.17±0.41	6.65±0.33
	Arable	5.00±0.84	4.00±0.86	2.21±0.37	3.94±0.61	6.70±0.40	5.85±0.45	3.97±0.31	5.62±0.39
	Other open	-	-	-	-	-	-	-	-
	Closed	4.73±0.36	4.49±0.40	3.33±0.20	3.03±0.22	6.90±0.18	6.87±0.20	3.30±0.16	4.62±0.16
	Open	5.46±0.89	4.58±0.91	2.38±0.36	4.56±0.50	7.37±0.38	6.75±0.44	4.16±0.27	6.06±0.27
Male	Closed canopy	3.14±0.96	1.00±0.00	3.00	1.35±0.15	5.18±0.54	1.00±0.00	4.56±0.18	1.67±0.16
	Open canopy	5.00±2.12	-	-	1.00±0.00	6.80±0.80	-	-	1.00±0.00
	Other woodland	-	-	-	-	-	-	-	-
	Woodland rides	-	-	-	-	-	-	-	-
	Grassland	-	-	4.50±0.35	2.00	-	-	4.56±0.18	2.00
	Arable	3.00	4.33±1.52	-	4.00	3.00	5.92±0.76	-	4.00
	Other open	-	-	-	-	-	-	-	-
	Closed	3.56±0.92	1.00±0.00	3.00	1.30±0.13	5.69±0.46	1.00±0.00	3.00	1.60±0.15
	Open	3.00	4.33±1.52	4.50±0.35	3.00±0.71	3.00	5.92±0.76	4.56±0.18	3.33±0.42
Mixed Sex	Closed canopy	9.00±1.99	6.00±2.05	-	8.12±1.01	11.63±0.77	8.11±0.88	-	10.26±0.33
	Open canopy	7.00±2.12	-	-	9.00±1.58	8.29±0.75	-	-	9.00±1.58
	Other woodland	-	-	-	-	-	-	-	-
	Woodland rides	7.00	-	6.50±1.06	6.00	7.00	-	6.85±0.42	6.00
	Grassland	-	-	-	-	-	-	-	-
	Arable	15.00	-	6.00	-	15.00	-	6.00	-
	Other open	-	-	-	-	-	-	-	-
	Closed	8.33±1.44	6.00±2.05	6.50±1.06	8.25±0.83	10.57±0.60	8.11±0.88	6.85±0.42	10.24±0.28
	Open	15.00	-	6.00	-	15.00	-	6.00	-

Table 6.17 Estimates of mean group size ± standard error and typical group size ± standard error for female, male and mixed sex groups at Tollard in each season and habitat type. Values without standard errors represent a single observation.

		Mean group size				Typical group size			
	Habitat	Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn
Female	Closed conifer	4.00±0.53	5.32±0.57	2.58±0.25	2.77±0.25	7.06±0.37	9.37±0.36	4.08±0.22	3.89±0.19
	Open conifer	4.00±1.11	4.22±0.44	1.84±0.22	3.48±0.48	7.36±0.55	5.86±0.27	2.68±0.25	5.03±0.29
	Other woodland	4.33±1.44	5.40±0.25	2.75±0.39	3.77±0.69	5.77±0.48	5.52±0.11	3.18±0.21	5.41±0.41
	Woodland rides	5.00±1.11	4.67±0.59	2.46±0.37	3.92±0.72	9.21±0.62	6.22±0.28	3.19±0.28	5.63±0.38
	Grassland	7.00±2.11	4.13±0.54	3.77±0.63	4.21±0.57	13.37±1.19	5.85±0.27	4.78±0.30	5.31±0.33
	Arable	9.00±1.16	7.36±1.32	3.64±0.53	6.43±1.12	11.82±0.32	13.29±0.60	6.63±0.36	9.16±0.39
	Other open	-	-	-	-	-	-	-	-
	Closed	4.23±0.44	4.92±0.32	2.38±0.16	3.23±0.22	7.63±0.28	7.77±0.22	3.60±0.15	4.70±0.15
	Open	8.31±1.07	5.78±0.76	3.65±0.44	5.32±0.66	12.27±0.41	10.69±0.45	6.25±0.29	7.63±0.31
Male	Closed conifer	1.00	2.40±0.61	4.00±0.71	1.00±0.00	1.00	3.17±0.37	4.25±0.37	1.00±0.00
	Open conifer	-	2.00	1.00	1.00±0.00	-	2.00	1.00	1.00±0.00
	Other woodland	1.00	-	-	1.00±0.00	1.00±0.00	-	-	1.00±0.00
	Woodland rides	1.00	2.50±1.06	1.00	-	1.00	3.40±0.60	1.00	-
	Grassland	-	2.00	-	1.40±0.22	-	2.00	-	1.57±0.20
	Arable	5.00	4.00±0.00	3.00±1.00	3.00	5.00	4.00±0.00	4.33±0.45	3.00
	Other open	-	-	-	-	-	-	-	-
	Closed	1.00±0.00	2.38±0.47	2.50±0.83	1.00±0.00	1.00±0.00	3.11±3.11	3.60±0.52	1.00±0.00
	Open	5.00	3.50±0.43	3.00±1.00	1.67±0.30	5.00	3.71±0.19	4.33±0.45	2.00±0.26
Mixed Sex	Closed conifer	-	5.60±1.19	3.00±0.71	4.83±1.14	-	6.86±0.50	3.33±0.42	6.45±0.57
	Open conifer	4.00	4.33±0.54	-	-	4.00	4.54±0.24	-	-
	Other woodland	6.00	-	-	-	6.00	-	-	-
	Woodland rides	-	5.00±2.12	-	-	-	6.80±0.80	-	-
	Grassland	-	11.00±3.54	-	-	-	13.27±0.97	-	-
	Arable	-	12.50±2.47	2.00±0.00	14.50±7.42	-	13.48±0.69	2.00±0.00	22.10±1.37
	Other open	-	-	-	-	-	-	-	-
	Closed	5.00±0.71	5.10±0.77	3.00±0.71	4.83±1.14	5.20±0.33	6.25±0.35	3.33±0.42	6.45±0.57
	Open	-	11.75±2.19	2.00±0.00	14.50±7.42	-	13.38±0.58	2.00±0.00	22.10±1.37

Table 6.18 Estimates of mean group size ± standard error and typical group size ± standard error for female, male and mixed sex groups at Tadley in each season and habitat type. Values without standard errors represent a single observation.

		Mean group size				Typical group size			
	Habitat	Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn
Female	Closed conifer	4.75±1.35	5.10±1.20	3.14±0.51	5.14±1.17	7.84±0.73	7.94±0.52	3.73±0.27	7.00±0.51
	Open conifer	3.67±0.81	4.00±1.10	2.39±0.41	3.50±0.91	4.73±0.41	5.50±0.53	3.65±0.32	5.86±0.53
	Other woodland	-	-	-	-	-	-	-	-
	Woodland rides	4.00±0.70	3.42±0.67	1.75±0.41	2.40±0.67	4.86±0.33	5.00±0.35	2.14±0.34	3.33±0.47
	Grassland	5.60±1.54	14.50±2.37	3.60±0.98	13.67±2.60	9.86±0.90	18.38±0.51	6.28±0.60	15.14±0.66
	Arable	3.64±0.86	2.80±0.33	3.25±1.39	1.80±0.33	5.85±0.55	3.00±0.21	5.62±0.87	2.11±0.26
	Other open	-	-	-	-	-	-	-	-
	Closed	4.19±0.62	4.15±0.59	2.48±0.30	3.77±0.62	6.11±0.38	6.43±0.31	3.53±0.22	5.99±0.34
	Open	4.57±0.89	10.60±2.13	3.50±0.81	6.25±2.26	8.19±0.61	17.03±0.58	6.10±0.49	12.80±0.90
Male	Closed conifer	-	-	-	-	-	-	-	-
	Open conifer	-	-	-	2.00	-	-	-	2.00
	Other woodland	-	-	-	-	-	-	-	-
	Woodland rides	-	-	-	-	-	-	-	-
	Grassland	-	2.00	2.00	-	-	2.00	2.00	-
	Arable	-	-	-	-	-	-	-	-
	Other open	-	-	-	-	-	-	-	-
	Closed	-	-	-	2.00	-	-	-	2.00
	Open	-	2.00	2.00	-	-	2.00	2.00	-
Mixed Sex	Closed conifer	-	10.00	-	-	-	10.00	-	-
	Open conifer	8.00±0.00	10.50±0.35	-	-	8.00±0.00	10.52±0.11	-	-
	Other woodland	-	-	-	-	-	-	-	-
	Woodland rides	-	-	-	-	-	-	-	-
	Grasslands	20.00±6.16	23.88±4.91	-	22.33±5.97	25.70±0.83	31.95±0.80	-	27.12±0.91
	Arable	8.00±0.00	-	-	-	8.00	-	-	-
	Other open	-	-	-	-	-	-	-	-
	Closed	8.00±0.00	10.33±0.27	-	-	8.00±0.00	10.35±0.09	-	-
	Open	17.00±5.30	23.88±4.91	-	22.33±5.97	23.62±1.01	31.95±0.80	-	27.12±0.91

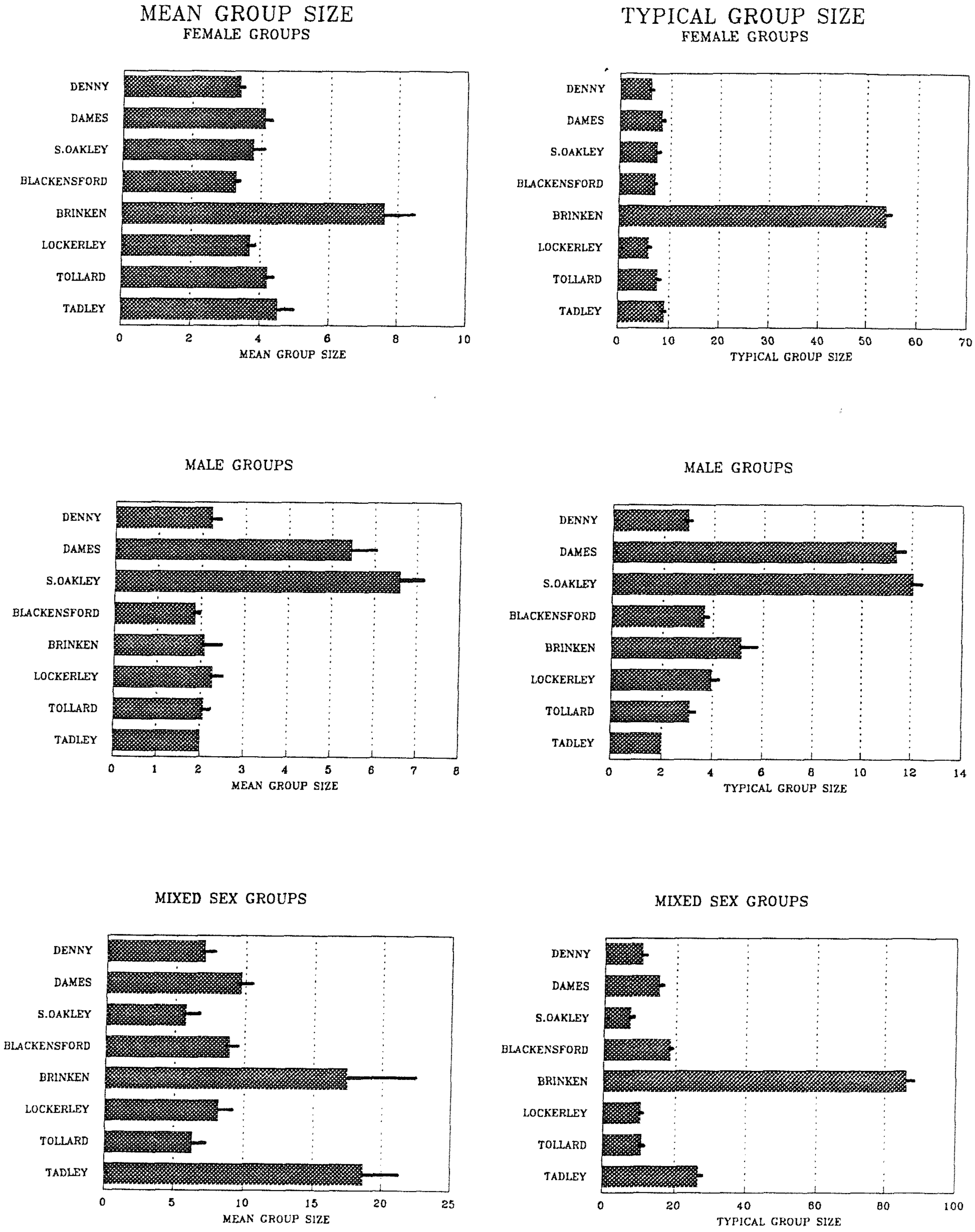
Table 6.19 Estimates of mean group size ± standard error and typical group size ± standard error for female groups per season and habitat category in each of the sites.

		Mean group size				Typical group size			
	Site	Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn
Woodland	Denny	3.26±0.19	3.74±0.21	2.10±0.16	2.39±0.16	4.83±0.13	5.91±0.14	3.96±0.20	3.58±0.13
	Dames Slough	3.25±0.26	4.11±0.67	2.33±0.19	2.44±0.17	4.45±0.15	8.14±0.63	4.10±0.19	3.60±0.15
	South Oakley	3.23±0.42	4.73±0.52	1.52±0.15	2.43±0.47	4.94±0.27	8.91±0.36	1.86±0.14	3.71±0.40
	Blackensford	4.17±0.26	4.49±0.28	2.06±0.17	1.97±0.07	6.18±0.17	6.60±0.15	3.30±0.17	2.84±0.08
	Brinken	4.08±0.37	5.67±0.67	2.17±0.22	2.75±0.16	5.83±0.22	7.78±0.30	3.24±0.19	3.51±0.10
	Lockerley	4.73±0.36	4.49±0.40	3.33±0.20	3.03±0.22	6.90±0.18	6.87±0.20	3.30±0.16	4.62±0.16
	Tollard	4.23±0.44	4.92±0.32	2.38±0.16	3.23±0.22	7.63±0.28	7.77±0.22	3.60±0.15	4.70±0.15
	Tadley	4.19±0.62	4.15±0.59	2.48±0.30	3.77±0.62	6.11±0.38	6.43±0.31	3.53±0.22	5.99±0.34
Open	Denny	7.09±0.94	6.69±0.69	4.50±0.61	3.00±0.53	11.19±0.38	8.75±0.26	7.47±0.40	4.42±0.36
	Dames Slough	8.70±0.95	8.94±0.88	6.40±0.91	6.32±0.81	11.06±0.40	11.82±0.31	12.45±0.59	8.30±0.26
	South Oakley	2.50±0.35	7.83±0.44	1.00	3.50±1.77	2.60±0.24	7.98±0.17	1.00	5.29±0.71
	Blackensford	6.96±1.32	8.97±1.31	2.62±0.50	4.16±0.57	13.50±0.67	16.22±0.49	5.37±0.57	6.12±0.29
	Brinken	10.67±1.87	38.53±8.81	7.52±1.84	4.05±1.07	22.51±0.71	102.94±1.46	43.01±1.88	19.69±1.65
	Lockerley	5.46±0.89	4.58±0.91	2.38±0.36	4.56±0.50	7.37±0.38	6.75±0.44	4.16±0.27	6.06±0.27
	Tollard	8.31±1.07	5.78±0.76	3.65±0.44	5.32±0.66	12.27±0.41	10.69±0.45	6.25±0.29	7.63±0.31
	Tadley	4.57±0.89	10.60±2.13	3.50±0.81	6.25±2.26	8.19±0.61	17.03±0.58	6.10±0.49	12.80±0.90

Table 6.20 Increased group size from woodland to open habitat calculated as the ratio of woodland group size to open group size in each study site. Values are calculated annually and seasonally using both mean and typical group size measures. Study sites are then ranked in order of increasing magnitude of woodland open group size ratio.

	Mean group size ratio					Typical group size ratio				
Site	Annual	Winter	Spring	Summer	Autumn	Annual	Winter	Spring	Summer	Autumn
Denny	1.9	2.2	1.8	2.1	1.3	1.8	2.3	1.5	1.9	1.2
Dames	2.7	2.7	2.2	2.8	2.6	2.4	2.5	1.5	3.0	2.3
S.Oakley	1.5	0.8	1.7	0.7	1.4	1.0	0.5	0.9	0.5	1.4
Black	2.1	1.7	2.0	1.3	2.1	2.7	2.2	2.5	1.6	2.2
Brinken	3.6	2.6	6.8	3.5	1.5	13.3	3.9	13.2	13.3	5.6
Lockerley	1.1	1.2	1.0	0.7	1.5	1.0	1.1	1.0	1.3	1.3
Tollard	1.5	2.0	1.2	1.5	1.7	1.5	1.6	1.4	1.7	1.6
Tadley	1.7	1.1	2.6	1.4	1.7	2.2	1.3	2.7	1.7	2.1
Smallest	Lockerley	S.Oakley	Lockerley	S.Oakley	Denny	Lockerley	S.Oakley	S.Oakley	S.Oakley	Denny
increase	S.Oakley	Tadley	Tollard	Lockerley	S.Oakley	S.Oakley	Lockerley	Lockerley	Lockerley	Lockerley
-	Tollard	Lockerley	S.Oakley	Black	Lockerley	Tollard	Tadley	Tollard	Black	S.Oakley
-	Tadley	Black	Denny	Tadley	Brinken	Denny	Tollard	Denny	Tadley	Tollard
-	Denny	Tollard	Black	Tollard	Tollard	Tadley	Black	Dames	Tollard	Tadley
-	Black	Denny	Dames	Denny	Tadley	Dames	Denny	Black	Denny	Black
Largest	Dames	Brinken	Tadley	Dames	Black	Black	Dames	Tadley	Dames	Dames
increase	Brinken	Dames	Brinken	Brinken	Dames	Brinken	Brinken	Brinken	Brinken	Brinken

Fig 6.1 Mean and typical group size of female, male, and mixed-sex groups in the eight study sites. Standard errors indicated by bar.



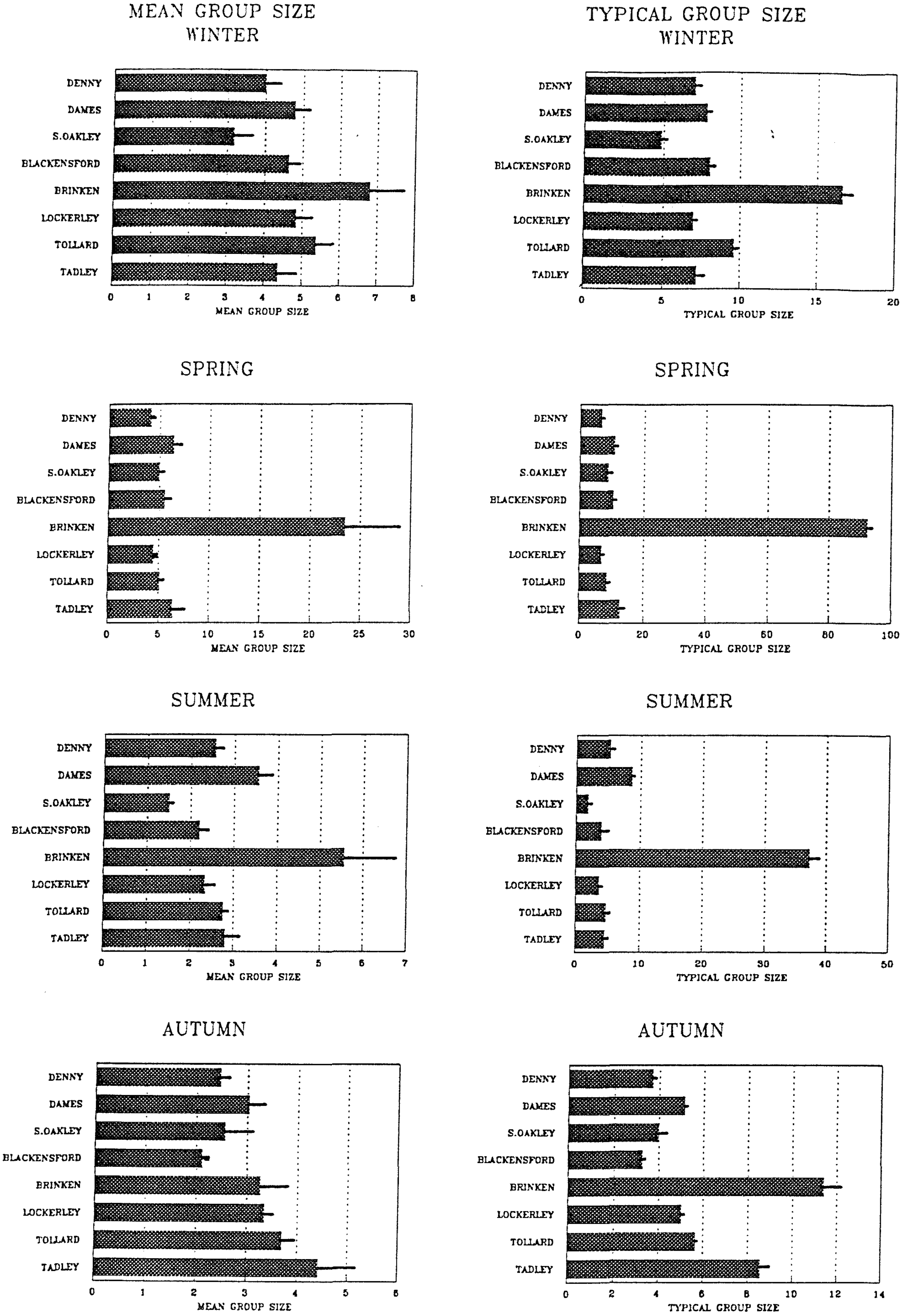


Fig 6.2 Seasonal estimates of female mean and typical group size in the eight study sites. Standard error indicated by bar.

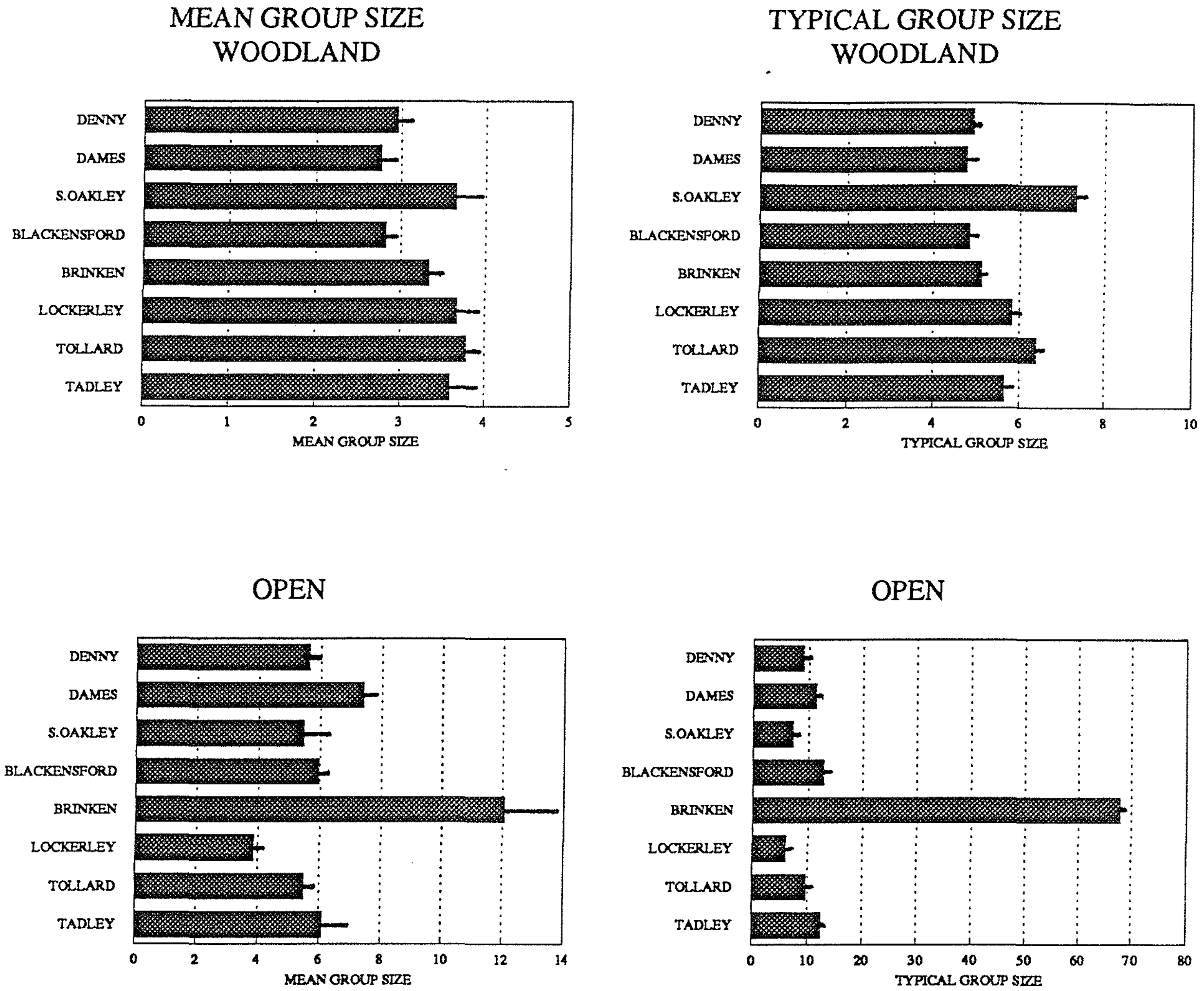


Fig 6.3 Mean and typical group size of female groups in woodland and open habitat. Standard error indicated by bar.

7. MATING SYSTEMS AND ECOLOGY

7.1. INTRODUCTION

Early reviews of mammalian mating systems concentrated on species differences in relation to their ecology (eg. Wilson 1975). Comparison within species, however, whether between populations living in different environments or within populations in different circumstances, avoid the problems of major differences between species masking subtle responses to environmental variation (Jarman 1982). Fallow deer occur in a wide range of environmental conditions, and are characterized by great flexibility in social systems (see Chapters 5 & 6), and thus provide a good opportunity to study the relationship between mating systems and ecology within a single species.

Fallow deer are traditionally described as exhibiting a mating system involving some degree of territoriality, with individual males establishing and defending noncontiguous reproductive territories, called 'rutting stands' and attracting females by auditory and olfactory cues (eg. Chapman & Chapman 1975). However, it is clear that considerably more variation in mating systems exists both between and within populations than has been previously recognized. In some populations non-territorial reproductive behaviour has been recorded (Alvarez et al. 1975; Schaal 1985a, 1987) whilst in others, reproductive aggregations analogous to leks have been observed (Schaal 1986; Pemberton & Balmford 1987; Clutton-Brock et al. 1988; Apollonio et al. 1989). This variation has not yet been completely documented; nor have the relationships yet been explored between the mating system adopted in any particular situation and factors of the population's ecology which might influence that system.

This chapter starts by defining the range of mating strategies adopted by individual male fallow deer in terms of a framework based on the degree and type of territoriality during the autumn rut. Utilizing this framework, the next section contrasts the mating systems of the New Forest populations to those of the agricultural sites. The final section examines which factors of the population and vegetational environment are most important in influencing the mating system adopted by the population.

Mammalian mating systems and ecology: a recap

A recent review of mammalian mating systems by Clutton-Brock (1989) suggested that much of the variation in male mating behaviour is attributable to four important characteristics of females: the extent to which the effective reproductive rate of females can be increased by male assistance in rearing offspring; the size of female ranges; the size and stability of female groups; and the density and distribution of females in time and space. Each of these is in turn affected by variation in the distribution of resources. Clutton-Brock's review has been outlined in detail in the general introduction to this thesis and will not be repeated here.

