Aspects of the ecology of the European woodcock Scolopax rustlcola L

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ASPECTS OF THE ECOLOGY OF THE EUROPEAN WOODCOCK

Scolopax rusticola L.

by

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ABSTRACT

The trends in the numbers of British breeding woodcock *Scolopax rusticola* and the Continental woodcock that visit Britain in winter were examined using ringing recoveries and bag records. The proportion of foreign: British woodcock present in S England and Wales is appreciably higher than in N England and Scotland.

Average annual survival rates for adult British and foreign-ringed woodcock were estimated as 58% and 54% respectively. Calculations of the annual production of young woodcock, based on British Trust for Ornithology nest record cards from Britain and on data collected in NE Derbyshire, suggested that too few young woodcock are produced to compensate for the current rate of adult mortality among British woodcock. Woodcock chick mortality was the key factor in an analysis of 15 years of data from Derbyshire. Overwinter loss was density-dependent and the main regulatory, or *k*, factor. This is important because it means that the arrival of Continental woodcock in Britain in winter probably increases mortality among the resident British birds. A simulation model based on the Derbyshire data was used to estimate the maximum sustainable shooting yield and the effectiveness of shooting bans in cold weather.

When feeding at night in winter, woodcock select grass fields in preference to arable fields and use areas dominated by grass. They probably select between the older fields on the basis of the relative availability of earthworms and other soil invertebrates, particularly leatherjackets, Tipulidae larvae. British woodcock are faithful to the natal or breeding site in winter and Continental woodcock exhibit lower wintering site fidelity. Woodcock experience higher mortality in cold winters, when freezing conditions prevent the birds feeding, and the recovery of the population following severe winters took three years. Most cold weather movements within Britain are probably only made by Continental migrants.

In the breeding season, woodcock selected areas of shrubby cover, typical of the edges of stands, within lowland mixed deciduous woodland. In an upland area of birchwood and heather moorland, feeding woodcock preferred dense young birch thickets although the birds nested in more open areas typically dominated by bracken *Pteridium aquilinum* and heather *Calluna vulgaris*. In both situations, the habitats used most intensively supported higher available densities of earthworms than habitats that were avoided.

Clearly, conversion of grassland to arable fields will reduce the area of suitable habitat for woodcock in winter. The loss of managed coppice in Britain in the last 50 years has probably contributed to the decline in the British breeding population, because coppice provides ideal habitat for breeding woodcock. The fact that woodcock do not breed in SW Britain may be due to increased overwinter mortality, because a high density of Continental woodcock occur there in winter.

For the late Monica Shorten, whose monograph
on the woodcock in 1974 provided the initial
impetus for further research on woodcock.

To David Caldow, whose great interest in
woodcock made the current study possible.

No part of this thesis has previously been submitted for a degree in this or any other university. The work described is my own except where duly acknowledged.

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Thanks to dad and Michael for encouragement.

1. GENERAL INTRODUCTION

1.1 Taxonomy

The European woodcock *Scolopax rusticola* belongs to the family Scolopacidae which consists of 22 genera and 86 species of wading birds, including curlews, sandpipers, godwits, stints, snipe and woodcock. There is a total of six species within the genus *Scolopax*, although *Scolopax rusticola* is the only species inhabiting the western Palearctic. The American woodcock *Scolopax minor* is found in the Nearctic whilst *S. saturata*, *S. celebensis* and *S. rochusennii* are limited to Indonesia and New Guinea and *S. mira* is confined to the Ryukyu Islands.

Although related to snipe, sandpipers and curlews, woodcock are rarely found in coastal habitats except on migration and are generally associated with woodland and farmland. Adults are of stout build, measure about 350mm from bill tip to tail tip and weigh about 300g. The highest weight is attained in November-December and drops to its lowest in early February (Rochford & Wilson 1982). Females are generally about 6g heavier than males throughout the year. The two arresting features of the woodcock's appearance are its long tapering bill (67-80mm) and its large dark eyes set back in the crown of the head. The woodcock is rarely seen on the ground due to its cryptic plumage and when disturbed in woodland it quickly disappears by means of a zig-zag flight. The woodcock is most frequently observed during the breeding season, when the male birds perform a conspicuous display flight involving a characteristic series of "croaking" and "sneeze" vocalizations.

1.2 Age and sex determination

First-year woodcock closely resemble adults and it is not possible to separate the two age classes in the field. In the hand, age is best determined on the basis of primary wear and the pattern of the primary coverts (Clausager 1973*a*). In first-year birds, the older primaries (p8-p10) are more worn and have generally lost the pale outer margin; the difference is more pronounced in spring than in autumn. The primary coverts of first-year birds generally have a chestnut distal fringe of 1.5-2.5mm wide whereas those of adult woodcock have a pale, narrow (1.0-1.5mm) distal fringe. Neither criterion alone is fully reliable but in combination 99% of birds can be aged successfully (Wilson, cited by Cramp & Simmons 1983).

The sexes are similar in plumage and morphology and despite several studies (Bettmann 1961, Clausager 1973*a*, Fadat 1968, 1972, 1973, McCabe & Brackbill 1973, Stronach *et al*. 1974, Rochford 1982), a reliable external character for sex determination still remains to be found in the European woodcock. At present, the sex of a proportion of birds can be determined on the basis of measurements. Using the ratio of tail: bill measurements, Clausager (1973*a*) was able to identify the sex of 42% of adult male woodcock and 46% of adult female woodcock with 99% certainty. He was able to identify 28% of first-year males and 20% of first-year females with the same degree of certainty. Rochford & Wilson (1982) applied discriminant analysis but all discriminant functions gave probabilities of misclassification of 23%-38%. This is in agreement with the findings of Stronach *et al.* (1974).

1.3 Distribution

World range

The distribution of the European woodcock varies seasonally and the best account of its world range is that of Vaurie (1965). The breeding range probably comprises the entire temperate and boreal Palearctic (Voous 1960) and apart from some scattered southern populations, the distribution limits lie between the July isotherms of 12°C in the north and 24°C in the south. In Norway, the northern distribution limit lies at 70°N, in Sweden and Finland at 66°N and further east it goes down to 64°N. In Siberia, the northern distribution is believed to end where that of the Siberian fir *Abies sibirica* finishes (Vaurie 1965). Island populations in the Azores, Madeira and the Canaries, as well as in Corsica, form the southern limit to the woodcock's distribution.

The southern limit to the woodcock's distribution on the mainland is less certain because here only high-altitude regions are inhabited. The limit runs through N Spain (Pyrenees), the mountainous parts of S France and N Italy and then south into the Tuscan Apennines. On the Balkan

Peninsula, the limit extends south into the Bulgarian Rhodope. In the lowlands to the east, the southern limit lies further north, following the southern edge of the taiga at about 50°N. The woodcock is distributed as far east as S Japan. Additional breeding populations occur south of the continuous distribution range in the central and W Caucasus (Kozlova 1962), in the northern mountains of Turkestan and along the N Himalayas, from N Pakistan to Bhutan (Vaurie 1965), where the species may be found at heights up to 4,000m.

The European population

About a third of the global woodcock population breeds in Europe and by far the largest numbers of breeding birds are found in the former USSR and Fennoscandia with over 90% of the European population occurring in these regions (Piersma 1986). These populations are migratory, wintering throughout western and southern Europe, but particularly in France, Spain, the United Kingdom and Italy. The breeding populations of NW Europe are largely sedentary (Cramp & Simmons 1983).

Birdlife International data (in prep.) suggest the woodcock has declined in over 80% of its European wintering range between 1970 and 1990. Unfortunately no trend data are available for Spain and the trend for the European population is based largely on a substantial decline in the French wintering population (Yeatman-Berthelot 1991). Paradoxically, the breeding population within Europe appears to have remained stable during the last 20 years, but this may be because the trends within most countries are only poorly understood. Fluctuations in the number of breeding woodcock in eastern Europe are the main cause for concern as such a large proportion of the breeding population is located in this region. The decline in the numbers of woodcock wintering in France suggests that there has been a reduction in breeding success or an increase in the rate of adult mortality amongst woodcock breeding in eastern Europe. Small increases in numbers of breeding birds have occurred in Belgium, the Netherlands (Teixeira 1979, Cramp & Simmons 1983), Denmark (Jespersen 1946, Clausager 1972) and Ireland (Hutchinson 1989) in the last century.

Changes in the distribution and population size of woodcock in Britain and Ireland

Up to 1826, the woodcock was known to nest in 20 English counties (including Devon, Cornwall and Somerset) but there were no records from Scotland or Wales and only one from Ireland (Shorten 1974). The species spread rapidly during the 19th century colonizing many parts of Scotland, Wales and Ireland; a change that has been ascribed mainly to the cessation of shooting in the breeding season and the protection of coverts for pheasants *Phasianus colchicus* (Alexander & Lack 1944, Alexander 1945-47). By the time of the Woodcock Inquiry in 1934-35, woodcock had been found breeding in every county of England and Wales except Anglesey and in all counties of Ireland and the Scottish mainland (Alexander 1945-47). Confirmation that woodcock were breeding on Anglesey was first obtained in 1969. The woodcock's breeding distribution appears to have changed little since 1940, with absences from Devon, Cornwall and S and W Wales (Witherby *et al.* 1940, Sharrock 1976, Lewis & Roberts 1993). The reason for the absence of breeding woodcock in these areas is still unclear. There was probably some expansion of range in S Scotland, Wales and E Anglia during the 1950s and 1960s due to the planting of new conifer forests (Parslow 1967, Avery & Leslie 1990), but the extent to which these were used by woodcock was never investigated. It seems likely that these forests are less suitable for woodcock now because they have reached the age where the canopy is closing (Lewis and Roberts 1993). Estimates of the size of the breeding population in Britain and Ireland can only be tentative because males are successively polygynous (Hirons 1979, 1980, 1981) and nests are very difficult to find. Sharrock (1976) suggested that the breeding woodcock population was in the order of 18,000-46,000 "pairs" (about 64,000 individuals) whilst Lewis & Roberts (1993) believe that the the current population is probably nearer 10,250-26,000 "pairs" (about 36,000 individuals).

Woodcock winter in all counties of the British Isles but generally avoid high ground in Scotland and N England (Lack 1986). They are thought to be more numerous on the east coast and in southern and western England and Wales (Tapper & Hirons 1983). The influx of Continental migrants in autumn is such that the British wintering woodcock population may number 800,000 birds (Hirons & Linsley 1989). This means that if there are equal numbers of young and adult British woodcock in winter, Continental woodcock comprise 84-91% of the wintering woodcock population in Britain. These migrants originate mainly from Fennoscandia and the former USSR (Cramp & Simmons 1983), but the number arriving from each country is unknown, as is the relative distribution of these birds with respect to the resident woodcock in Britain.

1.4 Habitat

The preferred breeding habitat is deciduous or mixed woodland (Clausager 1972) but conifer plantations are used up to the thicket stage (Shorten 1974, Marchant *et al.* 1990), as are large patches of bracken *Pteridium aquifolium* in upland areas. Clausager (1972) concluded that even in deciduous forests, the younger stands (aged 0-20 years as opposed to 21-100 years) were more densely populated. In Britain there is a higher incidence of breeding in large woods (>80ha), and woods of less than 10ha are rarely used (Fuller 1982). Clausager (1972) reported that in Denmark the minimum size of woods frequented by woodcock was 20-30ha. Kalchreuter (1983) suggested that in many cases increased disturbance by man in small woods was probably the limiting factor rather than woodland size itself. In Scotland, woodcock breed in sparse, scattered birchwoods and breeding woodcock have also been found on treeless islands off the Irish coast (Shorten 1974). An understorey of brambles *Rubus* spp., hazel *Corylus avellana*, holly *Ilex aquifolium* or bracken provides cover from avian predators (Hirons & Johnson 1987) and earthworm-rich soils are chosen by woodcock for feeding areas during the breeding season (Granval & Muys 1992). Wide rides and small clearings (2-4ha) are important to provide easy access and flight paths in large woods (Shorten 1974). Breeding success is thought to be low in years when there are very dry summers (Hirons 1988*a*) because earthworms are less available to the growing and recently fledged chicks.

The habitat requirements are less specific in winter and patches of gorse *Ulex europaeus*, willow *Salix* spp. scrub and *Rhodedendron* often hold woodcock during the day. This is probably because in winter woodcock become nocturnal and frequent nearby fields. Consequently, areas with permanent pasture or long-rotation grass leys within about 1km of woods are preferred as these types of fields support high densities of soil invertebrates (Hirons & Bickford-Smith 1983, Granval 1988). The woodcock experiences higher mortality in cold winters due to feeding sites becoming frozen (Baillie *et al.* 1986, Marchant *et al.* 1990).

1.5 Behaviour

Woodcock are most conspicuous during the spring and early summer due to the distinctive roding flights performed by male birds at dawn and dusk. Until the mid-1970s, the woodcock was believed to be monogamous and roding flights were thought to delimit the boundaries of exclusive territories (Tester & Watson 1973). During the last 15 years, thanks to radiotracking, great advances have been made in our understanding of the breeding behaviour of the woodcock. The species has been shown to exhibit successive polygyny, with dominant males fertilizing up to four females in a season (Hirons 1979, 1980, 1981). The pair bond lasts only three or four days, during which time the male follows the female closely. He then resumes roding and is believed not to revisit the female (Hirons 1980, 1981).

The age of first breeding in females has been reported as 12 months (Ostermeyer & Ferrand 1979, Hirons 1980), but it is not clear whether all females or only a proportion breed at this age. The gonads of first-year males are well developed by February-March (Stronach 1983) but the proportion of first-year males roding in a particular area seems to depend on the number of older males present. In Britain only a small proportion of first-year males are thought to rode (Hirons 1980), whereas in countries such as Sweden, where older males are removed by spring shooting, up to 50% of roding males may be first-years (Marcström 1988).

The breeding season in Britain is generally considered to extend from early March to mid-July. One of the earliest recorded instances of roding in Britain or Ireland was on 15 February (Raynsford 1959). The earliest woodcock clutch in Britain was found on 2 March (Vesey-Fitzgerald, cited by Shorten 1974) and the latest on 9 September (Savage, cited by Glutz von Blotzheim *et al.* 1977). In Denmark, 43% of clutches were found prior to 7 April in years when the mean March temperature was 0.5°C or more above average and only 13% were found before 7 April when the mean March temperature was 0.5°C or more below average (Clausager 1973*b*).

The nest is little more than a flat hollow measuring 13-15cm in diameter, usually lined with dead leaves or dry grass, and the mean clutch size is 3.8 (Alexander 1946) to 3.9 (Morgan & Shorten 1974). The female alone is responsible for incubation and the caring of the young (Shorten 1974, Hirons 1980). It has been suggested that the woodcock is double-brooded (Alexander 1945-47, Clausager 1972) but there are only two proven instances of this, where woodcock incubating eggs were seen surrounded by a brood of chicks (von Zedlitz 1927, cited by Glutz von Blotzheim *et al*. 1977, Jensen, cited by Pay 1937).

During the breeding season, woodcock feed in woodland by day and remain in cover to roost at night. In autumn, however, their behaviour changes and throughout the winter and early spring they are nocturnal and leave the woodland to feed on nearby fields. They return to cover approximately half an hour before dawn (Hirons & Bickford-Smith 1983) and roost during the day. It is thought that this change occurs because invertebrate food becomes relatively more available in fields in the winter (Hirons & Owen 1982). However, it may also be because woodcock foraging in woodland by day would be vulnerable to avian predators, which are known to be important in the breeding season when there is more cover than in winter (Hirons & Johnson 1987).

1.6 The impact of man on woodcock populations

The woodcock has been hunted throughout Europe by man for centuries and is still a highly valued quarry species amongst sportsmen. Under current legislation in Britain, woodcock may be shot between 1 October and 31 January in England and Wales and between 1 September and 31 January in

Scotland and Ireland. There is little information about the size of the annual bag because there is no legal requirement for hunters to submit details of the number of birds they kill. Game Conservancy Trust estimates, based on a survey of about 500 shoots, suggest that approximately 200,000 woodcock are killed in the UK per annum (Tapper & Hirons 1983). In order to determine the impact of shooting on both the resident British woodcock population and the population of overwintering Continental migrants it is necessary to know whether mortality due to hunting is additive or compensatory.

The extent of any compensatory response is determined by the degree of density dependence in mortality rates. In natural populations the relationship between hunting mortality and annual rates of survival is usually such that the mortality is neither totally additive nor totally compensatory. This has been demonstrated most clearly in wildfowl such as the mallard *Anas platyrhynchos* (Anderson & Burnham 1976). There are several mechanisms by which compensation for shooting mortality may operate. It may remove competition within the population for certain limiting resources such as food supplies, as in the mallard (Hepp *et al.* 1986), winter territories, for example in male red grouse *Lagopus lagopus scoticus* (Watson 1985, Watson & Jenkins 1968), or potential breeding sites. Alternatively, it may decrease the effect of density-dependent causes of mortality such as predation, as in the grey partridge *Perdix perdix* (Potts 1986), or disease. However, there is clearly a limit to the level of hunting that can be compensated for and even when partial compensation takes place shooting usually reduces the size of the breeding population (Potts 1986). In a population subjected to shooting, the rate of reproduction increases and the rate of natural mortality is reduced because the population density is reduced. The population stabilizes at a lower density than prior to shooting and has a higher growth rate. The strength of density dependence in breeding success and natural adult mortality determines the extent to which the population is reduced by given levels of harvesting (Robertson & Rosenberg 1988).

It is clear that in order to determine the likely impact of hunting on a given species, detailed knowledge of its biology is required. The woodcock does not readily yield information suitable for population studies and this is particularly the case with breeding females. This explains why, with the exception of Potts & Hirons (1983) who relied on bag data and age ratios amongst shot birds, there has been no attempt yet to investigate the influence of shooting on woodcock populations. The situation with regard to the hunting of woodcock in Britain is further complicated by the fact that the wintering population is comprised of both resident and migratory birds. It is conceivable that the current rate of harvesting can be compensated for by the resident British woodcock, but that it is damaging to the migrant population because these birds are likely to be harvested in several different countries whilst migrating to and from their British wintering grounds. In order to understand the impact of hunting on woodcock in Britain, information is clearly required on regional differences in the relative abundance of British and Continental woodcock in winter as well as regional differences in the hunting pressure.

Forestry practice in Britain clearly affects the woodcock population by altering the amount and type of habitat available to the species. Habitat loss has been invoked as the reason for the decline of the Atlantic population of the American woodcock (Dobell 1977), which has fallen by 2% per annum since the late 1960s. The factors responsible for habitat loss are thought to have been the closing of forest canopies, conversion of mixed stands to pure conifer stands, clear-felling for agriculture and drainage due to the regulation of rivers and for the enhancement of crop yields (Sanderson 1977, cited by Kalchreuter 1983). In S England there has been a net loss of woodland and covert since the 1930s due to the felling and fragmentation of old woodlands and the dissolution of former sporting estates (Marchant *et al.* 1990). There has been an 82% decline in managed coppice in Britain since 1950 (Warren & Key 1991) and some 30-50% of ancient semi-natural woodland has been lost. These losses may have been offset by the rapid increase in conifer afforestation during the 1950s and 1960s mentioned earlier (section 1.3)

Because woodcock feed primarily on farmland in the winter, they may be at risk from the effects of pesticides. Earthworms comprise an important component of the diet at this time of year (Hirons & Bickford-Smith 1983) and they are known to readily adsorb pesticide residues (Edwards &

Lofty 1977). Woodcock may therefore be contaminated by accumulation of these residues. Such an effect was demonstrated in the American woodcock during the early 1960s, which accumulated lethal doses of heptachlor epoxide that was applied in the Gulf States to control the imported fire ant *Solenopsis saevissima* (Stickel *et al.* 1965*a*,*b*). Chemicals on farmland may reduce the numbers of some soil invertebrates and thus deplete the woodcock's food supply. It has been shown recently that some molluscicides and fungicides are directly poisonous to earthworms and some other classes of soil invertebrates (Wiltshire & Glen 1989). The cattle anthelmintic *Ivermectin* has also caused some concern because it inhibits the larval development of certain Diptera and dung-beetles (*Aphodius* spp.) (Madsen *et al.* 1990).

1.7 The current status of the woodcock in Britain

The state of the British breeding woodcock population is very difficult to assess because there is no simple way to census the species. Woodcock nests are notoriously difficult to find and although counts can be made of roding males, these are of questionable value as the species is polygynous and, in any case, only a proportion of the males (mainly adult birds) rode (Hirons 1980). The British Trust for Ornithology's (BTO) Common Bird Census (CBC) index suggests a progressive decline in the British woodcock population which has become steeper since 1980 (Marchant *et al.* 1990). However, the CBC is not particularly suited to crepuscular species like the woodcock which do not hold breeding territories and it is not clear how reliably the CBC monitors the woodcock population. In addition, the CBC data are biased towards S England and it is now clear that woodcock are more numerous and have fewer gaps in their breeding distribution in N England and Scotland (Lewis & Roberts 1993). Nevertheless, the difference in the records of breeding woodcock between the BTO breeding bird surveys of 1968-72 (Sharrock 1976) and 1988-91 (Lewis & Roberts 1993) clearly indicates that there has been a decline in the size of the British breeding woodcock population.

Hunting statistics provide an indication of changes in the numbers of wintering woodcock from year to year, but yield no information on the British breeding population because of the large influx of Continental migrants. Game Conservancy Trust figures suggest an increase in the national woodcock bag since about 1974, but this may be due to an increase in pheasant shooting (Rands & Tapper 1986). The woodcock bag is also likely to be affected by the severity of the winter weather. Hirons & Linsley (1989) have suggested a new census method for woodcock in winter which involves counting feeding birds with a spot-lamp at night. However, there is as yet little information on the reliability of the technique and it is likely to be too labour intensive for a wide-scale survey.

In summary, it seems that there has been a decline in the population of British breeding woodcock population since 1980, with the largest losses in S England. The wintering population has remained at least constant and may have increased slightly, indicating that the same numbers of Continental migrants are continuing to visit Britain.

1.8 The present study

With the exception of surveys and literature reviews, the only research on the ecology of woodcock in Britain prior to this study was conducted by Dr. Graham Hirons, who was employed by the Game Conservancy Trust during 1977-86. The present study forms a continuation of Hirons' work and aims to answer some of the questions raised by it. Throughout this study unpublished data supplied by Dr. Hirons have been used to complement the current findings.

Research on the woodcock to date has focused largely upon the nature of the mating system (Hirons 1980, 1981, 1983), upon habitat use during the breeding season (Hirons & Johnson 1987) and on the use of fields in winter (Ferrand & Gossman 1988, Granval 1988). The main objective of this study was to determine the reason for the probable decline in the British breeding population. Breeding success and, in particular, chick survival is only poorly documented and this study involved the collection of breeding data so that the current rate of production could be compared with the annual adult survival rate estimated from ringing recoveries. Tests for density dependence in the production of young and in overwinter loss have been performed and the ability of woodcock populations to compensate for additional sources of mortality, such as shooting, has been examined. Information has been obtained on the relative distribution

of British and Continental woodcock in winter and regional differences in the harvest rate (the proportion of the birds present that were killed) due to shooting have been determined. The effects of increased pheasant shooting and cold winters on the size of the annual UK woodcock bag have been investigated. Habitat use and foraging behaviour by woodcock in winter and during the breeding season are described and the implications for the management of woodland and farmland are discussed.

2. SURVIVAL RATES AND MOVEMENTS OF BRITISH AND CONTINENTAL WOODCOCK IN THE BRITISH ISLES

2.1 INTRODUCTION

The woodcock is an important quarry species in Britain in winter and there is concern as to whether the current rate of mortality is causing this population to decline. The British population is estimated to number *c*.36,000 breeding birds (10,250-26,000 breeding "pairs", Lewis & Roberts 1993) which are supplemented by migrant birds in winter. Hirons & Linsley (1989) considered the total British wintering population to be *c*.800,000 birds, suggesting that migrants may outnumber resident birds by about 10:1. However, there is no information concerning the relative distribution of migrant and resident birds within Britain nor the degree of interchange between the different breeding populations. Some knowledge of the degree of philopatry of British woodcock is of importance in assessing the value of habitat management in areas where there are local declines.

The woodcock is relatively difficult to study in the field and there are certain aspects of its ecology that are unlikely to be determined by intensive local studies because of the difficulty in obtaining information from a large number of individuals. This chapter presents estimates of survival rates of British woodcock and Continental woodcock which winter in the British Isles. It describes the fidelity of British woodcock to the natal or breeding site as well as the origin, arrival and departure times of foreign birds, using the national ringing data held by the British Trust for Ornithology (BTO).