Interspecific differences in ungulate mating systems

Much of the early work on ungulate mating systems involved explanations of species-specific mating patterns in terms of their ecological correlates. The reviews of Jarman (1974), Estes (1974) and Leuthold (1977) on the comparative social organisation of African antelope are particularly well known. Jarman established main categories of social organisation and related these to the body size and feeding ecology of the species in each. Small-bodied antelope forage for highly nutritious, dispersed food items, usually in forest cover, and live in monogamous pairs in resource-based territories. Medium-sized antelope are intermediate feeders, occur in social groups of more variable size, and males are highly polygynous and defend resource based territories. In the largest bulk feeding species, female groups are very large, defence of a territory is no longer economic, and males adopt female defence strategies.

An identical approach has been adopted to account for inter-specific differences in the mating systems of cervids as, for example, in the review by Clutton-Brock et al. (1982). Species that live in closed canopy forests and are predominantly selective browsers occur singly or in small groups both in the breeding season and throughout the rest of the year. These include roe deer *Capreolus capreolus* (Bramley 1970) and moose *Alces alces* (Houston 1974) in temperate regions, and muntjac *Muntiacus muntjak* (Barrette 1977) and Bawean deer *Axis kuhlii* (Blouch & Atmosoedirdjo 1978) in the tropics and neotropics. In some species males defend territories overlapping female ranges whilst in others males range widely searching for females. Among species principally found in open canopy woodland or forest edge, typically intermediate feeders taking both browse and grasses, breeding systems vary widely. Territorial behaviour during the rut is thought to be typical for male fallow deer (Chapman & Chapman 1975) and sambar *Cervus unicolour* (Schaller 1967) whilst white-tailed *Odocoileus virginianus* (Hirth 1977), black-tailed *O.hemionus* (Kucera 1978), and chital *Axis axis* (Schaller 1967) bucks are described as forming temporary 'tending bonds' with oestrous females. The largest breeding groups are found in species occupying open habitats, such as red deer *Cervus elaphus* (Darling 1937) and elk *Cervus canadensis* (Struhsaker 1967), in which males typically collect and defend harems of females, and caribou *Rangifer tarandus*, in which males and females live in mixed sex groups and access to females is related to dominance rank (Lent 1965).

Intraspecific variation in ungulate mating systems

With the benefit of hindsight it is easy to be critical of these early attempts to categorize species mating systems. Over the last decade, rapid advances in evolutionary theory in combination with increasingly sophisticated field studies have led to greater understanding of the functional significance of social and reproductive behaviour (Clutton-Brock 1989). Mating systems are now seen as the outcome of reproductive strategies of individuals rather than the evolved characteristics of species (Bradbury & Vehrencamp 1977; Clutton-Brock & Harvey 1978; Wrangham & Rubenstein 1986). Variation in mating behaviour is expected both within and between populations as a consequence of the adaptive adjustment of individual behaviour to differences in the social and ecological environment (Rubenstein 1980; Dunbar 1982). The remainder of this introduction will consider examples of such intraspecific variation in the mating behaviour of medium to large antelope and deer.

Resource defence territoriality is the most common mating system among medium sized antelopes (Estes 1974). There are essentially two main types of resource defence in antelope, although it is best to regard these as extremes in a continuum (Gosling 1986). One is to defend a small part of a high quality patch of food which attracts large numbers of females, the second is to defend the whole of a food resource which is a long term food supply for a small number of females. Among several species the form of such territorial behaviour varies widely both between and within populations. A particularly good example of such flexibility is shown by topi *Damiliscus lunatus* in which male mating strategies appear to be adaptations to female movement and grouping patterns and competition with other males for access to females (Gosling in press). In the productive, homogeneous grasslands of the Serengeti, where high densities of topi congregate in the wet season, intrasexual competition is intense and male territories are very small (Duncan 1975). Where the vegetation is very heterogeneous, as in the Serengeti woodlands, females occur in small closed membership groups, intrasexual competition is low and males defend much larger territories which may encompass the entire home range of a female group (Duncan 1975). Along the ecotone between the plains and woodlands, territories of intermediate size are defended (Walther 1968). Topi mating strategies, however, are not limited to resource defence. Non-territorial following has been observed in the Ruwenzori National Park in Uganda where males abandon territories and move with large female groups on the open plains, and attempt to monopolize females within a small, mobile part of the herd (Jewell 1972). In other populations, male topi join leks and defend very small territories which contain minimal food resources (Duncan 1975; Montfort-Brahamn 1975). Gosling & Petrie (in press) suggest that topi leks arise when satellite males cluster around resource territories which are very successful because they contain high densities of females congregating in open areas for anti-predator reasons.

Similar flexibility is shown in other antelope species, although admittedly not on such a grand scale. Leks form in certain populations of Uganda kob *Kobus kob thomasi* (Beuchner 1961; Leuthold 1966), white-eared kob *Kobus kob leucotis* (Fryxell 1987), and lechwe *Kobus leche kafuensis* (Schuster 1976) as an alternative to resource defence territoriality. Resource defence itself is highly variable in impala *Aepyceros melampus* males, and appears to be largely a response to female flexibility in grouping and movement patterns (Jarman & Jarman 1979). Male hartebeest *Alcelaphus buselaphus* switch from resource defence to following when population density and intrasexual competition is low (Gosling 1974). Wildebeest *Connochaetes taurinus* in the Serengeti show clear differences in mating systems; in sedentary populations males defend resource based territories throughout the year, whilst in migratory populations mating occurs during the course of migration in small temporary territories, established for only a day or two and abandoned as the migration moves on (Estes 1969, 1974).

Intraspecific variation in cervid mating systems has received much less attention. An obvious parallel to migratory and sedentary wildebeest is the mating system variation shown by different populations of caribou. As previously described, Lent (1965) found that rutting behaviour of barren-ground caribou coincided with the autumn migration. The animals were aggregated and moving and the individual tending of oestrous females by dominant males was the only type of mating system observed. In neither migratory caribou nor wildebeest have studies been able to monitor the breeding success of individuals in mobile herds. In sedentary, woodland caribou populations, dominant males control loose harem groups from which females may come and go but subordinate males are excluded (Bergerud 1974).

More subtle variation has been documented in populations of white-tailed deer inhabiting environments contrasting in habitat structure and composition (Hirth 1977). The findings of this study in respect to social grouping have been presented in Chapter 6. In summary, Hirth demonstrated that among white-tails living in a savannah environment there was a marked increase in group size in open habitats. In woodland populations, group size changed little. Associated with this increased gregariousness was a change in breeding system. In woodland populations, interactions between the sexes were primarily between single males and single females, bucks forming a 'tending bond' upon locating oestrous females. In the savannah population, dominant males drove other males away from groups of females but did not try to herd females and maintain them in a cohesive group. Hirth surmised that the chasing of other males was the beginning of an evolution towards harem breeding, made possible by group living in open habitats. A similar progression towards harem breeding was demonstrated in the desert mule deer by Kucera (1978), who invokes the same ecological influences of open habitat and group living to account for this change from the more 'normal' temporary pair bonding of woodland populations (eg. Dasmann & Taber 1956). Both Hirth (1977) and Kucera (1978) stress the point that the whilst harem formation and defence was not shown, it is possible that if placed in an even more open habitat, where large groups might be more stable, *Odocoileus* species might evolve true harem behaviour.

Variation in fallow deer mating systems

As mentioned above, the 'species-specific' mating system of fallow deer has long been considered to be one of defence of noncontiguous territories called 'rutting stands' during a short reproductive period in autumn (eg. Cadman 1966; Chapman & Chapman 1975; Ueckermann & Hansen 1983). Male deer live in separate herds, often in geographically distinct areas throughout much of the year, move to female areas during the rut and briefly defend a territory, and then return to male groups. This view has persisted until very recently, despite early suggestions in the literature of mating system variation. Heideman (1973) and Espmark & Brunner (1974) both indicated that rutting territories and associated behaviour may be clustered, although they provided little or no data, and did not appear to attach any significance to their findings. Alvarez et al. (1975) suggested that non-territorial harem breeding occurred in a fallow population in Donana, S.Spain, however a more recent publication appears to contradict this, stating that territorial males attain highest mating success (Braza et al. 1986). Few of these studies provide quantitative data, and, in any case, comparison between studies is difficult due to variation in field methods and interpretation.

Schaal (1985a, 1987) first systematically described variation of mating strategies within a single population of fallow deer in Alsace, N. France, relating this to habitat openness and 'reproductive phase'. During the main autumn rut, in continuous woodland males adopted a territorial strategy of defending rutting stands and attracting females by advertisement, while in open habitats males were non-territorial and defended harems. Schaal also recognized a secondary winter reproductive phase, during which time male fighting and precopulatory behaviour was observed. In woodland habitats males adopted a following strategy in which temporary pair-bonds were formed, whereas mixed-sex groups including several males occurred in open habitats, and access to females was based on a linear dominance hierarchy. Schaal speculated that this variation was due to differences in the spatiotemporal distribution of food and its subsequent effect upon the distribution and abundance of females. Schaal (1986, 1987) subsequently described a lekking strategy observed in fallow at Jaegersborg Park, Denmark, in which up to twenty mature males aggregate on very small reproductive territories containing negligible resources. Other lekking populations were quickly discovered (Pemberton & Balmford 1987; Apollonio

1989; Langbein & Thirgood 1989) and several intensive studies initiated (Clutton-Brock et al. 1988, 1989; Apollonio et al. 1989, 1990). The results of comparative studies in British deer parks by Langbein (Langbein 1990, Langbein & Thirgood 1989) have done much to clarify the ecological parameters influencing mating systems in this species, and evaluation of these results will be delayed until the discussion of this chapter.

Objectives of the current study

In summary the objectives of this chapter are:

1. To clarify the range of mating strategies exhibited by male fallow deer in both wild and park populations.
2. To describe the range of mating systems adopted in the New Forest and agricultural fallow deer populations.
3. To examine which factors of the population and vegetational environment are most important in influencing the mating system of fallow deer.

7.2. METHODS

Data collection

Data were collected during observations made from 1987-1989 in three sites in the New Forest (Blackensford, Dames, Brinken) and during 1987-1988 in two agricultural populations (Lockerley & Tollard). Methodology differed slightly between sites and is summarized separately here.

In each year rutting observations were concentrated at Blackensford in the New Forest in order to concentrate effort on studies of alternative mating strategies and reproductive success. These data are presented in Chapter 8. Data presented in the current chapter were derived from censuses made from 1-4 times daily in which the location, activity, group size, and composition of each animal encountered was recorded. Male reproductive activity and social interactions were recorded opportunistically on these censuses. Individual adult males were recognized from a combination of coat and antler characteristics. The use of natural markings for individual recognition of large mammals is a widely used and accepted technique (eg. Clutton-Brock et al. 1982), especially suitable for fallow deer due to the presence of highly variable antlers. Identification and observation of individuals on the lek at Blackensford were made from hides 50m to the north and 20m to the south of the lek edge respectively. Observations were conducted at Blackensford on eighteen days in October 1987, sixteen days in October 1988, and thirty days in October 1989, with maximum single day gap between observation days.

The data presented for Dames Slough and Brinken are derived from censuses made once a day on visits to the study sites. Censuses were usually completed within three hours of dawn as human disturbance later in the day could be severe. Census data was collected in a similar manner as in Blackensford, with the location, activity, group size and composition of each animal encountered recorded. Reproductive activity and social interactions of males were recorded as above, however it was not possible to individually identify all mature males encountered. A limited number of focal animal watches were undertaken on some single territories, but this data is not presented here. Observations were conducted at a maximum four day interval throughout October (7-12 days sampling in each year) at Dames Slough (1987-1989) and Brinken (1988-1989).

Observations of reproductive behaviour were made on a more limited basis in the agricultural sites for logistic reasons. In both the 1987 and 1988 ruts, Lockerley was visited on four days at weekly intervals, whilst sampling at Tollard was limited to two days. In these restricted periods, data collection was mainly opportunistic during normal transect sampling of the sites. On locating reproductive activity, transects were interrupted and continuous observations collected until the animals moved from view. Due to the very low numbers of mature males in each site, it was possible to identify individually most reproductively active males on each day.

Ecological correlates

The habitat and population parameters investigated in relation to mating system variation between sites were habitat structure and composition, patterns of habitat use, male and female density, population dispersion, and female group size. These data have been previously presented and methodology can be found in the relevant chapter.

Population parameters presented in the analysis of variation between sites are based on transect data collected throughout the autumn season (September-November), and in each site did not vary between years. The intensity of sampling in the restricted area of the immediate vicinity of the Blackensford lek during the peak period of reproductive activity allows a more detailed assessment of localized density in each year of the study. A restricted area of 100 ha encompassing all known sites of reproductive activity was censused within three hours of dawn on each day of observations during the last two weeks in October (12, 10, 14 days respectively in 1987, 1988, 1989). Localized density was calculated as the average number of deer seen within this 100 ha area, reflecting not total density but the minimum density present at any one time. Group size and composition was recorded as in previous chapters.

7.3. RESULTS

Definitions: Strategies and Systems

In this presentation a clear distinction is made between the mating system of a population and mating strategies of individual males within that system. Male mating strategies are the specific behaviour patterns of individuals with the ultimate aim of achieving maximum lifetime copulatory success. The above definition is consistent with the game theory approach of Maynard Smith (1982) and Dunbar (1982). In many populations, alternative mating strategies may be adopted simultaneously by different males; additionally, individual males may switch from one strategy to another as social and environmental conditions change. The population mating system is the result of the combined strategies of all the individual males in the population.

Fallow mating strategies: the territoriality continuum

The wide range of mating strategies displayed by male fallow deer may best be viewed as a continuum, which can be arranged with respect to the degree and type of territoriality during the autumn rut (Fig 7.1). It is possible to identify particular reference points along this continuum, but in reality, one strategy grades imperceptibly into the next, making it difficult to define precise cut-off points. It is helpful, however, to distinguish broadly between those strategies in which single territories are held, those in which multiple territories are held, and those in which reproductive behaviour is non-territorial. The full range of mating strategies exhibited by fallow deer in both wild and park populations was described on this basis by Langbein & Thirgood (1989) and what follows is largely an updated version of ideas presented in that paper.

Single Territory ('Rutting stand')

The type of mating strategy traditionally described as typical for fallow deer (eg. Cadman 1966; Chapman & Chapman 1975) in which a single male defends an exclusive isolated reproductive territory. The defended area may vary greatly in both habitat type and size, such variation making precise description of a 'typical' stand difficult. Within wild populations, permanent territories have only been observed in woodland habitats; however here they occur in a range of forest types from closed canopy conifer to open canopy deciduous. The size of the defended area is also highly variable, ranging from 0.1 to 5.0 ha. The extent to which trophic resources are present on single territories varies; whilst some are located on or near areas of good grazing or under fruiting trees, the majority appear to contain little or nothing in the way of food.

Temporary territory

A strategy based on solitary territorialism as in the above case, but in which the territory is only defended for a relatively small proportion, often only 1 or 2 hours, of the day. Temporary territory holding males will readily leave their territories, often in pursuit of females, or to take up an alternative territory in a different part of their range. Temporary territories are often located on or near food resources, in which case they may be defended only when females are in attendance, or are situated to intercept major female movement paths.

Multiple stands

Multiple stands are the adjacent reproductive territories of several mature males, differing from single territories in not preserving the physical separation from neighbours characteristic of that strategy. As in single territories, the size of the defended area is highly variable from site to site. In many cases these territories are clustered together on or near food resources, particularly so when they are only of a temporary nature, and females may visit multiple stands for feeding as well as reproduction.

Leks

Leks have been defined by Bradbury (1981) as 'assemblies of territorial males which females visit solely for the purpose of copulation'. Males provide neither resources nor parental care and females have an opportunity for mate choice. The lack of significant trophic resources on fallow deer lek territories is a key distinction between this strategy and the preceding multiple stands. Lek territories are often greatly reduced in size, however neither this parameter nor the number of displaying males are good criteria for defining this strategy, due to their great variability from site to site.

Following

Following as a mating strategy involves a persistent association between a mature male and either solitary or groups of females which is not based on territoriality. Access to females is primarily by foraging or by prior holding of temporary stands to intercept female movements. Satellite behaviour on the periphery of territories of other males often develops into following of females when they leave the territory.

Harem defence

A harem is a group of females held by a single mature male for the purpose of obtaining exclusive mating rights. Other mature males are excluded from the group and the harem holder defends the females rather than a fixed territory. The harem holding buck will usually attempt to retain females within his group through extensive herding.

Dominance groups

A multi-male mixed sex group in which one male is dominant over all others and achieves most matings. Subordinate males are tolerated in the group and there is a relatively low level of male aggression. No territorial behaviour is exhibited and the bucks move with the large feeding groups of females and fawns.

The Blackensford mating system

The complex mating system at Blackensford was subject to detailed investigation in each of the three years of this study. The intensity of reproductive activity varied greatly between years and is summarised in the following sections with reference to Fig 7.2.

1987

The focus of reproductive activity was a small lek, situated on the boundary of two distinct habitats; half of the territories were located in a narrow belt of 35 year old Douglas Fir, the remainder in the adjacent open canopy Oak woodland. A maximum of nine lek territories were delineated by repeated censusing and confirmed by the mapping of boundary clashes. The territories were not all occupied simultaneously; the maximum number of mature bucks actively holding territories at any one time was seven. The two central conifer territories (C and D) contained no obvious trophic resources, initially being carpeted with fallen conifer needles and subsequently churned into ankle deep mud by the constant trampling of the deer. Territories C and D were each approximately 0.25 ha in total size, however most activity was concentrated in the northern halves of the territories near the edge of the open oak. Two peripheral territories (G & H) were established in the conifers to the west and east of the two central stands. The exact size and the extent to which these territories were defended was often difficult to determine. However, if the physical features of the conifer compartment were used to delineate the territory boundaries, which appeared likely, territories G and H were 0.5 and 0.8 ha in total size. Activity was concentrated on the boundaries with the two central territories, and the extent to which the remainder of the territory was used was uncertain.

The remaining territories were located in or on the edge of the adjacent open oak woodland to the north of the conifer block. Territories A, B, and E consisted of natural grassland with a high open canopy of mature oak. These territories contained limited resources which may have attracted females onto the lek. The exact territory boundaries were difficult to determine and almost certainly changed throughout the rut. The approximate boundaries were mapped by repeated censusing of the lek when bucks were in attendance and were estimated to comprise 0.4, 0.5, and 0.6 ha respectively. Territory I was situated on the boundary between the conifer block and the adjacent open oak in what was initially very thick bracken. In latter stages of the rut, the bracken was flattened by repeated trampling and the value of any available grazing deteriorated rapidly, eventually resulting in a quagmire similar to the central conifer territories. The area of territory I was estimated at 0.3 ha. The final territory F consisted of a very small area of less than 0.01 ha at the centre of the lek, focused around a single large beech tree on the border between territories C, D, I, and B.

The central conifer territories were occupied continuously by mature males throughout October. During the peak two weeks of the rut (October 14-28) a maximum of seven mature males were present on the lek during which time ten copulations were seen. The maximum number of deer seen on the lek at any one time was approximately 50 at 0800 hrs. on 23.10.87 (5 bucks, 15 yobs and prickets, 30 does and fawns).

Permanent single territories BH, BB and SE were established in three localities in close proximity to the lek (<0.5 km) during the peak of reproductive activity. These territories occurred in a variety of woodland habitats, ranged in trophic resources from plentiful to absent, and were representative of the great variability of single territory defence in fallow deer. Resident males remained on territories throughout much of the day. Three copulations were observed on single territories in 1987.

Temporary territories were established at four localities during the 1987 rut. Territories T1, T2 and T3 were on the periphery of the lek, typically formed in early morning or late evening, and appeared to be the response of bucks attempting to intercept females moving on and off the lek. These attempts had limited success, however it is not known whether these territories were permanently occupied at night. Territory T4 was established only during the middle of the day when female deer moved from the lek to feed in the open woodlands of Stinking Edge.

Non-territorial males were particularly common in Stinking Edge Wood and Beech Beds during the peak of the rut. Males appeared very mobile; during the early morning peak of activity non-territorial males were peripheral on the lek, then would follow female foraging movements out into Stinking Edge and Beech Beds during late morning and afternoon, and return to the lek in early evening. One non-territorial copulation was observed in Stinking Edge.

In total, twenty-three adult bucks were identified in eighteen days sampling. This was likely to be an underestimate of true numbers.

1988

The 1988 rut was characterised by a general reduction in reproductive activity throughout the area in comparison to 1987. This was particularly pronounced on the lek.

Despite early activity in the beginning of October, only two permanent territories were occupied on the lek, with two very temporary territories established in the ends of the conifers. The permanent territories were greatly expanded in size; one comprising conifer territories C and D, and the other open territories A, B and I. Territory turnover was low with two individual bucks holding these two lek territories for 17 and 12 days respectively. Eight copulations were seen on the lek, all in the central conifers. The maximum number of deer seen on the lek at one time was approximately 20 at 0800 hrs. on 19.10.88 (3 bucks, 7 yobs and prickets, 10 does and fawns).

Single territory BH was occupied throughout the rut, whilst use of single territories BB and SE was more intermittent. Few females were seen on these territories and no copulations were observed. Temporary territories T1, T2 and T3 on the periphery of the lek were more regularly occupied during the peak rut, with particularly T3 active in the latter stages. The open oak lek territory and T3 merged into one large 'domain of dominance' of a single buck during the last week in October.

Non-territorial males were rarely seen and there were no regular large scale movements of females associated with foraging. Twenty mature males were identified in sixteen sampling days, however ten of these were only seen on one or two days early in October and then appeared to leave the area.

1989

The 1989 rut at Blackensford is described in detail in Chapter 8 and only a very brief summary is presented here.

The focus of activity was the lek, which returned to the size and level of activity of the 1987 rut. The detailed structure of the lek in terms of territory size and location was identical to that observed in 1987. The lek was continuously occupied from 16.09.89-30.11.89, and during the peak of the rut up to seven territories were defended concurrently. A total of 58 copulations were observed on the lek. Details of territory occupancy and turnover, male interactions, individual copulatory success, and behavioural correlates of copulatory success are given in Chapter 8.

Single territories BB, BH and SE were occupied throughout the peak of the rut. Based on limited sampling, five copulations were seen on these territories. Temporary territories on the periphery of the lek did not form to the same extent as in the 1987 and 1988 ruts, similarly T4 was not occupied as this site was clear-felled during forestry operations in early 1989. Non-territorial following and satellite strategies were common throughout the rut and a single copulation was observed. In total 31 mature males were identified at Blackensford in 1989.

Blackensford: a summary

The Blackensford population exhibited a mixed mating system involving territorial defence of lek territories, single territories, and temporary territories, and non-territorial following of females. There was a marked decrease in reproductive activity in all strategies in 1988 in comparison to the other two years of the study. Data on reproductive success of alternative strategies is presented in Chapter 8. In 1987 and 1988 a minimum of twenty mature males were seen at Blackensford; this was likely an underestimate of the true numbers. A more detailed study in 1989 identified 31 individual mature males.

The Dames Slough mating system

Data on the distribution of reproductive behaviour was systematically collected in this geographical area of the New Forest in each of the three years of the study. Whilst the overall pattern of activity was similar in each year, the intensity of use of individual sites varied between years. A brief summary of each year is presented with reference to Fig 7.3. At certain sites (eg. Territory A) individual males were identified throughout the rut, however no systematic effort was made to recognize each male encountered in the area.

1987

Territories A, B, C and D were permanently defended by single mature males throughout the peak final two weeks of October. These territories were separated by over 500m in each case. The same buck was in situ on territory A from 2.10.87-26.10.87, however it was not known if other territorial males enjoyed the same longevity. Female deer were repeatedly seen on territories A, B and C (up to a maximum 17 does on territory A) but visibility was restricted on territory D and few females were ever visible. A single copulation was observed on territory A on 26.10.87.

Temporary territories T2, T3, T4 and T6 were occupied intermittently throughout the rut. It is not known whether the same bucks repeatedly returned to the same territory. Males did not appear capable of retaining females on temporary territories and their reproductive success is unknown.

Non-territorial males were frequently encountered throughout the study area. Males opportunistically followed groups of females as they were encountered. Since males were not individually recognizable it was impossible to accurately estimate the numbers of males pursuing this strategy.

The total number of mature 5 yr+ males active in this area during October 1987 was impossible to determine. The maximum number encountered on a single transect, including both territorial and non-territorial individuals, was nine, although it is impossible to state conclusively that these were separate individuals. This was almost certainly a underestimate, and it was likely that many more males moved in and out of the area during the rut.

1988

Territories A, B, C and D were similarly occupied by a single male throughout the peak two weeks of the rut. Reproductive activity at territory A was noticeably reduced in relation to the previous year eg. seven does maximum were observed at one time, and temporary stand T2 was never occupied. In contrast to the previous year, female deer continued to feed on the fields at Burley Lodge throughout October, and a single buck established a temporary territory (T1) on these fields whilst the females were present. The extent of territorial defence of this territory was unknown, and the male followed female groups back into Dames Slough Inclosure after early morning disturbance. No copulations were observed.

Reproductive activity at territories B, C and D appeared similar to the previous year. It was unknown whether a single individual male retained possession of each territory throughout the rut. No copulations were observed. Temporary territories T3, T4 and T6 were utilized to the same extent as in 1987. Non-territorial males were frequently encountered throughout the area; as in the previous year it was impossible to give a realistic estimate of the numbers of males adopting each strategy.

1989

Reproductive activity at territory A returned to the levels of 1987; a single male retained possession throughout the rut, female groups were consistently on the territory (maximum 11 does), and a single copulation was seen on 18.10.89. Temporary territory T2 was briefly occupied by at least two separate mature males during the peak two weeks of the rut. In contrast, female deer were not seen on the fields at Burley Lodge and no male activity was observed at the site of T1.

Reproductive activity was pronounced on territories B and C and in the immediate surrounding area, eg. T4 and T5. A single copulation was seen at C on 18.10.89. There was considerable evidence that B developed into a multiple stand during the absolute peak of the rut. On 1015 hr. on 18.10.89 four mature (5yr+) males were observed actively displaying and following 10-15 females in a restricted 0.25 ha area of open canopy conifer. Eight younger males were also present on the stand. This high level of activity continued for 20 minutes, until female deer left the stand following disturbance by a fight between two of the mature males. With the departure of the females, male activity abruptly ended and all males bar one left the stand. Similar activity was observed between 0830-1000 hrs on 20.10.89 at the same location. A maximum of 4 mature males, 15 young males, and 20 female deer and fawns were present in an area of approximately 0.25 ha. At no time was male-female contact observed, possibly due to continuous harassment of females by younger males. Activity on this stand was reduced on a subsequent visit at 0715 hrs on 25.10.89; a single mature male was present with six females.

Dames Slough: a summary

The mating system in this population was based on a mixture of permanent defence of single territories, temporary defence of single territories, and non-territorial following. In addition, in 1989 at least, there was some evidence of multiple territory reproductive behaviour, however more quantitative information at this one particular site is required. As males were not individually recognizable it is impossible to estimate either total numbers present or the numbers pursuing alternative mating strategies. Three copulations were observed on single territories.

The Brinken mating system

Data on the distribution of reproductive behaviour was collected during 1988 and 1989 in the same fashion as in the preceding site. Again the overall pattern of activity was the same but the intensity of use of individual sites differed between the two years. A brief summary of each year is given with reference to Fig 7.4. Individual males were not systematically recognized.

1988

Single territories A, B, C and D were permanently defended throughout the peak of the rut. The distance between the latter three territories was as little as 200m, although distinct boundaries could not be defined as each male moved extensively over an area of approximately 1 ha. It was not known whether a single male retained possession of each territory throughout the rut. During the peak of the rut, these single territories always contained females when undisturbed, however focal watches were not undertaken and no copulations were observed.