2.2 METHODS

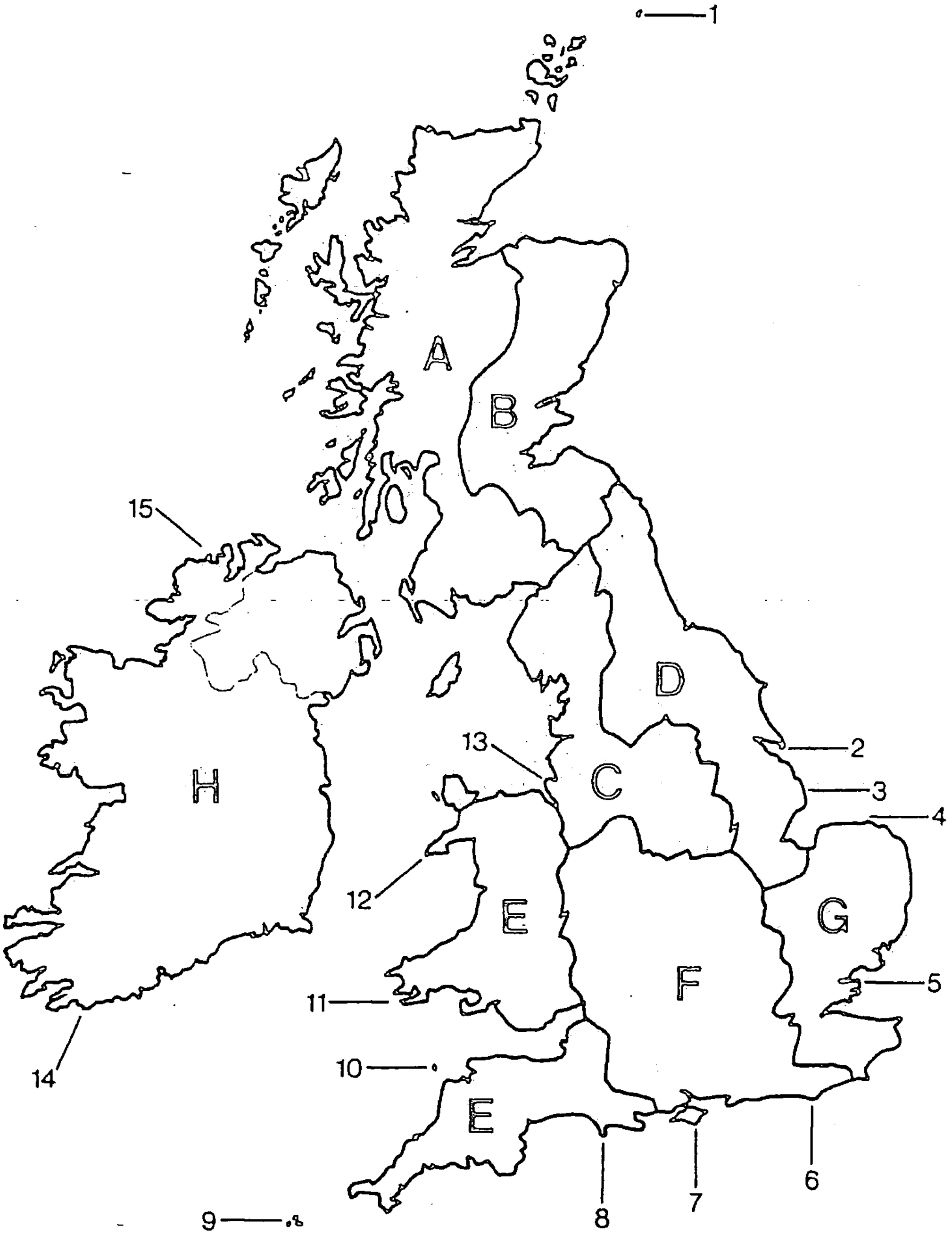
All ringing recoveries of woodcock found long dead (finding condition: not freshly dead, EURING code 3) were excluded from the analysis, together with a few recoveries containing other obvious inaccuracies. Details from 666 British-ringed woodcock and 226 foreign-ringed woodcock recovered in Britain and Ireland during the period 1909-1990 were used. Goodness-of-fit tests were performed on each recovery table to check whether there were any age-related survival effects (Appendix 2.1). No such effects were found among birds that survived beyond 1 April in the year after hatching and survival rates were calculated using Haldane's method for incomplete recovery data (Haldane 1955). This method was used instead of the more recent methods developed by Brownie *et al.* (1985) because the numbers of woodcock ringed each year were not available, meaning that a recapture rate could not be calculated for the Brownie *et al.* (1985) method. Adult survival rate was calculated from 1 April in the spring following ringing for woodcock ringed as full-grown birds (EURING age codes 2, 3, 4, 5, 6) and as chicks (EURING age code 1), and each year of life was taken as 1 April until 31 March (Appendix 2.1). This means that the estimates given for the survival of birds in their first year relate to the period from fledging until 1 April in the following year.

Since 89% of the recoveries were of shot birds, the extent to which these data represented mortality in the overall population was questionable. There was no significant difference in the proportion of birds shot between British-ringed adults, British chicks and foreign-ringed adults and chicks for recoveries made after 1 April in the year following ringing (Table 2.1), and the three data sets were combined to calculate survival rates for shot birds and for those found dead (excluding EURING finding circumstance codes 0 (unknown) and 99 (no information)). As there was a change from the use of aluminium rings to more durable monel and incoloy rings in Britain in 1960, the survival rates for woodcock marked with each type of ring were compared as were the proportions of recoveries made at least four years after ringing.

Table 2.1 Proportion of the woodcock recovered dead after 1 April in the year following ringing that were reported as "shot".

	Total recovered	Number shot	% shot	
British chicks	198	176	89	
British-ringed adults	138	123	89	
Foreign-ringed adults+chicks	104	94	90	
Total	440	393	89	$\chi^2=0.17$ (df=2) N.S.

Figure 2.1 Division of the British Isles into eight regions (*A–H*) and locations of bird observatories referred to in the text.
(1. Fair Isle, Shetland; 2. Spurn, E Yorkshire; 3. Gibraltar Point, Lincolnshire; 4. Cley and Blakeney, Norfolk; 5. Bradwell, Essex; 6. Dungeness, Kent; 7. St. Catharine's Point, Isle of Wight; 8. Portland Bill, Dorset; 9. St. Agnes, Isles of Scilly; 10. Lundy, N Devon; 11. Skokholm, Pembrokeshire; 12. Bardsey, Caernarvonshire; 13. Hilbre Island, Cheshire; 14. Cape Clear, Co. Cork; 15. Tory Island, Co. Donegal).



Calculations of parameters other than survival rates were based on all recoveries. For the purpose of seasonal analysis, the period from March to July was treated as the breeding season or spring, the months of August and September as autumn and the period from October to February as the non-breeding season or winter. For regional analyses, the British Isles were divided into eight compartments labelled *A-H* (Figure 2.1). To investigate the influence of cold weather on woodcock movements in winter, published data from 12 weather stations in central England giving average mean daily air temperatures for each winter month and for the period December-February (Manley 1974, Parker *et al.* 1991) were used. Information regarding the timing and locations of the first arrivals of migrant woodcock in the British Isles was obtained from bird observatory reports (Williamson 1958-1962). To determine whether the annual production of young was sufficient to maintain the British breeding population given the survival rates estimated from ring recoveries, estimates of nest success were determined using BTO nest record cards and estimates of chick survival to fledging were drawn from field data for the period 1988-1991 at a site in Derbyshire (Chapter 6).

2.3 RESULTS

2.3.1 Adult survival rate

The annual adult survival rate for birds shot (n=393) was 0.568±0.017 (±se) and was not significantly different from that for birds found dead (n=47, 0.608±0.059 (±se);

d=0.52, N.S.). There was therefore no evidence of an appreciable bias in the survival estimate arising from the shot sample. Of the woodcock found dead for which specific causes of death were given (n=35), most were killed by flying into wires or cables (n=13), as a result of accidental trapping (n=7) or by colliding with vehicles (n=5). Analysis of the data from birds recovered during October-February as first-years and as adults suggested that the proportion of all dead recoveries which were shot did not differ between age classes (British-ringed woodcock χ^2=0.02, df=1, N.S.; foreign-ringed woodcock χ^2=0.91, df=1, N.S.). Thus there was no evidence that first-year birds were more susceptible to shooting than adults.

Adult survival rates for woodcock ringed as adults (n=141) and as chicks (n=201) in Britain and Ireland and for those ringed abroad and recovered in Britain and Ireland (n=113) are given in Table 2.2. An assumption of estimating first-year survival was that the reporting rate was the same for adult and young birds. Evidence supporting this was the similar proportions of adults and first-years shot. The proportion of first-year woodcock among ringed birds shot at Lanarth, a sporting estate in Cornwall (Chapter 3), was not appreciably different from the proportion of first-years within the total sample ringed: in 1990/91 73% of the woodcock ringed (n=22) were first-year birds and 75% of the ringed birds shot (n=8) were first-years; in 1991/92 the proportions of first-years were 76% among ringed birds (n=72) and 82% among ringed birds that were shot (n=17). The annual adult survival rates estimated for British-ringed woodcock that were ringed as adults (53.3%) and as chicks (60.4%) did not differ significantly (d=1.31, N.S.). The survival of foreign-ringed birds visiting the British Isles (53.9%) was not significantly lower than that of birds ringed in the British Isles (57.9%; d=0.74, N.S.). The expectation of life once a young bird reached 1 April in its second calendar year was two years and therefore each adult can be expected, on average, to breed in two or three seasons.

Table 2.2 First-year survival and adult survival rates of British-ringed and foreign-ringed woodcock, 1909-1990.

	First-year survival (±se)	Annual adult survival rate (±se)	Expectation of further life of adults (years)
British-ringed chicks	0.472 ±0.024 (n=426)	0.604 ±0.022 (n=201)	2.03
British-ringed adults (n=141)		0.533 ±0.032	1.64
All British-ringed woodcock (n=342)		0.579 ±0.018	1.88
Foreign-ringed woodcock recovered in Britain and Ireland (n=113)		0.539 ±0.035	1.67

Estimation of the annual adult survival rate for British-ringed woodcock (adults and chicks) for three time periods suggested that adult survival was slightly lower during 1970-1990 (0.546±0.037 ±se, n=126) than during 1909-

1939 (0.606±0.023 ±se, n=185) and 1940-1969 (0.561±0.064 ±se, n=31), although there were no significant differences between any of the time periods; 1909-1939 vs. 1970-1990, d=1.05, N.S. and 1940-1969 vs. 1970-1990, d=0.15, N.S.

The annual adult survival rate for woodcock (adults and chicks) ringed prior to 1960 (n=200) was 0.607±0.022 (±se) and that for birds ringed from 1960 onwards (n=142) 0.538±0.035 (±se); the difference is not significant (d=1.27, N.S.). A higher proportion of the recoveries of woodcock ringed before 1960 were made four or more years after ringing; 19.5% compared with 12.0% of the recoveries of woodcock ringed from 1960 onwards. It seems unlikely that the aluminium rings did not survive the lifespan of woodcock, although it is possible that because the metal used for the rings after 1960 was more durable the difference in ring loss rates over time might conceal a real decline in survival.

There was no significant difference in the annual adult survival rates of woodcock ringed as chicks in Scotland (regions *A*,*B*) and in England and Wales (regions *C*-*G*); 0.596±0.028 (±se), n=131 and 0.652±0.047 (±se), n=61 respectively, d=0.74, N.S.

2.3.2 Philopatry

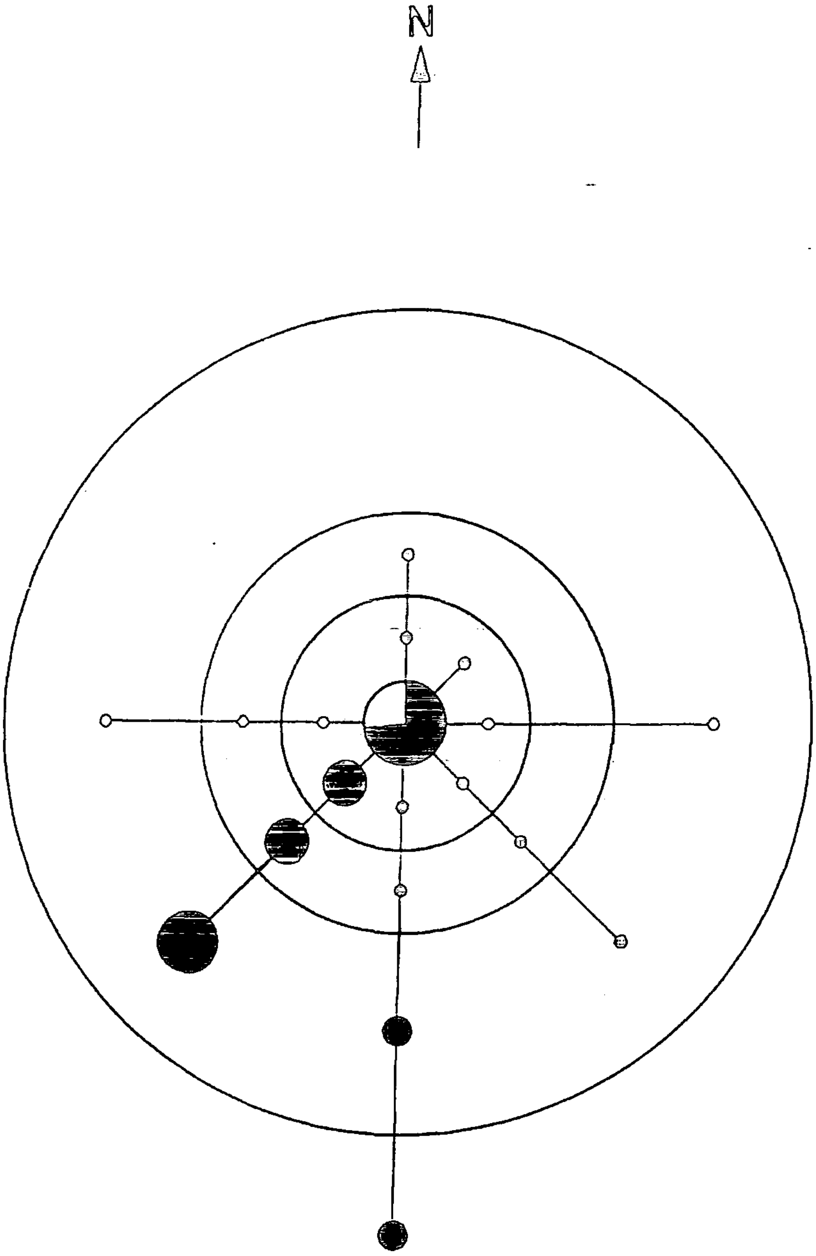
Forty-five British chicks were recovered during March-September in years following the year of ringing. Thirty-four (76%) were recovered within 10km of the ringing location, although five birds (11% of the breeding season recoveries) were recovered abroad (at distances greater than

500km). Of these three were found in Sweden (12 April 1948, 15 May 1940 and 25 May 1938), one in Norway (13 May 1932) and one in Russia (1 May 1940, near Moscow). The probability of a ringed woodcock being recovered abroad is obviously affected by the shooting seasons in each country, as some (the former USSR, the Baltic States, Romania, Hungary, Poland, former Czechoslovakia, Yugoslavia, Austria, Denmark and Sweden) still permit the shooting of roding birds during spring. None of the five recoveries were reported as shot but no specific causes of death were supplied. Two of the woodcock were first-years but the others were recovered in their third, fourth and seventh years. Of the 60 foreign birds ringed as chicks and recovered in the British Isles, none were found in the breeding season.

2.3.3 Fidelity to the natal or breeding site in winter

Data from 353 British-ringed chicks recovered in winter and 35 adults ringed in Britain and Ireland during May-September (presumed British) and recovered in winter were examined with respect to the distance and direction travelled. Adult recoveries were restricted to birds ringed in May-September because Continental woodcock are present in Britain until mid-April (see Table 2.6). In all, 51% were recovered within 10km of the place of ringing and 68% within 30km but 13% were recovered at distances of more than 500km. Of the birds that moved more than 100km from the place of ringing, 78% travelled south or south-west (Figure 2.2). Examination of the data for birds recovered when first-years

Figure 2.2 Distance and direction moved from the natal or breeding site by British woodcock in winter.
The concentric circles correspond to distance: 100km, 300km, 500km and 1,000km. The shaded area of the inner circle represents the proportion of birds moving <100km. The size of the black circles corresponds to the number of recoveries in each direction: 1-5, 6-10, 11-20 and >20.



and when adults revealed no significant differences in the direction taken or the distances moved (Table 2.3).

Table 2.3 Direction and distance moved from the natal or breeding site by British-ringed woodcock in winter (October-February).
Birds which moved less than 6km were excluded as the direction of movement was deemed unimportant for such local recoveries.

Age	Direction				
	N	E	S	W	Sample size
First-year	26	17	38	34	115
Adult	21	17	48	36	122
Total	47	34	86	70	237

$\chi^2=1.55$ (df=3) N.S.

Age	Distance (km)						
	<11	11-50	51-100	101-300	301-500	>500	*n*
First-year	99	38	10	6	12	28	193
Adult	98	35	5	20	14	23	195
Total	197	73	15	26	26	51	388
% distance	(51%)	(19%)	(4%)	(7%)	(7%)	(13%)	

Mann-Whitney U=18.0 (n=6,6) N.S.

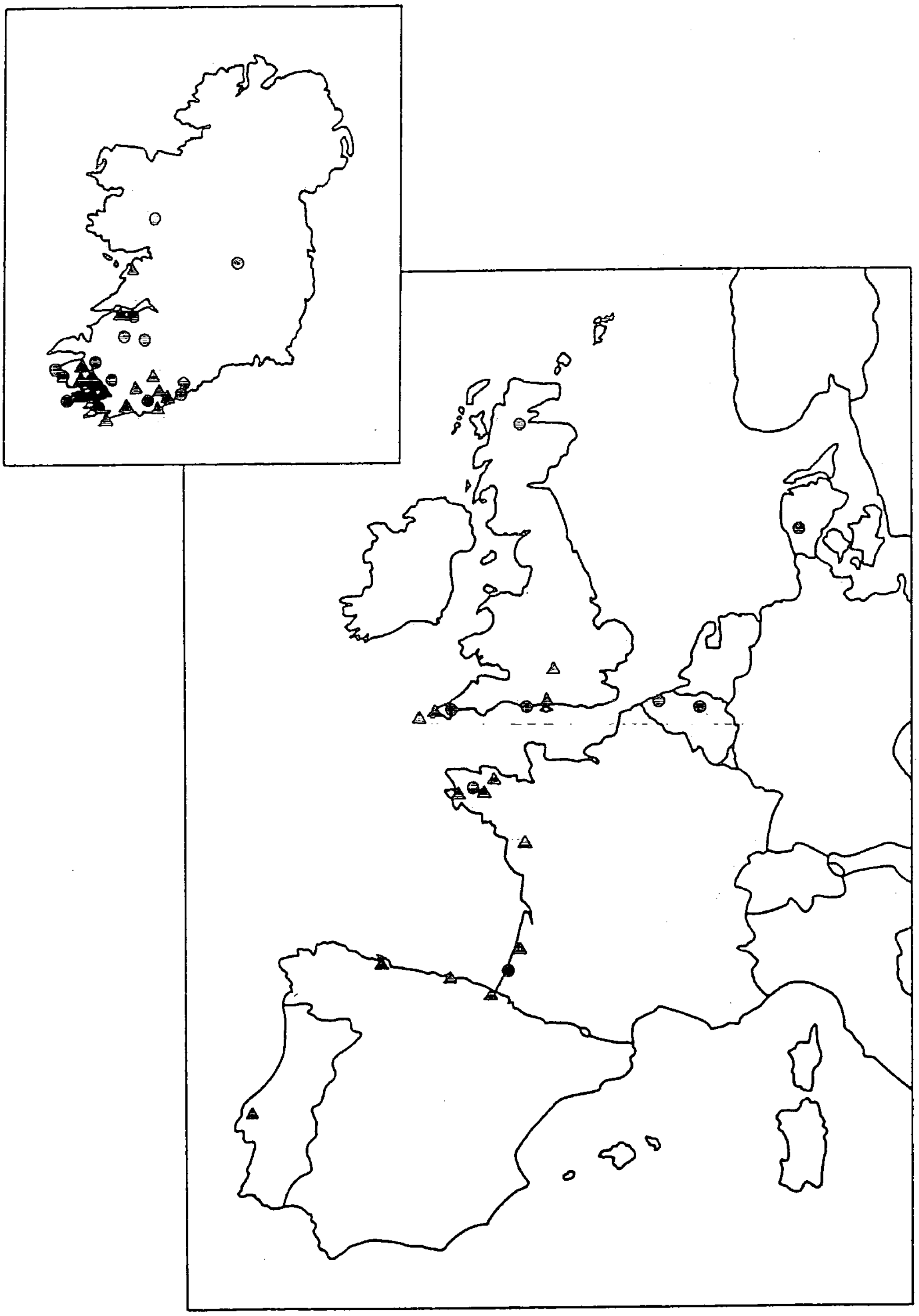
There was no evidence that woodcock recovered during December-February moved further when the mean December-February temperature in central England was low (<3°C); on the contrary fewer birds were recovered at distances greater than 500km during cold winters (Table 2.4). The mean temperature during the month of recovery did not affect the distribution of recovery distances either (Table 2.4). There was no correlation between the median recovery distance and the mean December-February air temperature in central England each winter ($r=-0.05$, $df=54$, N.S.).

Table 2.4 Distribution of recovery distances of British woodcock in relation to cold winters and cold spells within all winters.

	Distance (km)				
	<11	11-100	101-500	>500	*n*
Comparison between winters (mean Dec.-Feb. temperature in central England) for birds recovered during Dec.-Feb.					
Cold (<3°C)	19	10	13	2	44
Mild (≥3°C)	99	42	29	33	203
Total	118	52	42	35	247
			$\chi^2=8.76$ (df=3) $p<0.05$		
Comparison between recovery months within winters (mean Nov., Dec., Jan. or Feb. temperature) for birds recovered during Nov.-Feb.					
Cold (<3°C)	26	11	10	12	59
Mild (≥3°C)	149	66	38	38	291
Total	175	77	48	50	350
			$\chi^2=3.22$ (df=3) N.S.		

Fifty-one British woodcock (13% of winter recoveries) were recovered in Ireland, 30 of which moved more than 500km from their natal or breeding sites. All were ringed in Scotland or northern England. Fourteen birds (4%) were recovered in mainland Europe; seven in France, two in Belgium, three in Spain, one in Portugal and one in Denmark (Figure 2.3). The mean monthly temperature in central England during the months that these birds were recovered

Figure 2.3 Winter recoveries of British woodcock moving more than 500km from the natal or breeding site.
Triangles represent birds recovered in their first year following fledging, circles represent birds recovered as adults.

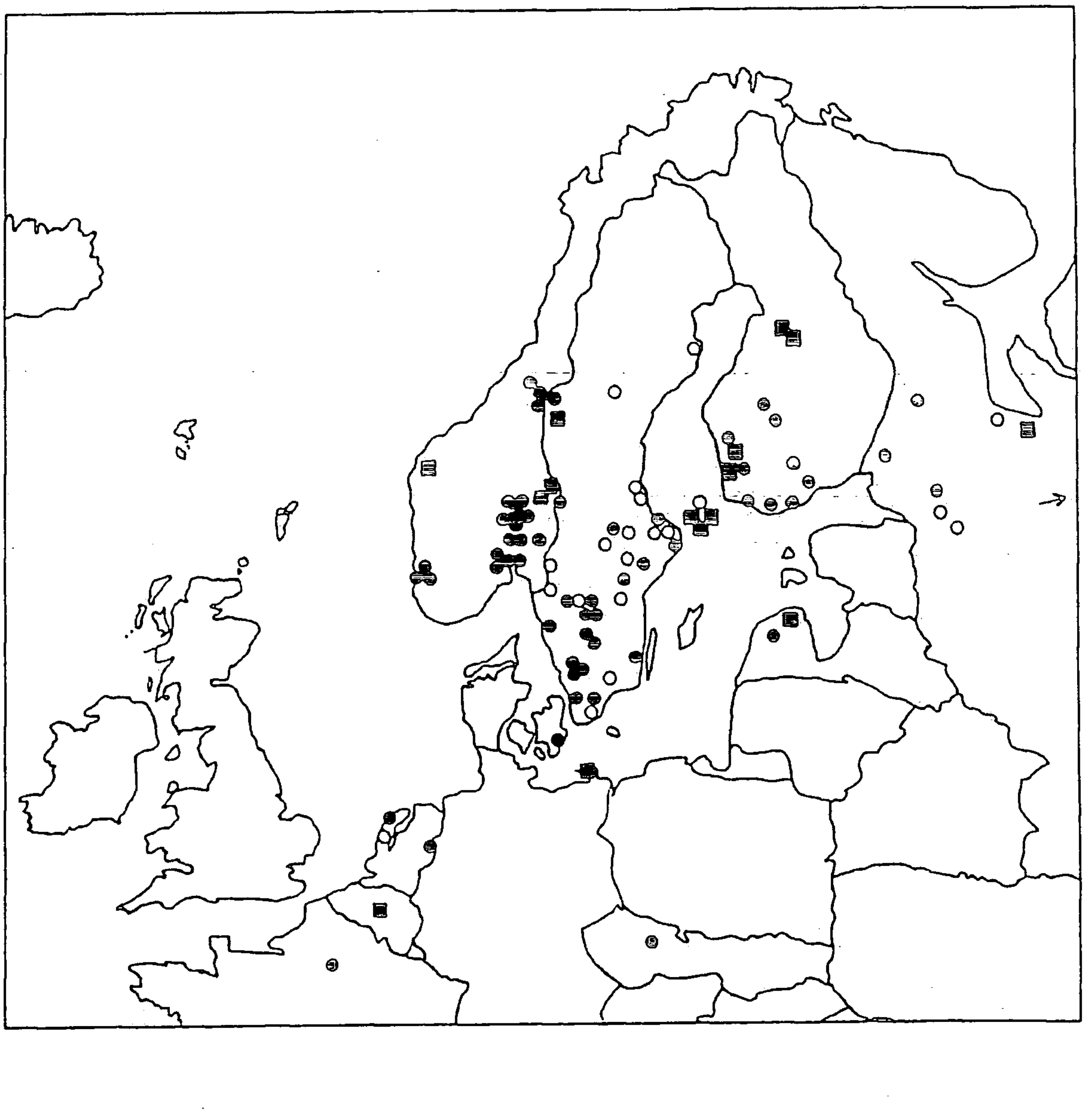


ranged from 0.4°C to 9.4°C and only 11 of the 65 recoveries were made during months with mean temperatures below 3°C. In total, 63% of the winter recoveries of British woodcock in Ireland and 86% of those on the Continent were made before 1 January, suggesting that in most cases the movements occurred before prolonged frosts or snow were encountered. Thus there is little evidence of "hard weather" movements out of the British Isles. Assuming that the recovery rates of ringed woodcock were similar in Britain and mainland Europe, the data suggest that only a small proportion (about 4%) of British woodcock are migratory, leaving Britain and Ireland as birds from mainland Europe are arriving.