Female deer remained in large numbers on the improved and natural grasslands at Queen's Meadow and Wide Lawn, particularly during early morning before human disturbance. Temporary territories were established at T1, T2 and T3 on the edge of open deciduous and grassland. These territories were formed in response to large groups (20-40 individuals) of feeding females. The extent to which territories were defended was uncertain, as was the reproductive success of individual males adopting this strategy. No copulations were observed and territories were abandoned when females moved into the woodland.

On one occasion (0815-0840 hrs, 20.10.88) four mature bucks were observed on a multiple stand at T2. At the start of observations each male was displaying and attempting to approach individuals in a group of approximately twenty females. No territory boundaries could be identified and male movement over a 1 ha area was pronounced. The activity ceased after a fight involving three of the bucks.

Non-territorial males were frequently observed throughout Brinken Wood and this appeared to be a common strategy in this site, although there is no data on individually recognized males to support this claim. The total number of mature bucks active in Brinken during the rut was unknown, however the maximum seen on a single transect was eleven.

1989

Single territories A, B, C and D were again defended throughout the rut; little information is available on either turnover of male ownership, female attendance, or male mating success. It is known that territory B was occupied by three different bucks between 15.10.89 and 25.10.89. No copulations were observed on any of these territories, however male competition for them was intense; five fights were observed within the main area of Brinken Wood during seven transects over the period 10.10.89-30.10.89.

In contrast to 1988, females were more evenly distributed throughout the study site and little reproductive activity was seen in the Queen's Meadow and Wide Lawn area. Temporary stands T4 and T5 were extensively used in early morning before human disturbance moved deer off the Warwickslade grasslands. Temporary multiple stands were observed on three occasions (13.10.89, 18.10.89, 20.10.89) at T4 for a total of 1 hour 55 minutes. The most extensive observations were obtained between 0700-0800 hrs. on 18.10.89 when three mature males separated by less than 50m actively displayed and approached female deer grazing in a dispersed group of 16 does and 7 fawns. Ten young males were present on the periphery of the female group. Two mounting attempts were observed by the same individual male but no copulations were seen. The distance between the males was maintained for 45 minutes until sequential fights involving all three mature males plus two younger males resulted in the mature males moving into woodland. The female deer were subsequently disturbed by a walker and dog.

Brinken: a summary

The mating system in this subpopulation of the New Forest was based on a mixture of permanent defence of single territories, temporary defence of single territories, and non-territorial following. In addition, in both years temporary multiple territories were established by males in areas extensively used by females for feeding. No information is available on the distribution of mating success between males adopting these alternative strategies, nor is it even approximately known how many mature males were active in Brinken during the rut.

The Lockerley mating system

The pattern of reproductive behaviour at Lockerley did not differ appreciably between years, hence a single account is presented with reference to Fig 7.5. In both years, a single mature (5+ years) male was observed in the main woodland block during October. Due to the very limited sampling, it is possible, but thought unlikely, that other mature males were present during the rut. In 1987, this buck was positively identified 17 times on three sampling days (October 18, 24, 25); in 1988 a similar buck was positively identified 9 times on three sampling days (October 16, 23, 30). Despite superficial similarity, there was no conclusive evidence that the same male was present both years. In addition to the single mature male, there was an unknown number of young males ('yobs') and yearling males ('prickets') present in the area of most reproductive activity. These immature males were not systematically identified, however the greatest number seen together at any one time was four yobs and three prickets. In both 1987 and 1988, the mature buck remained in residence in the main woodland block until the end of January, and was seen both in isolation and in the company of female deer. There was no firm evidence of winter reproductive activity.

Territorial behaviour was displayed at two sites, both in closed canopy conifer, separated by approximately 500m (Fig 7.3), and matched the description of a temporary territory. The mature male actively displayed and pursued females for a maximum period of 45 minutes whilst based on these territories. During this time all other males including prickets were excluded from an area of approximately 0.1 ha. Due to poor visibility in thick woodland continuous observations were not possible. The maximum number of female deer present at any time on one of the temporary stands was twelve. In contrast to the permanent single territories of the New Forest, the resident male was not observed displaying when females were absent from the stand. When the female group left the territory, the male abandoned territorial defence and pursued the females. The mature male was subsequently observed with female groups as much as 1 km away from the original territory. It was not possible to maintain visual contact with these highly mobile mixed-sex groups, and the extent of male-female contact was unclear. No copulations or mounting attempts were seen, and it is unclear whether the dominant mature male had exclusive mating access. The single mature male appeared able to maintain dominance by threat; no male-male physical contact (eg. fights) involving the mature buck was seen.

In summary, the mating system at Lockerley appeared, on admittedly limited observations, to be based on the temporary defence of two spatially distinct territories by a single mature male. These territories were only defended in the presence of females, and the resident male readily abandoned the territories to maintain contact with female groups. The extent and nature of male-female interactions in these mixed sex groups is unknown. The male strategy in this population appeared to be a mixture of temporary stand defence combined with non-territorial following.

The Tollard Royal mating system

As at Lockerley, the distribution and intensity of reproductive activity did not appear to differ between years and as such a single summary is presented with reference to Fig 7.6. Reproductive activity within the study area was centred on the 'island woodland' complexes of Chalkits, Farnham and Rotherley, among which most detail was obtained for Chalkits in each year. A single mature buck was resident in Chalkits on each of the four sampling days. It is unknown whether other bucks visited the copse during the rut. Within each year, the same buck was resident on both days, however 'ownership' of the copse changed between the two years. There were an unknown number of immature males in Chalkits in each year. In both years the buck had vacated the copse by November.

Activity in Chalkits was centred in the northern end of the copse in a 1 ha compartment of coppiced hazel. There did not appear to be a single rutting stand, and activity was equally distributed around the compartment. Additionally, the buck made frequent and long-lasting excursions throughout the copse, apparently in pursuit of females. Reproductive activity was exclusively in hazel coppice, resulting in few sightings of the buck and even fewer observations of male-female interactions. However, groaning was pronounced throughout the day, and the progress of the male throughout the copse could easily be followed. A possible interpretation of the Chalkits behaviour was that the whole copse (40.0 ha) could be considered as one large extended territory, however the extent to which it was defended against other males is unclear.

Fewer data are available for reproductive activity in the Rotherley and Farnham sites. In each year, a single mature buck was centred in each copse, but unlike Chalkits, the males did not restrict their activity to a single woodland. On two days in 1987, the Rotherley buck was observed in Rotherley Wood, Rotherley Firs and Animal Cover, three copses separated by 500m of arable land (Fig 7.4). Similarly, in 1988, a mature buck active in Farnham Wood was subsequently seen following a group of ten females nine days later in Hookswood Copse, approximately 1 km away (Fig 7.4). In both instances, positive identifications were made from drawings of antler shape. Detailed information of male-female interactions are not available, nor is detail of the intensity of male territorial behaviour, however it was clear that males did not occupy permanently defended territories. These two areas were frequently disturbed by forestry and gamebird rearing operations and the resident female deer were highly mobile.

In summary, the mating system at Tollard Royal appeared to be based on loose temporary territorial behaviour and following of female groups. Movement of females between widely separated woodland copses apparently resulted in similar behaviour by males. Nothing is known about the duration of association between bucks and female groups or about male reproductive success. It must be stressed that much of the above account is based on interpretation of the very limited data available.

Ecological correlates of mating systems

Variation between populations

In this section the variation in mating systems between the five study populations will be related to the ecological parameters of previous chapters: habitat structure and composition (Chapter 3); patterns of habitat use (Chapter 4); population density and dispersion (Chapter 5); and female group size (Chapter 6). This analysis concentrates on population differences and utilizes data collected over the three years of the study. All data have been previously presented and reference is made to the original tables and figures. For convenience of comparison significant variables are summarized in Table 7.1. The populations were divided into three categories on the basis of the degree and type of territoriality:

No permanent territories:	Lockerley and Tollard
Permanent single territories:	Dames and Brinken
Permanent multiple territories:	Blackensford

This division is based on the maximum development of male territorial behaviour in each site, and as such represents a slight modification of the scheme previously presented in Fig 7.1 and in an earlier publication (Langbein & Thirgood 1989), necessary because of the great variability in mating strategies displayed within wild populations.

Habitat structure

The mating system typical of each population was compared to the following structural parameters: grain size of all individual habitats, all woodland habitats, and all open habitats (Fig 3.14); amount of woodland to open edge (Table 3.6); and the occurrence of habitat change, both at individual habitat and woodland to open habitat levels (Fig 3.15). There was no relationship between any of the above parameters and the degree of territoriality displayed in the populations.

As previously mentioned (see Discussions, Chapters 3 and 6), whilst quantitative analysis of habitat structure has been based at the level of individual habitat types, it appears likely that this resolution was not warranted and, if anything, deer were responding in terms of their social organisation to a much coarser level of habitat resolution. Quantification at this coarse level is problematic and a more descriptive approach must be adopted.

Lockerley and Tollard were characterized by the discontinuous nature of woodlands, surrounded or interspersed with arable land and grasslands. In both cases the largest single woodland copse comprised less than 50% of the total woodland area in the study site (Fig 3.13). In contrast, the three Forest sites consisted of a single large woodland block with adjacent or enveloped grasslands or heathland. In each case the large woodland comprised more than 90% of total woodland area (Fig 3.13). In summary, discontinuous woodland appears to be associated with non-permanent reproductive territories (Table 7.1).

Habitat composition and utilization

The percentage woodland area varied greatly between the sites (Table 7.1), however the implications for mating systems are conflicting. The two sites in which non-permanent reproductive territories occurred (Lockerley and Tollard) contained the least amount of woodland, however the Forest site at which territoriality was most developed and lekking occurred (Blackensford) contained less woodland than at the two single territory Forest sites (Dames and Brinken).

Increased reproductive territoriality (eg. non-territorial -> lek) was associated with increased use of woodland in autumn, however the differences involved are slight (Table 7.1). Woodland use at Blackensford (92%) was significantly higher than at Tollard (75%) (G-test for independence, $p<0.05$) with the remaining three sites intermediary between the two but not significantly different statistically.

Population density and dispersion

There were very pronounced differences in female density between the two agricultural populations in which permanent territoriality was not shown and the three territorial New Forest populations (Table 7.1). Autumn female density was significantly higher at Dames, Brinken and Blackensford than at Lockerley and Tollard (Mann-Whitney U-tests, $p<0.001$). Density differences between the two agricultural populations were not significant, but Brinken density was higher than at Dames and Blackensford (Mann-Whitney U-tests, $p<0.001$). Similar trends were shown with autumn estimates of 2 yr+ male densities (Table 7.1). Male densities in the two agricultural populations were much lower than in the three Forest populations (Mann-Whitney U-tests, $p<0.001$). Differences between the two agricultural populations and between the three Forest populations were not significant. In summary, permanent reproductive territories appear to be associated with high population density; however, density alone can not explain the occurrence of permanent multiple territories.

Population dispersion also varied between the five sites but not in parallel with the degree of territoriality (Table 7.1). A relatively even distribution was shown both by a lekking population (Blackensford) and by a largely non-territorial population (Lockerley). As discussed in Chapter 5, the explanation for the generally uneven distribution of deer differs between the two environmental types; agricultural populations were concentrated on small woodlands whilst Forest populations were concentrated on small grasslands.

Female group size

In Chapter 6 it was shown that variation in female group size between the sites was most pronounced during the autumn. Is variation in the extent of male reproductive territoriality related to this variation in group size?

Autumn female group size in all habitats combined was smaller at Blackensford than the other four sites (Table 7.1; Mann-Whitney U-tests, $p<0.001$). Differences between the other sites were not significant. These overall values are inflated by the occurrence of large aggregations on favoured feeding areas in open habitats. It is arguable that female group size in woodland, where most daytime reproductive activity is observed, would be more likely to influence male mating strategies. How do woodland group sizes relate to observed mating systems?

Female groups in woodland at the lekking population at Blackensford were smaller than at all other sites (Mann-Whitney U-tests, $p<0.01$). Female groups in woodland in the largely non-territorial Lockerley and Tollard populations were larger than at all other sites (Mann-Whitney U-tests, $p<0.05$). Differences within mating system categories (eg. Lockerley and Tollard, Dames and Brinken) were not significant. In summary, there appears to be an association between decreased male territoriality and increased female woodland group size.

Ecological correlates of population variation in mating systems: a summary

The population mating systems observed in the current study were divided into three categories in which males either have:

1. No permanent territories
2. Permanent single territories
3. Permanent multiple territories

Category 1 populations (Tollard and Lockerley) were associated with relatively small discontinuous woodlands interspersed with open habitat, low autumn utilization of woodland, low density of females and of 2 yr+ males, and large female group size in woodland.

Category 2 populations (Dames and Brinken) were associated with relatively large continuous woodlands enclosing small islands of open habitat, intermediate autumn use of woodland, high density of females and of 2 yr+ males, and intermediate female group size in woodland.

The category 3 population (Blackensford) was associated with a large continuous woodland adjacent to a large continuous open heathland, high autumn use of woodland, high autumn density of females and of 2 yr+ males, and small female group size in woodland.

Ecological correlates of mating system variation at Blackensford

The preceding analysis concentrated on population differences between mating systems and possible ecological correlates. Population parameters such as male and female density and group size were obtained from dawn transect sampling for the whole autumn season (eg. September to November) for the entire study area. Previous analyses have shown that these parameters did not differ significantly between years (see Chapters 5 & 6) thus justifying presenting a single value for each site (see Table 7.1).

The intensity of sampling at Blackensford allows a more detailed assessment of the effects of localized density and resulting group size on reproductive behaviour. Within the limited temporal (October 15-28) and spatial (100ha around lek) confines of the peak period of reproductive activity at Blackensford, significant variation was shown between years in the densities of both female deer and 2 yr+ male deer (Fig 7.8). Female and male densities were significantly lower in 1988 than in 1987 and 1989 (Mann-Whitney U-tests, $p<0.001$), corresponding to the decrease in reproductive activity shown in that year.

In Chapter 6 it was suggested that high density populations were associated with small woodland group size. Was the between-year density difference at Blackensford reflected by a change in female group size? Mean female group size during October 15-28 within the 100ha woodland surrounding the lek did not change between the three years (Fig 7.8), suggesting that density alone may have been responsible for the change in reproductive activity.

7.4. DISCUSSION

The comparative approach adopted in this study and in parallel work by Langbein (1990) in park populations of fallow has clearly demonstrated the wide intraspecific variation in male mating strategies in this species. This discussion will concentrate on differences at the population level, contrasting the mating systems of populations in different areas, or of the same population in different breeding seasons, in relation to various parameters of the population's ecological environment. It is important to emphasize that the mating system of a population is the outcome of the reproductive strategies of individuals (Gosling & Petrie 1981; Wrangham & Rubenstein 1986; Clutton-Brock 1989). The mating system represents a level of organisation on which natural selection does not act (Petrie 1986), since selection is thought to act on individuals or genes rather than on groups or species (Hamilton 1964; Dawkins 1976).

The territoriality continuum: flexibility in male fallow deer

The mating strategies exhibited by male fallow deer may be broadly characterized by the degree and type of territorial behaviour during the autumn rut. In the current study, this ranged in intensity from non-territorial following of individual females or groups, through temporary and permanently defended single reproductive territories to the development of multiple territory systems and leks. Langbein (1990) observed a similar range in park populations of fallow, with the additional strategies of non-territorial harem defence and multi-male dominance groups.

Several of these mating strategies have been previously described in fallow deer; however, a lack of uniformity in defining such terms as 'rutting stands' and 'harems' makes interpretation of population differences difficult. Mating systems based on single non-contiguous reproductive territories ('rutting stands') have long been accepted as typical for the species (eg. Cadman 1966; Chapman & Chapman 1975; Ueckerman & Hansen 1983), and early, somewhat vague, suggestions that fallow bucks may aggregate during the rut (Heidemann 1973; Espmark & Brunner 1974) were largely overlooked. The situation is further confused by conflicting reports referring to a fallow population in Donana, S.

Spain, in which the population mating system has been described as both territorial eg. 'rutting stands' (Braza et al. 1986) and non-territorial eg. 'harems' (Alvarez et al. 1975). The latter publication has been frequently quoted as evidence for non-territorial breeding in this species (eg. Schaal 1987; Clutton-Brock et al. 1988). Lekking in fallow deer was first described by Schaal (1986) and a veritable flood of publications describing the same phenomenon in other populations has followed (Pemberton & Balmford 1987; Clutton-Brock et al. 1988, 1989; Apollonio et al. 1989, 1990).

The observations in the current study, and those of Langbein (1990) in park populations, led to a formal definition of different male mating strategies arranged along a continuum on the basis of degree and type of territoriality (Langbein & Thirgood 1989). Such definitions serve merely to characterize specific points along this continuum, and it is acknowledged that considerable overlap may exist between reproductive strategies. Such overlap is, for example, demonstrated by the change from temporary to permanent defence of a reproductive territory, or in the transition of a multiple stand to a 'true' lek. Nevertheless, it was believed that the described continuum of mating strategies provided a useful framework for the evaluation of the interaction of mating systems and ecology and, furthermore, earlier observations recorded in the literature could easily be located along this gradient. The previous lack of such an overall perspective has contributed to much of the current misunderstanding in the literature.

The recent review of male antelope mating strategies by Gosling (1986) provides a useful parallel to the territorial framework suggested in the current study. Gosling adopted a novel approach by recognizing as similar strategies which previous workers had categorized as different. He considers that male antelope have two main options if they are to maximize the number of times they mate. They can either 'follow' one or a group of females, which may also involve the active control of group members in a harem. Alternatively, they may adopt a 'sit and wait' strategy in which they wait in a part of the range that females visit and defend this area against other males. Such areas usually contain resources which are attractive to females but in certain cases, such as on leks, territories are very small, highly clustered, and contain insignificant food resources. This scheme fits well to that adopted in the present fallow studies. Following, harems and dominance groups are all non-territorial 'following' strategies; temporary and single territories, multiple stands and leks are all 'sit and wait' strategies. An important distinction between fallow deer and antelope, which appears to have been overlooked by some workers (eg. Clutton-Brock 1989, Gosling in press) is that single territorial defence by fallow bucks often does not involve resources. Whilst some territories, particularly in parkland, include or are adjacent to favoured grazing areas or fruiting trees, many territories in wild populations contain no obvious trophic resources. The attraction to females of mating on such territories must, presumably, lie with the identity of the male or his ability to control the territory against others.

Fallow mating systems and ecology

Most recent reviews of mammalian mating behaviour have suggested that male mating strategies are influenced by the spatial and temporal distribution of females, which is in turn affected by variation in resource distribution, predation pressure, the costs of social living and the activities of other males (Bradbury & Vehrencamp 1976, 1977; Emlen & Oring 1977; Clutton-Brock & Harvey 1978; Gosling 1986; Wrangham & Rubenstein 1986; Clutton-Brock 1989). As Gosling (1986) mentions, a major problem in testing sociobiological theory is the scarcity of information about intraspecific variation in mating strategies since interspecific comparisons can only suggest the major factors affecting social systems. Detailed information at the level of the individual animal and its response to different social and ecological environments is needed to understand the adaptiveness of particular strategies. Can the mating system variation observed in fallow deer be explained in these terms?

Schaal's (1987) studies of fallow deer in the Alsace and Jaegersborg provided the first links between mating strategies of males and the grouping patterns and sexual synchronisation of females. Schaal suggests that, in winter, female synchrony in oestrous is low, and thus few females are receptive at any time. In woodland, females are dispersed and males search for receptive females with whom they form tending bonds. In open habitat, females are more aggregated and males associate with females in large groups. Since these groups contain few receptive females, they are not economically defensible, and males tolerate the presence of other males. During the autumn, oestrous is highly synchronised and thus many females are receptive simultaneously. In woodlands, females are more dispersed and males compete for access to territories, to which receptive females are attracted. The large groups typical of open areas now contain many receptive females, and males compete for exclusive mating rights in unimale harems. Under certain conditions - and here Schaal suggests the importance of population density, numbers of adult males and sex ratio - males aggregate on territories containing negligible resources and form leks. Schaal's argument is elegant, and offers a plausible explanation for the variation in male mating behaviour observed; however, it lacks the conclusive evidence of comparative studies on populations exhibiting mating systems intermediary to those he describes.

In the current study, the lowest levels of territorial behaviour were shown by males in the agricultural populations. In these populations, female densities were very low and defence of a permanent reproductive territory would not be economical. Female groups in agricultural woodlands tend to be large, hence once a male has successfully attracted a female group to a temporary territory, it is probably more profitable to follow the females when they leave the territory than to remain and wait for the arrival of the next female group. Little detailed information is available regarding fallow ranging behaviour in any environment, however, it appears likely that female ranges in the agricultural sites are larger than in continuous woodland. Movement of females from one woodland copse to another was frequently observed, often involving distances of up to 1km. In these circumstances, males would have little option but to be highly mobile; defence of a permanent territory in an otherwise empty woodland copse would not result in high mating success. A further factor could be the very low densities of sexually mature male deer in these populations; in the atmosphere of reduced male competition, the onus may be more on finding receptive females than defending them.

The higher density, less aggregated populations in the New Forest were reflected by increased levels of male territoriality during the rut. In each of the Forest populations, however, a range of concurrent male mating strategies coexisted, encompassing both territorial and non-territorial strategies. These alternative mating strategies within populations are likely a reflection of one, or a combination, of several factors (Rubenstein 1980; Dunbar 1982). Males may be able to achieve similar lifetime reproductive success by adopting alternative mating strategies, which may be dependent upon the tactics adopted by others in the population. Alternatively, some males may be incapable of competing with other males to gain maximum access to females, and thus they may be making the 'best of a bad job' by accepting an inferior reproductive payoff. Detailed investigation of the relative costs and benefits of alternative male mating strategies in the Blackensford population are described in Chapter 8.

The lek system observed in each year at Blackensford represented a higher level of territorial organisation than that displayed in the other two Forest sites. Which ecological factors led to the occurrence of lekking in this population and not in the others? Autumn densities were no higher at Blackensford than at the other two sites, indeed if density alone was the critical factor then a lek should have occurred at Brinken. However by necessity, density assessments were based on transects throughout the autumn season and, in addition, reflected overall density throughout the study site. Localized density in the vicinity of the Blackensford lek was very high during the peak of the rut, and it may be this reason that caused the lek to form. This suggestion is given some support by the reduction in size of the lek in 1988, when female densities were very low. Why then do female deer concentrate in the Blackensford area during October? One possibility is that this area provides a rich source of acorns and beech mast, both known to be important constituents of fallow diet during the autumn and early winter (Jackson 1974, 1977). The acorn crop in 1988 was very poor, and this may have been a contributing factor to the relatively low densities of females at Blackensford in that year. Female deer remained on fields throughout the 1988 rut in all three study sites, and temporary rutting activity was observed on fields at both Dames and Brinken.

The Blackensford lek may therefore have been initiated by males placing their territories in or near the areas where females concentrate, however briefly, for a rich food supply (the 'hotspot' theory: Bradbury & Gibson (1983)). This in itself does not explain the extent to which male territories are clustered on the lek. The related idea that leks form because inferior males parasitize the females attracted to superior animals (the 'hotshot' theory: Beehler & Foster (1988)) may explain clustering but cannot account for the presence of several 'hotshots' on the same lek. Gosling & Petrie (in press) have suggested that lek formation in topi results from a combined process involving concentrations of females ('hotspots'), increased mating success of territorial males in these areas ('hotshots'), and then clustering of 'satellite' males in an attempt to parasitize these few very successful territories. This combination of the 'hotspot' and 'hotshot' theories provides a likely scenario for the initial evolution of the Blackensford lek. Once formed, females may prefer clusters of males because they facilitate mate choice (Alexander 1975; Bradbury 1981) or because they provide protection against dangerous harassment by several courting males (Wrangham 1980; Clutton-Brock et al. 1988).

If localized concentrations of females are a prerequisite for the formation of a lek, why does this mating system not occur at Brinken where females are highly aggregated on the improved grasslands at Queens Meadow? Numbers of adult males are unlikely to be a limiting factor; the adjacent fields of New Park contain the highest concentration of male deer in the Forest. The occurrence of temporary multiple territories on or near favoured feeding areas suggests that the same ecological pressures initiating lekking at Blackensford also operate at Brinken. Why then does a permanent lek not form? One likely possibility is that the high human disturbance in this area, particularly during the rut, does not allow the formation of permanent multiple territories. Feeding areas extensively used by deer at Brinken are almost exclusively on open grassland, and deer do not appear to concentrate in woodland to such an extent as at Blackensford. Few single territories in Brinken are 'permanent' in that they are occupied throughout the day; repeated disturbance results in extensive movements of female deer from one reproductive territory to another. Whether this explanation in itself is sufficient to explain the lack of a Brinken lek is unknown. Knowledge of the mating strategies adopted by males in the Brinken area is extremely limited; no information is available on male numbers or individual copulatory success and, of course, all observations were during daylight hours. The Brinken mating system remains possibly the most interesting option for further research on fallow reproductive strategies in the New Forest.

Langbein's (1990) parallel study of park populations of fallow provides an excellent comparison to the current project. Over the same three year period he was able to monitor the mating system adopted in nine separate park herds. Working in enclosed populations has the advantage that absolute assessments of density, sex ratio, and age structure are easily obtained. Langbein's study populations could be divided into the same three categories on the basis of the extent of male reproductive territoriality during the autumn rut (Langbein & Thirgood 1989). Adult buck density consistently emerged as the best predictor of the type of mating system adopted in park populations. Low buck density was associated with non-territorial mating systems, and the degree of territoriality progressively increased with buck density. In the three parks in which Langbein observed leks, both buck density per unit area and the actual numbers of adult bucks were very high. Doe density was also associated with the type of mating system, however separation between the parks was not as clear using this variable.

A functional explanation for the effects of density in these enclosed populations is complicated by the difficulty of isolating the effects of density from those of total numbers (Langbein & Thirgood 1989). At low population numbers, dominant males are able to successfully monopolize a high proportion of the population in a harem and density effects are minimal. When both buck and doe numbers are high, it is increasingly difficult for bucks to monopolize large proportions of the does using harem-type strategies as harems become too large to be economically defensible in light of the increased male competition. Defence of a territory becomes more viable with increasing doe density as the chance of it being repeatedly visited increases. With increasing buck densities, does in oestrous may avoid the heightened male harassment by congregating on defended areas.

Intraspecific variation in mating systems in cervids

The current study, in conjunction with that of Langbein (1990) and the earlier work of Schaal (1987), has demonstrated that fallow deer are highly flexible in their reproductive behaviour, both between and within populations. Mating systems encompass a wide range of territorial and non-territorial male strategies, and appear to be closely linked to population density. Increased male territoriality is associated with high male and female density; however environmental heterogeneity and local resource distribution may also influence mating patterns.

Whilst intraspecific variation in the mating strategies of male antelope have been widely reported (see Gosling 1986 for review) similar such studies are rare for cervids. A previous publication (Langbein & Thirgood 1989) concluded by suggesting that the mating system variation shown by fallow deer in relation to ecological parameters could well be replicated in other deer species if studied over a similar range of environmental conditions.

Recent reports in the literature indicate that this is in fact true. The mating behaviour of red deer stags has been extensively described as harem defence (eg. Clutton-Brock et al. 1982). Recent work in Donana, S. Spain, has shown that under certain conditions, males may defend reproductive territories, and suggests that these territorial males are the most successful in the rut (Carranza et al. 1990). Localized concentration of food in an otherwise low resource environment appears to make territories economically defensible. Reassessment of the mating behaviour of the closely related sika deer *Cervus nippon* suggests that a similar range of territorial and non-territorial strategies may be shown, although the environmental correlates of this variation are less well studied (Putman & Mann 1990). Other likely candidates for mating strategy flexibility are the widely distributed white-tailed and black-tailed deer of North America which occur at a range of densities in different environments. The study of cervid breeding systems may no longer be 'in its infancy' (*sensu* Clutton-Brock et al. 1982), but clearly there remains considerable scope for further comparative studies of species with a broad geographical and ecological distribution.

7.2. SUMMARY

1. The range of mating strategies displayed by male deer may best be viewed as a continuum, arranged with respect to the degree and type of territoriality during the autumn rut. Seven mating strategies may be broadly distingusished: following, harems, dominance groups, temporary territories, single territories, multiple territories and leks.
2. Territoriality was most developed in the Blackensford population in the New Forest. In this site, males adopted the alternative mating strategies of defending lek territories, single territories and temporary territories, and non-territorial following.
3. The New Forest populations Brinken and Dames Slough differed from Blackensford in that leks did not occur. There was some limited evidence of temporary multiple stands forming in responce to female feeding aggregations.
4. Territoriality was least developed in the agricultural populations Lockerley and Tollard Royal. In these sites, males loosely defended temporary territories which were readily abandoned to follow female groups.
5. The lowest levels of territorial behaviour were associated with low density, highly aggregated populations inhabiting small discontinuous woodlands interspersed with open habitat.
6. Permanent reproductive territories were associated with relatively high density, less aggregated populations inhabiting continuous woodland with adjacent open habitat.

7. Lekking was associated with very high localized density possibly initiated by female aggregation at food resources.
8. Mating system variation within populations between years appeared due to the density and distribution of females, which was in turn affected by the abundance and distribution of food.

Table 7.1 Ecological correlates of mating system variation between populations. All environmental and population parameters explained in text.

Site	Mating Strategies	Environment 'Type'	% Woodland	Autumn % use of woodland	Autumn male density deer/100ha	Autumn female density deer/100ha	Autumn dispersion	Autumn female group size combined	Autumn female group size woodland	Autumn female group size open
Tollard	Temp territory Following	Island woodland Continuous open	19	75	0.2 ± 0.1	4.8 ± 0.7	7.4	3.70 ± 0.24	3.23 ± 0.22	5.32 ± 0.66
Lockerley	Temp territory Following	Mosaic woodland open	41	81	0.8 ± 0.4	7.7 ± 1.0	5.4	3.35 ± 0.21	3.03 ± 0.22	4.56 ± 0.50
Dames	Single territory Temp territory Following Multiple territory (?)	Continuous woodland Island open	81	82	6.8 ± 3.2	34.6 ± 4.4	10.6	3.03 ± 0.25	2.44 ± 0.17	6.32 ± 0.81
Brinken	Single territory Temp territory Following Multiple territory (?)	Continuous woodland Island open	79	85	9.0 ± 7.8	83.0 ± 20.0	4.1	3.26 ± 0.44	2.75 ± 0.16	4.05 ± 1.07
Blackensford	Lek Single territory Temp territory Following	Continuous woodland Continuous open	51	92	10.4 ± 6.9	35.1 ± 4.2	5.1	2.12 ± 0.08	1.97 ± 0.07	4.16 ± 0.57

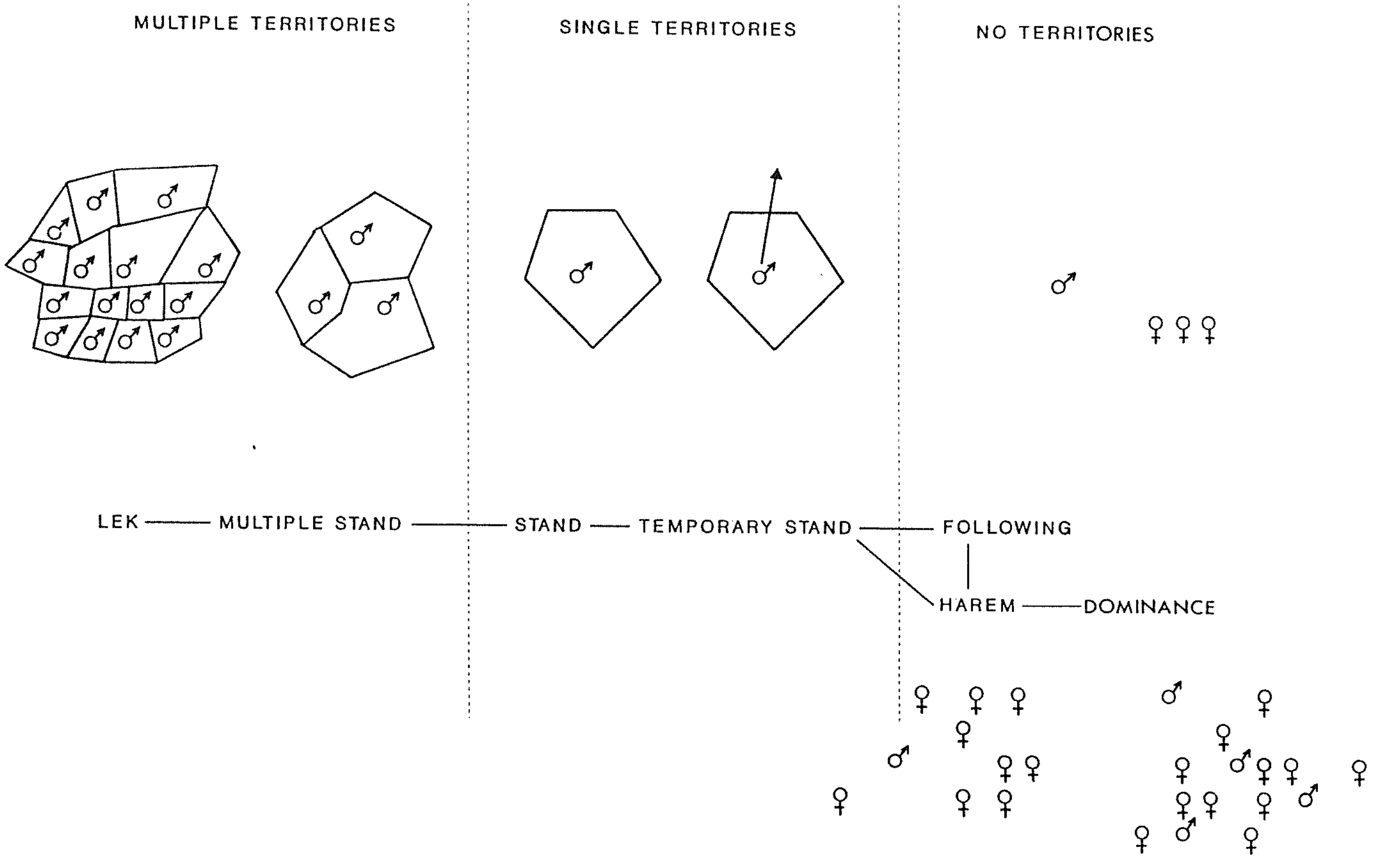


Fig 7.1 Schematic view of the range of observed variation in fallow deer mating systems.

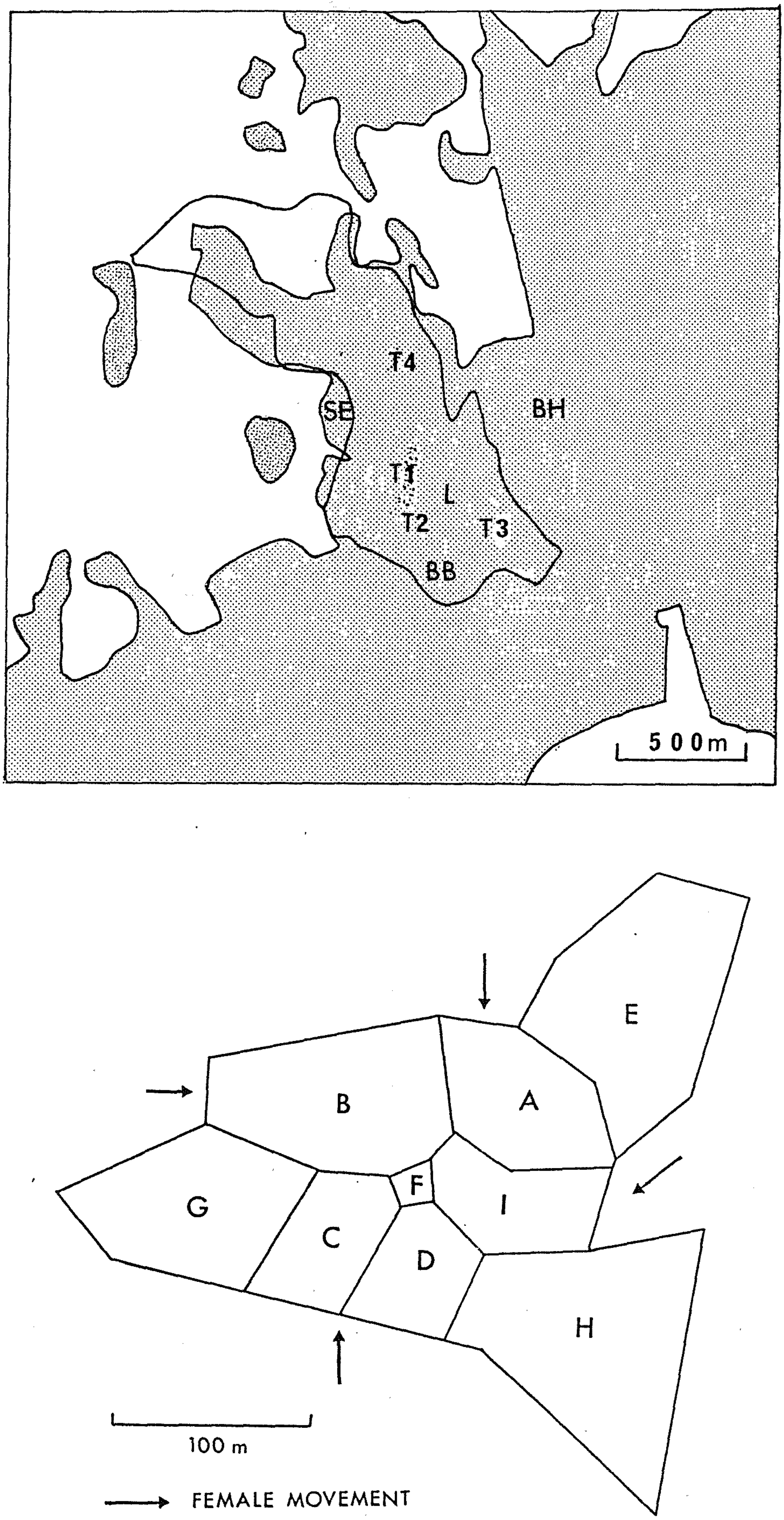


Fig 7.2 Distribution of reproductive activity at the Blackensford study site showing location of lek (L), single territories (BB, BH, SE) and temporary territories (T1, T2, T3, T4). Details of lek territories shown at larger scale below. See text for details.

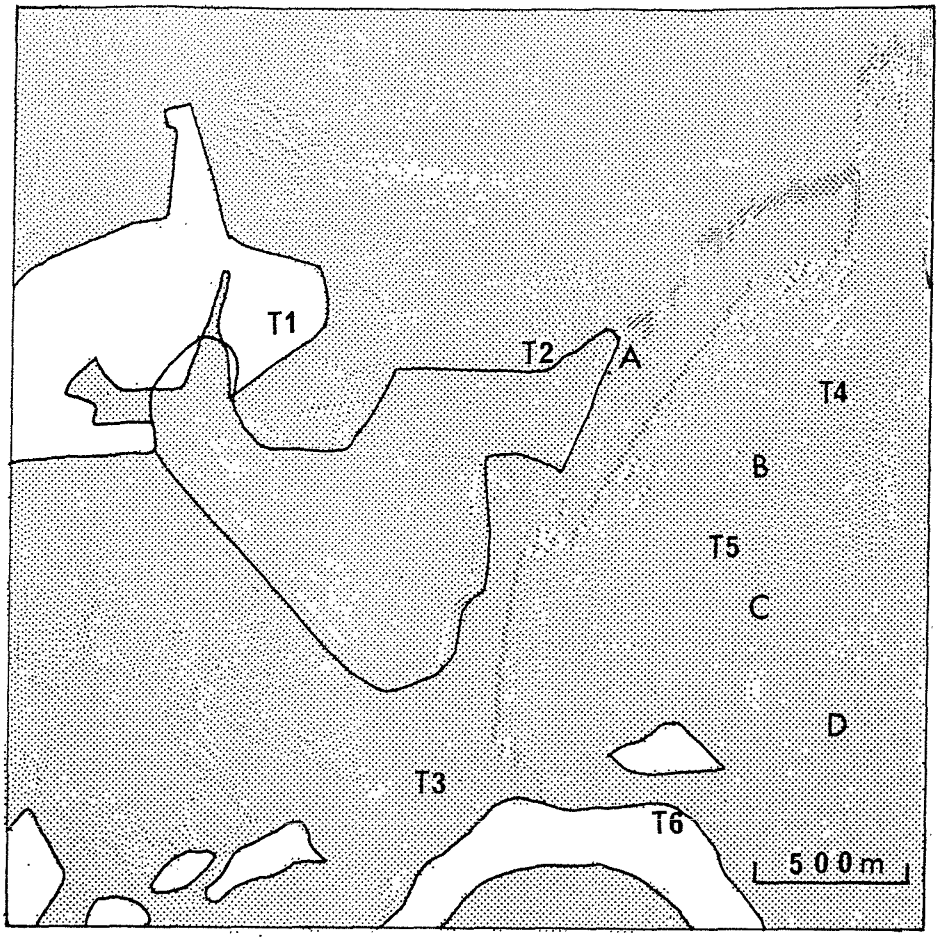


Fig 7.3 Distribution of reproductive activity at the Dames Slough study site showing location of single territories (A, B, C, D) and temporary territories (T1, T2, T3, T4, T5).

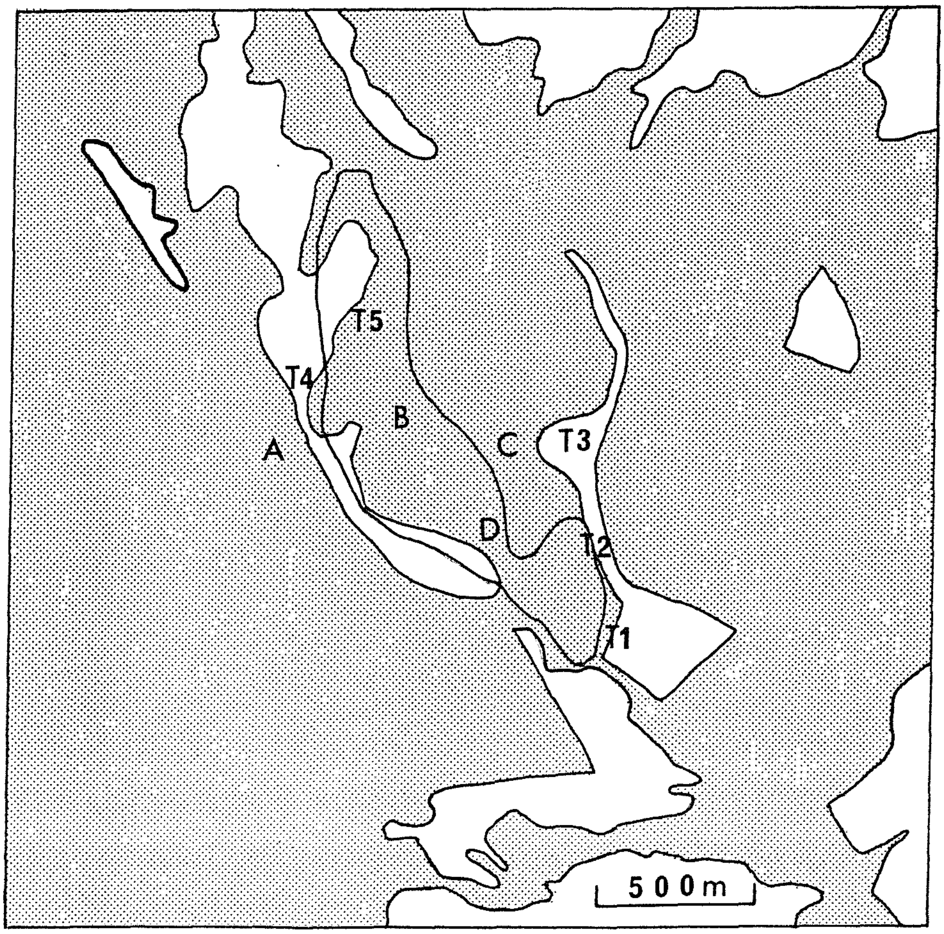


Fig 7.4 Distribution of reproductive activity at Brinken showing location of single (A, B, C, D) and temporary (T1, T2, T3, T4, T5) territories.

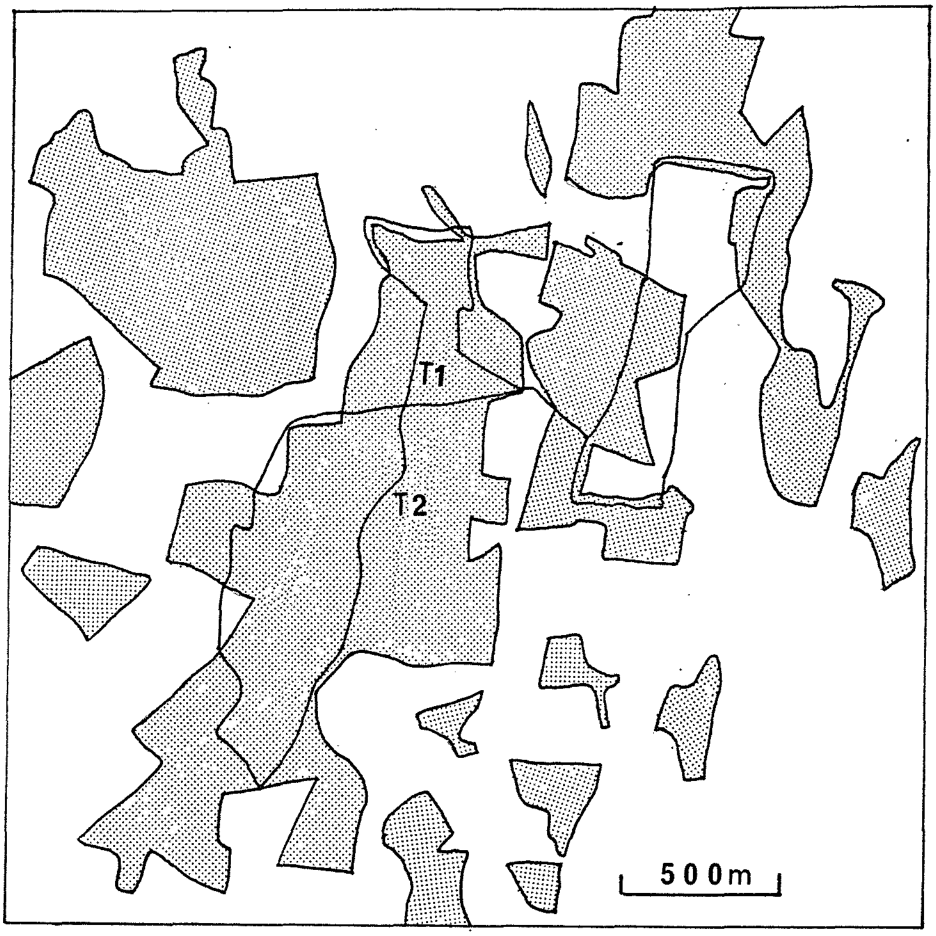


Fig 7.5 Distribution of reproductive activity at the Lockerley study site showing location of temporary territories (T1 & T2).

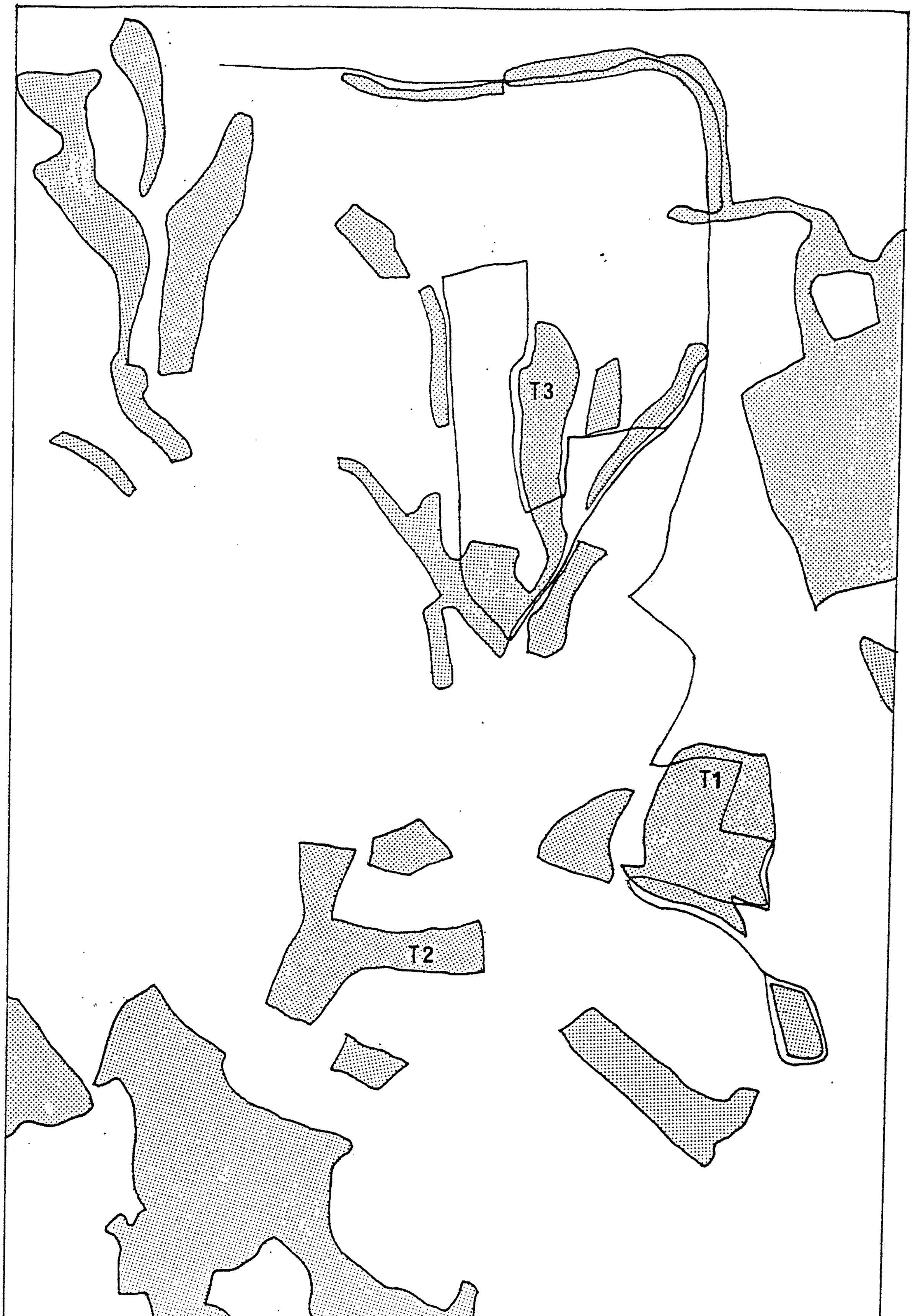
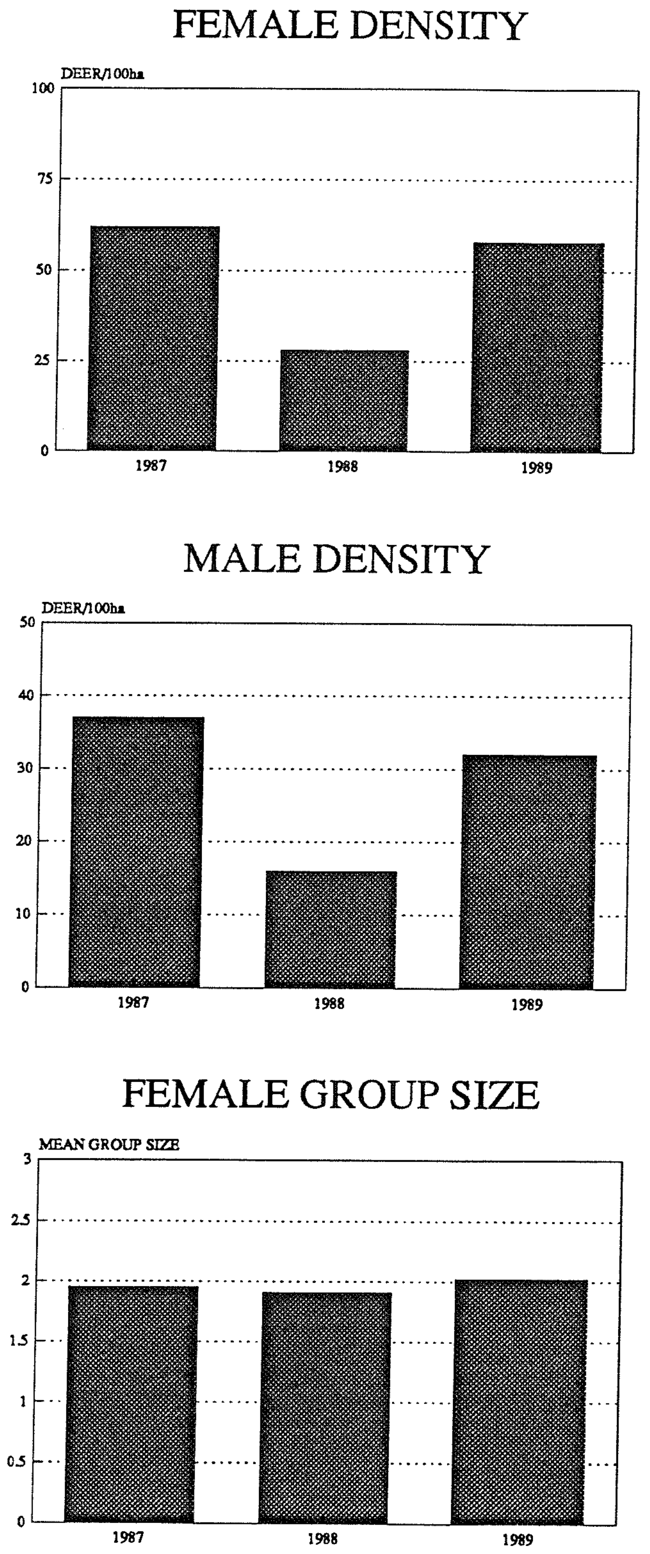


Fig 7.6 Distribution of reproductive activity at the Tollard Royal study site showing location of temporary territories (T1, T2, T3).

Fig 7.7 Density and group size estimates within a limited 100 ha area in the vicinity of the Blackensford lek, October 15-28, 1987-1989. Estimates based on morning transects.



8. ALTERNATIVE MATING STRATEGIES AND REPRODUCTIVE SUCCESS

8.1. INTRODUCTION

It is clear from Chapter 7 that in wild populations of fallow, unlike the situation in parks (Langbein 1990), mixed mating systems, where a variety of individual strategies exist side by side, are not uncommon. In the Blackensford site in the New Forest, for example, males adopt the alternative mating strategies of lekking, single territory defence, and non-territorial following. This situation lends itself ideally to intensive study to determine the relative reproductive success of males adopting the different strategies. The current chapter describes the spatial and temporal distribution of reproductive activity at Blackensford and presents data on copulatory success of males adopting alternative mating strategies. Work was concentrated in the autumn rutting season of 1989, but additional data are available from observations carried out in 1987 and 1988.

Alternative mating strategies

An increasing number of field studies of mammalian reproductive behaviour have shown that males may adopt alternative mating strategies, both between and within populations. There are three principle explanations for such variation (Rubenstein 1980; Dunbar 1982). The first is that a particular strategy may be optimal under certain environmental or social conditions. Mating strategy variation between populations has been recorded in many species, as for example in topi *Damiliscus lunatus* (Gosling 1986, in press) and in fallow deer (Schaal 1987; Langbein & Thirgood 1989), and the relationship between ecological variables and mating strategies is now increasingly clear (see Chapter 7). Particularly convincing is a shift in mating strategy within populations, as the social or environmental conditions change between years. Such a shift was recently demonstrated in pronghorn antelope *Antilocapra americana* where the death of the majority of mature males during a severe winter was followed by a mating strategy change from territoriality to harem defence (Byers & Kitchen 1988). Similar within-population flexibility has been recorded in fallow deer, where changes in either male or female densities between years have resulted in variation in the extent of territorial behaviour and the occurrence of leks (Langbein & Thirgood 1989).