2.3.4 Origins of foreign migrants wintering in the British Isles

The origins of wintering woodcock were determined from recoveries of birds ringed abroad as adults during May-September or as chicks and from birds ringed in Britain and Ireland in winter (October-February) and recovered abroad during May-September (Figure 2.4). The majority of recoveries were of birds ringed in Norway, Sweden and Finland. In order to determine the relative contribution of overwintering migrants from each country it was necessary to relate the number of birds ringed to the size of the breeding population in each state. This was done by comparing the ringing totals for woodcock, published in Kalchreuter (1983), with the number of birds recovered in the British Isles that were ringed during the same period

Figure 2.4 The origin of woodcock wintering in the British Isles as determined from ring recoveries.
Filled squares represent adult woodcock ringed abroad during May-September and recovered in the British Isles in October-February. Filled circles represent woodcock ringed as chicks abroad and recovered in the British Isles in October-February. Open circles represent adult woodcock ringed in the British Isles in October-February and recovered abroad in May-September. The arrow corresponds to a bird recovered near Perm, Russia (58°N 56°E). The distribution of the recoveries of woodcock that were ringed in the British Isles in winter can be explained by the fact that shooting is permitted during July and August in Sweden and from April until mid-May in the former Soviet Union.



(Table 2.5). The final ringing year varied between 1970 and 1973 for different countries with the exception of the former Soviet Union for which ringing totals were only available up to 1954. The proportion of birds recovered in Britain and Ireland was then multiplied by the estimated breeding population in each country (Piersma 1986) and expressed as a percentage of the total value for all the countries, thereby providing an index of the proportions of the populations wintering in the British Isles.

Table 2.5 The relative proportions of woodcock from each country of origin wintering in Britain. (Data from Kalchreuter (1983) and Piersma (1986)).
Where breeding populations have been quoted as "pairs" in Piersma (1986), the figures have been doubled to give the approximate number of individuals and where ranges were quoted, the midpoint has been taken. No estimate is available for the size of the breeding population in the former Soviet Union and a value of 1,000,000 birds has been used as an approximation.

Country	Number of birds ringed	Number of recoveries in Britain	% recovered in Britain	Estimated breeding population	Index
Norway	331	14	4.2	69,000	9.6
Sweden	1,079	27	2.5	150,000	12.4
Finland	879	17	1.9	400,000	25.2
Former USSR	284	3	1.1	(1,000,000)	(36.4)
Denmark	249	11	4.4	3,500	0.5
Germany	549	15	2.7	>9,000[a]	0.8
Netherlands	690	43	6.2	5,000	1.0
Belgium	>155	1	0.6	2,200	<0.1
France	66	0	0	20,000	0
Britain	6,088	404[b]	6.6	64,000[c]	14.0

[a] Information only available for East Germany.
[b] Winter recoveries only.
[c] This estimate of the size of the British breeding population has been used instead of the more recent estimate of Lewis & Roberts (1993) because it is more applicable to the time period for which the ringing recoveries have been examined here.

As many birds originated from Finland as from Norway and Sweden combined. The former Soviet Union probably contributed a large number of woodcock to the British wintering population but more information is required about this important breeding area. It is clear that only very small numbers of woodcock came to the British Isles from Germany, the Netherlands, Belgium and France and that the majority of these were birds ringed on migration (see Figure 2.4 and Table 2.5).

2.3.5 Arrival and departure times of foreign migrants

The proportion of foreign woodcock (adults ringed during May-September and chicks) recovered in Britain and Ireland increased until the end of December and declined after January (Table 2.6). The latest ringing date for a woodcock ringed abroad and recovered in Britain during the same season was 25 December (a bird ringed in the Netherlands and shot in Suffolk the following day). Thus there was little evidence of cold weather movements in January and February into Britain from the Continent although this has frequently been assumed. The first and last recoveries of foreign-ringed birds were on 12 October and 15 April respectively. Some foreign-ringed birds (4% of all foreign recoveries) remained in Britain during March and into April, by which time many resident females would have laid eggs (Chapter 6).

The mean recovery latitude and longitude (Table 2.6) indicate that there is a net movement of British birds south and west during December, January and February and then a relatively rapid movement back north and east in March. The pattern for foreign-ringed birds indicates that they move rapidly south and west during October and the mean recovery latitudes for November to January suggest that the majority of foreign birds are to be found further south in Britain than British birds during this period. The information for foreign-ringed woodcock in February, March and April is based on only seven recoveries, but there appears to be no eastward movement of these birds in Britain until March.

Table 2.6 The temporal and spatial distribution of winter recoveries of British and foreign woodcock (adults ringed during May-September and chicks) within the British Isles. Each degree of latitude is equivalent to *c*.111km and at 50°N each degree of longitude is equal to *c*.72km.

Month of recovery	Ringing location						
	Britain			Abroad			
	n	Mean latitude (°N)	Mean longitude (°W)	*n*	Mean latitude (°N)	Mean longitude (°W)	% foreign
October	38	55°59'	3°54'	2	51°10'	1°12'	5.0
November	98	55°03'	3°59'	14	52°51'	5°25'	12.5
December	119	54°24'	3°52'	29	53°01'	3°44'	19.6
January	99	54°13'	4°08'	27	53°01'	4°27'	21.4
February	20	54°04'	5°49'	4	53°08'	4°16'	16.7
March+ April	12	55°06'	3°02'	3	51°06'	0°34'	20.0

Surprisingly few records of woodcock were made at bird observatories during 1958-61 and these generally involved small numbers of birds. The data suggest that the first Continental arrivals usually occur during the second week in October in northern Britain and about ten days later in southern Britain (Table 2.7). By far the largest number of woodcock recorded at any of the observatories were seen at Fair Isle, where about 50 per day were seen during peak passage in average years but more than 300 were seen on 6 November 1961 (Williamson 1962). More than 1,000 were recorded on 27-28 October 1976 (Thom 1986). Of five recoveries of woodcock ringed abroad and found on Fair Isle or ringed on Fair Isle and recovered abroad, three were Swedish birds and two were from Denmark.

Table 2.7 First sighting dates of woodcock at British bird observatories, autumn 1958-1961. (Data from Williamson 1958-1962).

Coastal location and observatories (see Figure 2.1)		Number of first dates recorded	Mean first date during 1958-61
NE Scotland	1	3	12 October
SE England	2,3,4,5	5	14 October
SW England	9,10,11	5	24 October
N Wales	12,13	2	24 October
Ireland	14,15	2	25 October
S England	6,7,8	4	30 October

The recovery dates of all foreign-ringed woodcock recovered in the British Isles in winter revealed no significant difference in the time of recovery between birds ringed north of the 54°N latitude line (Norway, Sweden, Finland, Denmark and the former Soviet Union) and those ringed to the south (Germany, the Netherlands, Belgium and France) (Table 2.8).

Table 2.8 Recovery dates of foreign-ringed woodcock recovered in the British Isles according to the region of ringing.

Ringing region	Recovery period in the British Isles							Total
	Before 16 Nov	16-30 Nov	1-15 Dec	16-31 Dec	1-15 Jan	16-31 Jan	1-28 Feb	
North of 54°N	13	11	20	20	25	24	7	120
South of 54°N	7	12	15	26	20	16	4	100

χ^2=4.53 (df=6) N.S.

2.3.6 Relative adundance of foreign woodcock in the wintering population in the British Isles

The ratio of foreign to British recoveries in winter was highest in south and western Britain (Table 2.9). These proportions, of course, are dependent on the number of woodcock ringed in the British Isles and in each of the countries from which migrants arrived and therefore do not represent the true proportions of foreign to British birds in each region. Nevertheless, the data support the evidence from mean recovery latitudes (Table 2.6) that foreign-ringed woodcock winter further south in Britain than British-ringed woodcock. The number of recoveries, particularly of British-ringed birds, is low in SW England and Wales (region *E*) and this is likely to be due to the scarcity of woodcock as a breeding species in this region (Lewis & Roberts 1993).

Table 2.9 The regional distribution of winter recoveries of British-ringed and foreign-ringed woodcock in the British Isles.

Origin of birds	Region of recovery				
	Scotland (*A*,*B*)	England			Ireland (*H*)
		North (*C*,*D*)	South (*F*,*G*)	SW+ Wales (*E*)	
British Isles	177	85	25	9	77
Continent	5	9	21	12	29
% foreign	2.7	9.6	45.7	57.1	27.4

$\chi^2=87.6$ (df=3) $p<0.001$
(data pooled for S England and SW England + Wales)

2.4 DISCUSSION

2.4.1 British woodcock

The British woodcock is typically sedentary, exhibiting a high degree of philopatry. Ringing recovery data suggest that it usually winters close to its breeding areas but about 13% of British woodcock move south-west to Ireland and about 4% move southwards to mainland Europe. These movements do not appear to be induced by cold weather, as supposed by Alexander (1946), since they occur largely before January, when Continental woodcock are arriving in Britain. Instead, it is probable that a small component of the British woodcock population is truly migratory.

Woodcock ringed in Britain and Ireland have an estimated annual adult survival rate of 57.9±1.8% (±se). This value is similar to the estimates of 63% and 59.3%

calculated from smaller samples by Lack (1943) (n=203) and Boyd (1962) (n=251) respectively. It is slightly lower than the adult survival rates for other similar-sized waders such as the black-tailed godwit *Limosa limosa* (63%), lapwing *Vanellus vanellus* (66%) and redshank *Tringa totanus* (68%) (Cramp & Simmons 1983). This may be because woodcock are more frequently shot in winter or because they utilize a different type of habitat. There is no evidence for a significant decline in the annual adult survival rate since 1909.

It is possible to calculate the breeding success required by woodcock in the British Isles to maintain the population with a 57.9% adult survival rate. As woodcock are polygynous, only the number of females is important. The assumption has to be made that there was no sex-specific difference in mortality rate because there were no data to examine adult survival rates on the basis of sex (only a small proportion of woodcock can be sexed with confidence). If we consider 100 females, 42.1 will die each year and will need the same number of female young produced from 100 females in any year to reach breeding age. Assuming that the proportions of each sex at hatching are equal, each female will need to raise 0.84 young to breeding age. With a first year survival rate from fledging of 47.2%, it will be necessary to fledge 1.78 young per female to meet this need. With a mean clutch size of 3.89, a hatching success of 44% of clutches, relaying of unsuccessful clutches (giving an effective 70% hatching success) and 7% addled eggs (Chapter 6), then 2.53 chicks are produced annually per female. Fledging success is estimated by me as 45% (Chapter 6) resulting in 1.14 chicks fledging per female, which is appreciably lower than the required number of 1.78. These data predict a decline in the British woodcock population and this is borne out by a long term decline in the BTO Common Birds Census data (Marchant *et al.* 1990). Nevertheless, the errors associated with the estimates of survival and breeding success used in the above calculation are such that the estimated rate of population change has a wide confidence interval. This uncertainty means that no firm conclusion can be drawn about whether the British woodcock population is increasing, stable or decreasing. Another consideration is that the breeding success data are from a single, possibly unrepresentative, site and should be treated with caution. Since most recoveries are of shot birds, it is possible that overall the survival rate in the British Isles is slightly higher than estimated here due to areas where there is no shooting or where the intensity of shooting is only low. Some evidence of such areas arises from five birds which survived for more than eight years (when only one would have been expected, Appendix 2.1). The author knows of areas where woodcock are present in winter, mainly at low densities, but where they are not shot. Such areas may be playing an important role in maintaining the British population of woodcock.

On the evidence of recoveries, 11% of British young woodcock were reported on the Continent in the breeding season. This is almost certainly an exaggerated proportion, enhanced by the shooting of roding birds in certain areas, but this genetic exchange is interesting and important. Such examples could be considered abmigration and are often explained by British birds pairing with Continental migrants in the wintering area and returning to the migrants' breeding area. Such an explanation seems unlikely in woodcock since there is no good evidence of pair formation prior to migration and long term pairing is very unlikely as the species is polygynous. There are no records of ringed Continental woodcock remaining to breed in Britain or Ireland.

2.4.2 Continental woodcock

The woodcock breeding on the continent of Europe are largely migratory and about 730,000 may overwinter in Britain (Hirons & Linsley 1989, Lewis & Roberts 1993). The adult survival rate of foreign-ringed birds recovered in Britain and Ireland is 53.9±3.5% (±se), which is not significantly different from the survival rate of British woodcock. The fact that the survival rates are comparable suggests that most foreign birds return to the British Isles in successive years and that this behaviour is not solely a characteristic of, for example, young birds. If they did not return, the survival rate of Continental-ringed woodcock would be lower owing to the shortage of older birds reported in Britain and Ireland. It was not possible to estimate wintering site fidelity for Continental woodcock in this study but it is thought to be relatively high, with about 14% of a sample of 402 birds returning to four study sites in Ireland in subsequent winters (Wilson 1983) and was estimated as 69% on the basis of ringed woodcock returning to a site in Cornwall (Chapter 3). Clausager (1974) estimated the mean annual adult survival rate for woodcock ringed in Scandinavia to be 49.4% (n=227). He deduced that each female would have to produce 2.94 fledged young per year in order to maintain a stable population and concluded that a considerable proportion of the Scandinavian females must produce two successive broods each year in order to achieve this. At present, there are only two records of double-brooding in woodcock (von Zedlitz 1927, cited by Glutz von Blotzheim *et al.* 1977, Jensen, cited by Pay 1937), but females losing eggs or chicks are able to lay a second clutch of eggs (Hirons 1983).

Continental woodcock do not arrive in the British Isles until the second week in October. There is no evidence that birds from the more northerly breeding populations of Fennoscandia and the former Soviet Union arrive earlier than birds from Germany, the Netherlands, Belgium and France. Relatively few foreign-ringed woodcock overwinter in Scotland and by far the highest proportion of foreign-ringed birds is found in southern England and Wales. The density of wintering woodcock is higher in SW England; for example, the density in Cornwall is three times greater than in Wiltshire and up to ten times greater than in Derbyshire (Chapter 3). There is therefore likely to be a large proportion and a large number of foreign woodcock wintering in SW England and Wales, further south than many British woodcock. Within Britain the largest numbers of woodcock are shot in western areas, particularly in SW England (Tapper & Hirons 1983, Chapter 3), and a large proportion of the birds that are killed each winter are therefore undoubtedly foreign migrants. It seems unlikely that many Continental woodcock breed in the British Isles despite the fact that foreign-ringed birds are present until mid-April. In Cornwall, an area where no woodcock breed (Lewis & Roberts 1993), a few birds (presumed to be Continental) from the wintering population are present until the end of March and these birds simply continue their winter pattern of behaviour and do not engage in roding (Hoodless, pers. obs.). In any case, roding alone does not provide proof that breeding has taken place. Shorten (1974) reported that roding woodcock were seen on the Scilly Isles at the time of the spring migration, but that no nest was ever found there. Witherby *et al.* (1940) state that passage birds may rode in localities where they do not stay to breed.

3. THE DENSITY AND DISTRIBUTION OF WOODCOCK IN WINTER

3.1 INTRODUCTION

The wintering woodcock population in Britain consists of birds of both British and Continental origin and is thought to number approximately 800,000 individuals (Hirons & Linsley 1989). Migrant woodcock from Fennoscandia and the former USSR constitute about 84-91% of this population (Chapter 1) and most arrive in Britain during October and November (Alexander 1946). The BTO *Atlas of Wintering Birds* shows the species to be generally distributed over much of Britain and Ireland with the exception of high ground in Scotland and N England (Lack 1986). However, the precise distribution and regional abundance of woodcock in winter is poorly understood due to the species nocturnal habit at this time of year. To date, only indirect assessments have been possible through the use of bag records as an index of absolute woodcock numbers (Tapper & Hirons 1983). The total number of woodcock shot in Britain each year is estimated to be *c*.200,000 birds (Tapper & Hirons 1983) but nothing is known about regional differences in the proportion of birds killed or about the level of harvest that can be sustained.

The purpose of the work described in this chapter was to determine directly woodcock densities in four counties (Cornwall, Wiltshire, Derbyshire and Co. Durham) and to find out how the proportion of woodcock shot varied between different shoots and different parts of the country. Winter densities of brown hares *Lepus europaeus* which, like woodcock, are nocturnal and make use of fields, can be assessed by means of spot-lamp counts (Barnes & Tapper 1985). The value of this method for determining winter woodcock densities was assessed in Cornwall. Although dazzling with a spot-lamp has become a recognized technique for catching woodcock for ringing in winter (Gossman *et al.* 1988) and counts of woodcock made with a spot-lamp have been used to investigate feeding preferences between different types of fields (Ferrand & Gossman 1988) the potential of the method as a census technique has not been exploited. Because the woodcock that can be seen feeding in fields at night rest in woodland during the day, information from shoots concerning the number of birds in particular woods can be used to calculate equivalent densities of birds at night and provide independent estimates for comparison with spot-lamp estimates.

The accuracy of spot-lamp counts is likely to be affected by four factors. 1. The efficiency of the observer in detecting woodcock present on the fields. This is not a problem provided the same observer covers the same study area during a season, because a measure of the efficiency can be gained from data collected on shoots. 2. Disturbance of the woodcock, in particular flushing of birds when attempting to catch them for ringing. 3. Night to night variability in the distribution of birds between fields. 4. Immigration and emigration of birds during the census period. The effect of these factors was examined in Cornwall.

Winter site fidelity has important implications for birds since familiarity with the distribution of food sources or with potential predators can affect survival (Spaans 1977, Hestbeck *et al.* 1991). However, if the suitability of potential wintering sites varies from year to year and these changes are perceived by the birds, they may actively select the most favourable areas each winter (Nichols *et al.* 1983). Recaptures of ringed birds at the same wintering sites in Ireland have provided some evidence for site fidelity in woodcock (Wilson 1983), but such an approach neither allows the estimation of a survival rate to the following winter nor the proportion of the birds alive exhibiting site fidelity. In order to determine the proportion of the woodcock alive that returned to winter in Cornwall during this study, the methodology of Hepp *et al.* (1987) and Cuadrado *et al.* (unpublished) was used to compare survival rate estimates based on the recovery data from woodcock ringed in Cornwall with the recovery data from woodcock ringed throughout Britain and Ireland in winter.

Bag records can provide a useful indication of the trend in wintering woodcock numbers provided they are interpreted with care. In some European countries, all hunters are required to report the total number of each game species killed in order to obtain a game licence. Such a system has been in operation in Denmark since 1940, enabling the annual bag for each species to be monitored (Strandgaard 1964, Strandgaard & Asferg 1980). There is no such legal requirement in Britain and bag returns are submitted on a voluntary basis to a scheme set up by the Game Research

Association in 1961. This is now run by the Game Conservancy Trust which receives 400-500 bag returns each year. Continuous records for each year from the same sporting estates or farms over several decades are the most useful, provided there have not been changes in the number of guns or the number of days shooting between seasons. However, the relatively large number of contributors to the Game Conservancy Trust scheme ensures that the inclusion or removal of a particular shoot in a given year does not have an appreciable influence on the mean bag.

Tapper (1988) has described the problems involved in interpreting British bag records. Those of most importance with respect to the woodcock are that the sample is non-random, consisting of a group of self-selected enthusiasts, that contributors may drop out of the scheme when shooting becomes impractical leading to underestimates of declines, and that the bag of one species may be affected by changes in the shooting pressure on another species. It has been suggested that the increase in the number of woodcock shot in the last decade is a consequence of increased pheasant *Phasianus colchicus* rearing and a greater number of days devoted to pheasant shooting (Tapper & Hirons 1983). In this chapter, the relationship between the pheasant bag and the woodcock bag has been examined on a regional basis. The influence of winter temperature on the woodcock bag has also been investigated.

3.2 STUDY SITES

Most of the fieldwork was conducted in Cornwall because the relatively large numbers of woodcock there facilitated the collection of data for testing different methods of density estimation. Sites in Wiltshire, Derbyshire and Co. Durham were studied so that regional differences in woodcock density could be determined.

Cornwall

South-west Britain appears to be favoured as a wintering area by woodcock because of its abundance of normally frost-free pasture. The Lizard Peninsula, in particular, is renowned for the numbers of woodcock shot there. Woodcock do not breed in Cornwall (Lewis & Roberts 1993) and ringing recoveries indicate that a high proportion of the woodcock wintering in SW England are Continental migrants (Chapter 2). The first birds arrive in October and most depart in late February and early March. Only two woodcock ringed on the Lizard Peninsula in winter have been recovered in the breeding season, both in the former USSR. The agriculture of the region is predominantly dairy and sheep farming, and the climate in winter is mild with an average daily mean temperature in January of about 7.5°C, and usually less than ten days each year with minimum temperatures below 0°C.

Attention was focused on two estates on the Lizard Peninsula: Lanarth, located 4km from the sea on the east of the Peninsula (grid reference *SW 7621*) and Trelowarren, situated centrally on the Peninsula about 2km south of

Mawgan Creek on the Helford River (grid reference *SW 7223*). For the purpose of this study, Lanarth was divided into two areas; one around Lanarth farm and the other about 3.3km south-west, near Traboe Cross. Both estates consisted of a patchwork of relatively small fields (median size 4.5ha), a high proportion of which were grass (permanent pastures and leys); 77% at Trelowarren and 86% at Lanarth. Trelowarren had extensive areas of mature woodland, which were mainly deciduous (ash *Fraxinus excelsior* and oak *Quercus robur*) but with some mixed and coniferous areas as well. At Lanarth, there were some smaller blocks of deciduous woodland which had been largely invaded by *Rhodedendron*, but there were also relatively large areas of uncultivated *Calluna/Molinia* moorland with scattered clumps of gorse *Ulex europaeus* and sallow *Salix* spp. At Traboe Cross, the only nearby woodland consisted of a coniferous plantation (46ha).

Shooting took place on the main area at Lanarth once a year during the week following Christmas, although there were smaller shoots on a number of outlying areas during November and January. Shoots occurred at Trelowarren approximately once every two weeks from December until mid-January but pheasants were the principal quarry here unlike at Lanarth where only woodcock were shot.

Wiltshire

Fieldwork was carried out at Clarendon Park Estate (grid reference *SU 1928*) which lies about 5km east of Salisbury. A large proportion of the area was devoted to growing cereals, and arable fields outnumbered grass fields by about 16:1. Daytime cover was afforded by a single large block (about 360ha) of mixed woodland which occupied approximately 25% of the area of the estate. In addition, the fields in the north-east half of the estate were interspersed by a network of narrow deciduous shelterbelts. Pheasant shoots were conducted on the area throughout the winter.

Derbyshire

Work was conducted on tenanted farmland surrounding Whitwell Wood (grid reference *SK 5278*), a 171ha deciduous plantation in NE Derbyshire, about 24km south-east of Sheffield. The agriculture of the area was almost entirely arable and crop fields outnumbered grass fields by about 18:1. The predominant crops were winter cereals and oilseed rape. Other than Whitwell Wood, diurnal cover consisted of two relatively large deciduous woods (approximately 31ha and 42ha in size) and eight small woods and copses (sizes 2-21ha). The climate can be severe in hard winters with sustained periods of frost or snow. No shooting took place on the study area but pheasant shoots were conducted on a few neighbouring farms and on Welbeck Estate which is situated about 6km south-east of the study area.

Co. Durham

Work was conducted on part of the Raby Estate in lower Teesdale, the study area being situated midway between Staindrop and Hamsterley Forest (grid reference *NZ 0322*). The area consisted entirely of a mixture of improved and unimproved pasture fields which supported mainly sheep and a few beef cattle. Several relatively small coniferous woods (4-25ha) were distributed throughout the area but diurnal cover was also afforded by large areas of bracken and *Calluna*-dominated heath in some parts of the study area. Shooting took place on the area twice each winter; once in late November and once in late December, although shooting continued throughout the season on the rest of the estate.

3.3 METHODS

3.3.1 Density estimation from spot-lamp counts

The principle of spot-lamp counting was to search a known area on several nights, recording the number of woodcock seen, so that an estimate of the density of birds present could be derived. Prior to commencing the counts, the size of each field at the study sites was determined from a 1:25,000 O.S. map and each was assigned a code-letter. The counts were conducted during two week periods coinciding with the occurrence of a new moon as the woodcock were more settled at these times (Gossman *et al*. 1988). They were made using a 300,000 CP quartz halogen lamp, powered by a 12v powerpack, and all except those in Derbyshire were done on foot. The counts in Derbyshire were conducted from a vehicle because the density of woodcock there was relatively low and the use of a vehicle enabled larger areas to be searched. In cases where it was not possible to see entire fields from the vehicle, arcs of view were estimated. The fields were searched in a different sequence each night. To assess night to night variability in the distribution of woodcock between fields and disturbance of the birds during the spot-lamp counts, data collected from 12 fields at Trelowarren and 11 fields at Lanarth in Cornwall during 1990/91 and 1991/92 were used to test for differences in the mean number of woodcock seen per field and the mean number seen per night. Subsets of the complete dataset were selected such that there was no more than one missing value for any field or any night in a particular analysis.

The densities of woodcock in Wiltshire, Derbyshire and Co. Durham were lower than in Cornwall and areas of at least 3km^2 were searched in each region to ensure representative density estimates. Counts made in November and early December were pooled to give pre-shoot densities and counts made in late January and February were used to calculate post-shoot densities. A number of woodcock were caught and ringed in Cornwall each year and it was possible to sex some of these birds using the ratio of the tail to bill measurements (Clausager 1973*a*). The proportion of each sex in the samples was amended according to the ability of Clausager's functions to discriminate each age and sex group[1] and the sex ratio amongst the woodcock wintering in Cornwall was examined for any bias caused by shooting or differential migration. In addition, the tail: bill ratio of all the woodcock measured alive was plotted against the

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[1] Clausager (1973*a*) was able to classify with 99% certainty 42% of the males and 46% of the females in a sample of 156 adult woodcock, and 28% of the males and 20% of the females in a sample of 135 first-year birds using the tail: bill ratio. The criteria for classification were: adults, >1.20 male <1.10 female and first-years, >1.20 male <1.00 female.

cumulative percentage of the number of birds, using probability paper. This provided a method of testing for a departure from an equal sex ratio without the need to know the sex of the individuals, thus enabling the data from all the birds to be used.