Such an explanation accounts for differences between populations, or within populations, between different years, but alternative mating strategies often occur simultaneously. One possibility is that some males may be poor competitors, limited by phenotype, and are simply 'making the best of a bad job' in a suboptimal mating strategy (Dawkins 1980). In some cases, competitive ability is age dependent and, unable to compete with older rivals, younger animals may attempt to sneak copulations. A good example is in elephant seals *Mirounga angustirostris*, where young seals have no chance of defending a harem themselves and instead attempt to steal copulations by pretending to be a female and joining a large bull's harem (Le Beouf 1974). The 'satellite' strategies adopted by some male waterbuck *Kobus ellipsiprymnus* not only enable males to sneak copulations from territory holders, but also increase the likelihood that satellites will eventually take over the territory (Wirtz 1981, 1982). In general, individuals employing 'best of a bad job' strategies would have lower mating success than others adopting optimal strategies.

A second explanation for mating strategy variation within populations is that the best strategy for an individual to adopt may depend upon the strategies adopted by other males in the population. Under these circumstances a mixture of strategies may coexist as a mixed evolutionarily stable strategy (ESS)(Dawkins 1980). If two alternative strategies observed in nature are examples of a mixed ESS, then they should, on average, yield the same fitness payoff in terms of matings. In practice, realistic measurements of the costs and benefits of alternative strategies are difficult to obtain. Alternatives within a mixed ESS may consist of distinct options such as 'follow' or 'be territorial' but are more likely to show continuous variation (Dawkins 1980). Measurements must also ideally be in terms of lifetime reproductive success (Clutton-Brock 1988) and are thus complicated by the fact that individual males may themselves switch strategy during their lifespan.

Alternative strategies and male mating success in ungulates

The occurrence of alternative mating strategies within some ungulate populations offers the opportunity to investigate the costs and benefits of different strategies. Have the results of existing studies been sufficient to say whether alternative strategies are 'the best of a bad job' or are examples of mixed ESSs?

Studies of mating success of individuals adopting non-territorial following strategies as an alternative to territorial defence are very limited. Non-territorial strategies are relatively rare in antelope and only in oryx *Oryx beisa*, hartebeest *Alcelaphus buselaphus cokei* and topi have both strategies been recorded in a single species (Gosling 1986). In one topi population in Uganda, non-territorial 'herdmaster' males coexist with resource defence males (Jewell 1972); however, no information on relative reproductive success is available. In fallow deer, Schaal (1987) observed both territorial 'rutting stands' and non-territorial harems; however, few copulations were recorded in his Alsace study site. Extrapolation of copulatory success from the numbers of females in reproductive groups, as attempted in some fallow studies (eg. Braza et al. 1986), is of questionable validity, as such groups are likely to be fluid in composition and may well be formed for reasons other than reproduction. Investigation of the reproductive success of non-territorial strategies in male ungulates remains problematic due to difficulties in observability, although the future use of DNA fingerprinting (Jeffreys et al. 1985) is likely to improve the reliability of estimates of paternity.

Lek breeding is an uncommon mating system that has only been described in five ungulate species: Uganda kob *Kobus kob thomasi* (Beuchner 1961), white-eared kob *Kobus kob leucotis* (Fryxell 1987), topi (Montfort-Brahamn 1975), lechwe *Kobus leche kafuensis* (Schuster 1976) and fallow deer (Schaal 1986). In lek breeding species, males congregate on small clustered mating territories which females visit solely for the purpose of copulation (Bradbury & Gibson 1983). Lekking in ungulates rarely occurs as a pure strategy within populations, but usually as an alternative to single or resource territory defence (Gosling in press).

Intensive studies of Uganda kob and fallow deer have suggested that males holding lek territories have much higher mating rates than any of those that hold single territories (Buechner & Schloeth 1965; Leuthold 1966; Schaal 1987; Clutton-Brock et al. 1988). In the two enclosed fallow populations studied by Schaal and Clutton-Brock et al., over 90% of all observed copulations were by lek males, with relatively fewer copulations recorded for single territory males, apparently offering support for the 'best of a bad job' theory. However both of these studies concentrated effort of observation upon the lek and may have underestimated copulatory success by non-lekking males. Additionally, mating success was measured over a limited time scale of at most three or four reproductive seasons. As Gosling & Petrie (1981) have suggested, the benefits of increased mating rate on leks do not come without costs; males are exposed to intense competition, tend to feed very little and are likely to lose body condition rapidly. In contrast, males on resource territories away from the lek suffer less competition and are thus able to maintain breeding status for longer periods of time in any one season as well as between years. Gosling & Petrie have suggested that although successful lekking is a high cost - high benefit strategy and resource defence low cost - low benefit, both may be equivalent because some males can hold resource territories for longer. Evidence from kob and fallow deer support this theory; territory turnover is faster on leks in both species (Beuchner & Schloeth 1965; Clutton-Brock et al. 1988). However, the restricted time scale of the fallow rut in comparison to the aseasonal breeding of kob might suggest that differences between strategies must be additive over several years.

Why do female ungulates mate on leks ?

If male mating success is much higher on lek territories than in single territories, as suggested by Clutton-Brock (1989), this provides an obvious selection pressure inducing males to congregate on leks. What are the corresponding pressures inducing females to mate on leks?

One possibility is that females benefit from reduced predation by mating on leks because of the presence of other animals. Such a suggestion has been made for topi (Gosling & Petrie in press) and also in some Tetraonid leks (Wittenberger 1978) but has been dismissed as a general explanation by Clutton-Brock (1989), who points out that in many lekking ungulates, females are found in smaller groups when on leks than when off them.

A second possibility is that females benefit from increased opportunities for mate choice on leks because of the numbers of males to choose from, the opportunity to compare males closely, and the ability to monitor the choices of other females (Alexander 1975; Bradbury 1981; Bradbury & Gibson 1983; Losey et al. 1986). Evidence of mate choice on leks is equivocal however, and even if it does occur, it is not necessarily a reason that females mate on leks (Clutton-Brock 1989). How females might benefit from choosing certain males is controversial and difficult to answer from existing field data. Because males contribute only sperm to females, it is likely that benefit is genetic: females choose males with genetic traits for either survival or mating or both (Krebs & Harvey 1988).

A final possibility is that oestrous females are exposed to dangerous harassment by courting males and congregate on leks because clustered territories offer better protection than isolated territories (Wrangham 1980). Clutton-Brock et al. (1988) suggest that this may be a factor promoting lekking in fallow deer, although in practice such a theory is difficult to test.

It may be that these theories are not exclusive, and furthermore as Gosling (1986) notes, lekking may have evolved under different selection pressures in different species.

Male mating success on leks and female mate choice

Male mating success on leks is not evenly distributed; in all species a small proportion of males perform the majority of copulations and the majority of males do not mate at all (Bradbury & Gibson 1983). Mating success amongst lekking fallow deer has been shown to be similarly skewed; studies on park (Schaal 1987; Clutton-Brock et al. 1988) and wild (Apollonio et al. 1989) populations suggest that the most successful five or six bucks account for up to 90% of all copulations.

If females do actively choose males on leks, which criteria are used to select mates? Mate choice cues can conveniently be bracketed into two classes whose relative importance has been controversial: spatial and phenotypic. Early work on avian (Kruijt et al. 1972; Wiley 1973; Lill 1974) and ungulate (Beuchner & Schloeth 1965; Beuchner & Roth 1974) leks indicated that mating success was not equally distributed across the lek; in particular, central lek territories were the most successful. It is possible therefore, that if competition for these central territories is very intense, as might be expected, then it provides females with an indirect measure of male quality. Recent reassessment of sage grouse *Centrocercus urophasianus* leks, however, has shown that these 'mating centres' are not stable in time, and the central position of successful territories may result from males clustering around the current centre of activity (Gibson & Bradbury 1986).

If spatial effects are minimal, as suggested above, which phenotypic cues do females use to distinguish among the males on a lek? In sage grouse, there are no correlations between mating success and any measured morphological trait of individual males, such as size, but there is a strong correlation between mating success and display rate (Gibson & Bradbury 1985). Similar correlations between courtship display and mating success have recently been demonstrated in black grouse *Tetrao tetrix* (Kruijt & de Vos 1988) and long-tailed manakins *Chiroxiphia linearis* (McDonald 1989).

Age, size, fighting success, and dominance are correlated with male reproductive success in many polygynous mammals (Geist 1971; Le Boeuf 1974; Clutton-Brock et al. 1982) and it seems likely that a similar relationship would hold on ungulate leks. The available evidence, however, is limited and contradictory. Gosling & Petrie (in press) suggest that successful topi males on leks were large, whilst the majority of unsuccessful males were small, however they were unable to show a consistent relationship between these two variables. Mating success on a fallow deer lek was correlated to antler size and fighting success, as well as display rates and territory position (Clutton-Brock et al. 1988). However, teasing apart the independent effects of each factor from spurious effects due to correlations between them is difficult. Contradictory results have been reported from another lekking fallow study in which agonistic interactions on the lek appear unrelated to reproductive success; in this population lek attendance and territory location were the main determinants of the number of copulations achieved (Apollonio et al. 1989). These latter two variables may be an indirect measure of male quality, however, as only males in superior body condition can defend a lek territory throughout the rut.

Objectives of the current study

In summary, the aims of this chapter are:

1. To assess the spatial and temporal distribution of reproductive activity at Blackensford.
2. To investigate the reproductive success of male deer pursuing lekking, single territory defence and following strategies.
3. To analyze the behaviour of lek males and determine the correlates of male mating success.

8.2. METHODS

Data collection

During 1987 and 1988, observations of reproductive activity were made at Blackensford as part of a wider survey investigating ecological correlates of mating system variation (see Chapter 7 and Langbein & Thirgood 1989). The site was visited on eighteen days in October 1987 and sixteen days in October 1988. In each year, data were collected on the location and activity of individually recognized males encountered during regular patrols of the site. A census of a restricted area of 100 ha around the lek was made from 1-4 times daily and the identity, location, activity, and group size and composition of each animal encountered were recorded. Identification and observation of males on the lek was made from two natural hides 50m to the north and 20m to the south of the lek edge.

During 1989, observations of reproductive activity were made each day from October 1-30, with weekly surveys conducted in September and November to establish the approximate dates of initiation and termination of territoriality. Intensive observations began on October 9, the date that the first adult female was seen on a reproductive territory, and continued until November. In order to maintain continuous observation of the lek and to enable simultaneous sampling of the single territory and following strategies, a field assistant was employed for this part of the study (October 1-30). We were able to recognize individually a total of 31 mature males by a combination of coat and antler characteristics. Whilst we can not state that other males did not visit the area during the rut, we are satisfied that we accounted for all reproductively active males.

Three types of behavioural data were collected. Firstly, the lek was monitored continuously from dawn to dusk from a hide approximately 50m to the north of the lek. Visibility on the lek was improved in comparison to previous years by forestry thinning operations in the conifers the previous spring. Scans of the entire lek were made at 10 minute intervals. For each territory, we recorded the identity of the territorial male and the number of females. A continuous record was kept of fighting, mounting and successful copulations. Ejaculations were easily identified for the buck leaps upright, propelling the doe forwards.

Secondly, the single territories were systematically watched from vantage points for two hours each per day of the intensive observation period (October 9-30). Buck recognition was often difficult in the dense vegetation of some territories; considerable time and effort was expended to ensure that a positive identification of the resident male was obtained for each day. Continuous or uninterrupted focal watches of males were not possible due to the poor visibility; however, it is unlikely that any copulations were missed during observations because of the typically long duration of fallow courtship and conspicuous nature of ejaculation. In contrast to the lek territories no agonistic behaviour was seen on single territories during the 1989 rut.

Finally, observations of non-territorial males were obtained opportunistically during a daily patrol of the area and whilst moving from one territorial site to another. The identity of individual males encountered, activity, group size and composition were recorded. Attempts were made to follow males undetected, although this was only rarely successful. More frequently, undisturbed observations of non-territorial males interacting with females were obtained when these individuals moved onto the periphery of single territories. In these circumstances, all male-female interactions were noted.

Data analysis

The analysis involved the following measures:

Territory tenancy. The number of days for which an individual buck held a territory. Where bucks were holding the same territory in the morning as they had held the previous evening, it was assumed that they had held it overnight.

Territory turnover. The turnover of males on individual territories was calculated as:

$$T = \text{Number of changes in territory ownership} + 1 \ / \ \text{Number of sampling days}$$

Agonistic behaviour. Direct interactions between bucks were subdivided into three categories on the basis of the level of escalation.

1. Non-contact interactions.
   Includes active or passive displacement of one male by another with no physical contact, and parallel walks and other forms of assessment by mature males.

2. Antler clashes.

   Brief contact between males of less than 30 seconds with no obvious outcome. Often but not always between neighbouring territory holders.

3. Escalated fights.

   Fights lasting more than 30 seconds or with a definite winner and loser.

   In most analyses categories 2 and 3 are combined simply as fights.

Reproductive success. The number of ejaculations seen performed by a male during observations.

Lek attendance. Three parameters of lek attendance were defined.

1. The number of days on a central conifer territory.
2. The total territory-holding days on the lek.
3. The total lek days regardless of territoriality.

Number of consorting females. Three measures of the number of consorting females on male territories were defined.

1. Daily number of consorting females. The total number of females seen on a male's territory during regular scans of the lek, divided by the number of scans in that day.
2. Mean number of consorting females. The average daily number of consorting females on all days in which copulations were observed on the lek.
3. Occupancy number of consorting females. The average daily number of consorting females on all days in which copulations were observed on the lek and the buck held a lek territory.

Fighting. Two measures of fighting were defined.

1. Number of fights. The total number of antler clashes and escalated fights within a given time period.
2. Fighting rate. The number of fights per day on the lek.

Dominance. Using only fights with a clear outcome, a dominance hierarchy was calculated using the index of Clutton-Brock et al. (1979) in which the rank of an individual is weighted according to the rank of his opponents. Dominance was calculated as:

$$D = (B + b + 1) / (L + l + 1)$$

where B is the number of different bucks that the individual was seen to beat and b is the sum of the individuals that they were seen to beat; L is the number of different bucks that the individual was seen to lose to and l the sum of the individuals that beat them.

Statistical analyses

Most variables were not normally distributed therefore standard non-parametric statistics were employed (Siegel 1956).

8.3. RESULTS

Spatial and temporal distribution of reproductive activity

This section describes the distribution in space and time of reproductive activity during the main autumn reproductive period at Blackensford. It is based on data collected during September-November 1989, supplemented by, and contrasted to, data from 1987 and 1988.

Spatial distribution of territories

The spatial distribution of the lek and single stand territories during October 1989 is shown in Fig 8.1. As in previous years, the lek was located in an area of 4.0 ha on the boundary between two habitats; half the territories were in closed canopy conifer and half in open canopy oak. The spatial organisation of the lek has been described in detail elsewhere (see Chapter 7) and only a brief summary will be given here. A total of nine separate territories were established on the lek at some stage during the 1989 rut, although a maximum of only seven territories were defended concurrently. Reproductive activity was concentrated on the northern edge of the conifers (Fig 8.2). The conifer (G, C, D, H) and border (F, I) territories contained no trophic resources, whilst the oak territories (A, B, E) contained limited amounts of grazing and acorns.

In 1989 three single stand territories were permanently defended during the peak two weeks of the rut in the Blackensford area (Fig 8.1). Both the Blackensford Hill (BH) stand and the Beech Beds (BB) stand were located approximately 400m away from the centre of the lek, thus losing visual contact whilst remaining within the acoustic range of male groaning. There was no reason to believe that these two territories were simply peripheral territories of the lek, although females were regularly intercepted moving from one site to the other.

The BH stand was situated in the middle of a block of 35 year old Douglas Fir 400 m to the north-east of the lek. The stand contained no trophic resources of any sort and deer were never seen to feed whilst on the territory. The size of the territory was difficult to estimate, as no male-male interactions were recorded during the 1989 rut, however the area regularly used by the resident buck rarely exceeded 1 ha.

The BB stand was located a similar distance to the south-west of the lek in an area of closed canopy beech. Limited amounts of beech mast were available, however it is unlikely that these were the principal attraction for females as much better feeding areas were located nearby. Again the absolute territory size was difficult to estimate, and a size of less than 1 ha is likely.

The final stand was situated 700 m to the north-west of the lek in the naturally regenerated Scots Pine woodland known as Stinking Edge (SE). The daily focus of this stand was highly mobile and typified the variable nature of fallow territoriality. The area contained several meadows providing good grazing and usually contained a high density of deer. The location of reproductive activity varied on an hourly basis in response to the distribution of females. If this entire area was considered as one large territory, it would comprise approximately 5 ha.

Temporary stand holding bucks were less common in 1989 than in previous years and there were no areas in which this was a regularly occurring mating strategy. Non-territorial mating behaviour was by contrast widespread throughout the Stinking Edge and Beech Beds areas (Fig 8.1). Much of this non-territorial behaviour appeared in the form of satellite bucks attempting to parasitise the territorial males by intercepting females moving onto rutting stands, or following females when they were moving between reproductive and feeding areas.

Initiation and duration of territoriality

Mature bucks were first seen in the Blackensford area on September 16 and limited territorial behaviour started shortly afterwards. The first buck (B1) to show attachment to a specific territory was subsequently very successful in achieving matings (11 matings between Oct 18-21, ranking third in mating success out of a total 31 males). Initially territorial behaviour was limited to the lek, with territories 'A' and 'C' being the focus of activity from Sept. 16 onwards, and maintaining a resident male until the end of October (Fig 8.2). Subsequently, a mature male and accompanying sub-adult males maintained a presence on and in the immediate vicinity of the lek until late November, although no territorial behaviour was shown.

A feature of this and previous ruts was the initial establishment of relatively large territories on the lek, and subsequent subdivision of such territories as the peak of the rut approached. Thus initially only two territories on the lek were defended, focused on 'C' and 'A' respectively, but extending beyond the limits of those territories during the peak of the rut. With increased satellite male encroachment, temporary peripheral territories were created, and by mid-October some had become more permanently established (Territories 'D' & 'I', Fig 8.2). The opposite phenomenon occurred at the end of the rut, with the peripheral territories being abandoned, and the remaining central territory males expanding their domain to include some or all of the peripheral territories. This progression from late September through October is shown in Fig 8.3.

The establishment of single stand territories largely followed the pattern of peripheral lek territories, with occupation on a short term basis of one to three days in early October, and continuous territorial defence starting on October 16, the date of the first observed copulation. There was a suggestion from this and the previous two years that the early occupation of the 'BH' stand was more continuous than the data show. Repeated observations of the same individual as resident, separated by short absences, suggested that one male maintained control over the stand. Visibility on this territory was poor and sightings of inactive or lying animals problematic, therefore it is possible that a buck standing silently on the periphery of the territory could be missed.

Territory tenancy and turnover

The duration of territory holding by individual bucks appeared to vary between lek and single stand territories, with particularly territory 'C' having a very fast turnover of males (Fig 8.4). However, the great variation within categories, and the small sample size, prevented this relationship from being validated statistically. Similarly, the average duration of territory occupancy by individual males did not vary significantly between the lek and single stands.

Tenancy data from 1987 and 1988 was difficult to interpret, as there were considerable gaps in the sampling regime (Days with data available: 1987: 18/30; 1988: 16/30). However, these periods were largely concentrated outside of the peak two weeks of mating activity when territory ownership changes were less frequent, and it was possible to reconstruct comparable continuous tenancy records. When a male occupied a territory on both the days before and after a missing data point, it was assumed that his tenancy was uninterrupted. If an unobserved change in ownership occurred, the unaccounted-for time was divided between each male.

Tenancy duration in 1987 was similar to 1989, characterised by great variability between territories, and no significant differences between the lek and single stands. In 1988, a year in which there was a marked reduction in reproductive activity (see Chapter 7), tenancy time on all territories was much longer than in the other years. Two individual bucks dominated the lek, holding the two permanently occupied territories for seventeen and twelve days respectively. Again, however, sample size was too small to show a significant difference either between years, or between lek and single stand territories.

A useful contrast could be made between the turnover of males on territories at Blackensford and elsewhere in the New Forest where permanent multiple territory mating systems do not exist. Data on recognized males is very limited, however where it does exist (Dames Slough 1987, 1988, 1989; Vinney Ridge 1988, 1989), individual male occupancy of single stands was continuous throughout the rut.

Spatial and temporal distribution of fights

Direct interactions between mature males in 1989 were only observed on or in the near vicinity (<100 m) of the lek, and thus all analyses of fighting data refer to this limited area. This is in contrast to the ruts of 1987 and 1988 when escalated fights were observed on both the Blackensford Hill (BH) and Stinking Edge (SE) stands, and occasionally heard elsewhere. It is very likely that during the 1989 rut interactions between males did occur off the lek, but simply were not seen for logistic reasons.

The breakdown of a total 132 male-male interactions on the lek was: 38 non-contact, 26 antler clashes, and 68 escalated fights. Fights occurred on all territories but were concentrated on the boundary between territories C, D, F, & I (71/94 total fights). Fallow fighting behaviour often involves a prolonged display element in which the bucks assess each others competitive ability (eg. parallel walk) which may result in the actual combat occurring a considerable distance away from the original interaction. In such cases the location of the first interaction has been used in the analysis. Most fights involved at least one territorial male (71/94 total fights), if not one of the two central conifer territory males (45/94 total fights).

Direct interactions between bucks were first seen on the lek on October 4, with the first escalated fight occurring on the lek on October 10. Fights were then observed on every day on the lek until October 28, after which time they were not seen (Fig 8.5). However, continuous observation of the lek was terminated at this time and it is possible, but unlikely that further agonistic interactions occurred.

Whilst fights occurred daily on the lek from October 10-28 inclusive, their occurrence throughout this period was significantly different from a random (Poisson) distribution (Chi-square=10.1, p<0.01). There is a suggestion of a cyclical trend, with a periodicity of three to four days between peaks of fighting (Fig 8.5). In the early part of the rut (eg. October 10-18) this periodicity is quite clear with a single day as the peak; however, during the period of maximum copulations (see below), high levels of fighting occurred on successive days before decreasing. In general, however, there appeared to be one or two days of intense fighting activity, followed by two or three days of relative calm. Of course this analysis is restricted to daytime observations, and there was strong circumstantial evidence of high levels of fighting at night.

At a finer scale, the non-random distribution of fighting is even clearer. Subdivision of daylight hours into six two-hour time periods, over the same period October 10-28, reveals the highly clustered nature of fighting activity (Fig 8.6) (Chi-square=28.1, $p<0.001$). The incidence of fighting clearly stimulated further fighting activity. In one prolonged bout of fighting (0820h-1040h October 19) ten individual bucks were involved in a minimum of twelve fights. Whilst this was exceptional, short periods of up to an hour of intense activity were common. Fighting activity on the lek often appeared to attract other males to the lek, and sequential fights were frequent. Thus a central stand holding buck was often forced to fight two or three challengers in succession. The sudden appearance of bucks on the lek during periods of increased fighting suggested strongly that some individuals remained on the periphery of the lek, hidden to the view of the observer. The adaptive value of such a strategy is obvious: remain resting on the periphery, move in on signs of male-male activity, and possibly usurp an injured or exhausted territory holder.

Fight duration

Whilst fighting activity was common throughout a relatively long period in October (10-28 inclusive) and certainly occurred in the week preceding the first matings, it is possible that the intensity of individual encounters was not constant throughout the rut. Clutton-Brock et al. (1979) showed that both the frequency and duration of fights between red deer stags peaked in the first two weeks in October, coinciding with the peak period of conceptions. Comparison of the duration of escalated fights on the lek during October 1989 revealed no significant difference between five-day time periods (Fig 8.7). However, fight duration can not be taken as a simple measure of the intensity of male competition, as many other factors, such as the competitive ability of the combatants, could influence this parameter.

Temporal distribution of matings

The first successful copulation was seen on lek territory 'C' on the October 16, although an unsuccessful mating sequence involving sixteen mounting attempts had been observed on the previous day. Subsequently, matings occurred on the lek on every day until October 28, rising to a peak of fifteen on October 23, and declining again until a final burst of four successful copulations on October 28 brought activity to a close (Fig 8.8).

Matings off the lek were seen on October 17, 22, 23, 24(two), & 28, thus appearing to show a similar distribution to the lek matings. It is impossible to state with any certainty whether or not non-lek matings occurred before or after this time, although there is circumstantial evidence from this and other studies that matings do occur in November, December and January.

Subdivision of rut: prerut and peakrut

It is possible to divide the main October rut into two distinct periods on the basis of the distribution of fighting and mating (see Figs 8.5 & 8.8); the Prerut, which in 1989 encompassed the period October 2-15, during which time territorial interactions occur but no matings, and the Peakrut, from October 16-28, when most mating occurs. Obviously there would be slight changes from year to year in the exact date of transition from one category to the other. This division and terminology will be emphasized in much of the analyses that follow.

Relationship between fighting and mating

There was no correlation between the total number of fights and the number of matings seen in each territory. Defence of the more successful territories was generally more continuous than the others, so this relationship was reexamined using the average number of fights per day the territory was occupied; however the correlation was still non-significant.

The relationship between fighting and mating can be considered in terms of their distribution in time on the lek on individual days throughout October 1989 (superimposing Figs 8.5 & 8.8). It is clear that in addition to the fighting-only days of the prerut, there are days of relatively low mating during the peakrut in which fighting is a common occurrence. Similarly, a high level of mating on a given day is not necessarily associated with increased fighting. For example, the level of fighting on the peak mating day (October 23) was lower than that of the preceding day. Taken overall, there was no correlation between the level of fighting and mating on individual days, even when this analysis was restricted to the thirteen days of the peakrut. However a weak correlation (r_s=0.82, p=0.10) was obtained when the same data were lumped into five day time periods (Fig 8.9), suggesting that a period of increased fighting was associated with high levels of mating, if not vice versa. The overriding trend in the occurrence of fights, however, appears to be the cyclical pattern described earlier, with the periodicity shortening as the day of maximum copulations approaches. The timing of this intensification of fighting activity precedes the peak day by a complete cycle of four days, which raises the intriguing question of whether males are able to predict the date of peak oestrous several days in advance, and adjust their behaviour accordingly.

The relationship between fighting and mating may also be considered at a finer scale, in terms of occurrence in two hour time periods from dawn to dusk summed over the whole peakrut (Fig 8.10). There was no significant correlation, either positive or negative, between these two parameters, although certain trends can be seen in the data. The two hours after dawn are characterised by low levels of mating and high levels of fighting. Subsequently, the number of matings increase and remain at a high level until late afternoon, when they sharply drop during the final period before darkness. In contrast, fighting levels steadily decrease from their peak after dawn to a minimum during the afternoon, then rise sharply again in the period before darkness. Whilst the correlations are not significant, these data are supported by subjective observations that suggest that fighting activity disrupts matings. Similar findings have been reported for fallow leks elsewhere (Clutton-Brock et al. 1988; Apollonio et al. 1989).

Individual distribution of fighting and mating

In the previous section the distribution of fighting and mating was considered in terms of the population, or, more specifically, the subset of males which were active on the lek. The level of fighting followed a cyclical trend, with activity intensifying as the copulatory peak was reached, then subsequently tailing off. The logical next step is to investigate fighting and mating behaviour at the individual level, to determine whether similar trends are shown. Unfortunately, sufficient data for such an analysis was only available for a few individuals, which in this case were the three most successful copulatory males.

Great variation existed in the temporal distribution of fighting and mating between the three most successful bucks (Fig 8.11). There was insufficient data to support the suggestion that individual fighting activity intensified on the days immediately before peak copulations. Although statistically insignificant due to small sample size, each buck had many more fights before his individual peak copulatory day than after. There was no evidence that the fighting success of individuals changed before and after this date; however, the relative infrequency of interactions after the peak copulatory day restricts such comparison. Subjective impressions from field observations suggested that most bucks remained on successful territories until exhausted, and were incapable of winning fights after being usurped. The exceptions were the two top copulatory bucks (B2 & B20), who having fought their way onto the central conifer territories by the peak copulatory day, remained in situ until mating was completed. There was no evidence that the dominance rank of the opponents of individual bucks changed throughout the rut; however, the post-peak copulatory period was characterised by increased frequency of challenges to territory holders by immature males.

Reproductive success of alternative strategies

This section considers the distribution of successful copulations between the alternative mating strategies of lek territoriality, single stand territoriality, and non-territorial following. It then goes on to describe the mating success of individual males adopting these strategies, and the distribution of copulations on different lek territories. Finally, individual male flexibility in mating strategy is investigated.

Distribution of matings between lek, single territory & non-territorial males

Of the total of 64 copulations observed at Blackensford during October 1989, 58 were seen on the lek, with single territory and non-territorial males apparently contributing relatively little (Fig 8.12). This very unequal distribution (90.6% lek matings) is comparable to published figures for other lekking populations of fallow deer (Jaegersborg 91.6% (Schaal 1987), Petworth 94% (Clutton-Brock et al. 1988)).

However, such an analysis is very misleading, as limits to manpower resources did not allow an equal amount of time to be spent in observation of males adopting the three mating strategies. Whilst the lek was watched continuously during daylight hours from October 10-30, thus including the 13-day period of the peakrut, it was only possible to observe the single territories for two hours each per day, with observations of non-territorial males being made largely on an opportunistic basis. If the observed number of matings on the three single stand territories are weighted by a correction factor of 6x, to make the observation times equivalent to that of the lek territories (Table 8.1), a very different picture of mating distribution is revealed (Fig 8.12). Clearly, the estimated proportion of matings occurring on single stand territories in this population is much higher than those which have been reported for other lekking populations. The contribution of non-territorial males to the total number of matings cannot be reliably estimated at this time.

Obviously, any such manipulations of real data involve a number of assumptions and it is necessary to justify the correction before any further conclusions are drawn.

Assumptions of the correction

1. Matings occur over the same 13 day period on stands and lek.

Matings on the lek occurred on each day from October 16-28, reaching a peak on October 23. Single stand matings were seen on October 17, 22, 23, 24(two), 28 and activity appeared to follow the same trend as on the lek.

2. Matings are equally distributed throughout the day, hence the two hour sampling periods provide a representative estimate of activity.

Suitable data are not available to answer this question for activity on single stands, therefore it is necessary to use comparable data from the lek. When the distribution of matings on the lek were examined in terms of six two-hour time periods from dawn to dusk, matings were equally distributed across the four central periods, the exceptions being the first two hours after dawn and the last two hours before dusk, which were characterized by low levels of mating and high levels of fighting. Sampling of single stands rarely occurred during these latter periods as both observers were required to record male-male interactions on the lek. Thus by concentrating observations on the four central periods it is possible that a slight over-estimation of single stand mating activity occurred. Obviously, another assumption is being made that mating distribution throughout the day on stands parallels that of the lek.

3. All matings on the lek were seen.

Whilst such a statement can not made with absolute certainty, it is felt that due to the generally long duration of fallow deer courtship (up to 19 mounts over 25 minutes), and the relatively violent act of copulation in which the female is usually knocked forwards, that few if any matings were missed on the lek during daylight hours.

4. What happens at night?

This is the unknown factor in all investigations of fallow deer mating behaviour. Other studies of lek breeding populations of fallow have suggested that mating occurs at the same level during the night as during the day (Schaal 1987; Clutton-Brock et al. 1988). There is, however, little direct evidence from these studies that this is indeed the case, few if any actual night-time copulations being witnessed.

An attempt to gather objective data on this question was made in the 1989 rut. Instantaneous observations were made with a red filter spotlight on five nights during the peakrut from a vantage point close to the lek. The limitations of such a "freeze-frame" view are obvious, however it was possible to get a good indication of the spatial organisation and level of activity on the lek.

The results of this very preliminary investigation were both surprising and contradictory. On the three nights prior to the maximal copulatory date, spotlighting suggested that activity levels, in terms of numbers of male and female deer on the lek, were at least as high as on the preceding days. Levels of groaning, which have been shown to be correlated to mating activity by Clutton-Brock et al. (1988), were similarly high, although this parameter was not systematically measured. However, night-time activity was more widely dispersed over the lek, with the oak territories A, B, I, and E and the adjacent open grassland north of the lek more widely used by females. Most significantly, the rigid territorial spatial structure of the lek appeared to break down at night, with the dominant, conifer territory (C & D) holding bucks of the previous day moving out of their territories onto the rest of the lek, apparently in response to the movement of females. It was impossible to determine whether these bucks maintained their dominance status during the night; however in five out of the six cases, individual bucks retained their original territories on the following day.

In contrast, on the two nights in which observations were made after the maximal mating day, reproductive activity was greatly reduced. Few if any females were on the lek, no groaning was heard, and the dominant males were seen lying silently on their territories. In both cases these observations were made at 10:00 pm, and by the following morning activity had resumed its previous high level.

Taken as a whole, the available data largely satisfy the questions posed by the first three assumptions, and justify the correction factor of the preceding analysis. The corrected data certainly provides a more realistic picture of the mating distribution than the uncorrected data, but it singularly fails to answer the question of non-territorial matings. The question of nocturnal matings remains totally unresolved, however it does not invalidate the weighting of the non-lek day-time copulations. Until this question is properly addressed, the data presented above remains at best an approximation of the true mating distribution.

Distribution of matings between individuals

This analysis was taken further to consider the reproductive success of individual males adopting the three alternative mating strategies of lek territoriality, single stand territoriality and non-territorial following. The distribution of copulatory success between mature males differed significantly from the Poisson series that would have been expected had matings been distributed at random (Chi-squared = 31.8, $p<0.001$; Fig 8.13). The three most successful bucks achieved 78% of all observed copulations in the population. In addition to the ten successfully copulating bucks represented in Fig 8.13, there were also 21 males which achieved no matings.

No attempt has been made to reproduce the correction factor of the previous analysis to make allowance for the time difference of observation between individuals; however it is clear that even based on a limited sampling period of only two hours a day, two single stand bucks achieved more copulations in two hours than eight of the twelve lek bucks in twelve hours. Observations of the same population on a less intensive basis during the 1987 and 1988 ruts offers supporting evidence; four of twenty-two copulations over the two years occurred off the lek and, in 1987, two single territory bucks ranked joint third in copulatory success (Table 8.2).

Distribution of matings between lek territories

Successful matings were not randomly distributed between the nine lek territories (Chi-square= 31.8, $p<0.001$; Table 8.3). 90% of all observed matings occurred in two territories (C & D in Fig 8.2) which were located in the middle of the conifer block on the southern side of the lek. With one exception, all copulations occurred in or on the edge of the conifers.

Territory 'C' was consistently the most successful. Copulations occurred in this territory on every day bar one of the peakrut, and on only two days did more matings occur elsewhere (Table 8.3). However, this includes the top copulatory day (October 23) when eleven matings were seen on Territory 'D'.

Individual flexibility in mating strategy

Drawing a tentative conclusion regarding the mating success of individual males adopting alternative reproductive strategies, the data suggest that within a given year, successful lek bucks attain higher mating success than single stand bucks, who in turn get more matings than unsuccessful lek bucks. The mating success of bucks adopting non-territorial following strategies remains largely a mystery. This conclusion does not take into consideration the possibility of bucks attaining copulations in more than one strategy within a single year. Such individual behavioural flexibility certainly does occur, however its frequency is unclear, as is the extent it varies from year to year.

In the 1989 rut, one individual male (B21 in Fig 8.13) achieved copulatory success both in a non-territorial strategy (October 22) and later on the lek (October 27). Of eighteen males who defended either single or lek territories for at least one day during this year, ten were also observed interacting with females in a non-territorial strategy (Table 8.4). Peripheral males frequently left the lek and were subsequently observed with female groups. Such opportunistic behaviour is not surprising; however it was not clear whether or not males left the lek specifically to forage for females. Switching between territorial strategies was less common. Of the thirteen males which held lek territories, only three were also seen on single stands, and in each case for only a single day. However, one buck lost or abandoned his single stand territory after more than two weeks defence, spent less than an hour on the lek and was successful in obtaining a 'sneaky' mating.

Data from the 1987 and 1988 ruts generally support these findings (Table 8.4). In both years a large proportion of males were non-specialists (65% in 1987; 45% in 1988). Switching between single territory and lekking strategies was more common in 1987 (50% of all lek males) than in 1988 and 1989 (40% and 31% of all lek males respectively).

At a finer scale, individual flexibility in mating behaviour may also be demonstrated on the lek. Copulations on the lek in 1989 were dominated by three individual males, each of whom achieved successful matings on a central lek territory for a period of four to six days. However, these individuals did not become successful overnight; each invested considerable time in defending peripheral lek territories before gaining or regaining control of the central territory and thus achieving mating success. Males B1 and B2 were the first bucks to establish territories on the lek (on September 16 and October 2 respectively) and were subsequently in situ on most days until their periods of copulatory success (see Fig 8.4). The top copulatory buck (B20) arrived later in the rut (October 16) but subsequently spent six days on a peripheral territory before fighting his way into a central position.

Correlates of male mating success on the lek

It is clear from the previous section that male mating success on the lek is highly skewed, with a few successful males obtaining the great majority of copulations. Fig 8.14 shows the distribution of mating success on the lek in terms of territories and individuals; over 90% of copulations occurred on two of the nine lek territories, whilst the three most successful males accounted for more than 85% of the matings. Both of these distributions of matings are significantly different from a Poisson distribution (Chi-squared =31.8, $p<0.001$; Kolmogorov Smirnov D=0.65, $p<0.001$).

Why were some males more successful than others? To resolve this question individual reproductive success was related to certain aspects of male mating behaviour on the lek. The parameters considered were lek attendance, number of females on territory, fighting and dominance.

Lek attendance

Three parameters of lek attendance were considered in this analysis: the number of days on a central conifer territory (C & D in Fig 8.2), the number of total territory-holding days on the lek, and the number of total lek days regardless of territoriality. Data was separately analyzed for three time periods: the prerut (October 2-15), the peakrut (October 16-28), and a combined value for the total rut (October 2-28); and for three groups of individual bucks: all 22 bucks which visited the lek, the 12 bucks which held territories on the lek during the peakrut, and the 8 bucks which successfully mated on the lek.

Most variables were not normally distributed, therefore for this and the following analyses, non-parametric Spearman rank correlations were used. The data were reanalysed using Mann-Whitney U-tests, both between successful and unsuccessful males, and between successful males with >10 and <10 matings; in each case the results were similar to the rank correlation, which for simplicity are presented alone. The results of the correlation matrix are summarized in Table 8.5.

Mating success was significantly correlated to the number of days spent defending a central conifer territory (rs=0.81, p<0.01), particularly during the peakrut (rs=0.89, p<0.01). This relationship remained significant when only the bucks which copulated were included in the analysis, both for the total rut (rs=0.90, p<0.05) and the peakrut (rs=0.93, p<0.01). The other lek attendance parameters, total territory days and total lek days, were of reduced significance and were largely an artifact of the previous strong relationship. To briefly summarize, successful bucks spent more time on the lek defending central conifer territories than unsuccessful bucks (Fig 8.15).

Number of consorting females

The daily number of consorting females was calculated as the total number of females seen on a male's territory during regular scans of the lek, divided by the number of scans in that day. This measure differs from the 'harem size' of Apollonio et al. (1989) in that, for each individual male, it may include non-territorial periods when he was absent from the lek and thus not recorded as attracting females to a lek territory. It was thought that this provided a more accurate measure of the attractiveness of males to females, and was less affected by temporary occupancy of territories containing large numbers of females. Using the same logic, the mean number of consorting females was calculated by taking the average number of consorting females for all thirteen days of the peakrut, including days in which males were absent from the lek and thus holding no lek females.

The mean number of consorting females was positively correlated to reproductive success, whether the analysis included all 22 lek bucks (rs=0.90, p<0.001), the 12 bucks which held lek territories (rs=0.92, p<0.001), or the 8 copulatory bucks (rs=0.98, p<0.01). For all territorial males combined, the daily number of consorting females was higher on copulatory days than on non-copulatory days (Mann-Whitney U-test, U=5.6, p<0.001; Fig 8.16).

For the three males which copulated on three or more days, and achieved at least 10% of all copulations, there was a positive correlation between the daily number of matings and the daily number of consorting females (rs=0.99, N=6, p<0.05; rs=0.74, N=10, p<0.05; rs=0.75, N=13, p<0.01). The average daily number of consorting females of each of these males was higher on days in which they mated than days in which they did not mate (Mann-Whitney U-tests, p<0.05).

It should be clear that mean number of consorting females is not independent of lek attendance; long periods of central territory occupancy result in a relatively high values for this parameter (Spearman rank-correlation rs=0.94, N=12, p<0.01). For this reason, an alternative summary statistic was calculated, called the occupancy number of consorting females, by taking the average daily number of consorting females for all days in the peakrut in which a buck held a lek territory. The occupancy number of consorting females was significantly correlated to mating success when this analysis included non-copulatory bucks (rs=0.88, N=22, p<0.01; rs=0.76, N=12, p<0.05); however the correlation was not significant when only males that copulated were considered. What this suggests is that on any given day, a moderately successful buck may attract as many females as a very successful buck, and that mating success is closely related to the number of days in which a buck can attract a large harem. Additionally, in a small lek such as Blackensford, where typically each day mating is dominated by a single buck, the timing of harem holding is important. The most successful buck overall held a central conifer territory on the maximal mating day, whilst the second ranking buck occupied a similar position on the two following days. Thus optimal timing appears a critical factor.

Fighting

Fighting behaviour was considered in two contexts, firstly the total number of fights in which each buck was involved, and secondly the fighting rate, calculated as the number of fights per day on the lek. In this analysis antler clashes and escalated fights were combined into a single category. These measures were calculated separately for each of three time periods: prerut, peakrut, and a combined measure for the total rut; and analyzed for each of the three groups of bucks: the 22 lek bucks, the 12 territorial lek bucks, and the 8 copulatory lek bucks.

The number of fights over the total rut was positively correlated to mating success for all categories of bucks (Table 8.6). This relationship was particularly strong for fights during the peakrut; implying that most successful bucks were involved in a large number of agonistic encounters during this period. Surprisingly, the number of fights in the prerut period was independent of mating success.

Fighting rate, in terms of fights per day, was similarly correlated to mating success in the peakrut and total rut periods, but only when non-copulatory bucks were included in the analysis (Table 8.6). Fighting rate in the prerut period was independent of copulatory success.

The number of fights a buck engaged in was positively correlated to the length of time he spent on the lek (Table 8.7). Fighting rate, in terms of fights per day on the lek, was also positively correlated to lek attendance, in particular the number of days spent in a central conifer territory (Table 8.7).

Dominance

A dominance hierarchy was calculated using the index of Clutton-Brock et al. (1979) in which the rank of an individual is weighted according to the rank of his opponents. This index included all interactions with a definite +/- outcome, including spatial displacements without contact. The index was calculated separately for interactions in the prerut and peakrut periods, and as a total rut measure of dominance. The relationship to mating success was determined initially for all interacting bucks and separately for the eight copulatory bucks.

The dominance index including all interacting males during the peakrut was correlated to mating success ($rs=0.66$, $N=15$, $p<0.05$). Mating success was independent of dominance in the prerut and as a combined measure for the total rut. Relative mating success in the copulatory buck category was not related to dominance in any period.

Peakrut dominance was significantly correlated to the number of fights in the peakrut ($rs=0.54$, $N=15$, $p<0.05$) but was independent of fighting rate. Dominant individuals in the peakrut spent more days on central lek territories ($rs=0.57$, $N=15$, $p<0.05$) but dominance was not related to other lek attendance parameters.

8.4. DISCUSSION

Distribution of reproductive activity

The lek was the focus of reproductive activity throughout the rut in this particular site. The initiation of territoriality by males in mid-September was first displayed here; a continuous presence by one or more mature bucks was maintained throughout October; and a post-rut concentration of mature males and young 'hopefuls' continued on into late November. These results were largely replicated in each of the three years of the study. The early occupation of lek territories is in contrast to the fallow population studied by Clutton-Brock et al. (1988) where territorial defence was initiated on single resource territories with the subsequent occupation of lek territories occurring as a gradual process.

Differences in tenancy time between lek and single stand territories, with a higher turnover on leks, have been demonstrated for several ungulates, including fallow deer (Clutton-Brock et al. 1988), Uganda kob (Buechner & Schloeth 1965), and possibly topi (Gosling in press). Similarly, turnover of territories on a kob lek was faster in the centre than on the periphery (Floody & Arnold 1975). In contrast, Apollonio et al. (1990) working on a wild population of fallow with small leks of comparable size to the Blackensford population, demonstrated both a very low turnover of lek males and no difference in tenancy time between successful and unsuccessful territories. In the current study the data on territory turnover was too variable to identify any clear distinctions between the lek and single stands, or differences within the lek. It may be that the whole subpopulation was quite unstable, with high turnover on the lek resulting in a similar action on at least some of the adjacent single stands. This instability was likely to be the result of the competition for females; a reduction in female density in 1988 resulted in longer tenure of both lek and single stand territories. Similarly, males occupying single stand territories in non-lekking areas typically retain possession for the duration of the rut.

Competition for the lek territories was intense. Fighting in cervids is dangerous (Geist 1986) and at least one male received fatal injuries as a result of a fight on the lek. Fights on the lek followed a cyclical trend with a three to four day periodicity between peaks of activity. Within each day, agonistic activity was concentrated in the mornings and evenings, with a lull during the afternoon. The incidence of fighting clearly stimulated further fighting, and sequential bouts involving up to ten individuals were not uncommon. In my view these prolonged bouts of fighting resulted in the dominance hierarchy being re-established, and were followed by relatively stable periods with few agonistic interactions.

The number of fights in a territory was not related to the copulations achieved. This result differs to those of Floody and Arnold (1975) and Fryxell (1987) who, working with different subspecies of kob, reported an association between the level of fighting on lek territories and indirect measures of reproductive activity, such as numbers of females. The results presented here are similar to the fallow study of Apollonio et al. (1990), but a different interpretation is given. Apollonio et al. consider that fighting may be of limited importance in a male's ability to hold a successful lek territory; dominance is established before the rut and social relationships are not strongly affected by the outcome of interactions on the lek. In the Blackensford lek, a simpler explanation may suffice. Successful males did not always fight in their own territories, in particular, there was a very high incidence of fighting in the territories bounding the central territories. However, one or other of the two successful 'bucks of the day' was involved in just under half of all interactions.

Alternative strategies and reproductive success

Copulations occurred in non-lek strategies. This result is perhaps the most interesting and controversial of the current study. Other studies of lek breeding mammals have suggested that males holding territories on the lek have much higher mating rates than any of those that hold single territories off the lek (Buechner & Schloeth 1965; Leuthold 1966; Schaal 1987; Clutton-Brock et al. 1988; reviewed in Clutton-Brock 1989). Work on fallow deer by Schaal (1987) and Clutton-Brock et al. (1988) has indicated that over 90% of matings occur on the lek. Clearly the 65%/35% division between lek and alternative strategies which has been suggested here for the Blackensford population needs explaining.

Since the estimation of total copulations off the lek is based on weighted data, there must be a real possibility that it is inaccurate. However, there is no doubt that at least some non-lek individuals do get matings, and 9% of the total matings in only 17% of observation time is compelling evidence. Furthermore, recent work on black grouse has shown that a single solitary male obtained a higher lifetime copulatory success than the most successful males on an arena in the same population (Kruijt & de Vos 1988). Gosling and Petrie (in press), working on topi leks, have independently come to the same conclusions as those given here; namely that successful lek males mate at a higher rate than males in single territories, but that unsuccessful males on leks achieve fewer matings than either. Unfortunately, however, their conclusions are largely based on indirect measures of reproductive success, as few copulations were observed.

Whilst it is indisputable that, in the studies of Schaal (1987) and Clutton-Brock et al. (1988), over 90% of observed copulations were by lek males; more than 50% of females of breeding age in these confined populations were unaccounted for in their observations. These studies made the assumption that copulatory behaviour on the lek continues at the same rate during the night as day, and thus multiplied lek copulations by two to take account of nocturnal matings. Nocturnal matings have been observed on kob leks (Floody & Arnold (1975), but as yet little direct evidence exists for fallow deer. Given that nocturnal matings do occur, we do not know if the skew in mating success in favour of lek males remains consistent at night, or whether in fact other strategies become more profitable when visual cues to territory defence and mate choice break down.

It is most likely that there were real differences between the populations. It has been previously suggested that wild populations of fallow deer display a greater range of concurrent mating strategies than enclosed park herds (Langbein & Thirgood 1989). This may be due to the increased diversity of habitat, and its subsequent effects upon the distribution and localized density of the deer. Males may be less able to accurately predict, on both a short term (daily) and long term (yearly) basis, the availability of oestrous females, and hence it is advantageous to maintain a degree of plasticity in their repertoire of reproductive strategies. The mating activity at Blackensford involved a small subset of perhaps 200 animals out of a total population in the New Forest estimated at

2000 (Putman 1986a). In this population, lekking was a rarely occurring alternative strategy, and the majority of copulations probably occurred on single territories.

Fallow bucks were not all specialists; some individuals switched from one strategy to another as mating opportunities dictated. Whether this individual flexibility is forced on animals as a result of losing a territory, or is a positive, voluntary response resulting in increased mating success is unclear. The data suggest that following is probably an opportunistic strategy, exhibited by most if not all males at some time in the rut, but one that does not result in high copulatory success (a 'side-payment strategy' (Dunbar 1982)). Switching between the territorial strategies of lekking and single stands was more common in fallow deer than other ungulates. Very few Uganda kob or topi males switched between lek and single resource territories (Leuthold 1966; Montfort-Brahamn 1975; Gosling et al. 1987), and Gosling & Petrie (in press) suggest that males on topi leks may be smaller than their contemporaries on resource territories, and are thus limited by their phenotype rather than opting to specialize in a behavioural alternative.

Mate choice on leks

Copulatory success on the lek was highly skewed, both in terms of territories and individual males. Over 90% of matings occurred on two adjacent territories, located in the middle of the conifer belt on the southern side of the lek. These two territories were not in the physical centre of the lek, although they were the centre of daytime activity. The view that females choose to mate with centrally-located males has dominated the literature on lekking in both ungulates (Buechner & Schloeth 1965; Buechner & Roth 1974) and birds (Kruijt et.al. 1972; Wiley 1973; Lill 1974). Reinterpretation of this data has suggested that this 'centre effect' may be due to males relocating their territories around successful males, hence the central location of successful territories may be a result and not a cause of their success (Gibson & Bradbury 1986). In the fallow lek studied by Apollonio et al. (1990), copulations mainly occurred on territories at one end of the lek near a path regularly used by females, and the lack of suitable display sites surrounding these territories was suggested as the reason why peripheral territories were located at the other end of the lek. At Blackensford, a complicating factor is that the lekking arena is located on two quite distinct habitats, and there may well be differences in nocturnal and diurnal female distribution. With one exception, daytime copulations occurred in, or on the edge, of the conifers; the possibility that matings during the night occur in the open can not be discounted in explaining why these apparently unsuccessful territories were all located on one side of the lek.

Male phenotypic or behavioural cues are also thought to be important in influencing female mate choice on leks. Recent work on avian leks suggests that differences in the rate of courtship displays are correlated to male mating success (Gibson & Bradbury 1985; Kruijt & de Vos 1988; McDonald 1989). Opinions differ on whether phenotypic or location cues are important for fallow deer. Apollonio et al. (1989, 1990) suggest that females choose mates largely on the basis of territory location, but acknowledge that male competition for favoured sites may result in an indirect selection for male quality. In an experimental manipulation by Clutton-Brock et al. (1989), when successful males were induced to relocate their territories, differences in the mating success of bucks persisted, suggesting that females were choosing their mates on the basis of phenotypic cues independent of location.

At Blackensford, there was typically one 'mating centre' at any one time. Simultaneous matings by two bucks were rare. Thus there was a fair degree of female unanimity in mate choice. However, the mating centre was not fixed, and there were several switches between the two central conifer territories that occurred whilst the same males were in residence. In these circumstances a behavioural cue must have been utilized by the females to choose between the two bucks. Differences in rates of male display were not systematically measured and therefore can not be discounted. An alternative hypothesis is that females choose between males on their relative ability to offer protection from other, often younger males. Unfortunately, this hypothesis is to a certain extent unfalsifiable; females will only remain on territories when harassment is at a minimum, thus comparison of protection levels concurrently offered by lek males is impossible. Interestingly, the avoidance of male harassment has also been invoked by Clutton-Brock (1989) as a factor inducing females to mate on leks.

Correlates of male mating success on lek

Successful males spent more time on the lek, particularly in defence of a central conifer territory. Lek attendance would not be without costs, both in terms of injuries and energy expenditure. Vehrencamp et al. (1989) demonstrated that the daily energy expenditure of male sage grouse increased significantly with increased display rate and time spent on the lek. Red deer stags lose about 20% of body weight during the rut (Mitchell et al. 1976), and active fallow bucks are likely to suffer a similar loss (J. Langbein pers. comm.).

Possession of favoured territories resulted in large numbers of consorting females, however mating success was more dependent upon the timing and duration of female holding than actual size. This association between reproductive success and female numbers is limited to the lek, and the presence of females on single territories or consorting with non-territorial males should not be used as an indirect index of mating success.

Fighting success and social dominance are correlated to male reproductive success in many polygynous mammals (Geist 1971; Clutton-Brock et al. 1982; Le Boeuf & Reiter 1988). Not surprisingly, successful fallow bucks fought more often, both in absolute numbers and in terms of fighting rate, and tended to win most interactions with other males during the peakrut period of copulatory activity. However, agonistic interactions between bucks on the lek in the prerut period did not appear to be important in influencing eventual mating success. In contrast to the study of Apollonio et al. (1989), the male social hierarchy at Blackensford changed constantly throughout the rut. Individual males were unable to maintain a dominant position for more than a week. It is therefore suggested that bucks who established a dominant position early in the rut, before copulations occurred, may simply have 'peaked too soon', and were subsequently too weak to maintain that position during the optimum period.

To lek or not to lek ?

A fallow buck arriving at Blackensford during the middle of October is confronted with a choice of several options. He may opt to play a non-territorial role, a 'low-cost low-benefit' strategy in the terminology of Gosling & Petrie (1981), which may be forced upon him by his poor competitive ability, making the 'best of a bad job' (Dawkins 1980), or as part of a long term strategy involving conserving his resources for future years when he might be more capable of winning territorial fights.

Alternatively, he may attempt to take over a territory, either on or off the lek. There is little information available on the costs of winning and defending a single territory; escalated fights occur, but less frequently than on a lek territory. Therefore we can assume that, in common with other ungulates (Gosling 1986), single territory defence is less costly than lek territory defence. Copulatory success on single territories is unlikely to reach the level of the most successful lek males within a single year; however the lower costs involved may mean that single territory males may retain better body condition throughout the rut, and thus have a better chance of surviving to reproduce in following years. Measurement must be in terms of lifetime reproductive success (Clutton-Brock 1988), and longitudinal studies of known individuals are necessary to determine the relative payoffs of the alternative mating strategies.

Why do unsuccessful males stay on the lek ?