Analysis of data from eight woodcock radiotracked during November and December 1992 (Chapter 4) showed that on average 7% of woodcock failed to leave their diurnal covers each night (9 from 124 bird-nights) and so counts were corrected for this before densities were calculated. The density estimates for Cornwall refer solely to grass fields because woodcock were only occasionally seen on winter cereal or ploughed fields and in any case these fields only comprised a small proportion of the Cornish study areas. Density estimates for Wiltshire and Derbyshire include data from counts made on grass and cultivated fields. Count data for Cornwall and Derbyshire for the winter of 1988/89 were supplied by Dr. G. Hirons as were details of woodcock ringed on the Lizard Peninsula during 1978/79-1980/81 and 1986/87-1988/89.

3.3.2 Density estimation using shoot data

The main area at Lanarth was studied because shooting only took place there once a year but approximately one third of the annual woodcock bag for the entire estate was killed on the day. During the course of the shoot the location of each drive was marked on a 1:10,000 map and the numbers of woodcock flushed and shot per drive were recorded. The positions where any ringed birds were shot were noted. In an attempt to define the boundary of the study area in a manner which had biological meaning, the distances flown by woodcock from their diurnal covers to fields to feed at night were examined using data from radiotagged birds (Chapter 4) and birds ringed on fields that were recovered during shooting.

Two methods were used to estimate the number of woodcock present in the study area on the shoot day. In the first, the number of woodcock flushed on the shoot was corrected for the flushing efficiency (the proportion of the birds present that were disturbed by the beaters), the proportion of birds flushed twice and the proportion of woodland within the study area that was driven. It was not possible to determine annual estimates of the flushing efficiency and the proprotion of woodcock flushed twice, but Lack (cited by Bickford-Smith 1980) estimated that the number of woodcock present was equal to 90-95% of the number of woodcock flushed, on the basis of radiotagged birds flushed during the course of a simulated shoot. The number of woodcock flushed was corrected by 0.93 in this study and the first estimate of the number of woodcock (N) was calculated by:

$$N = 0.93nW/w$$

where n = number of woodcock flushed
W = total woodland in study area (km^2)
w = woodland driven during shoot (km^2)

It was assumed that the woodcock were distributed between the woods in approximate proportion to the area of each wood. No correction was made for woodcock from woods not driven that were feeding on fields outside the study area. However, due to the heterogeneous distribution of woods in this part of Cornwall it was likely that a similar number of woodcock moved into the area from woods located outside the boundary, although this was not proved.

The second method of estimating the number of woodcock in the study area employed the Lincoln index with small sample correction (Bailey 1952):

$$N = R(s+1)/(r+1)$$

$$se = \sqrt{\frac{R^2(s+1)(s-r)}{(r+1)^2(r+2)}}$$

where R = total woodcock ringed
s = total woodcock shot
r = ringed birds recovered shot

The assumption was made that all of the ringed birds were still alive and in the study area on the shoot day. This method was used so that the degree of immigration and emigration between the period of spot-lamp counting and the shoot day could be assessed by comparison with the density estimate calculated from the number of woodcock flushed on the shoot day. The number of ringed woodcock expected to be shot (E), assuming no immigration or emigration, could be estimated by calculating the number likely to be at risk from the proportion of woodland driven. The number of ringed woodcock likely to be shot from those at risk could then be estimated from the proportion of the woodcock flushed that were killed:

$E = Rsw/0.93nW$

where R = total woodcock ringed
n = number of woodcock flushed
s = number of woodcock shot
W = total woodland in study area (km^2)
w = woodland driven during shoot (km^2)

3.3.3 Calculation of wintering site fidelity

Woodcock were ringed at Lanarth and Trelowarren, Cornwall during November-February each winter and ringed birds were recovered during the shoots on the two estates. The recoveries of woodcock ringed at Lanarth and Trelowarren provided an estimate of survival (S) as the proportion of the individuals alive in year n that were still alive and returned to the same wintering site in year n+1. The parameter (1-S) therefore included both deaths and failure to return to Lanarth and Trelowarren. A survival rate estimate calculated from the recoveries of woodcock ringed throughout Britain and Ireland during the winter (October-February), using the national ring recovery data for 1909-1990, reflected only survival since the recovery data came from a much larger area. It was assumed that individuals returned to Britain and Ireland and that wintering sites were not chosen from throughout Europe.

It was therefore possible to test the null hypothesis that the probability of returning to the same wintering site, given that the bird was alive, was equal to unity (Cuadrado *et al.* unpublished); in other words, that the survival rate estimates from woodcock ringed and recovered in Cornwall and from the national ring recovery data were equal. If the null hypothesis was rejected, the probability of returning to the same wintering site could be estimated from the ratio of the two survival rates (Hepp *et al.* 1987).

Constant annual adult survival rates were calculated for the Cornish and the national ring recovery data using Haldane's method for incomplete recoveries (Haldane 1955). Recoveries made during the winter of ringing were excluded from both datasets and the analyses were restricted to woodcock that were shot. For the national data, each year was taken as 1 March-28/29 February and the recoveries of woodcock ringed at Lanarth and Trelowarren were excluded.

3.3.4 Bag records and harvest rate estimation

The main shoots at Trelowarren and Lanarth were attended in the winter of 1991/92 as were a few shoots on nearby areas. The total number of woodcock flushed and shot and the number of pheasants shot were recorded for each shoot. Similar information was obtained for 26 shoots throughout Britain in December 1992 by the Game Conservancy Limited's regional advisors. For the purpose of this study, the term "harvest rate" has been used to describe the proportion of the woodcock present (= the corrected number flushed) that was shot. At the end of each shoot in Cornwall, the woodcock were aged according to Clausager (1973*a*). A sample of 20 birds was sexed by dissection.

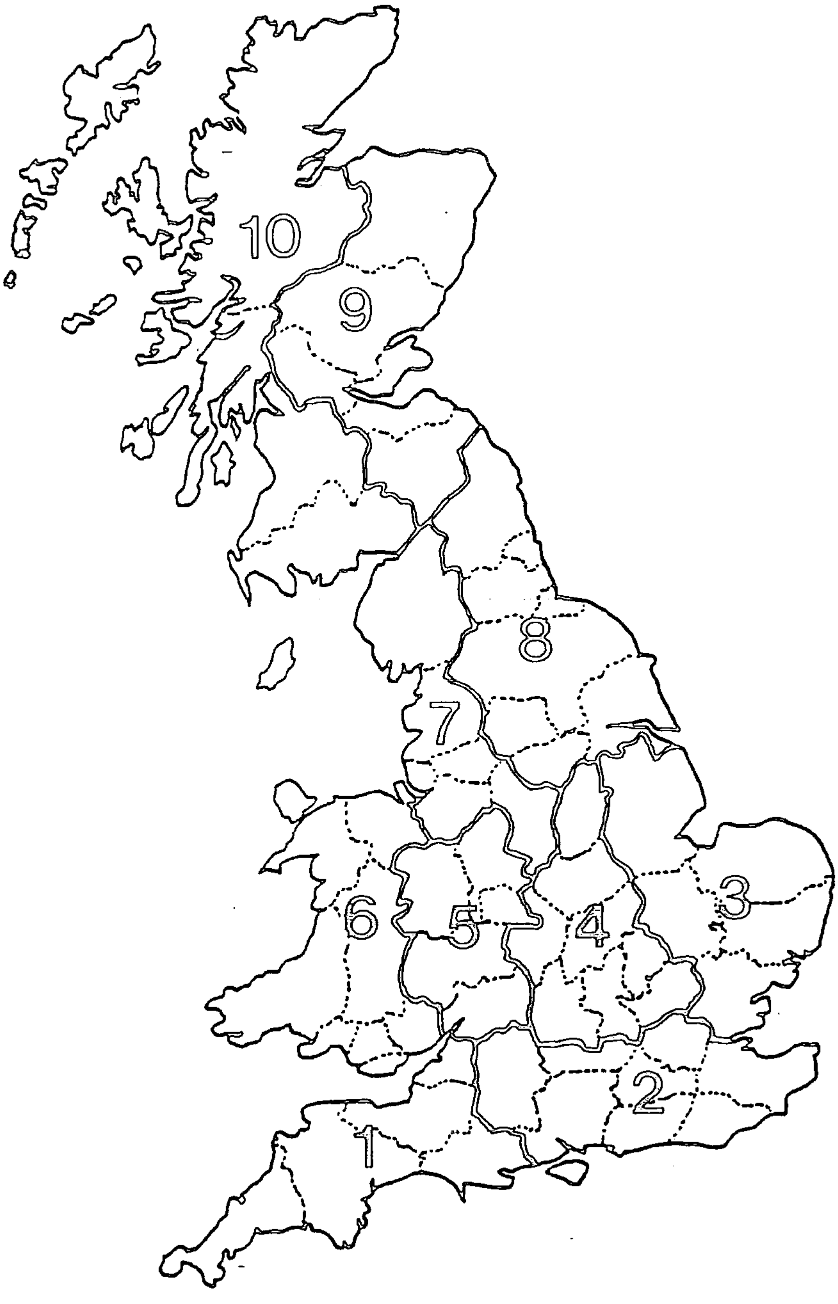
Bag records from the Game Conservancy Trust's National Game Census were used to provide information on the distribution of woodcock throughout Britain in winter and to determine regional trends. The locations of shoots

Figure 3.1 The distribution of shoots contributing to the Game Conservancy Trust's National Game Census in 1977.

contributing to the scheme are shown in Figure 3.1. Most of England was well represented with the exception of Cornwall, but relatively few records were received from W Scotland or Wales. For the purpose of regional analyses, Britain was divided into ten areas (Figure 3.2). Ireland was excluded because very few Irish records were received. Where possible, shoots with records for every year during the period of interest were used to determine trends. In all cases, shoots killing no woodcock were included in calculations of the mean bag to reduce the risk of any declines being underestimated.

Regional trends in the annual woodcock bag were corrected for the annual pheasant bag and compared with the uncorrected trends. One problem with the National Game Census bag data is that the number of days shooting is not recorded with the annual totals for each species killed. It was therefore assumed that an increase in the pheasant bag resulted from an increase in the number of days shooting or an increase in the area of woodland driven, both of which would have produced a larger woodcock bag. It was assumed that there was no increase in the pheasant bag due simply to the shooting of larger numbers of pheasants on the same shoot days, as this would not have produced a larger woodcock bag. These assumptions are validated by Tapper & Hirons (1983) and Tapper (1992) who believe that the increased pheasant bags during the late 1970s and during the 1980s were due to an increase in the number of days shooting.

Figure 3.2 The Game Conservancy Trust's National Game Census regions.
(1 SW England, 2 SE England, 3 East Anglia, 4 East Midlands, 5 West Midlands, 6 Wales, 7 NW England, 8 NE England, 9 E Scotland, 10 W Scotland).



The relationship between the number of pheasants and the number of woodcock shot was determined by plotting the mean pheasant bag against the mean woodcock bag for each year for Britain as a whole and for each region, and determining the correlation coefficient. As a check that the relationship between the means was representative of the relationship on individual shoots, the pheasant bag was plotted against the woodcock bag for all shoots in Britain in 1968/69 and 1987/88. This was not done for all years due to the large numbers of shoots involved and 1968/69 and 1987/88 were chosen in order to give data for a representative range of pheasant bags (1968/69 mean bag 29.1 pheasants/km^2, 1987/1988 mean bag 49.0 pheasants/km^2). The woodcock bag was corrected for the number of pheasants shot each year using three methods, the results of which were compared. The first two methods employed the residuals from the regression of the woodcock bag on the pheasant bag and the woodcock: pheasant ratio. The third method ammended the woodcock bag in proportion to the annual variance in the pheasant bag:

$$\text{Corrected woodcock bag for year } n = W_n + rW_x(P_x - P_n)/P_x$$

where W_x = mean woodcock bag for the period 1961-1992
W_n = woodcock bag in year n
P_x = mean pheasant bag for the period 1961-1992
P_n = pheasant bag in year n
r = correlation coefficient between the pheasant and woodcock bags

All three methods gave very similar results in terms of the trends of the corrected woodcock bags in all regions. For the purpose of graphical presentation, the figures for the third method are given as they are in the same units as the uncorrected bag trends.

The influence of winter air temperatures on the annual mean woodcock bag was investigated using the coldest of the monthly means for December and January in each of the years 1961/62-1990/91, given in Manley (1974) and Parker *et al.* (1991).

3.4 RESULTS

3.4.1 Night to night variation in spot-lamp counts, Cornwall

There were significant differences in the mean number of woodcock seen on each field over all nights during the pre-shoot periods at Lanarth and Trelowarren in both 1990/91 and 1991/92 and during the post-shoot period in 1990/91 at Lanarth and 1991/92 at Trelowarren (Table 3.1, Appendix 3.1). For neither estate were there significant differences in the mean number of woodcock seen per night over all fields for any of the time periods (Table 3.1, Appendix 3.1). It was decided that spot-lamp counts were sufficiently reliable to enable representative estimates of woodcock density to be determined from counts conducted over a few nights.

Table 3.1 Variation in woodcock numbers between fields and between nights in Cornwall (two-way ANOVA).
Pre-shoot data for 1990/91 given as an example.

	Trelowarren				Lanarth (main area)			
Field/ night	Field code	Mean birds/ field	Date	Mean birds/ field/ night	Field code	Mean birds/ field	Date	Mean birds/ field/ night
Pre-shoot 1990/91								
1	B	2.60	28 Nov	1.43	B	12.40	3 Dec	2.57
2	C	0	29 Nov	3.00	D	2.40	4 Dec	3.57
3	D	0	30 Nov	2.50	E	0.20	5 Dec	2.86
4	E	2.00	1 Dec	3.25	F	0	6 Dec	2.71
5	J	1.80	10 Dec	0.57	J	0.80	7 Dec	2.83
6	K	5.00			P	3.00		
7	Q	6.00			BA	1.25		
8	T	0.60						
Fields	F=12.77		df= 7,20	p<0.01	F=34.76		6,23	p<0.01
Nights	F= 0.90		df= 3,20	N.S.	F= 0.49		4,23	N.S.

	Trelowarren			Lanarth (main area)		
	F	df	Sig.	F	df	Sig.
Post-shoot 1990/91						
Fields	1.99	5,13	N.S.	17.02	3,3	p<0.05
Nights	1.65	3,13	N.S.	0.00	1,3	N.S.
Pre-shoot 1991/92						
Fields	4.28	6,29	p<0.01	82.60	4,11	p<0.01
Nights	2.53	5,29	N.S.	2.98	3,11	N.S.
Post-shoot 1991/92						
Fields	7.08	6,10	p<0.01	3.97	3,5	N.S.
Nights	0.61	2,10	N.S.	0.51	2,5	N.S.

3.4.2 Woodcock densities in Cornwall from spot-lamp counts

Woodcock densities in Cornwall for the last five winters, calculated from spot-lamp counts, are presented in Table 3.2. The woodcock reached their highest density on the

Lizard Peninsula during the winter of 1989/90 and were present at their lowest density in 1992/93. Up to four times as many woodcock were present in some parts of the study area before shooting in 1989/90 as in 1992/93. However, the large standard errors (particularly for Traboe Cross) in 1989/90 indicate that there were large changes in the density of birds and probably large-scale movements of woodcock through the study area. The density of woodcock on the main area at Lanarth was significantly higher than that at Trelowarren (paired t-test on $\log_{10}$ transformed data; pre-shoot data only $t=8.13$, $df=4$, $p<0.01$; pre-shoot and post-shoot data $t=3.60$, $df=8$, $p<0.01$).

Table 3.2 Mean woodcock densities (birds/km^2 grass fields ±se) on the three Cornish study areas, determined by spot-lamp counts.
The number of counts is given in parentheses.

Year	Trelowarren	Lanarth (main area)	Lanarth (Traboe Cross)
1988/89			
Pre-shoot	21.5 ± 4.1 (6)	27.6 ± 4.4 (10)	28.6 ± 6.8 (2)
Post-shoot	5.0 (1)	17.0 ± 4.3 (2)	6.8 (1)
1989/90			
Pre-shoot	41.0 ±11.8 (4)	70.6 ±19.9 (2)	65.6 ±51.4 (3)
Post-shoot	18.2 ± 4.8 (10)	15.9 ± 2.1 (4)	12.3 ± 1.8 (4)
1990/91			
Pre-shoot	31.5 ± 6.0 (6)	47.7 ± 4.3 (6)	--
Post-shoot	19.5 ± 5.5 (4)	24.8 ± 6.3 (7)	16.5 ± 8.7 (2)
1991/92			
Pre-shoot	16.9 ± 4.3 (13)	26.4 ± 2.7 (16)	14.8 ± 3.9 (8)
Post-shoot	10.4 ± 1.0 (3)	19.9 ± 2.8 (9)	27.0 ± 5.9 (4)
1992/93			
Pre-shoot	11.5 ± 2.6 (7)	16.2 ± 4.4 (8)	10.8 ± 2.5 (4)

3.4.3 Comparison of woodcock densities in different parts of England from spot-lamp counts

The densities of woodcock estimated from spot-lamp counts in Wiltshire, Derbyshire and Co. Durham were all lower than those in Cornwall and, with the exception of 1989/90, the lowest densities were recorded in Derbyshire (Table 3.3). There was clearly a high density of woodcock in Derbyshire as well as Cornwall in 1989/90 and the birds remained throughout the winter. The magnitude of the difference in the density of woodcock between 1989/90 and the other winters in Derbyshire was surprising and suggested an influx of woodcock from elsewhere. The density of woodcock was clearly lower in Cornwall and Wiltshire following the main period of shooting, but because immigration and emigration of woodcock were not accounted for, the difference between the pre-shoot and post-shoot densities cannot be assumed to provide a reliable estimate of the overwinter mortality. Shooting appears to have been relatively unimportant in Derbyshire and Co. Durham, but there was undoubtedly some immigration of woodcock to the counting area following shooting in Derbyshire in 1989/90 and in Co. Durham in 1991/92, because the density of woodcock increased after the shooting had finished.

Table 3.3 Mean woodcock densities at sites in four counties in England before shooting (November to mid-December) and after shooting (mid-January to February) (birds/km^2 fields ±se): grass fields, top row; crop fields, bottom. The number of counts is given in parentheses. Data have been pooled for the different estates within each area.

Year	Cornwall	Wiltshire	Derbyshire	Co. Durham
1988/89				
Pre-shoot	25.7±12.1(18)	--	7.2 (1)	--
		--	0.0 (1)	
Post-shoot	11.4± 7.3 (4)	--	--	--
		--	--	
1989/90				
Pre-shoot	55.7±49.9 (9)	4.6 (1)	10.2 (1)	--
		0.0 (1)	19.3 (1)	
Post-shoot	16.4±11.4(18)	--	2.5±0.5(2)	--
		--	20.4±2.9(5)	
1990/91				
Pre-shoot	39.6±14.9(12)	10.3±1.6(2)	--	--
		0.0 (2)	--	
Post-shoot	21.8±13.9(13)	6.8 (1)	6.1±2.9(2)	--
		0.0 (1)	0.0 (2)	
1991/92				
Pre-shoot	20.5±13.4(37)	13.6±2.9(3)	11.6±8.3(2)	4.6±5.0(3)
		0.0 (2)	0.0 (2)	
Post-shoot	19.9± 9.8(16)	10.0±6.8(3)	8.3±1.2(3)	7.4±5.0(4)
		0.0 (2)	0.0 (3)	

3.4.4 Woodcock density estimated from shoots at Lanarth, Cornwall

The mean distance of all the flights to fields made by the eight radiotagged woodcock tracked during November and December 1992 was only 289±195m (±sd, maximum=780m, n=32). Hirons & Bickford-Smith (1983) monitored 66 flights made by five woodcock and reported the mean distance as 444±388m (±sd, maximum=1370m). The mean recovery distance of 17 woodcock ringed on fields and shot in woodland during 1991/92 was greater, at 908±533m (±sd, maximum=2160m), although this might be an overestimate of the distance of flights between woodland and fields as some of the ringed woodcock could have changed their diurnal resting sites between ringing and recovery. Excluding the recovery distances of two woodcock for which this was suspected gave a mean recovery distance of 786±417m (±sd, maximum=1390m, n=15). The estimates of the maximum distance likely to be flown by woodcock at night on the basis of the radiotracking study by Hirons & Bickford-Smith (1983) (1370m) and the ringed woodcock that were shot (1390m) were then similar. For the purpose of this investigation, the study area was therefore defined as the area enclosed by a 1370m wide strip of land surrounding each of the woods of interest.

The study area (excluding roads and buildings) defined in this manner on the basis of the woods driven during the shoot on the main area at Lanarth was 12.27km^2 in 1990/91 and 1992/93 and 11.82km^2 in 1991/92. The small difference was because one of the woods that was driven was different in 1991/92. Woodland comprised approximately 10% of each area, fields 70% and moorland 20%. The estimates of woodcock density for each winter and the values of the parameters used in the calculations are given in Table 3.4.

Table 3.4 Woodcock densities (birds/km^2 grass fields) estimated from the shoot at Lanarth (main area) in 1990/91-1992/93 and values of the parameters used in the calculations.

	1990/91	1991/92	1992/93
Number of woodcock flushed during the shoot, *n*	159	137	66
Number of woodcock shot, *s*	91	75	37
Number of woodcock ringed prior to the shoot, *R*	20	54	11
Number of ringed birds recovered, *r*	3	7	1
Total woodland (km^2) in the study area, *W*	1.24	1.19	1.24
Woodland driven (km^2) during the shoot, *w*	0.49	0.51	0.49
Area of grass fields (km^2) in the study area, *p*	8.59	8.19	8.59
Method 1: Corrected number of woodcock flushed			
Estimated number of woodcock in the study area	374	297	155
Density of woodcock on grass fields at night (birds/km^2)	44	36	18
Method 2: Lincoln index			
Estimated number of woodcock in the study area (±se)	460 (±201)	513 (±162)	209 (±117)
Density of woodcock on grass fields at night (birds/km^2 ±se)	54 (±23.4)	63 (±19.8)	24 (±13.6)

The harvest rate (= the proportion of the woodcock present in the woods that were driven that was shot) was similar each year; 1990/91 61%, 1991/92 59% and 1992/93 61%. The two shoot methods produced different density estimates in all three years suggesting that some immigration or emigration occurred, particularly in the second year, violating the assumptions of the second method (Lincoln index). When compared with the mean densities calculated from spot-lamp counts, there was better agreement with the densities calculated by the first shoot method (corrected number of woodcock flushed) (Table 3.5). This was expected because the second shoot method (Lincoln index) was dependent on the proportion of ringed woodcock shot and since only small numbers of birds were ringed each year, the figure for the proportion shot was relatively inaccurate. This explains the large standard errors of the estimates of the number of woodcock in the study area from the second shoot method (Table 3.4).

3.4.5 Evidence for immigration and emigration

The fact that the density estimate derived by the second shoot method in 1991/92 was so high implied that the assumption of no immigration or emigration was violated. The number of ringed woodcock recovered during the shoot was lower than expected in all three years (1990/91 three compared with five, 1991/92 seven compared with 14, 1992/93 one compared with three). Comparison of the density estimate from the first shoot method with that from the spot-lamp method in 1991 suggested that woodcock arrived on the Lizard Peninsula between mid-December, when spot-lamp counting finished, and the shoot day (30 December). Examination of the spot-lamp data for November and December 1991 suggested that a similar arrival of woodcock occurred during 4-6 December (Table 3.6).

Table 3.5 Comparison of woodcock density estimates (birds/km^2 grass fields) for Lanarth (main area) from spot-lamp counts and shoots during 1990/91-1992/93.

	1990/91		1991/92		1992/93	
Method	Density (birds/ km^2)	Spot-lamp density as % of shoot density	Density (birds/ km^2)	Spot-lamp density as % of shoot density	Density (birds/ km^2)	Spot-lamp density as % of shoot density
Spot-lamp, December data	48		30		16	
Shoot method 1: Corrected number of woodcock flushed	44	110%	36	82%	18	90%
Shoot method 2: Lincoln index	54	89%	63	47%	24	67%

Emigration of ringed woodcock would also have led to the high density estimate of the second shoot method and confirmation that emigration took place was indicated by ring recoveries from outside the study area. Three of the woodcock ringed at Lanarth in November and December 1991 were shot in early January 1992 on a farm about 8km south-west and one bird (first-year, sex unknown) ringed on 15 November 1991 was shot in S Wales on 26 December 1991.

Table 3.6 Temporal change in woodcock density (birds/km^2 grass fields) on the basis of spot-lamp counts and the estimated number of woodcock in the study area at Lanarth (main area) during November 1991 to February 1992.

6-11 Nov.	30 Nov. -4 Dec.	6-9 Dec.	10-12 Dec.	Shoot day, 30 Dec.		1-7 Feb.
				Before shoot	After shoot	
Woodcock density (birds/km^2 grass fields ±se)						
20 ±3.7	21 ±6.6	32 ±2.1	33 ±1.7	43	34	16 ±2.4
Woodcock in study area (assuming 100% spot-lamp efficiency)						
161	174	260	266	355	280	134

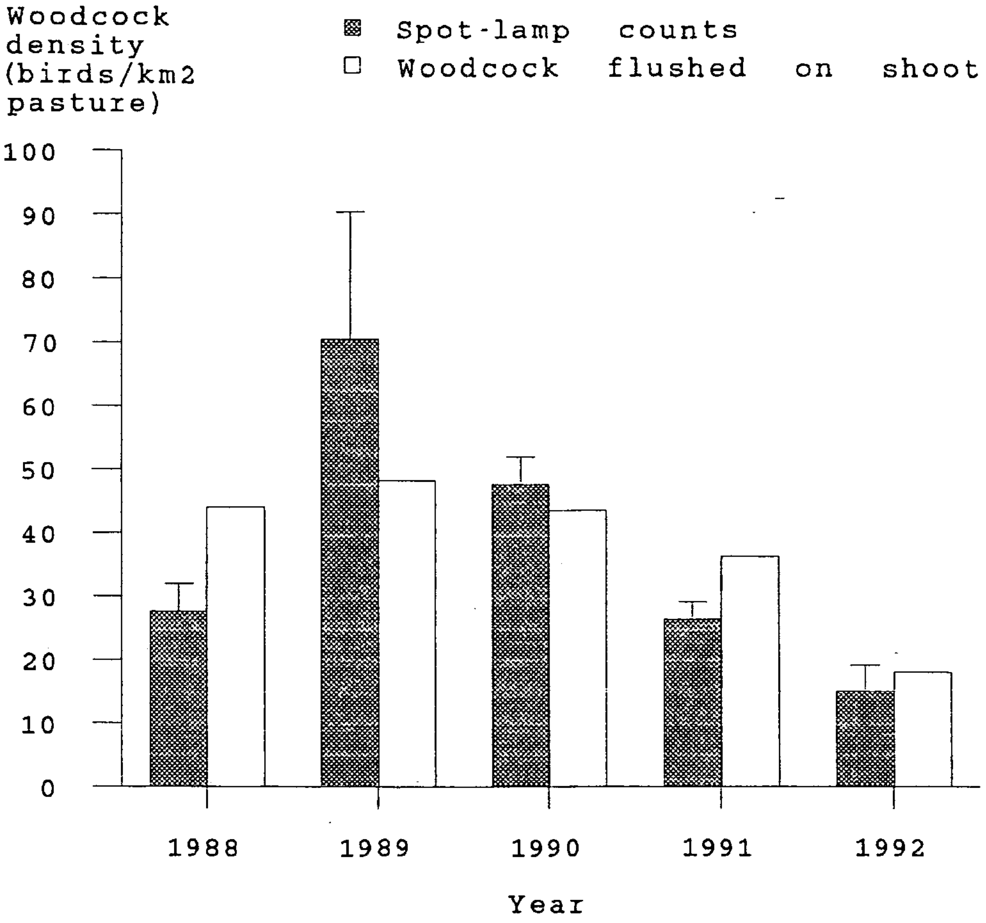
The efficiency of the spot-lamp counts (i.e. the proportion of the woodcock present on fields that were seen) was not known but the woodcock densities estimated by the spot-lamp method and the first shoot method were in approximate agreement. Assuming the counts were 100% efficient, the number of woodcock in the study area at Lanarth during each count period was calculated (Table 3.6). It was thus estimated that there was a net gain of 194 woodcock between 11 November and the shoot day on 30 December. By assuming that the woodcock ringed during this period had an equal chance of being recovered outside the study area as within it, the proportion of woodcock leaving the area was estimated from the proportion of recoveries outside (4/11 = 36%). It was therefore concluded that of the 161 woodcock present in early November, 58 were likely to have left the study area before 30 December and hence there must have been a total influx of 252 woodcock to produce the net gain of 194 birds. In other words, approximately four woodcock arrived on the Lizard Peninsula for every one that left during November and December. It was not possible to determine whether woodcock continued to arrive in the area during January, but there was a net loss of 146 birds, suggesting that by this time the balance had switched to emigration.

Comparison of woodcock densities from spot-lamp counts and from the shoots (according to the first shoot method) at Lanarth during each of the last five winters, suggests that the pattern of immigration and emigration might not have been the same each year (Figure 3.3). There may have been net immigration at Lanarth in late December in 1988 and 1991, and net emigration in 1989, following an exceptionally high density of woodcock (71±20 birds/km^2 ±se) in early December. However, as it was not possible to calculate the error associated with the density estimated from the number of woodcock flushed, it is possible that the results are consistent with a null hypothesis of no movement by woodcock through the area and large errors of density estimation.

3.4.6 Wintering site fidelity

During the winters 1978/79-1980/81 and 1986/87-1992/93 a total of 276 woodcock were ringed at Lanarth and Trelowarren in Cornwall and 29 (10.5%) were recovered on these estates in subsequent winters (Appendix 3.2). The constant annual adult survival rate for the woodcock that returned to Cornwall was 0.38±0.10 (±se), and a

Figure 3.3 Comparison of the estimated woodcock densities from spot-lamp counts and the number of woodcock flushed on the main day shoot at Lanarth for 1988/89-1992/93. (Error bars are +1se).



goodness-of-fit test suggested that the Haldane model provided a reasonable fit to the data (χ^2=0.11, df=2, N.S.).

Of the woodcock ringed throughout Britain and Ireland in winter (October-February), 105 were recovered in subsequent years. A goodness-of-fit test suggested that the Haldane model provided a reasonable fit to these data (χ^2=7.70, df=4, N.S.; Appendix 3.2) and the constant annual adult survival rate for the national ring recoveries was estimated as 0.55±0.04 (±se). The annual survival rate estimate from Cornwall was lower than this, but not significantly different (d=1.62, N.S.). The non-significant result is probably due to the small number of recoveries in the Cornish sample. It is nonetheless clear that the woodcock at Lanarth and Trelowarren exhibited relatively high wintering site fidelity as the ratio of the two survival rates (the national one measuring survival only and the Cornish one measuring survival and winter site fidelity) is 0.69. Evidence that wintering site fidelity was not 100% comes from three winter recoveries in France and one in Lincolnshire of woodcock ringed on the Lizard Peninsula. The three birds shot in France were recovered on 10 February 1980 (ringed as a first-year 21 January 1979), on 12 December 1988 (ringed as an adult on 14 January 1988), and on 15 November 1989 (ringed as a first-year on 2 December 1988). The bird shot in Lincolnshire was ringed as a first-year on 2 February 1980 and recovered on 25 December 1980. The dates of these recoveries suggest that these woodcock were not killed on migration.

3.4.7 Age and sex ratios among woodcock wintering on the Lizard Peninsula, Cornwall

The woodcock population wintering on the Lizard Peninsula exhibited an unusual age and sex structure. During 1988/89-1991/92 the percentage of first-year birds among those shot ranged from 72%-79% at Lanarth (n=114, 148) and from 62%-65% at Trelowarren (n=16, 57). These age ratios were confirmed by the percentage of first-year birds among those ringed; for example 76% in 1990/91 (n=24) and 75% in 1991/92 (n=86) at Lanarth. The sex ratio among adult woodcock on the Lizard Peninsula was such that there was a significantly higher proportion of females (Table 3.7). A plot of the tail: bill ratio for 64 adult woodcock measured alive against the cumulative percentage of the number of birds, using probability paper, gave an inflexion point at 74%, suggesting that 74% of the adult woodcock caught on the Lizard Peninsula were females. There was no significant difference in the proportions of males and females among the first-year birds, although there were more males (Table 3.7). A point of inflexion was obtained at 35% in a plot of tail: bill ratio against the cumulative percentage of the number of birds for 149 first-year woodcock, implying that only 35% of the first-year woodcock caught on the Lizard Peninsula were females. It was not possible to determine whether a similar sex ratio was maintained from year to year due to the relatively small numbers of woodcock ringed each year.

Table 3.7 Sex ratio among the woodcock wintering on the Lizard Peninsula, Cornwall during 1987/88-1992/93.

Method of sex determination	Adults		First-years	
	Male	Female	Male	Female
Dissection of shot birds	3	10	3	4
Measurement of live birds	14	24	23	11
Total	17 (33%)	34 (67%)	26 (63%)	15 (37%)
χ^2 goodness-of-fit test	$\chi^2=5.67$, df=1, $p<0.05$		$\chi^2=2.95$, df=1, N.S.	

3.4.8 Woodcock shooting in the United Kingdom

Data from the National Game Census for the period 1988/89-1992/93 revealed that 73% of shoots killed woodcock but that only 6% killed more than five birds/km^2 per annum (Figure 3.4). There was some regional variation in the proportion of shoots killing woodcock, with the highest proportions in Wales (100%) and SW England (90%) and the lowest in N England (69%) and Scotland (59%) (Table 3.8). Virtually all the shoots in central and S England and Wales killed pheasants, and NW England and W Scotland were the only regions where the proportion of shoots killing woodcock was greater than the proportion killing pheasants.

Figure 3.4 The distribution of the size of annual woodcock bags in Britain, based on the mean annual bag per shoot during 1988/89-1992/93 (mean number of shoots=465).

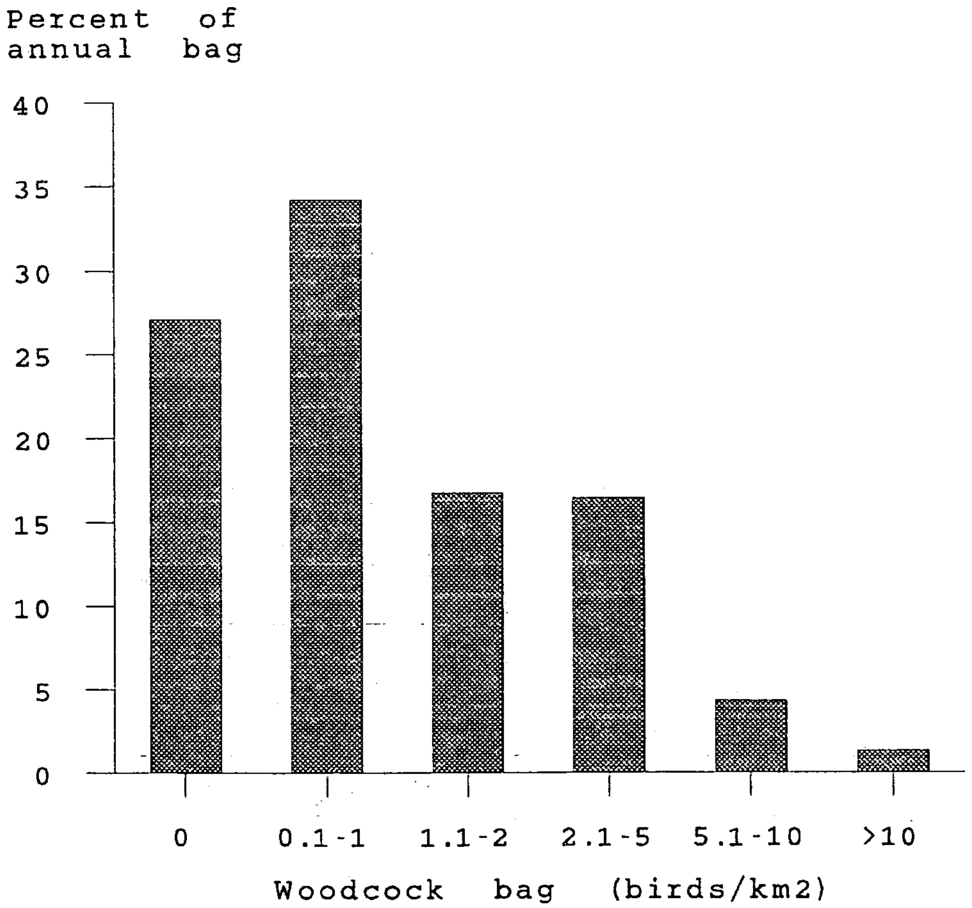


Table 3.8 Regional differences in the proportion of shoots killing woodcock and pheasants, five year mean 1988/89-1992/93.

	Region	Mean number of shoots per year	Mean proportion killing woodcock	Mean proportion killing pheasants
1	SW England	31	90%	99%
2	S England	60	77%	99%
3	E Anglia	73	76%	100%
4	E Midlands	27	82%	99%
5	W Midlands	25	76%	98%
6	Wales	9	100%	100%
7	NW England	28	66%	61%
8	NE England	57	72%	80%
9	E Scotland	77	62%	69%
10	W Scotland	59	56%	49%

The highest mean annual woodcock bags were shot in SW England and E Anglia, where they were approximately twice the size of those taken throughout the rest of England and Wales and seven to ten times greater than those in Scotland (Table 3.9). The largest numbers of pheasants killed per woodcock were in central and S England. Calculation of the mean annual woodcock bag for 1988/89-1992/93 by county revealed that the largest numbers of woodcock killed each year were in Cornwall, the Isle of Wight, Powys, Dyfed, Humberside and Cleveland (Figure 3.5).

Data from the shoots surveyed in December 1992, where the numbers of woodcock flushed were counted, revealed large differences in the harvest rates between the individual shoots in each region (as shown particularly by the standard deviations for S England and Yorkshire, Table 3.10). A one-way ANOVA on the arcsin-transformed percentages was not significant (F=2.62, df=4,29, N.S.) and the only significant

Figure 3.5 The mean annual woodcock bag per county during 1988/89-1992/93.

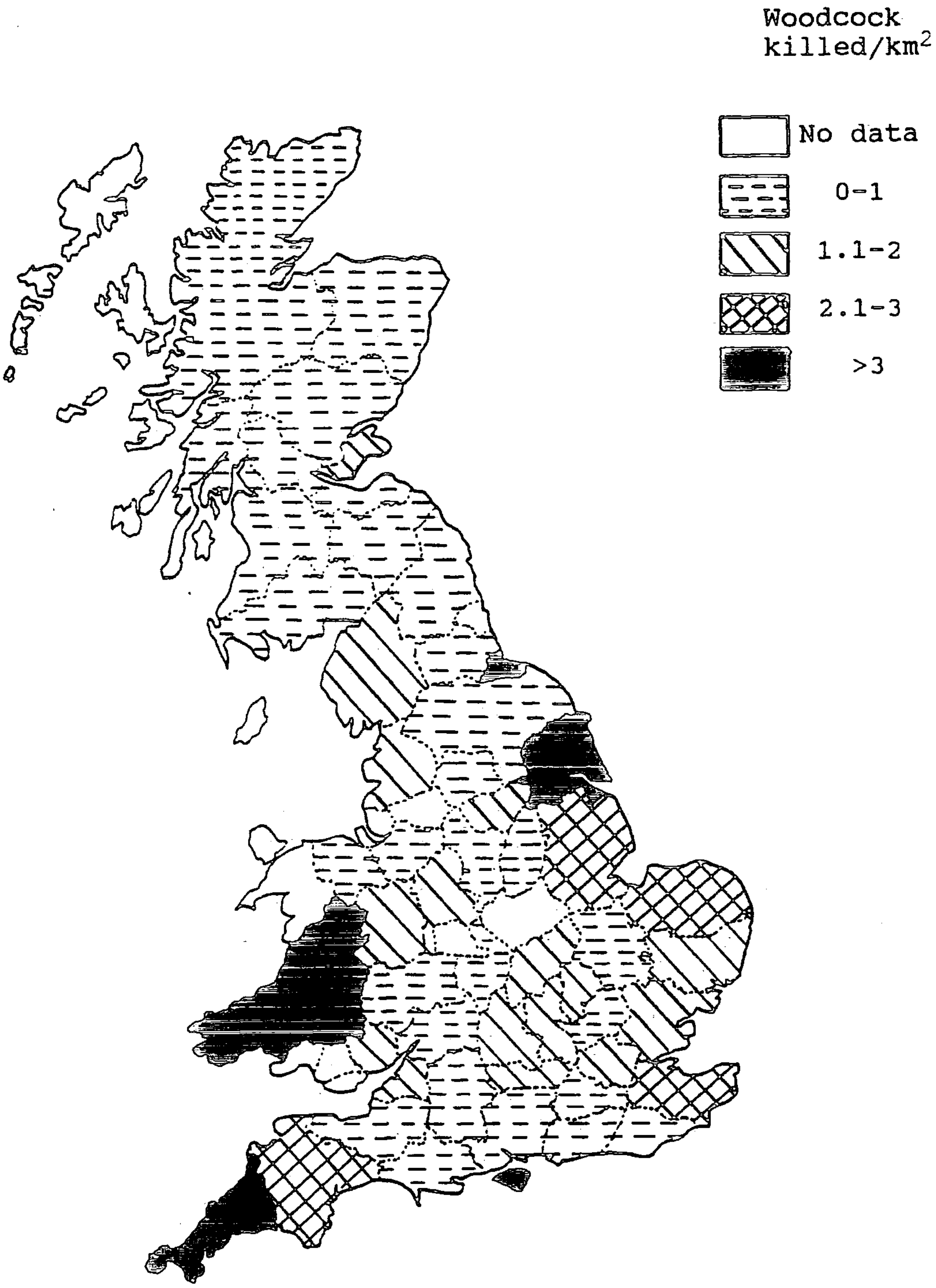


Table 3.9 Regional differences in the annual woodcock and pheasant bags and the number of pheasants killed per woodcock, five year mean 1988/89-1992/93.

Region	Mean annual woodcock bag (birds/km^2)	Mean annual pheasant bag (birds/km^2)	Mean number of pheasants killed per woodcock
1 SW England	2.21	148.3	67
2 S England	1.03	257.7	250
3 E Anglia	2.07	144.0	70
4 E Midlands	1.08	188.1	174
5 W Midlands	1.03	225.7	219
6 Wales	1.12	165.1	147
7 NW England	1.29	71.5	55
8 NE England	0.75	39.9	53
9 E Scotland	0.29	24.5	84
10 W Scotland	0.22	8.8	40

regional difference revealed by the Duncan multiple range test was between the mean harvest rates in Cornwall and in Clwyd and Shropshire. Excluding Lanarth, the harvest rate on the other Cornish shoots averaged about 35% of the woodcock present. Lanarth was unique in terms of both the number of woodcock shot and the harvest rate (59%). However, it is clear from Figure 3.4 that shoots such as Lanarth are uncommon and contribute little to the annual woodcock bag for the UK, which is undoubtedly comprised mainly of woodcock killed on pheasant shoots.

Table 3.10 Regional differences in the mean harvest rate of woodcock on shoots and the ratio of pheasants to woodcock killed (Cornwall December 1991 and January 1992, other regions December 1992).

Region	Number of shoots	Mean harvest rate (%) ±sd	Mean number of pheasants killed per woodcock
Cornwall	8	41 ±10.5	5
Surrey, Wiltshire, Hampshire & Dorset	6	20 ±39.9	574
Clwyd & Shropshire	3	3 ± 4.5	143
Yorkshire	3	20 ±21.3	29
S Scotland	14	13 ±15.3	59

3.4.9 Trends in the number of wintering woodcock

The annual mean woodcock bag for the UK since 1961 does not show a simple trend, but has four distinct peaks, in 1961/62, 1978/79, 1984/85 and 1990/91 (Figure 3.6). The periods of 31 December 1978-1 March 1979 and 3 January 1985-20 February 1985 are among those identified as "cold winters" by Ridgill & Fox (1990) on the basis of frozen ground at more than half of 13 coastal weather stations at 09.00 GMT. There was also a relatively cold mean December air temperature during 1961/62. Comparison of the annual mean woodcock bag for the UK with the coldest of the mean monthly air temperatures for December and January of each year gave a significant negative relationship ($r=-0.40$, $df=28$, $p<0.05$; slope=-0.032; Figure 3.7). Negative relationships were found in all five of the areas examined separately; SW England and Wales (NGC regions 1+6), central

Figure 3.6 The trend in the annual mean woodcock bag for 1961/62-1992/93 as represented by the National Game Census shoots in all regions. (Error bars are ±1se).

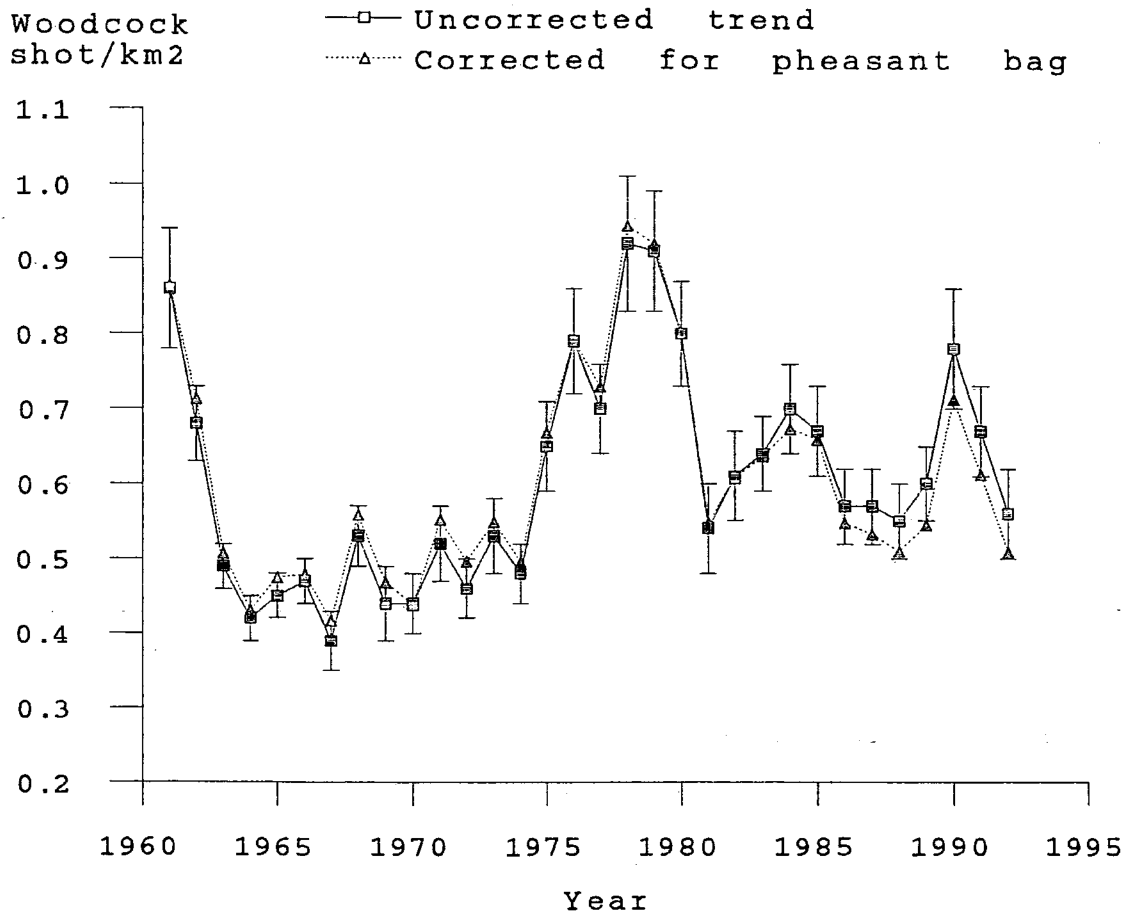
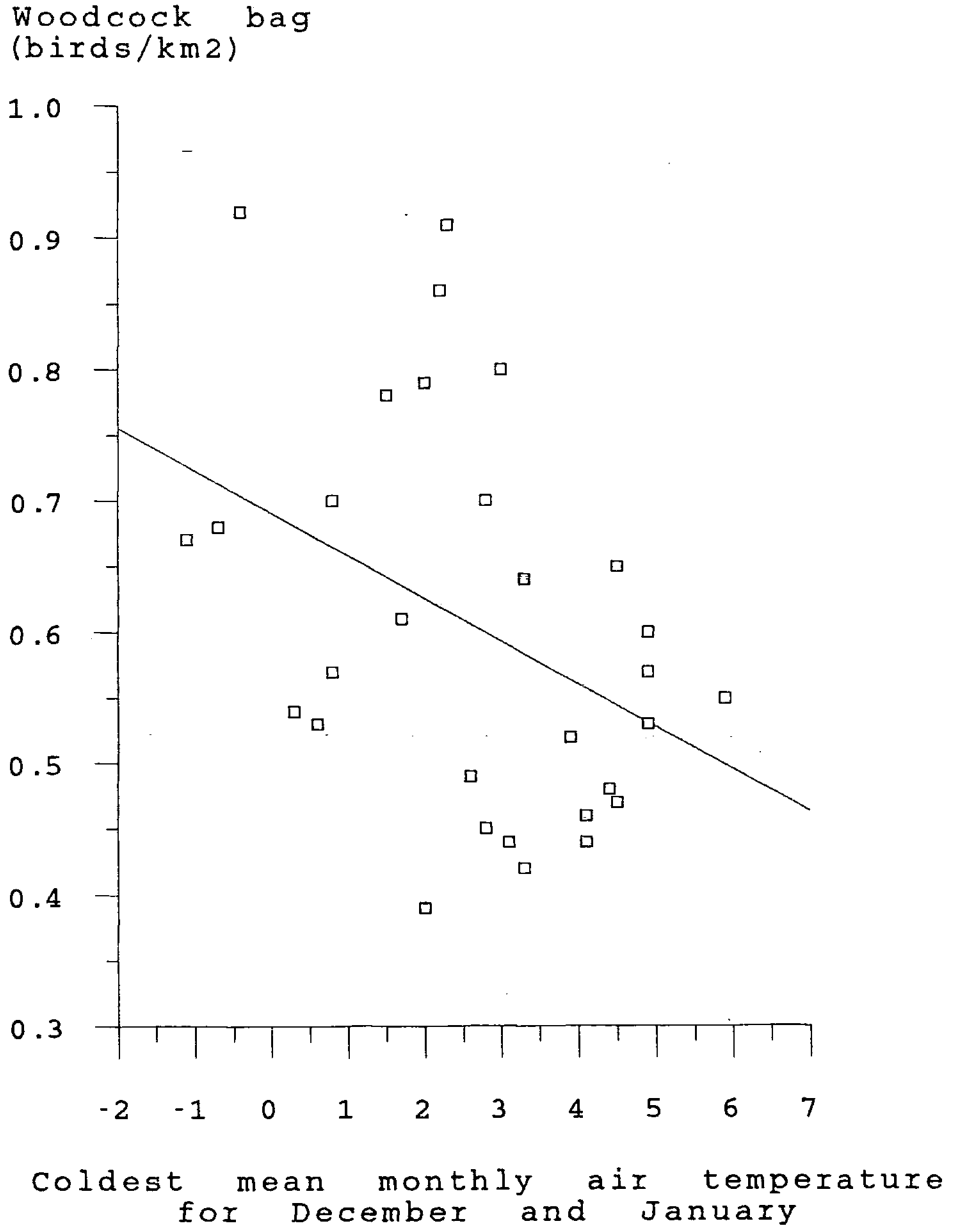


Figure 3.7 Relationship between the annual mean woodcock bag for the UK and the coldest of the mean monthly air temperatures for December and January in central England, for the winters 1961/62-1990/91.
Mean monthly air temperature data taken from Manley (1974) and Parker *et al.* (1991).