It is clear that mating success on the lek is highly skewed, with only a few individual males gaining copulations. The benefits for these males are obvious, but why should the majority of unsuccessful males remain if mating opportunities are available elsewhere ? Recent work by Gosling & Petrie (in press) on topi suggests that on average lek males are smaller than males in the resource territories around the lek, and may be incapable of winning the fights necessary to acquire good quality resource territories. These small males may pursue a 'satellite' strategy around successful males on leks in hope of obtaining 'sneak' copulations. Although quantitative data are not available in the current study, it seems unlikely that this is the case for fallow deer. It is also difficult to imagine that males attain fitness benefits other than matings from staying on the lek; indeed, even unsuccessful males are exposed to an increased level of potentially dangerous fighting.

One possible explanation can be deduced from observations of the behaviour of successful males on the lek. Most of these males spend their first few days on peripheral lek territories, before fighting their way onto successful territories. As previously stated, few males attain copulations during their initial period on the lek. These males often appear to initiate interactions with the resident territory holders, and may well be playing a 'waiting game' until the residents are sufficiently weakened to be usurped. Those males which remain on peripheral territories and never become very successful may simply mistime their final push. However, the possibility of gaining a successful territory, and the associated mating benefits that go with it, may be sufficient to entice these males to remain on the lek.

8.5. SUMMARY

1. During the 1989 rut at Blackensford, male deer adopted the alternative mating strategies of lek territory defence, single territory defence, and non-territorial following.
2. The lek was the focus of reproductive activity thoughout the rut and was characterised by the continual presence of mature males, high turnover of territory ownership and high incidence of fighting.
3. Fighting activity followed a cyclical trend with a three to four day periodicity and was concentrated in the mornings and evenings. Most fights occurred on or near successful territories.
4. Copulations were seen on the lek on each day from October 16-28, rising to a peak of 15 matings on October 23. Non-lek copulations were seen from October 17-28.
5. Individual male mating success was highest on the lek, but unsuccessful lek males got fewer matings than some single territory males off the lek. The mating success of non-territorial behaviour, which was adopted by most males at some time durng the rut was uncertain. Non-lek matings were higher than those reported in other lekking ungulate populations.

6. Males were not specialists; individuals commonly changed mating strategies.
7. Copulatory success on lek was highly skewed both in terms of territories and individual males. Over 90% of all copulations occured on two adjacent territories on one side of the lek, whilst the three most successful males accounted for more than 85% of the matings.
8. Successful males spent more time on the lek, particularly in defence of the two central conifer territories, and attracted more females to their territories.
9. Successful males fought more often and tended to win most fights. Fighting and dominance in the beginning of the rut was unrelated to mating success.
10. Further data are needed on the lifetime reproductive success of males adopting alternative mating strategies.

Table 8.1 Calculation of estimated matings during October 16-28, 1989 for lek, single territory and following strategies.

	Lek	Single territories			Follow
		A	B	C	
Daily hours observation	12	2	2	2	?
Total hours observation	156	26	26	26	?
Observed matings	58	3	2	0	1
Correction factor	-	6x	6x	6x	?
Observed (Estimated) matings	58	(18)	(12)	(0)	???

Table 8.2 Observed distribution of copulations between individual males at Blackensford during the 1987 and 1988 ruts.

Year	Buck	Observed copulations		
		Lek	Single territory	Follow
1987	A4	3	-	-
	A5	-	2	-
	A6	-	1	1
	A7	2	-	-
	A8	3	-	-
	A15	2	-	-
	Total	10	3	1
1988	B8	6	-	-
	B11	1	-	-
	B13	1	-	-
	Total	8	0	0

Table 8.3 Observed distribution of copulations on lek territories during 1989 rut.

Date in October	Lek territory								
	A	B	C	D	E	F	G	H	I
16	-	-	2	-	-	-	-	-	-
17	-	-	2	-	-	-	-	-	-
18	-	-	2	-	-	-	-	-	-
19	-	-	1	-	-	-	-	-	-
20	-	-	3	-	-	-	-	-	-
21	-	-	5	-	-	-	-	-	1
22	1	-	2	2	-	-	1	-	2
23	-	-	4	11	-	-	-	-	-
24	-	-	6	-	-	-	-	-	-
25	-	-	5	-	-	-	-	-	-
26	-	-	-	2	-	-	-	-	-
27	-	-	1	-	-	-	-	-	1
28	-	-	4	-	-	-	-	-	-
Total	1	-	37	15	-	-	1	-	4

Table 8.4 Numbers of male fallow deer adopting specialist and non-specialist mating strategies in the Blackensford population during the 1987-1989 ruts.

	1987	1988	1989
Lek only	5	3	2
Single Territory only	0	2	3
Non-territorial only	3	6	13
Lek and Single territory	4	1	3
Lek and Non-territorial	4	3	7
Single territory and Non-territorial	2	2	2
Lek, Single territory and Non-territorial	5	3	1
Total	23	20	31

Table 8.5 Spearman rank correlation coefficients between individual male mating success and lek attendance parameters during 1989 rut. Sample size in parentheses.
** p<0.01, * p<0.05

		Central conifer days	Total territory days	Total lek days
Prerut	All bucks (22)	0.45 *	0.17	0.05
	Territorial bucks (12)	0.41	0.01	0.01
	Copulatory bucks (8)	0.34	0.31	0.31
Peakrut	All bucks (22)	0.89 **	0.71 **	0.63 **
	Territorial bucks (12)	0.92 **	0.45	0.39
	Copulatory bucks (8)	0.93 **	0.72 *	0.68 *
Total rut	All bucks (22)	0.81 **	0.65 **	0.53 **
	Territorial bucks (12)	0.89 **	0.49	0.31
	Copulatory bucks (8)	0.90 **	0.76 *	0.69 *

Table 8.6 Spearman rank correlation coefficients between individual male mating success and fighting parameters during the 1989 rut. Sample size in parentheses.
** p<0.01, * p<0.05

		Number fights	Fighting rate
Prerut	All bucks (22)	0.06	0.04
	Territorial bucks (12)	0.09	0.01
	Copulatory bucks (8)	0.28	0.14
Peakrut	All bucks (22)	0.79 **	0.68 **
	Territorial bucks (12)	0.76 **	0.56 *
	Copulatory bucks (8)	0.72 *	0.56
Total rut	All bucks (22)	0.69 **	0.60 **
	Territorial bucks (12)	0.65 *	0.57 *
	Copulatory bucks (8)	0.85 **	0.41

Table 8.7 Spearman rank correlation coefficients between individual male fighting and lek attendance parameters during the 1989 rut. Sample size in parentheses.
** p<0.01, * p<0.05

		Number fights	Fighting rate
Prerut	Central conifer days (15)	0.70 **	0.46 *
	Total territory days (15)	0.62 *	0.50 *
	Total lek days (15)	0.78 **	0.47 *
Peakrut	Central conifer days (16)	0.73 **	0.42 *
	Total territory days (16)	0.79 **	0.06
	Total lek days (16)	0.76 **	0.05
Total rut	Central conifer days (22)	0.85 **	0.55 **
	Total territory days (22)	0.81 **	0.31
	Total lek days (22)	0.80 **	0.22

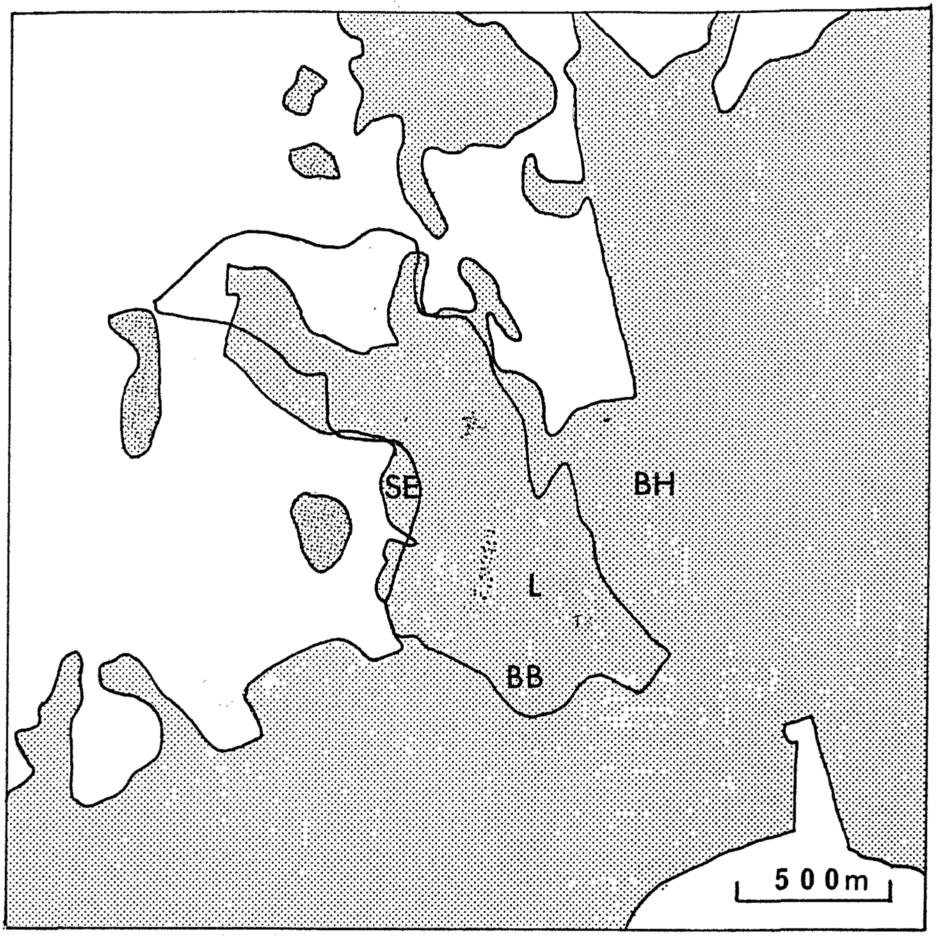


Fig 8.1 Distribution of reproductive activity at Blackensford October 1989 showing location of lek (L) and single territories (BH, BB, SE).

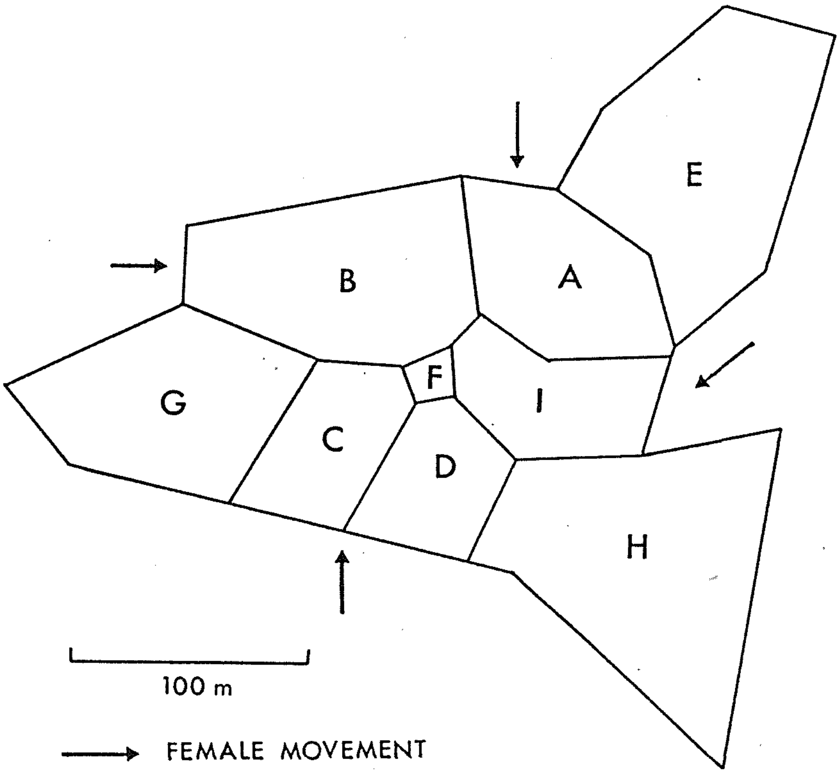
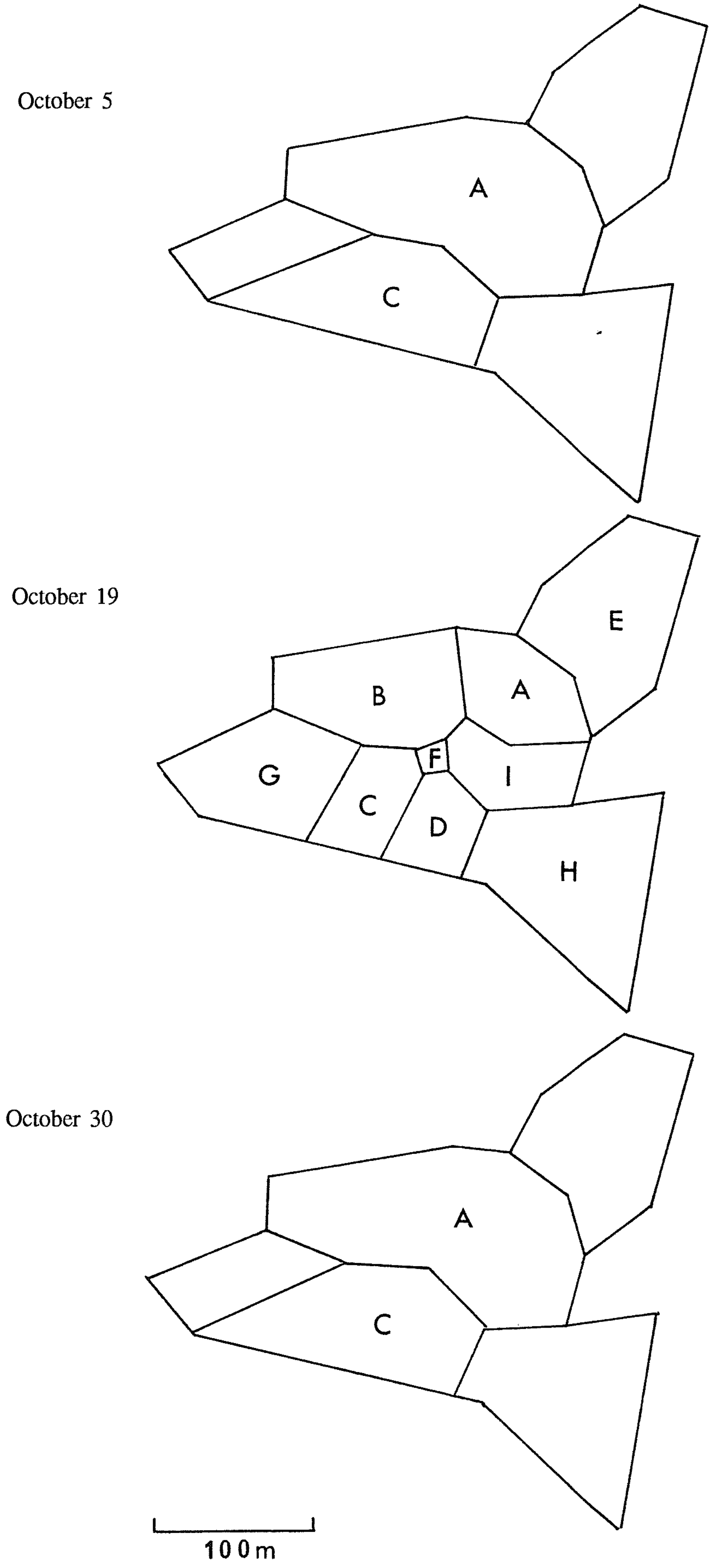


Fig 8.2 Distribution of territories on Blackensford lek during October 1989.



October 5

October 19

October 30

Fig 8.3 Change in territory size on Blackensford lek during October 1989 rut. See text for details.

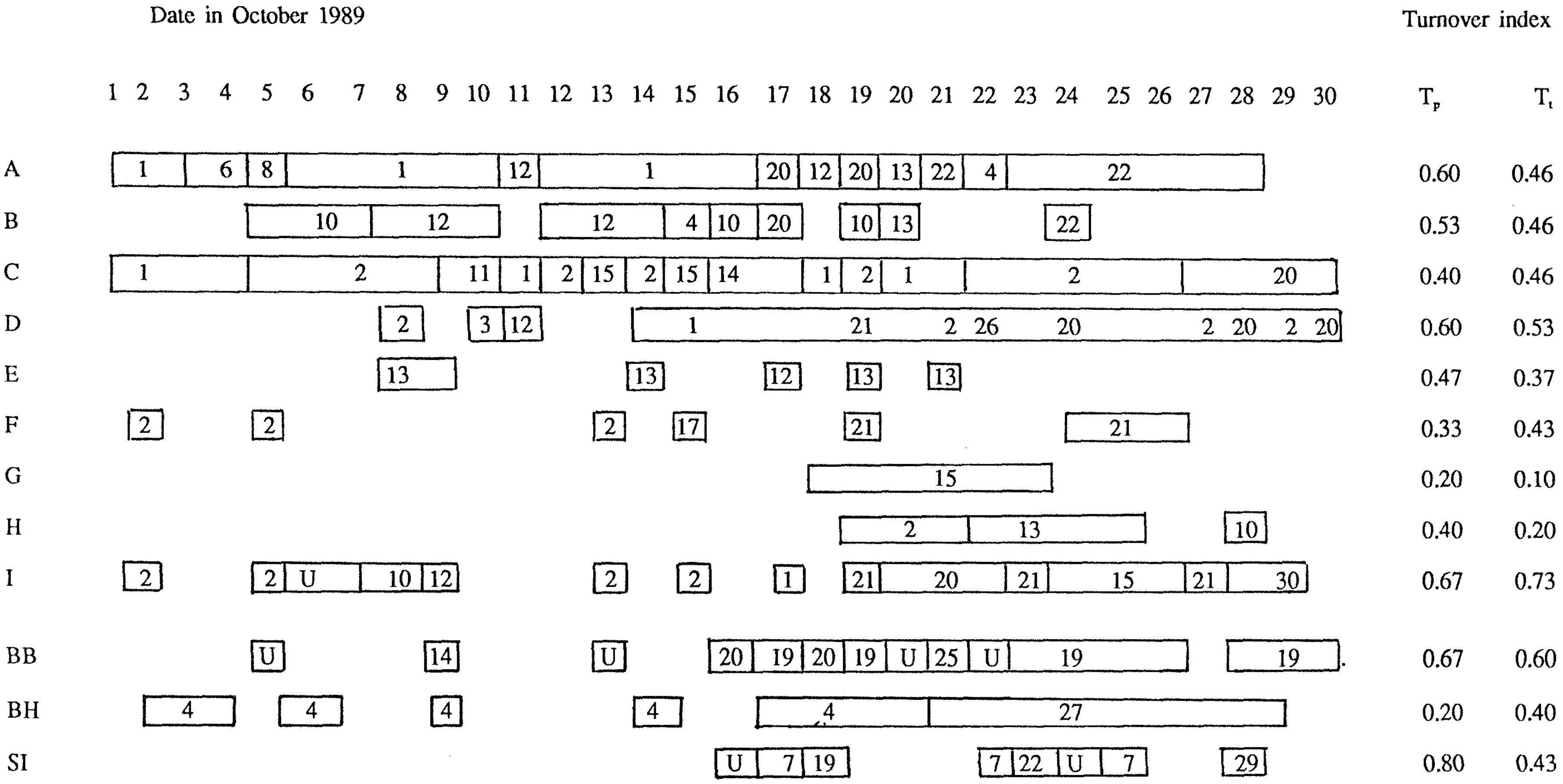


Fig 8.4 Duration and turnover of territory tenancy by male deer at Blackensford during October 1989.
Lek territories: A, B, C, D, E, F, G, H, I
Single stand territories: BB, BH, SI
Buck identification numbers: 1-30
Unidentified Bucks: U
Turnover index peakrut: T_p
Turnover index total rut: T_t

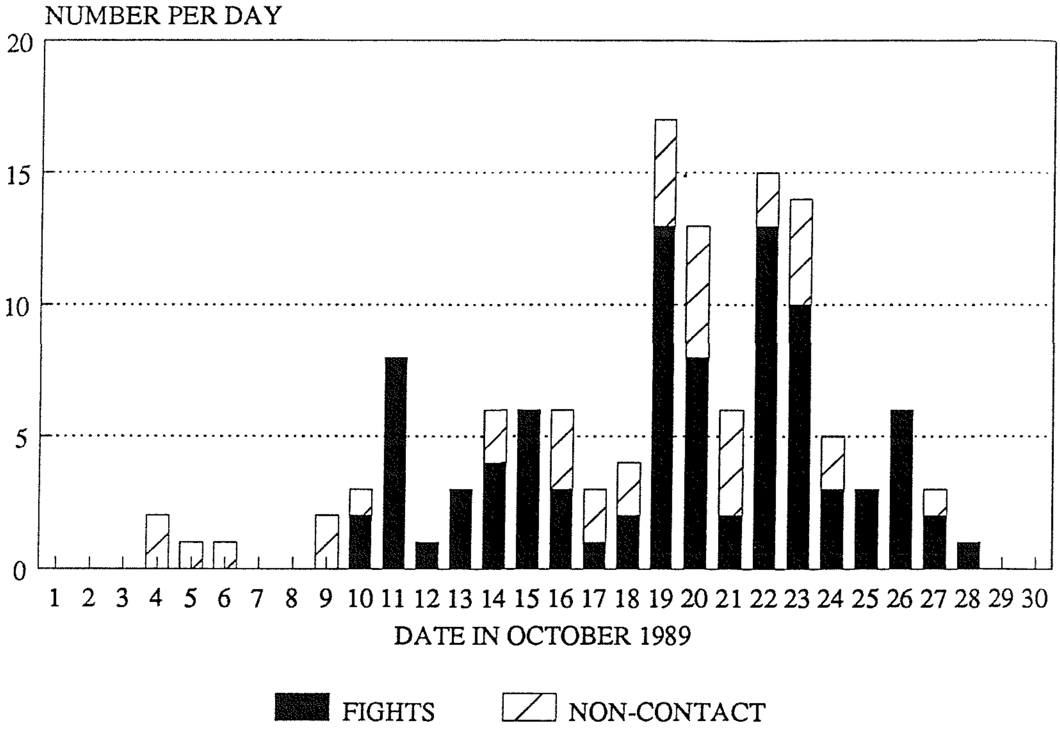
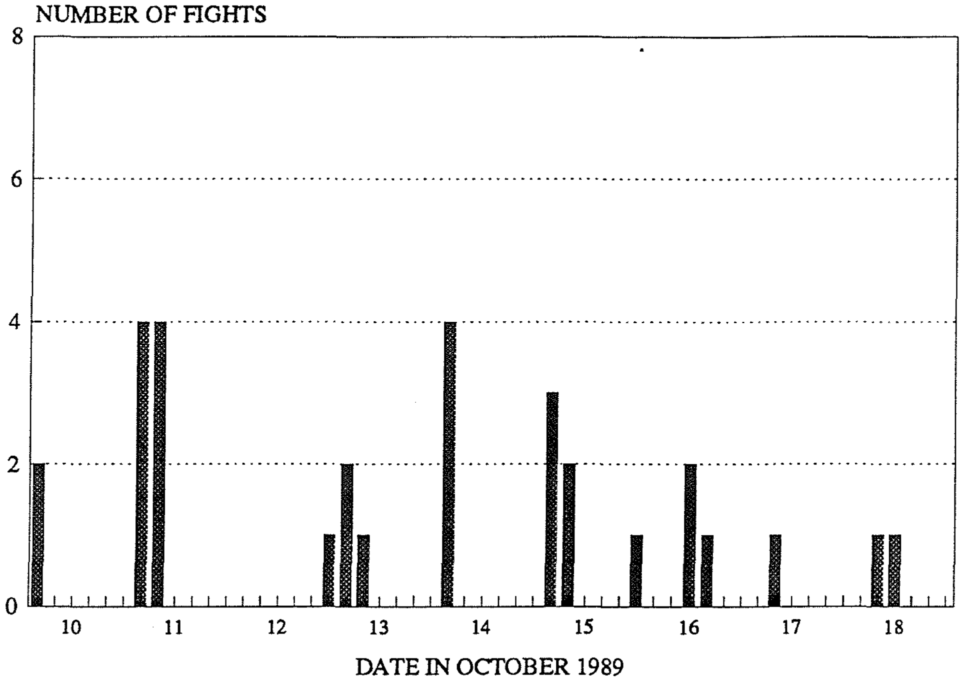
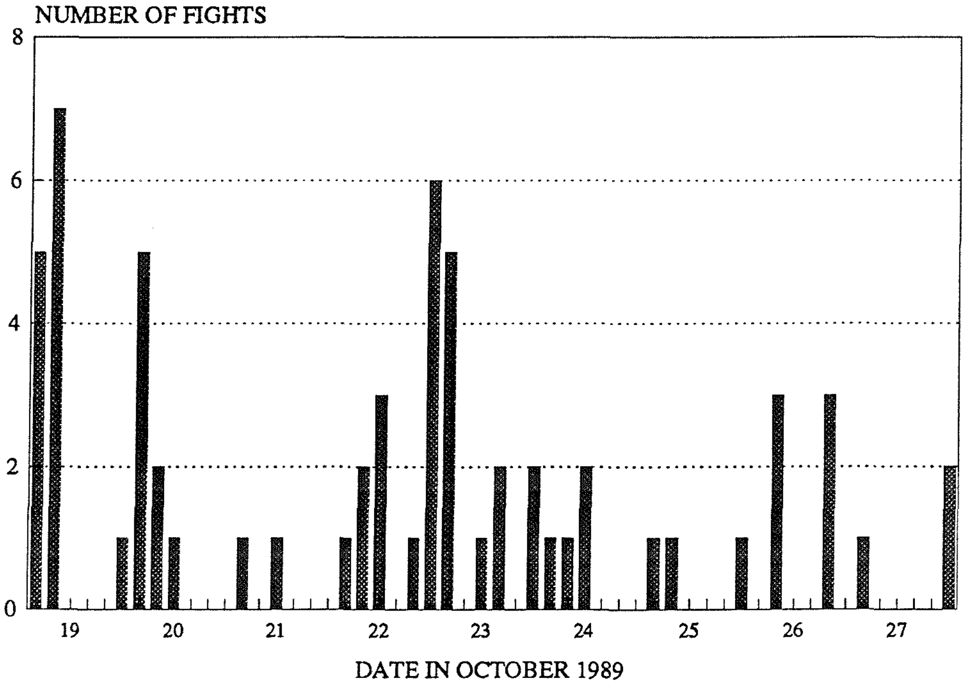


Fig 8.5 Temporal distribution of male-male interactions on the lek in October 1989.

Fig 8.6 Number of fights on the lek per two hour time period in each day during October 10-27. Time periods: 0700-0859 hrs, 0900-1059 hrs, 1100-1259 hrs, 1300-1459 hrs, 1500-1659 hrs, 1700-1900 hrs.





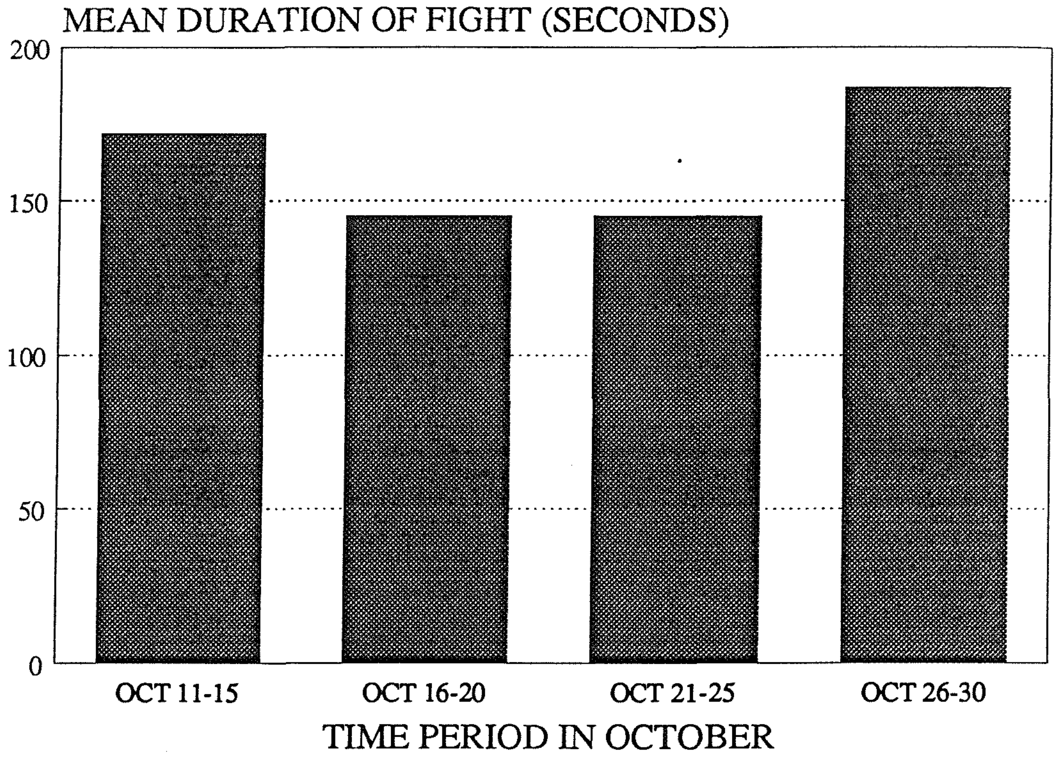


Fig 8.7 Duration of escalated fights on the lek during five day time periods.

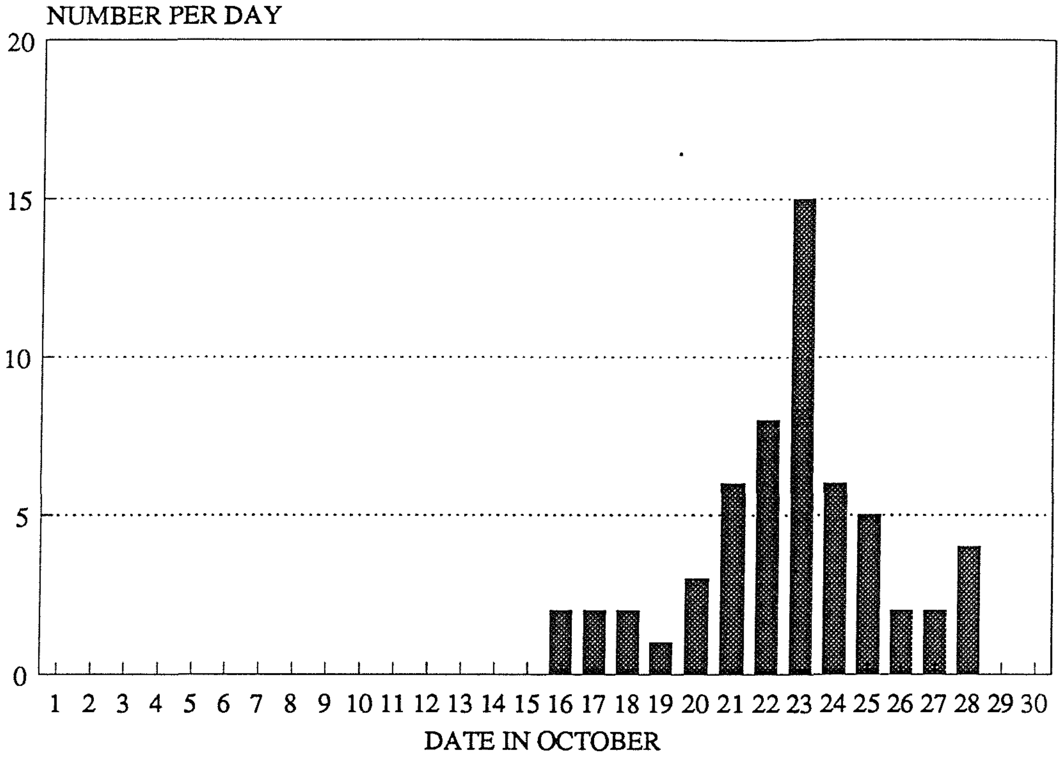


Fig 8.8 Temporal distribution of copulations on the lek during October 1989.

Fig 8.9 Distribution by date of matings and fights on the lek during October 1989.

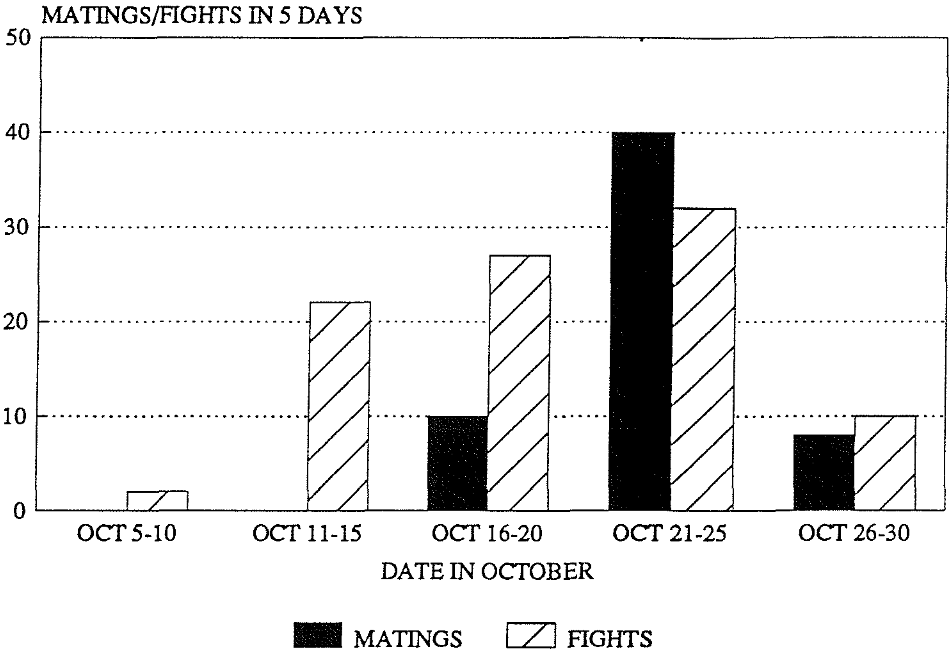


Fig 8.10 Distribution by time of matings and fights during the peakrut (October 16-28, 1989).

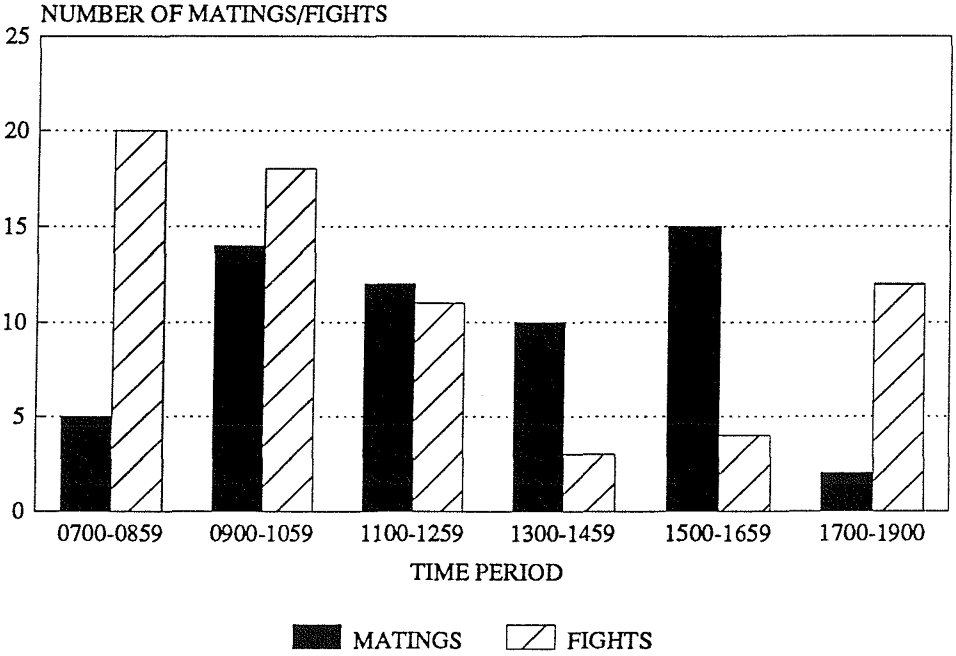
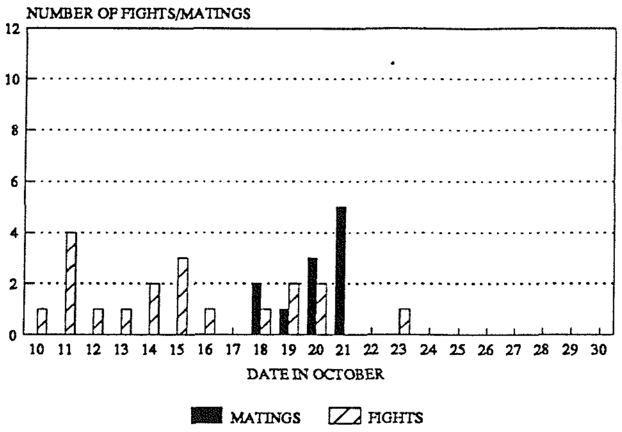


Fig 8.11 Distribution by date of the matings and fights of the three most successful bucks on the lek during Ocotber 1989.

TWINFISH



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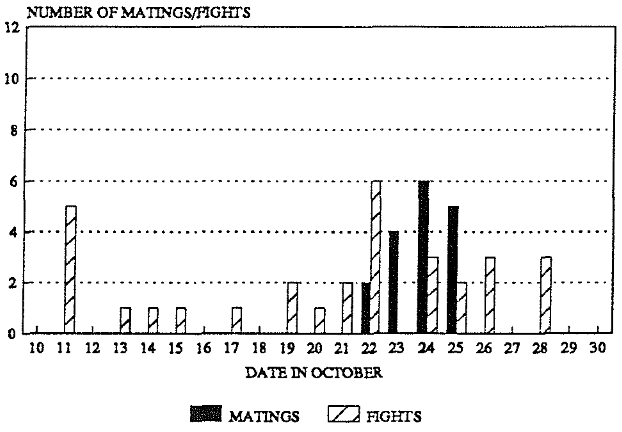

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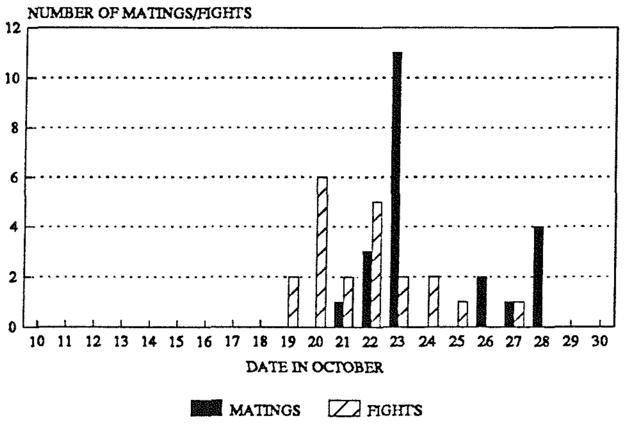


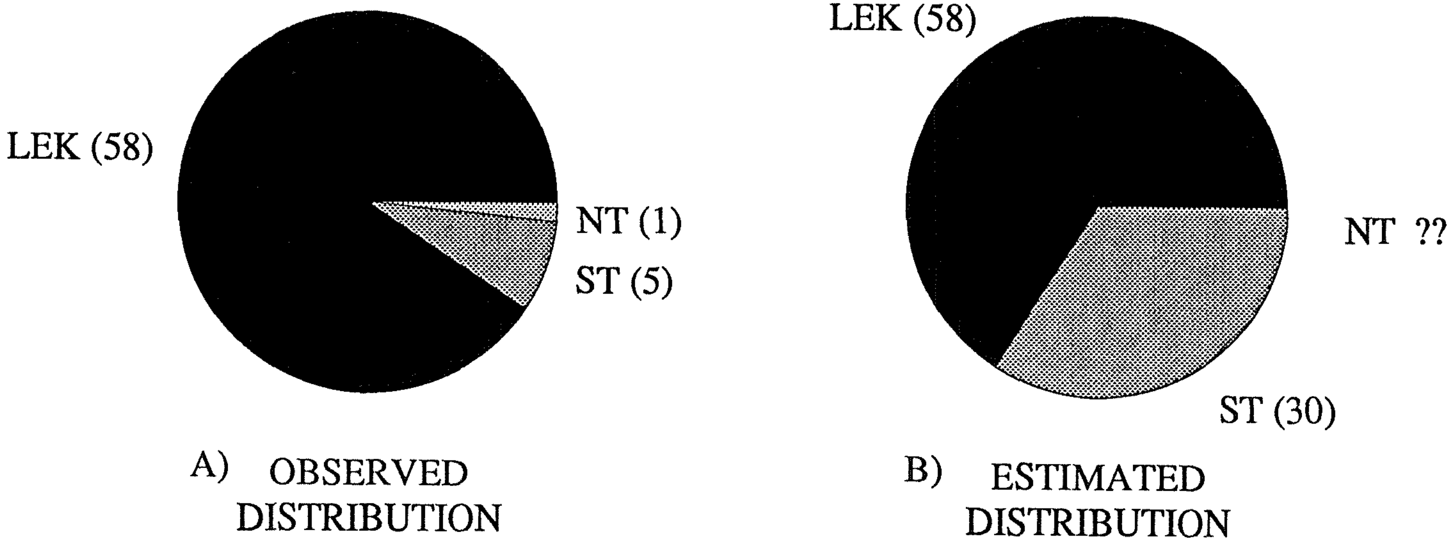
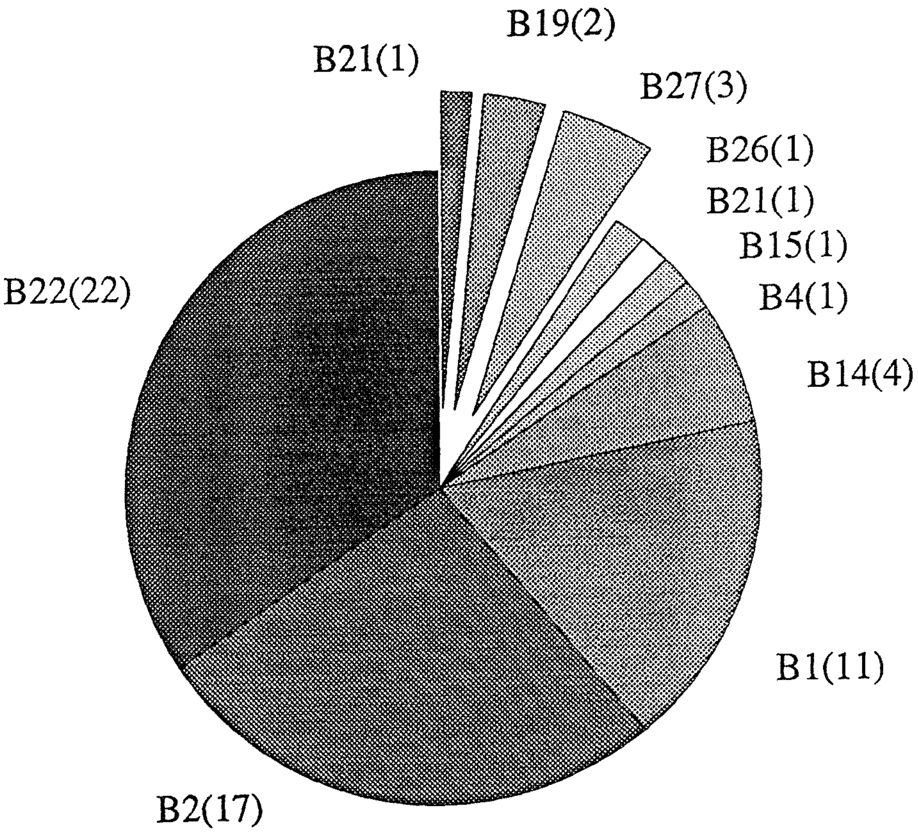
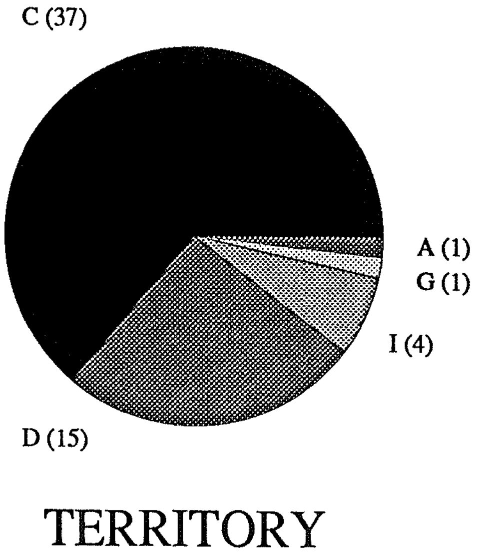


Fig 8.12 Distribution of copulations between lek, single territory (ST) and non-territorial (NT) males. Numbers in parentheses indicate number of copulations.

Fig 8.13 Individual distribution of mating success between males at Blackensford during October 1989. Numbers in parentheses indicate numbers of copulations. Exploded pie segments indicate non-lek matings.



+ 21 BUCKS NO MATINGS



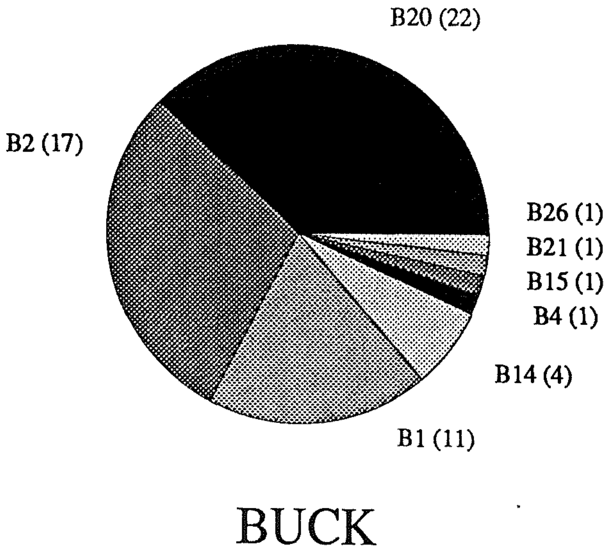


Fig 8.14 Distribution of copulations on the lek in different territories and by different bucks. Numbers in parentheses indicate the number of copulations.

Fig 8.15 Number of days attending lek for bucks achieving >10% of total matings, bucks achieving <10% of total matings, and bucks achieving no matings.

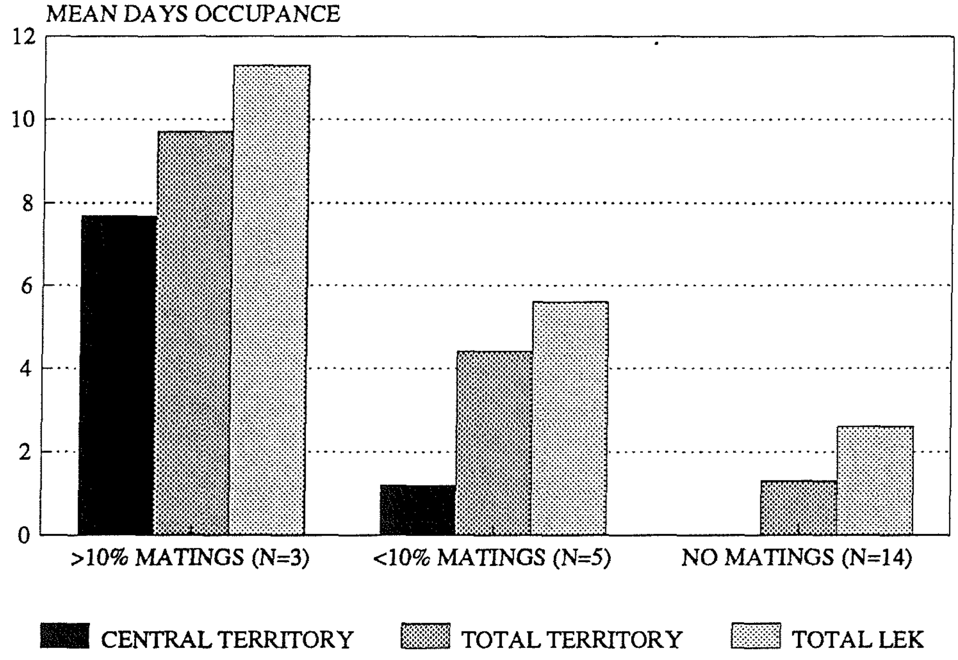
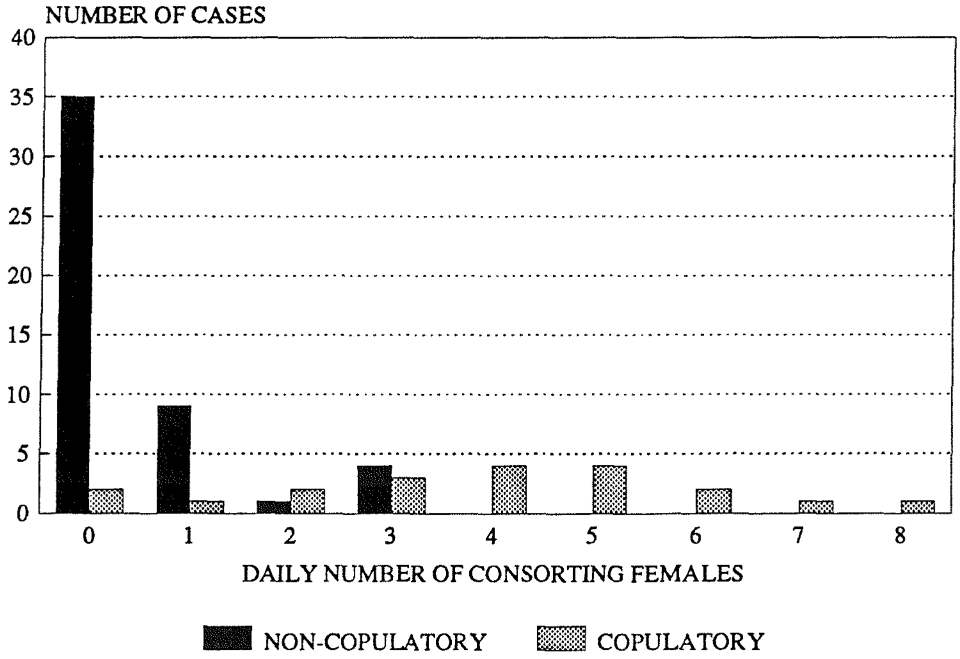


Fig 8.16 Distribution of daily number of consorting females on lek territories for copulatory and non-copulatory days.



9. GENERAL DISCUSSION

The principal objective of this thesis was to examine grouping patterns and mating systems of fallow deer in relation to characteristics of the population structure and vegetational environment. This study has shown that fallow deer are marked by their flexibility in adapting to differing environmental circumstances, and as such provide an ideal 'model species' to investigate the interactions between the social and ecological environment and the social systems of large mammals. This discussion briefly summarizes the major conclusions of the thesis, the outstanding questions, and finally the wider implications of the study.

Despite occurring in environments as markedly different in habitat composition and structure as the New Forest and the agricultural study sites, patterns of habitat use showed great similarity across the study sites in terms of utilization of woodland and open habitats. Even in the relatively open agricultural environment, fallow remain principally a woodland-inhabiting deer. Differences between the two main environmental types were more pronounced in respect of characteristics of the populations themselves. Densities were much higher in the New Forest populations, and there was considerable variation within and between categories in sex ratio. These two characteristics appeared to influence the extent of winter and spring sexual segregation exhibited by the populations. Males joined female groups when male numbers were low, possibly responding to the same ecological factors initiating female grouping. In the New Forest, 'mixed-sexing' was the result of temporary aggregations of females and young males. In contrast, mixed-sex groups in the agricultural sites contain males of all ages and may have been of a more permanent nature.

The size of social groups was strongly influenced by season, habitat openness, habitat structure and population density. A common seasonal pattern existed across all sites, with female groups largest in winter and spring, decreasing during parturition in early summer, and increasing again after the autumn rut. Male group size was smallest during the rut and varied little throughout the remainder of the year. In common with most ungulates, fallow group size was largest in open habitats. Between different populations, variation in the extent of change in group size between woodland and open habitats may have been influenced by habitat structure and population density. High density populations inhabiting large continuous woodlands were characterised by small groups in woodland and large groups in open habitats. In contrast, in low density populations inhabiting small discontinuous woodlands group size was less variable. Isolating the effects of habitat structure and density was not possible in the current range of study sites.

The flexibility in fallow grouping patterns was matched by the variation in mating systems. Males adopted a range of mating strategies which could be broadly classified according the degree and type of territoriality during the autumn rut. In the low density agricultural populations, male territoriality was reduced and males followed groups of females throughout their range. In the higher density New Forest populations a wide range of male mating strategies existed including leks, multiple stands, single territories, temporary territories, and non-territorial following. Increased territoriality and the development of multiple territory mating systems was associated with an increase in male and female density. Lekking may be initiated by locally high densities of females aggregating near favoured feeding resources. In one population in the New Forest, lekking occurred as an alternative strategy to single territory defence and non-territorial following. In this population, copulatory success was highest on the lek, but unsuccessful lek males achieved less copulations than some single territory males away from the lek.

Despite the advances in knowledge of fallow deer biology over the last decade, several major questions remain unanswered. Little is known of male or female ranging behaviour in any environment, and the few data available are based on winter observations of a small sample of individually recognized females, in what could be considered an atypical environment. Further information from individually marked animals is needed to investigate the dynamics of group formation and the cohesion of social groups. Ideally such studies would be conducted in both the forest and agricultural environments, however the need is more urgent in the latter case, in view of the widespread distribution of fallow deer in the agricultural landscape. Such a study would by necessity be based on intensive radio-telemetry and the capture and tagging of a substantial proportion of the population.

The feeding ecology of female fallow deer has been intensively studied in the New Forest; however, little information is available on forage selection in males. Faecal samples were collected throughout the year in the current study to facilitate comparison of male and female diets on separate and distinct ranges, but were not analyzed due to limits of time. A useful contrast could be made with sex differences in diet in agricultural fallow deer, with possible implications for population differences in the extent of sexual segregation.

More information is needed on male mating strategies, particularly in low density populations. The intensive work at Blackensford in the New Forest revealed that an accurate interpretation of the costs and benefits of alternative mating strategies may only be gained from continuous observation. Therefore, further studies should concentrate on single populations rather than encompass a range of sites. At Blackensford, more data are needed on the reproductive success of single territory and non-territorial males in relation to lekking males. Additionally there is an urgent requirement for nocturnal studies of reproductive activity. Ultimately, male success must be interpreted in terms of lifetime copulations, and longitudinal studies encompassing the reproductive lifespan of individually known animals are needed. The mating system studies reported in this thesis have largely concentrated on males, and future research could emphasize the female role in shaping mating systems through examining aspects of mate choice.

What are the implications of the current study for research into the relationship between the social and ecological environment and social systems of large mammals? Fallow deer show marked flexibility in patterns of social grouping and mating systems. This flexibility can be demonstrated at two levels. Populations living under different ecological circumstances show different sociobiological attributes. At a finer scale, it has been shown that individual social strategies may vary within populations. In the current study, individual variation has been shown only for male mating strategies, however it is likely that individual variation in other aspects of male and female social strategies are pronounced. As stated at the beginning of the thesis, a social system is the sum of the behaviours of the individual animals in the population. Variation between population social systems must therefore be explained as the result of changes in individual behaviour. Social system variation at the population level in mammals has been recognized for many years; future studies must concentrate on individual variation to help explain the evolution of mammalian societies.

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