$r=-0.40$, $df=28$, $p<0.05$; slope=-0.032



and S England (NGC regions 2+4+5), E Anglia (NGC region 3), N England (NGC regions 7+8) and Scotland (NGC regions 9+10), but the only significant relationship was for the annual mean woodcock bag in E Anglia ($r=-0.44$, $df=28$, $p<0.05$; slope=-0.246).

The most stable phase of the UK bag trend occurred during 1963/64-1974/75 where the bag averaged about 0.46 bird/km^2 (Figure 3.6). The woodcock bag since 1980 has averaged about 0.65 bird/km^2 but there has been a series of relatively cold winters (1981/82, 1984/85, 1985/86 and 1986/87) as well as a dramatic increase in the number of pheasants shot during this time. The increase in pheasant shooting was such that the annual bag approximately doubled between 1980/81 and 1990/91 (Figure 3.8). There was no significant relationship between the annual mean pheasant bag for the UK and the annual mean woodcock bag for the UK during the period 1961/62-1992/93 ($r=0.20$, $df=30$, N.S.; slope=0.003). There was also no significant correlation between the pheasant bags and the woodcock bags for all the National Game Census shoots in 1968/69 and 1987/88 ($r=0.001$, $df=926$, N.S.). These results suggest that the increase in pheasant shooting had little effect on the total UK woodcock bag (Figure 3.6). The woodcock bags for 22 Scottish shoots where no pheasants were shot, with records for every year since 1961/62, showed a similar pattern to the trend for the UK as a whole, but the peak in the mean bag in 1978/79 was less pronounced and there was a proportionately larger peak in the mean bag in 1990/91 (Figure 3.9).

Figure 3.8 The trend in the annual mean pheasant bag for 1961/62-1992/93 as represented by the National Game Census shoots in all regions. (Error bars are ±1se).

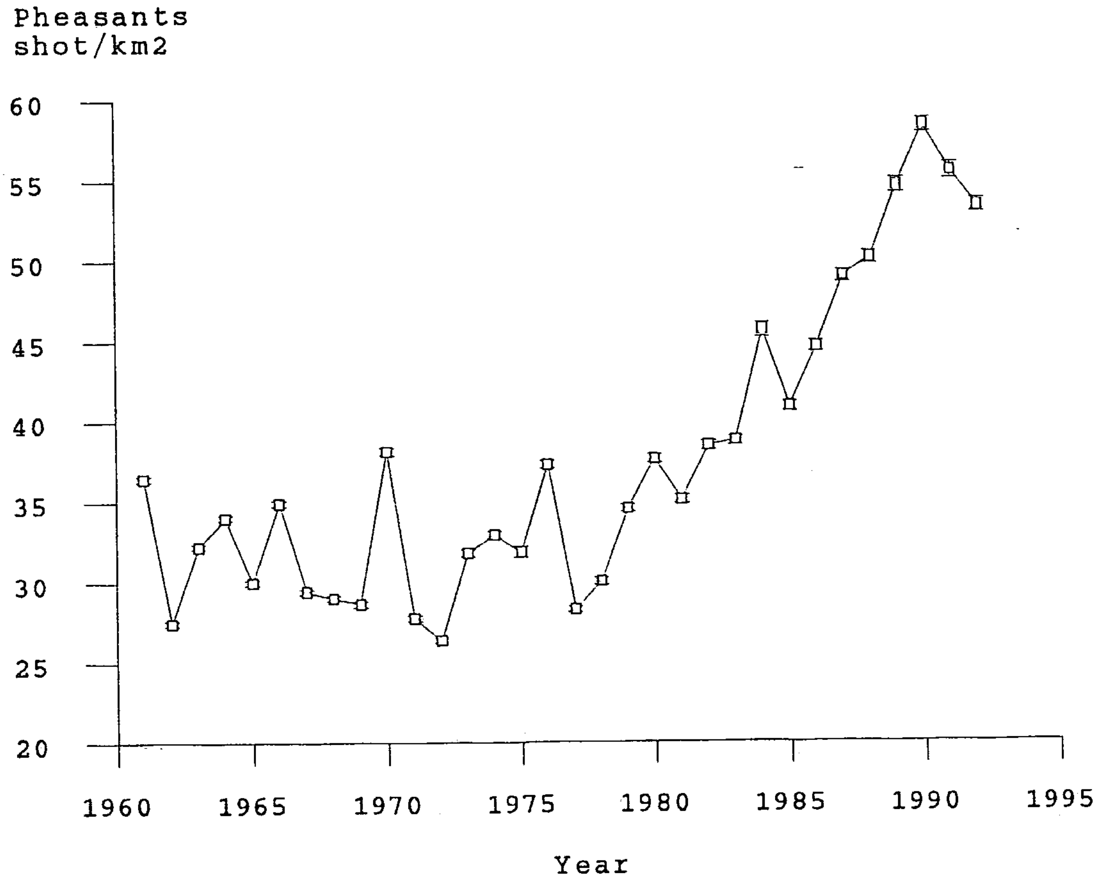
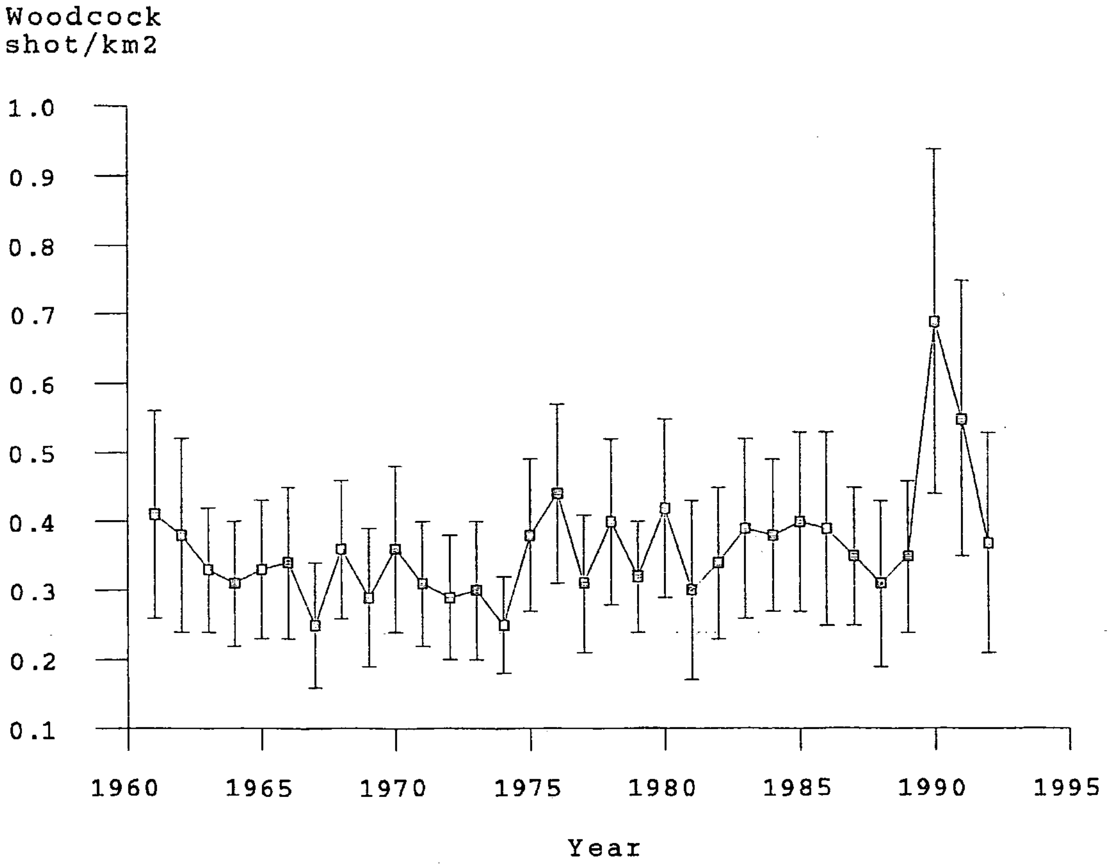


Figure 3.9 The trend in the annual mean woodcock bag for 1961/62-1992/93 for 19 Scottish shoots killing woodcock but no pheasants. (Error bars are ±1se).



The mean annual woodcock bag for 19 shoots throughout Britain with near complete records for every year since 1900, yielded a trend with three phases (Figure 3.10). During the period 1906-1914 the mean bag was relatively stable and fluctuated around 1.0 bird/km^2. Following the First World War, there was a gradual decline in the mean bag from 1.1 birds/km^2 in 1924 to 0.5 bird/km^2 in 1974, although unusually large bags were taken during the hard winters of 1961/62 and 1962/63. Since 1974 the size of the mean annual woodcock bag has increased sharply to approximately 1.3 birds/km^2 (with the exception of 1992).

SW England and Wales

SW England and probably Wales are the regions with the highest densities of wintering woodcock and, not surprisingly, the annual mean woodcock bags have generally been higher here than in any other region, with the exception of E Anglia in certain years. Because relatively few woodcock breed in SW England and Wales (Lewis & Roberts 1993), the annual mean bags from these regions provide the best indication of changes in the number of Continental woodcock overwintering in Britain from year to year.

Large numbers of woodcock were shot during the cold winter of 1962/63 (mean bag 2.60 birds/km^2), probably because they were concentrated in SW England (Dobinson & Richards 1964). The mean woodcock bag fell to 1.25 birds/km^2 in 1963/64 and gradually declined to 0.75 birds/km^2 over the next four years, before starting to pick up again in 1968/69

Figure 3.10 The trend in the annual mean woodcock bag for shoots throughout Britain with continuous records (bag totals for every year) for the period 1900/1-1992/93. (Standard errors omitted for clarity).

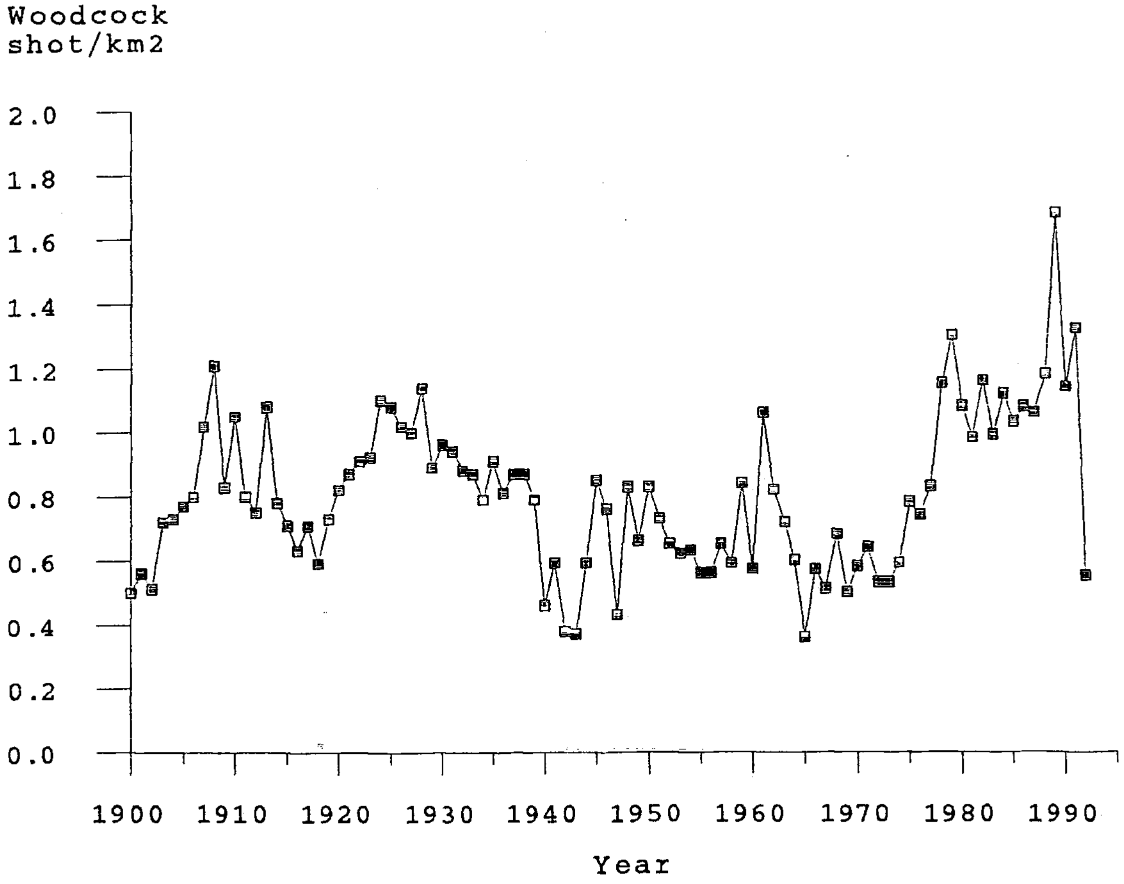
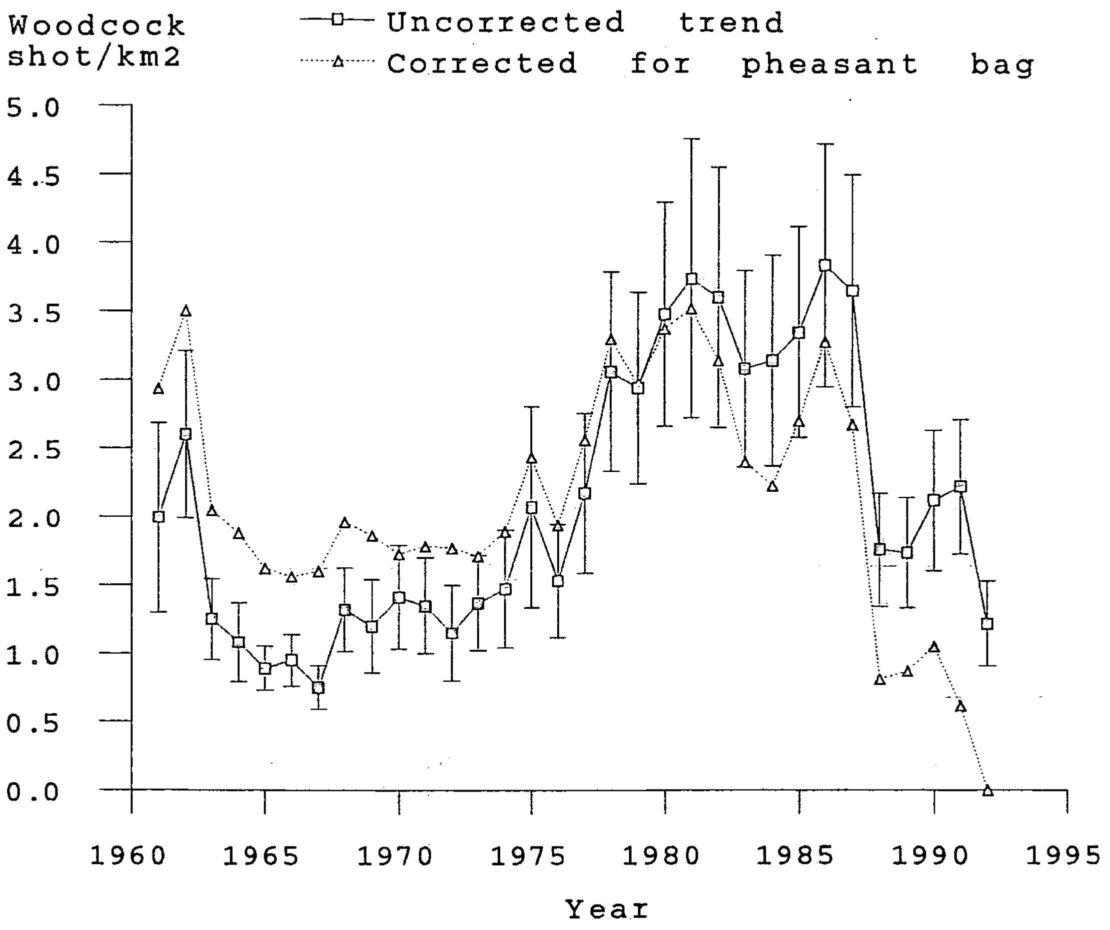


Figure 3.11 The trend in the annual mean woodcock bag for SW England and Wales (NGC regions 1 and 6) for 1961/62-1992/93. (Error bars are ±1se).



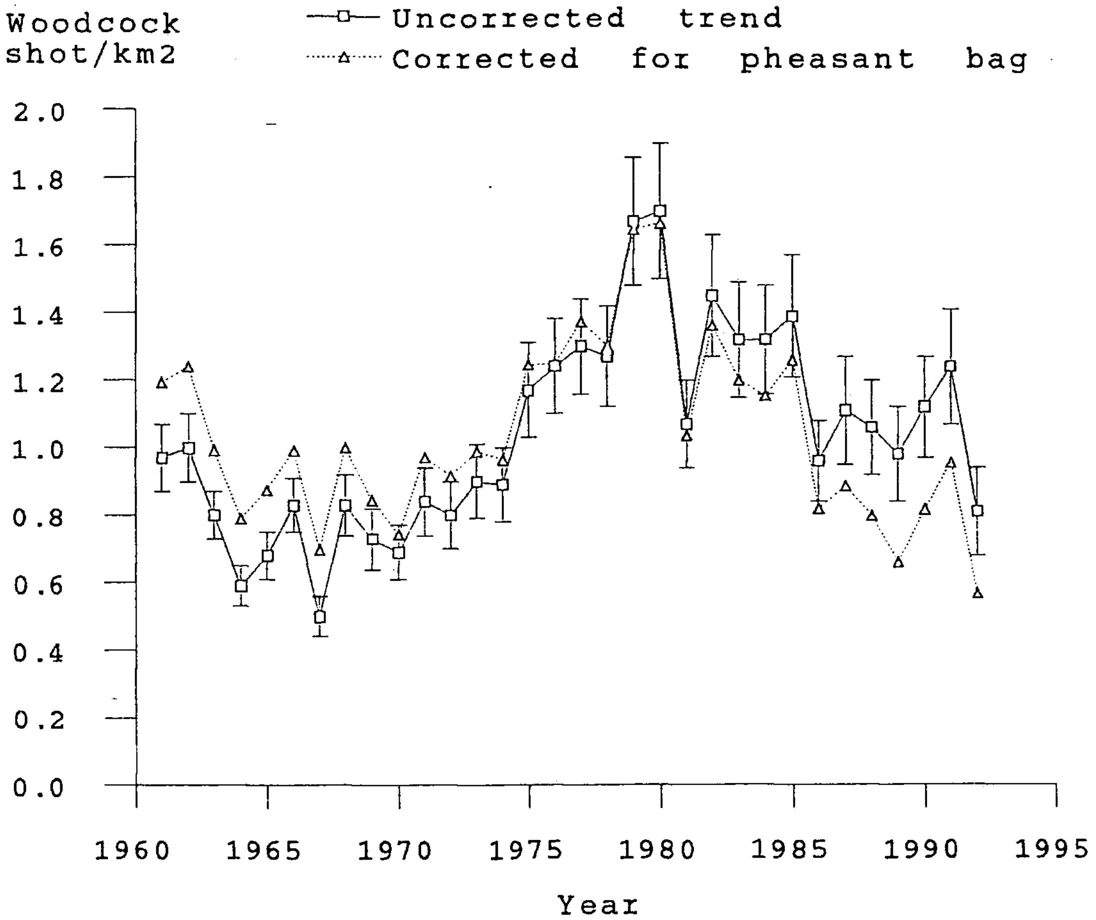
(Figure 3.11). The annual mean bag slowly increased until 1977/78 and there then followed a period of ten years of very large woodcock bags averaging approximately 3.5 birds/km^2, although there was greater variation between individual shoots. During this period there were two peaks in the colder winters of 1981/82 and 1986/87, indicating that more woodcock than usual were shot. This might have been because woodcock were concentrated in the south-west or because they were more vulnerable to shooting in cold weather.

There was a significant correlation between the annual mean pheasant bag and the annual mean woodcock bag for these regions during 1961/62-1992/93 ($r=0.69$, $df=30$, $p<0.001$). This meant that the annual mean woodcock bag was high during the 1980s, but that it would actually have fallen sharply during 1988/89-1992/93 were it not for the increased frequency of pheasant shooting (Figure 3.11).

Central and S England

The uncorrected woodcock bag trend for central and S England (Figure 3.12) was similar to that for SW England and Wales, and there was a significant positive correlation between the annual mean woodcock bags for the two regions ($r=0.70$, $df=30$, $p<0.001$). The increase in the mean woodcock bag in central and S England during the cold winter of 1962/63 was relatively small and the subsequent recovery was relatively quick compared to SW England and Wales, taking only three years. As for SW England and Wales, there was a substantial increase in the annual woodcock bag from 1970/71

Figure 3.12 The trend in the annual mean woodcock bag for central and S England (NGC regions 2, 4 and 5) for 1961/62-1992/93. (Error bars are ±1se).



to 1980/81 (mean bags 0.69 birds/km^2 and 1.70 birds/km^2 respectively) and then a more gradual decline to 0.81 birds/km^2 in 1992/93.

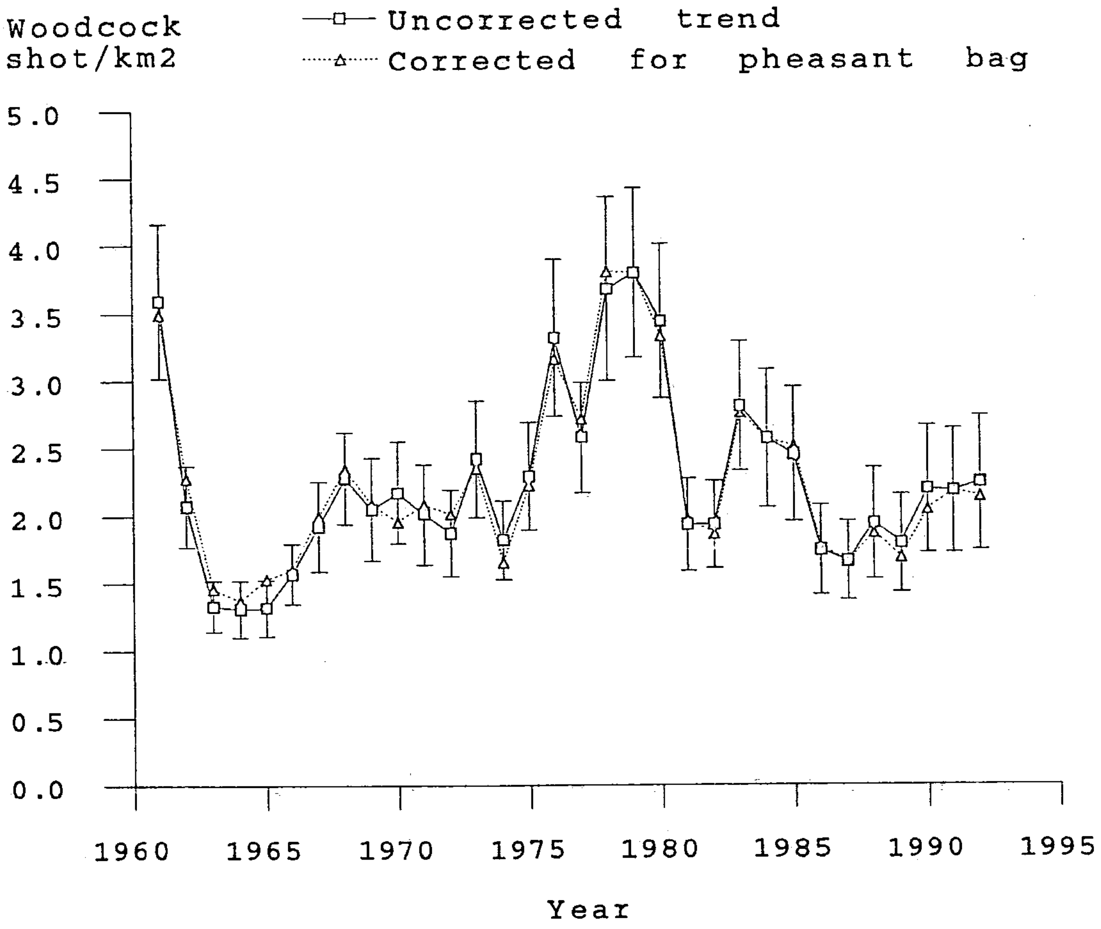
There was a significant correlation between the annual mean pheasant bag and the annual mean woodcock bag during 1961/62-1992/93 in central and S England ($r=0.45$, $df=30$, $p<0.01$). However, the increase in the annual woodcock bag occurred before the largest increase in pheasant shooting: during 1970/71-1980/81 the mean pheasant bag increased by 28.0 birds/km^2, whereas during 1980/81-1989/90 it increased by 88.4 birds/km^2.

E Anglia

The annual woodcock bag trend for E Anglia is characterized by peak mean bags in 1961/62, 1976/77, 1978/79, 1979/80 and 1983/84 (Figure 3.13). Unlike in SW England and Wales and central and S England, the mean bag for 1961/62 was considerably higher than that for 1962/63. The size of the mean bags for 1981/82-1992/93 was only slightly higher than those for 1967/68-1975/76 and the trend for 1986/87-1992/93 was one of a gradual increase, compared to the trends for SW England and Wales and central and S England for these years, which showed declines.

There was no significant correlation between the annual mean pheasant and woodcock bags in E Anglia ($r=0.26$, $df=30$, N.S.) and the correction to the woodcock bag trend on the basis of the pheasant bag made a negligible difference. The significant negative correlation between the uncorrected annual mean woodcock bag and the coldest of the mean monthly

Figure 3.13 The trend in the annual mean woodcock bag for East Anglia (NGC region 3) for 1961/62-1992/93. (Error bars are ±1se).



air temperatures for December and January in E Anglia ($r=-0.44$, $df=28$, $p<0.05$), suggested that woodcock did not normally leave E Anglia at the onset of cold weather as expected from Tapper & Hirons (1983). Central and S England and SW England and Wales are the regions likely to receive any woodcock leaving E Anglia in cold winters, and the mean annual woodcock bags for E Anglia might be expected to be negatively correlated with the mean annual bags for these regions. The relationships between the annual mean woodcock bags corrected for the pheasant bag for E Anglia and central and S England ($r=0.75$, $df=29$, $p<0.001$) and E Anglia and SW England and Wales ($r=0.45$, $df=29$, $p<0.05$), however, were significantly positive, again suggesting that few woodcock left E Anglia in cold weather.

N England and Scotland

The uncorrected woodcock bag trends for N England and Scotland (Figures 3.14 and 3.15) were very similar, with a stable phase from 1961/62-1974/75 and peak bags in 1976/77, 1978/79, 1984/85 and 1990/91. The correlation between the two trends was significant ($r=0.81$, $df=30$, $p<0.001$), but they were quite different from the three previous bag trends for S England and Wales. The annual mean woodcock bags for N England and Scotland should provide a better indication of the state of the British breeding woodcock population, because the relative number of foreign to British woodcock wintering in these regions is much lower (Chapter 2). The mean woodcock bags for the cold winter of 1962/63 were little different from those in other years, presumably

Figure 3.14 The trend in the annual mean woodcock bag for N England (NGC regions 7 and 8) for 1961/62-1992/93. (Error bars are ±1se).

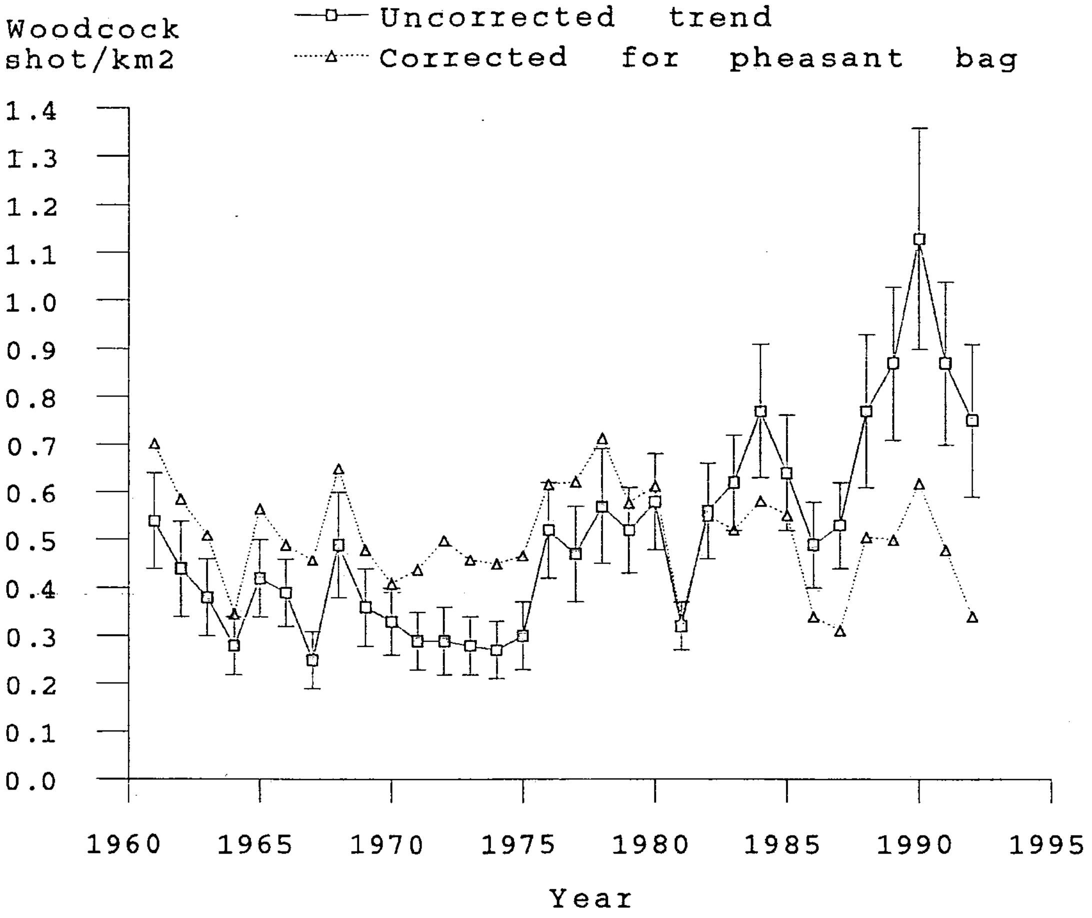
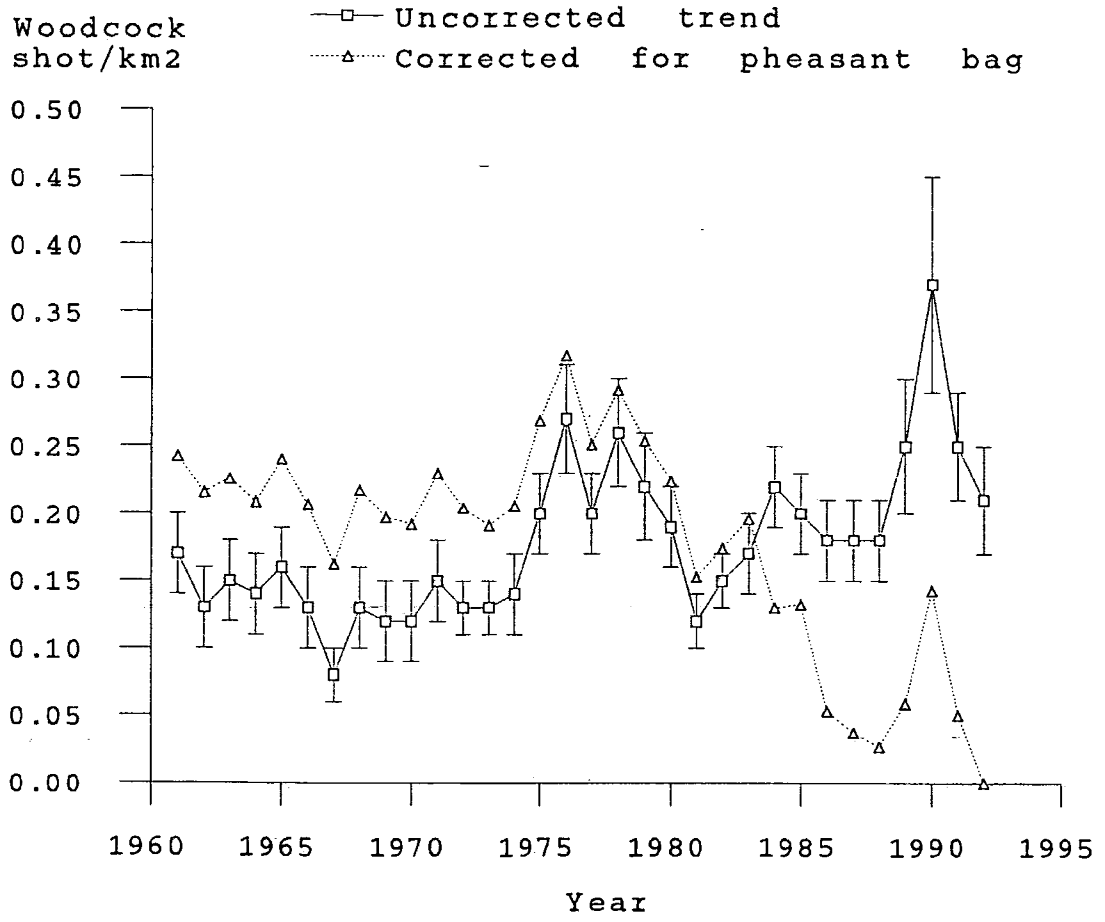


Figure 3.15 The trend in the annual mean woodcock bag for Scotland (NGC regions 9 and 10) for 1961/62-1992/93. (Error bars are ±1se).



because there were not the concentrations of woodcock (probably mainly Continental birds) that were seen in parts of S England. The very high mean woodcock bags in N England and in Scotland in 1990/91 probably reflect a good breeding season: the woodcock at Whitwell Wood, Derbyshire certainly reared more young than average during 1990 (Chapter 6).

Pheasant shooting appears to have had a greater influence on the size of the mean annual woodcock bags in N England and Scotland than in S England, presumably because relatively few pheasants were shot per woodcock in these regions prior to the main increase in pheasant shooting during the 1980s. The correlations between the annual mean pheasant and woodcock bags were 0.87 (df=30, $p<0.001$) for N England and 0.65 (df=30, $p<0.001$) for Scotland. The mean pheasant bag in both N England and Scotland remained fairly stable during 1961/62-1974/75 but increased rapidly during 1975/76-1990/91 from 15.8 birds/km^2 to 54.4 birds/km^2 in N England and from 4.5 birds/km^2 to 17.3 birds/km^2 in Scotland. The indication from the woodcock bag trends corrected for the mean pheasant bags is that there was no increase in the size of the wintering woodcock populations in N England or Scotland during the 1980s. The corrected trend for N England suggests a relatively stable wintering population since the early 1960s, whilst that for Scotland implies that there has been a sharp decline in wintering woodcock since 1980.

3.5 DISCUSSION

Spot-lamp counting proved to be a reliable method for assessing woodcock density in winter and should be of particular value for monitoring woodcock numbers in areas where no shooting takes place and information cannot be gained from bag records. The Lizard Peninsula clearly supported high densities of wintering woodcock and the mild climate and predominance of grass fields probably contributed to making the area attractive for woodcock. The spot-lamp counts in Cornwall, Wiltshire, Derbyshire and Co. Durham suggested that woodcock densities were generally lower in central and N England in most years compared with S England and highlighted the scale of the difference in winter between mild western regions such as Cornwall, where no woodcock breed (Lewis & Roberts 1993), and the main breeding areas in N England and Scotland. The low densities of woodcock in Derbyshire were probably partly due to the very low proportion of grass fields in the area (Chapter 4).

The number of woodcock wintering in Britain each year is clearly dependent on the size of the annual influx of birds from Fennoscandia and Russia, which is estimated to make up about 84-91% of the wintering population (Chapter 1). Annual differences in the number of Continental woodcock arriving will be most noticeable in S Wales and SW England where few woodcock breed. The increased numbers in Cornwall during 1989/90 suggest that 1989 was a good breeding season on the Continent and that the influx of migrant woodcock was larger than usual.

In certain circumstances, shoot data can clearly provide a useful indication of woodcock numbers in a given area. For instance, the fact that the shoots in Cornwall were conducted in a similar manner each year and that the harvest rates were similar from year to year, meant that the woodcock bag was a direct reflection of the woodcock density at the time of each shoot. Care is obviously needed when comparing woodcock densities calculated from shoots in different parts of the country because the harvest rate is likely to differ between areas, such that bag records may give a misleading impression of relative density.

Wilson (1983) concluded that wintering site fidelity was relatively high among woodcock in Ireland because 14% of the birds ringed at four sites returned in subsequent winters. However it is not possible to estimate a survival rate or the proportion of the woodcock alive that returned to Ireland from this figure. In the present study it was estimated that 69% of the woodcock alive each winter returned to the Lizard Peninsula. It has previously been assumed that the woodcock population wintering on the Lizard Peninsula, Cornwall is relatively stable, with few birds arriving or leaving between mid-November and mid-February (Hirons & Bickford-Smith 1983, Hirons & Linsley 1989). However, evidence from this study indicated that, in some years at least, both immigration and emigration took place during December. These were not just local movements, because one of the woodcock that left Lanarth in mid-winter moved 139km north-east to S Wales. This bird was in its first year, as were three of the four birds that were recovered at different wintering sites in subsequent years (section 3.4.6). Only two of these birds could be sexed with certainty, but both were males. Although currently based on very little evidence, there is a suggestion that the different age and sex groups amongst the woodcock on the Lizard Peninsula were behaving differently, with most of the woodcock passing through being first-year males. This was as expected, given that there was a high proportion of first-year birds on the Lizard Peninsula (about 70%) and that a larger proportion than expected were males (about 65%).

There were no additional ringing recoveries from the national dataset of woodcock ringed in SW England in their first winter (October-February) and recovered in subsequent winters, to support the possibility of a difference in wintering site fidelity between first-year and adult woodcock. There were three recoveries of woodcock ringed in their first winter in parts of S Ireland where woodcock do not breed (Lewis & Roberts 1993) and recovered the following year. One bird ringed in Co. Mayo on 22 January 1975 was recovered 13km from the place of ringing on 19 November 1976, one bird ringed in Co. Clare on 29 February 1980 was recovered in N Yorkshire on 27 October 1980, and the remaining bird was ringed in Co. Mayo on 17 December 1980 and recovered in S Yorkshire on 21 November 1981. These recoveries suggest that some first-year woodcock use different wintering sites in subsequent years, although the time of recovery of the second of these birds means that it might have been shot on migration back to Ireland.

At present, it is not known what causes differences in the timing and extent of immigration and emigration between years. The weather is likely to be important but the mean December air temperatures in central England were relatively mild during 1988/89-1992/93. It is possible that even in those years when the number of woodcock appeared to remain constant, there was in fact a movement of individuals through the study area on the Lizard Peninsula. The fact that there may be immigration and emigration throughout the winter in some years means that spot-lamp counts conducted in November and February cannot be used to estimate overwinter loss. Assuming that the situation with regard to the movement of Continental woodcock during the winter is similar in other parts of S England, where resident birds are also present, it is clearly impossible to assess the impact of a series of shoots upon the resident woodcock in a given area.

The average proportion of first-year woodcock among the wings received from Cornwall in the Woodcock Production Survey (a survey of woodcock wings collected from hunters throughout Britain and Ireland by the British Association for Shooting and Conservation) for the period 1981/82-1986/87 was 64% (Harradine 1988), a figure similar to those found at Trelowarren and Lanarth. This survey included wings from Lanarth but nevertheless provided some evidence that there was a relatively high proportion of first-year birds among the woodcock on other shoots in Cornwall. Comparison of the proportions of British woodcock ringing recoveries made by shooting during the first year and in later years suggested that first-year birds were unlikely to be more susceptible than adults to being shot (Chapter 2). Indeed, the Woodcock Production Survey showed variations in the age ratio amongst samples of woodcock that were shot throughout the country and in eastern England there was a bias towards adults.

Further evidence is required to support the finding of a biased sex ratio among adult woodcock on the Lizard Peninsula. Nevertheless, since the wintering woodcock population in Cornwall consists predominantly of Continental migrants and there is a suggestion from the only two spring ring recoveries that the woodcock on the Lizard Peninsula originate from the former USSR, it is conceivable that the predominance of females among the adult birds results from the shooting of roding males on the breeding grounds. Alternatively, the age and sex biases on the Lizard Peninsula may be indicative of a differential migration pattern similar to that recognized for a number of migratory waterfowl species, such as the pochard, *Aythya ferina*, and the tufted duck, *Aythya fuligula* (Salomonsen 1968). In these species the adult males leave the breeding grounds before the females and arrive on the wintering grounds first. The females and young have to move further south to find suitable wintering sites. As mentioned previously, there was a suggestion that most of the woodcock passing through the study area on the Lizard Peninsula were first-year birds. The occurrence of a high proportion of females among the adult woodcock at Lanarth gives some cause for concern about the large woodcock bags killed there.

The size of the woodcock bag in any particular year appears to depend on the winter temperature and the number of pheasants shot, the relative importance of these factors varying between different regions of Britain. The increase in pheasant shooting during the 1980s caused a larger change in the annual mean woodcock bag in N England and Scotland than other parts of Britain, because relatively small numbers of pheasants were previously shot in these regions. In central and S England and E Anglia, the areas traditionally renowned for pheasant shooting, it is likely that there was a proportionately smaller increase in the number of days devoted to pheasant shooting during the 1980s. The mean woodcock bags in Scotland and parts of N England were probably relatively low for two reasons. Firstly, grouse shooting is more important than pheasant shooting in these areas and very few woodcock are flushed during grouse shoots. Also, the open season for woodcock does not commence until 1 September in Scotland and 1 October in England, compared with 12 August for red grouse *Lagopus lagopus scoticus* and there are no Continental migrants present until October. The second reason is that an appreciable proportion of Scottish woodcock overwinter in Ireland (Chapter 2).

During the severe winter of 1962/63, unusually large numbers of woodcock were concentrated in the south and western counties of England and Wales (Dobinson & Richards 1964). On the basis of the mean woodcock bags per county during a mild winter (1979/80) and a cold winter (1980/81), Tapper & Hirons (1983) suggested that there was a redistribution of woodcock within Britain during cold winters. If this is the case, it probably only involves Continental migrants, as there is no evidence from ring recoveries that British woodcock move further from their natal or breeding sites in cold winters or cold spells within winters (Chapter 2). It is plausible that the resident and the migrant woodcock might follow different strategies in cold weather, because whilst the resident birds would probably benefit from remaining in the same place due to familiarity with the site, the migrant birds would lose little by moving as they would probably be more likely to encounter unfrozen feeding areas elsewhere. There is no direct evidence that more woodcock arrive in Britain during cold winters than mild ones, but there is a suggestion of this from increased numbers of observations of woodcock on the coast in cold winters (Dobinson & Richards 1964, Marchant 1982, Cramp & Simmons 1983). There is some evidence that woodcock experience increased mortality during cold spells (Ash 1964, Dobinson & Richards 1964, Baillie *et al.* 1986). Lapwings *Vanellus vanellus* feed in fields during the winter and are likely to encounter the same difficulty as woodcock in obtaining food during freezing conditions. Peach *et al.* (1994) have shown that both the adult and first-year survival rates of lapwings are lower in cold winters.

The indication from the annual woodcock bag trend for the UK is that the wintering population has remained relatively stable since 1961. Although the mean woodcock bags were larger during the 1980s this cannot be taken as an indication of larger numbers of overwintering migrants because the increase occurred at a time when there was a series of cold winters and an increase in pheasant shooting. During the phase of greatest increase in the woodcock bag in the UK (1974/75-1980/81) there was no increase in the bag in Denmark (Strandgaard & Asferg 1980), where woodcock are shot on passage from Scandinavia to Britain and other countries (Clausager 1974). Clearly, the trend in the annual mean woodcock bag for the UK is not a good measure of the status of the resident British breeding population, but the bags for Scotland and N England can provide some indication of how woodcock are faring in the main breeding areas because relatively few Continental woodcock winter there (Chapter 2). The woodcock shot in Scotland during September are undoubtedly resident birds and if these were recorded separately from the total annual bag they would provide a good guide to annual changes in the size of the post-breeding woodcock population.

4. THE FORAGING BEHAVIOUR OF WOODCOCK IN WINTER

4.1 INTRODUCTION

Breeding woodcock are associated with woodland and scrub, but in winter they are only dependent on these habitats for resting places and they feed at night in fields. Woodcock generally fly out from their diurnal resting places about 30 min. after sunset and return about 30 min. before sunrise and their diet in winter consists largely of earthworms and leatherjackets (Tipulidae larvae) (Hirons & Bickford-Smith 1983). Woodcock probably feed at night in winter because it provides the most profitable and safest feeding opportunities: the "preference hypothesis" proposed for nocturnal foraging in wildfowl and shorebirds by McNeil *et al.* (1992). There are much higher densities of earthworms in fields than in woodland and they are more available at night (Ralph 1957). Furthermore, avian predation is thought to influence the choice of feeding areas by woodcock during the breeding season when they are active in woodland during the day (Hirons & Johnson 1987) and in winter, when there is little ground cover, this factor is likely to be even more important. The fact that fields are used at night is consistent with the observation that most bird species, with the exception of some owls, engaged in flight at night utilize open habitats, well away from obstacles and clear of complex vegetation (Martin 1990).

Hirons & Bickford-Smith (1983) have shown that woodcock typically fly only short distances to feed at night (mean distance ± sd = 444±388m, maximum=1370m) and occupy small home ranges (9-22ha). However, their study relied on only five radiotagged individuals which were monitored in late winter and the intensity of radiolocations was insufficient to provide data on the pattern of field use each night. Waders foraging in flocks during the day have been shown to exhibit preferences between fields for feeding in winter, lapwings *Vanellus vanellus* and golden plovers *Pluvialis apricaria* choosing old pasture (>25 years old) over young pasture (<4 years old), cereal fields and plough (Barnard & Thompson 1985) and oystercatchers *Haematopus ostralegus* selecting grass leys in relation to the time since they were last ploughed (Heppleston 1971). This behaviour has been attributed to the higher density of earthworms in old pasture and the greater spatial and temporal predictability in the distribution of worm-rich patches. There is a suggestion that woodcock prefer permanent pastures over leys and cereal fields (Ferrand & Gossman 1988) but the reasons for this have not been determined.

Lapwings and golden plovers are able to use visual cues, such as the presence of other birds, the density and height of the grass and the number of worm casts and burrows, to locate the most profitable feeding areas (Barnard & Thompson 1985). Similarly, oystercatchers feed by sight during the day, but switch to tactile feeding at night (Hulscher 1976). Woodcock are almost certainly dependent on tactile feeding and in common with many scolopacid species, they possess many touch-sensitive nerve endings, such as Herbst's corpuscles, in the bill tip and a trigeminal expansion of the forebrain (Pettigrew & Frost 1985). Woodcock possess large eyes in relation to the size of the head, a characteristic that probably aids them in the initial location of fields at dusk, although large eyes have been suggested as an advantage for nocturnal foraging in plovers (Dugan 1981, Pienkowski 1983).

The purpose of the work described in this chapter was to examine the extent to which woodcock distinguished between fields of different food availability and to investigate some of the factors that may have acted as cues in the choice of feeding locations.

4.2 STUDY SITES

Fieldwork was conducted on the Lizard Peninsula, W Cornwall (grid reference *SW 7220*) because relatively large numbers of woodcock were known to winter there (Chapter 3) and their behaviour could be more easily studied than in other parts of the country.

4.3 METHODS

4.3.1 Identification of woodcock feeding sites

In order to assess differences in the use of different types of field by woodcock, 26 fields of five different types (permanent pasture, grass ley of three ages and winter wheat) were searched with a spot-lamp in mid-November 1992.

Woodcock feeding sites within fields were identified by marking the positions where woodcock were flushed from fields during spot-lamp counts in 1991 and 1992 with 0.5m canes. In cases where the bird was not disturbed, a cane was placed at the point of observation and notes were made on the distance and direction of the bird from the cane. The cane was then moved to the bird's feeding location the following morning.

4.3.2 Radiotracking and home range analysis

Radiotracking was used to obtain data on the sizes and utilization of home ranges by woodcock. Thirteen woodcock were caught on fields at night during 19-26 November 1992 (three at Trelowarren and ten at Lanarth) by using the spot-lamp to dazzle them. They were fitted with single-stage radio-transmitters (Biotrack Ltd., Wareham, Dorset) weighing 2g which were attached by means of figure eight harnesses made from 5mm elastic (Amlaner *et al.* 1978, Hirons & Owen 1982). Six of the transmitters had mercury tilt-switches which produced different pulse rates according to whether the woodcock were sitting or walking.

The woodcock were located with a portable M-57 receiver (Mariner Radar, Lowestoft, Suffolk) and a three-element Yagi antenna by following the path of increasing signal strength to within about 40m of the bird, when precise location by triangulation became possible. A diurnal position fix was recorded every two days and one to four radiolocations were determined each night. The maximum range of transmitter detection was about 300-400m when the birds were in cover by day and 500-700m at night when the birds were present on fields. Although the precise location of the birds could be determined in the field, difficulty was sometimes encountered in relating this location to its position on the map. This was especially true when birds were active in the centre of large fields (>15ha) and for this reason the size of grid squares chosen for recording radiolocations was 50m x 50m.

The radiotagged woodcock were monitored from 22 November until 12 December 1992 and the home range was regarded as the restricted area encompassing the diurnal resting sites and nocturnal foraging sites used by each bird during this period. The sizes of home ranges were calculated by means of minimum convex polygons (Mohr 1947, Southwood 1966) and 95% harmonic means (Dixon & Chapman 1980) using the program RANGES IV (Kenwood 1990). The minimum convex polygon was used because it is a non-parametric technique which is robust with regard to temporal autocorrelation of radiolocations (Swihart & Slade 1985, Harris *et al.* 1990) and is the most useful technique for comparing range size between studies. The harmonic mean is a widely used parametric method which is sensitive to areas of increased activity within the range. The distorting effect of fixes close to grid intersections in the harmonic mean method was reduced by adjusting the fix coordinates to the centre of each grid square (Spencer & Barrett 1984).

For comparison of total home range size between individual woodcock, the minimum convex polygon and harmonic mean range areas were assessed for the first 28 radiolocations for each bird. For two woodcock (birds 247 and 298) where fewer than 28 radiolocations were obtained, the home range size at 28 radiolocations was estimated from the increase in range size between five and 12 radiolocations, which was compared with a regression of the increase between five and 12 radiolocations against the home range size at 28 radiolocations for the other radiotagged woodcock (Harris *et al.* 1990). The regression equations are:

minimum convex polygon home ranges $y=-1.88+0.53x$

95% harmonic mean home ranges $y=0.15+0.24x$

where y is the home range size at 28 radiolocations and x is the increase in range size from five to 12 radiolocations. The nocturnal home ranges were similarly corrected to their size at 22 radiolocations on the basis of the increase in range size between five and ten radiolocations. The regression equations used for correcting the nocturnal home ranges are:

minimum convex polygon home ranges $y=-1.34+0.50x$

95% harmonic mean home ranges $y=2.74+3.25x$

where y is the home range size at 22 radiolocations and x is the increase in range size from five to ten radiolocations.

Two of the woodcock (one at Trelowarren and one at Lanarth) were monitored automatically for two nights each using a Rustrack chart recorder, with a chart speed of 10cm/h, linked to the radio receiver (Hirons & Owen 1982, Kenward 1987). Bouts of activity were characterized by fluctuating signal levels whereas a constant chart trace was produced when the woodcock were immobile. The equipment was set up so that the birds could be detected within a 108° arc upto a distance of 300m in front of the antenna (an area of approximately 8.5ha). The range of detection was verified during the day using a spare radiotag. Additional data for two bird-nights and four bird-days were supplied by Dr. G. Hirons. The activity charts from the woodcock monitored in this way were divided into 5 min. periods and each period was scored according to whether or not the bird was active. Percentage activity in each hour of the day and night was calculated from the proportion of active periods.

4.3.3 Measurement of parameters to determine the reasons for the use of particular fields by woodcock

Differences between field types

Invertebrate availability and relative soil softness were measured for 26 fields comprised of permanent pastures, three ages of grass leys and winter wheat during November 1992. Invertebrates were sampled using a soil auger (110mm diameter, 95cm^2 surface area) to remove cores to a depth of 70mm, the average length of the woodcock bill. A total of 10-28 pairs of randomly sited soil cores were taken from each field between the hours of 21.00 GMT and 01.00 GMT and placed in labelled polythene bags. Samples were hand-sorted within 42h of collection and all invertebrates greater than 2mm in length were counted and stored in 10% formalin. Hand-sorting was used because it is the most effective technique

(Heppleston 1971, Edwards & Lofty 1977). Chemical extraction techniques are thought to result in an overestimate of deep-dwelling species such as *Lumbricus terrestris* that are forced up and an underestimate of surface-dwellers such as *Allolobophora chlorotica*, *A. caliginosa* and *A. rosea* that tend to move down (Barnard & Thompson 1985). In addition, chemical extraction was difficult to perform at night and is known to be less efficient when the soil is waterlogged (Satchell 1967), as was the case for some of the fields sampled.

Broken worms estimated to be more than half the length of the intact animal were counted as whole worms. *Lumbricus terrestris* were counted separately from all the other species of earthworms. Invertebrates other than earthworms were grouped. They included dipteran larvae, particularly leatherjackets (Tipulidae larvae), and adult and larval Coleoptera. The biomass of the earthworms and other soil invertebrates was measured as wet weight to the nearest 0.001g. As weights were determined after preservation in formalin, a correction for weight loss during storage was determined by weighing a sample of 20 earthworms alive and after two months storage in 10% formalin. The value of the correction was x1.08, which was applied to the measured earthworm wet weights. No separate correction was determined for the other soil invertebrates and the same correction of x1.08 was used. A relative measure of soil softness between fields was obtained from the mean depth (mm) of ten drops of a pointed steel rod (weight 468g, with the end 200mm milled to a width of 2mm) from a height of 2m; a method similar to that employed by Lofaldli *et al.* (1992). This measure is hereafter referred to as the soil penetrability.

The predictability of available earthworm density and other soil invertebrate density within fields was examined by taking repeat samples from the same locations; three samples at three locations in each of five different fields at Trelowarren on two or three nights. The fields chosen were all used by woodcock at some stage during the spot-lamp counting and consisted of two permanent pastures, a second year ley, a first year ley and a winter wheat field.

Comparison of fields visited and avoided by woodcock

Differences in invertebrate availability, soil penetrability and grass length were examined for 17 fields, all permanent pastures or old leys (>2 years in grass), that were classified into three groups according to their use by feeding woodcock. These groups were fields in which woodcock were seen during all visits in November 1992, in which they were seen on 33-75% of visits and in which they were never seen.

Regression analysis between fields

Twelve independent variables describing each of 12 fields were measured in November 1991 and 14 independent variables were measured in 20 fields during November 1992, for use in a forward stepwise multiple regression to determine the factors most influencing the choice of field by woodcock at night. The variables that were entered in the regression analysis are given in Table 4.1. Fields that were

Table 4.1 Summary of the variables used in a multiple regression analysis to explain the choice between fields by feeding woodcock in winter.

Dependent variable

Mean woodcock density (number/km^2)

Independent variables

1. Area of field (ha)

2. Length of the field perimeter
3. Percentage hedgerow in field boundary
4. Percentage woodland in field boundary

5. Distance from centre of field to edge of nearest wood (m)

#6. Field type: (a) Permanent pasture
(b) Ley in grass for >2 years
(c) 2nd-year ley
(d) 1st-year ley

#7. Grazing: (a) No livestock
(b) Horses
(c) Cattle for half the winter
(d) Cattle all winter
(e) Sheep

8. Grass length (mm) (1992 only)

#9. Soil moisture: (1992 only) (a) No moisture in topsoil (2cm)
(b) Moisture in topsoil (2cm)
(c) Some water on soil surface
(d) Field surface covered by 0-1cm water
(e) Field surface covered by >1cm water

10. Soil penetrability (mm)

*11. Mean available earthworm density (no./m^2)
*12. Mean available earthworm biomass (g/m^2)

*13. Mean available density of other invertebrates (no./m^2)
*14. Mean available biomass of other invertebrates (g/m^2)

#Where there was more than one category per variable, dummy matrices were used.

*Of these variables only 11 and 13 or 12 and 14 were used in the same analysis.

either visited or avoided by woodcock were included but the analysis was restricted to grass fields. The analyses were conducted twice; once using invertebrate density and once using invertebrate biomass. The coded variables field type, grazing intensity and soil moisture were substituted by dummy matrices before entry into the multiple regression. The percentages of hedgerow and woodland in the field boundary were arcsin transformed.

Plots of the studentized residuals against the mean woodcock density and each of the independent variables were examined for violations of the assumptions of linearity, equality of variance and normality made in multiple regression analysis (Norusis 1988). These revealed that the assumptions were met and that none of the variables required transformation. Sokal & Rohlf (1981) state that the number of observations in a multiple regression analysis must be at least one greater than the number of independent variables, but that larger samples relative to the number of independent variables are desireable. For this reason, the set of independent variables was split into two groups and two separate analyses were conducted to determine the effect on the selected predictor variables. This made no difference to the result in either year.

Comparison of feeding and random sites within fields

Invertebrate density in the top 7cm of soil and soil penetrability were determined at 15 feeding locations within permanent pastures and old leys (>2 years in grass) identified during spot-lamp counts, and at 15 paired random locations. Each paired random location was sited 150m from a feeding location in a random direction. Each pair of feeding and random locations were within the same field. Ten soil samples were taken at each of the feeding and random sites.

4.4 RESULTS

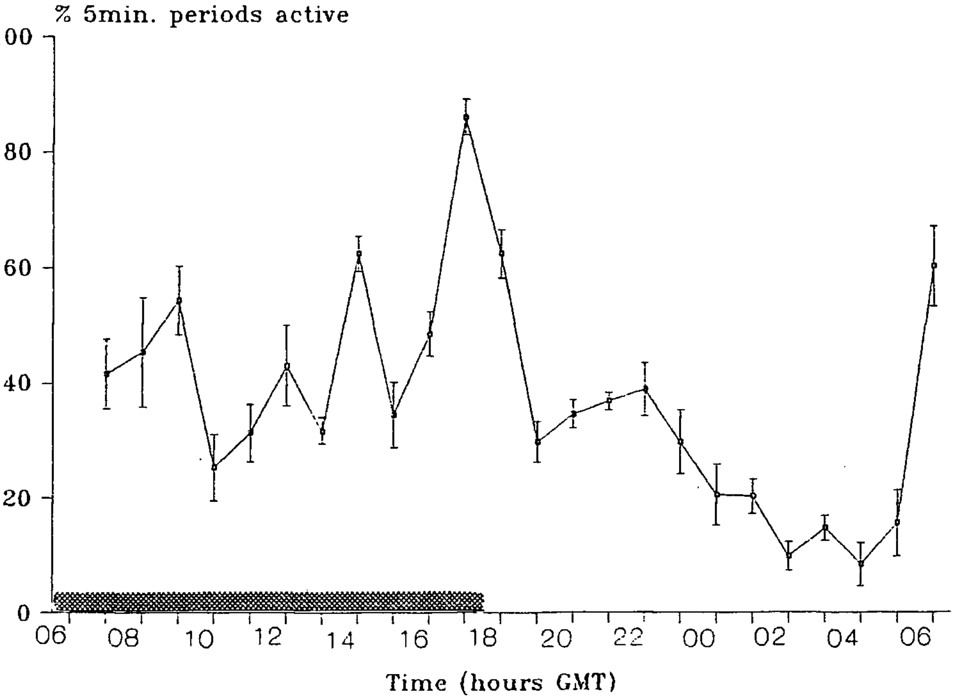
4.4.1 Activity pattern of the radiotagged woodcock

Of the 13 woodcock tagged in November 1992, eight yielded information for ten to 22 days each and a mean of 29 radiolocations was obtained for these birds (Appendix 4.1). Of the five birds which did not provide any useful information, four were lost within two nights of tagging and one remained in the study area but could not be detected due to interference. It was shot on 31 December 1992 within 1km of the place of marking. Extensive searches of the study area were conducted for the four missing birds by night and day, but it was concluded that they left the area soon after tagging. None were shot later in the season. No adverse effects on behaviour resulting from radiotagging were perceived among the woodcock that remained on the study area, although three of the woodcock never returned to the fields where they were caught. One bird (228) was recaptured at the end of the study and two (349 and 336) were shot later in the same winter (31 December and mid-January), both within 1km of their tagging locations.

The radiotagged woodcock were most active just after flying out to fields to feed at dusk and just before returning to woodland at dawn (Figure 4.1). They were as active during the day as during the night but the periods of activity were of shorter duration in the day (means; day, 4.3 min., n=60; night, 6.9 min., n=39). This degree of activity during daylight hours was unexpected as the woodcock moved only very short distances (<30m) within the woodland during the course of a day. Nevertheless, these data relate only to whether the birds were active and not to whether they were feeding. There did not appear to be distinct feeding and resting periods at night although the radiotagged woodcock were undoubtedly least active between 02.00 GMT and 06.00 GMT. On average, the radiotagged woodcock were only active for 17±17 min./h (±sd, n=11 hours; 19.00-06.00 GMT) during the night.

On at least six nights (5%) from a total of 112 bird-nights monitored for all the radiotagged woodcock, certain individuals left their resting places to feed on fields appreciably later than usual or returned appreciably

Figure 4.1 Twenty-four hour activity pattern of radiotagged woodcock on the Lizard Peninsula, Cornwall in winter (n=4 bird-days, 6 bird-nights). (Error bars are ±1se; shaded bar indicates the period of daylight).

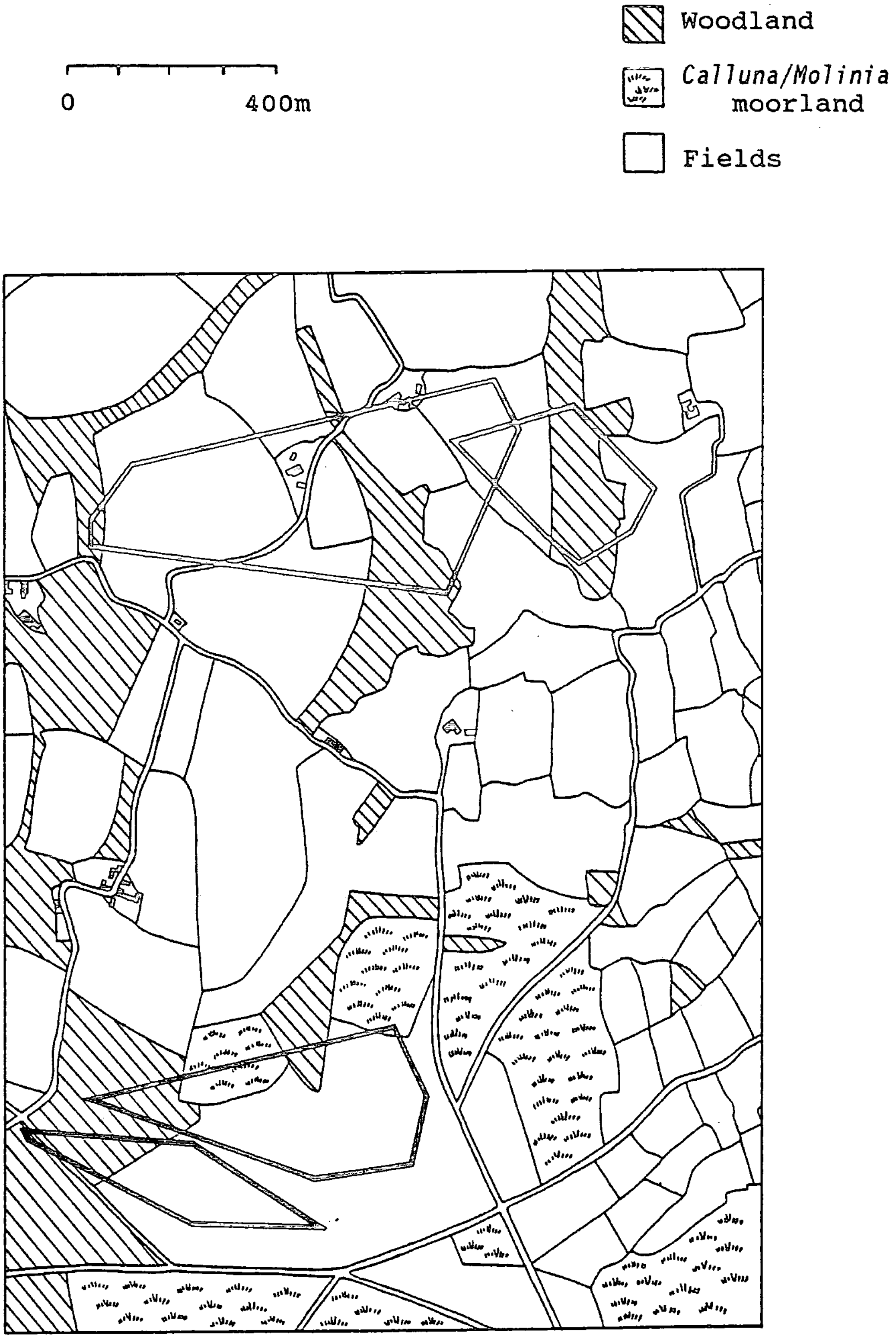


earlier. The latest recorded woodland radiolocation followed by a field radiolocation was 01.35 GMT and the earliest woodland radiolocation to have been preceeded by a field radiolocation was 00.30 GMT. Three of the eight radiotagged woodcock each spent at least one entire night in woodland. There was no consistency between birds with respect to the nights on which this occurred. Two of the woodcock flew to moorland instead of fields on a total of eight nights (7% of the bird-nights monitored). These birds did not move during the night and it was assumed that they were not feeding on the moorland.

4.4.2 The home range of woodcock in winter

Each of the woodcock used fields and woodland close to the point of capture (Figure 4.2) and the mean distance flown from cover to fields used for feeding was 322±175m (±sd, maximum 620m, n=8 birds). The size of standardized minimum convex polygon home ranges used by each bird during the period of study ranged from 7-58ha (Table 4.2). Asymptotic areas derived from plots of the number of radiolocations (*x*) against home range size (*y*) (Stickel 1954, Hawes 1977) were reached for the six woodcock for which 28 or more radiolocations were obtained after 9-30 radiolocations. A mean incremental range area plot (Kenward 1982) for these six birds revealed that on average the asymptote was reached after 23 radiolocations. Home range asymptotes were not reached for birds 298 and 247 because too few radiolocations were obtained (n=12 and n=19). The complete home ranges include areas that were

Figure 4.2 Minimum convex polygon home ranges of four radiotagged woodcock at Lanarth, Cornwall during 22 November-12 December 1992.



simply flown through by the birds at dusk and dawn. In the case of bird 247 at Traboe Cross, the relatively large home range results from the fact that the fields in this area are interspersed by large tracts of moorland, which account for approximately 34ha (83%) of the total uncorrected range area. The radiotagged woodcock exhibited high fidelity to their woodland resting sites and five of the eight birds used the same site throughout the study period. One of the woodcock was accidentally flushed from its resting place during the day and flew 137m to a new site. It continued to use the new resting site following the disturbance and did not visit the old site again. The mean distance of the diurnal resting sites from the nearest woodland or ride edge was 29±11m (±sd). The very small nocturnal ranges showed that the birds repeatedly returned to a small number of fields to feed and indicated that particular fields were selected.

Only occasionally did any of the woodcock change the field in which they fed during the course of one night. From a total of 55 pairs of consecutive radiolocations, recorded at approximately two hour intervals, within nights, field changes only occurred in four cases (7%). The two birds monitored automatically both remained within the area of detection (8.5ha), and certainly in one case in the same field, for the duration of each night. There was more variation in the field used for feeding by each bird between nights, although certain fields were used for up to 11 consecutive nights (Figure 4.3). The number of fields used by each radiotagged bird and the time between field changes

Table 4.2 Home range areas of eight woodcock radiotracked on the Lizard Peninsula, Cornwall during the period 22 November-12 December 1992.
Total home ranges (calculated from day and night radiolocations) are standardized on 28 radiolocations and nocturnal ranges (calculated from night radiolocations only) are standardized on 22 radiolocations.

Radio freq.	Number of radio-locations		Minimum convex polygon area (ha)		95% harmonic mean area (ha)	
	Total	Night	Total	Nocturnal	Total	Nocturnal
Lanarth						
218	36	29	7.4	5.4	4.7	2.7
228	28	22	9.1	7.9	8.3	5.6
247	19	13	57.5*	57.9#	55.6*	29.8#
319	31	27	27.3	21.5	16.6	16.9
349	37	30	9.6	7.0	3.7	2.0
Trelowarren						
298	12	10	15.0*	11.2#	4.1*	5.4#
309	36	31	12.5	10.5	4.5	2.3
336	30	25	29.1	21.6	21.4	12.9

*Estimate of home range size at 28 radiolocations derived from the increase in range size from five to 12 radiolocations.

#Estimate of home range size at 22 radiolocations derived from the increase in range size from five to ten radiolocations.

The nocturnal minimum convex polygon home range for bird 247 and the nocturnal harmonic mean home range for bird 298 obviously cannot be larger than their respective total home ranges. The discrepancies are due to the use of different equations for the estimation of the nocturnal and total home ranges for these birds.

The home range for bird 247 was larger than the home ranges for the other birds because the fields used by bird 247 were separated by large tracts of moorland. These comprised approximately 83% of the uncorrected total home range areas.

Figure 4.3 Patterns of field use at night by eight radiotagged woodcock on the Lizard Peninsula, Cornwall during 19 November-12 December 1992.

Different letters represent different fields. The diagonal hatched blocks indicate nights spent on moorland, the cross-hatched blocks indicate nights spent in a dense hedgerow and the black blocks indicate nights spent in woodland.

Black circles indicate when the birds were accidentally flushed.

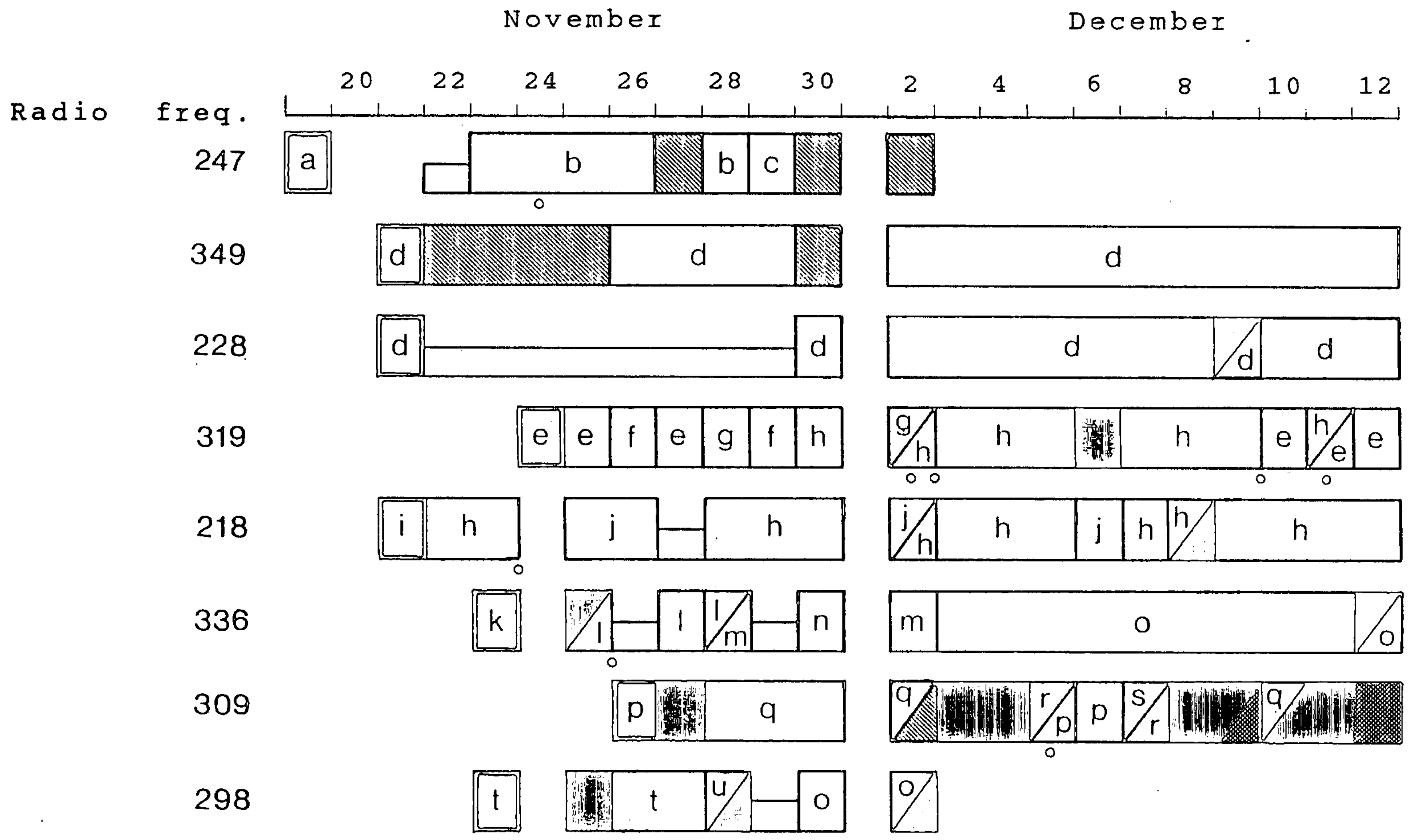


Table 4.3 The number of fields visited by eight woodcock radiotracked on the Lizard Peninsula, Cornwall during 22 November-12 December 1992 and the mean time spent on a field before changing to another field.
Changes between and within nights are included but the night of initial capture is excluded. Changes induced as a result of disturbance by the observer are omitted.

Radio freq.	Number of nights monitored	Nights spent in woodland or on moorland	Total no. of fields visited	Total no. of changes	Mean time (nights) between each change of field*
Lanarth					
218	18	0	2	5	2.4
228	12	0	1	0	(≥12.0)
247	9	3	2	1	5.0
319	17	1	4	7	1.8
349	20	5	1	0	(≥15.0)
Trelowarren					
298	6	1	3	2	1.5
309	15	7	4	4	1.8
336	15	0	4	4	1.3

*The nights spent on the last field visited have been excluded because the interval until the next change of field was incomplete. For this reason a mean interval could not be calculated for birds 228 and 349.

is summarised in Table 4.3. Bird 228 was not located on any of the fields within 1km of its diurnal resting place for eight nights following tagging and it is not known how many fields were used during this period. The mean time between each change of field was not significantly different between individuals (F=0.72, df=5,18, N.S.) or between the birds at Trelowarren and Lanarth (F=0.97, df=1,22, N.S.). The mean distance between the different fields used by the radiotagged woodcock on different nights was 327±134m (±sd). Birds 228 and 349 behaved differently, in so far as they did not change fields at all. This may have been because they both visited a particularly large field (22.6ha). Examination of the movements of 16 ringed woodcock recaptured during the winter they were marked revealed that ten had stayed in the same field and that six (38%) had made appreciable movements (mean±sd, 1018±261m) to new fields. There was no significant difference in the mean time between marking and recapture for the two groups of birds (recaptured in same field 24±28 days (±sd); recaptured in different fields 28±34 days (±sd); t=0.26, df=14, N.S.).

On eight occasions radiotagged woodcock were accidentally flushed by the observer whilst radiolocations were being made. In only one instance did the bird return to the same field that night. In the other seven cases the birds moved short distances (mean 395m) to fields which they had used on previous nights (adjacent fields in three cases). One bird flushed from the same field on two separate nights flew to the same location within the same new field. These fields were used for one to three nights following the disturbance.

4.4.3 Evidence for selection between fields by woodcock at night

Spot-lamp counts revealed significant differences in the mean number of woodcock seen per field, as demonstrated in Chapter 3. The difference in woodcock numbers between fields was confirmed by the counts on 12 fields at Trelowarren and 24 fields at Lanarth during November and December 1991. The mean number of woodcock per field ranged from 0 to 7.83 and one-way ANOVAs were significant; Trelowarren $F=3.38$, $df=11,75$, $p<0.01$; Lanarth $F=8.86$, $df=23,69$, $p<0.01$. Plots of the number of woodcock against field size gave linear relationships with $r^2=0.26$ ($n=12$) at Trelowarren and $r^2=0.25$ ($n=24$) at Lanarth, suggesting that field size alone only explained a small proportion of the variation in field use by woodcock. The differences in field use were still significant when based on woodcock density per field (Trelowarren $F=3.77$, $df=11,75$, $p<0.001$; Lanarth $F=4.98$, $df=23,69$, $p<0.001$) and woodcock density has therefore been used to examine the importance of other field parameters.

Examination of the spot-lamp counts conducted in November 1992 with respect to the use of different field types by woodcock revealed a clear preference for permanent pastures (Table 4.4). The significance of field type with respect to the available invertebrate biomass and soil penetrability is shown in Figure 4.4. The density and biomass of earthworms and other soil invertebrates per field were highly correlated (earthworms $r=0.73$, $df=19$, $p<0.001$; other soil invertebrates $r=0.73$, $df=19$, $p<0.001$) and the pattern of available invertebrate density against field type were similar to those for biomass.

The earthworm biomass available to woodcock was highest in permanent pasture but a similar biomass was present in second-year leys. The earthworm biomass in winter wheat fields and first-year leys was approximately half that found in permanent pasture and leys older than two years and the difference between the five groups of fields was

Figure 4.4 Differences in (a) woodcock density, (b) soil penetrability, (c) available earthworm biomass and (d) the avialable biomass of other soil invertebrates with field type (1 permanent pasture, 2 grass ley >2 years old, 3 second-year ley, 4 first-year ley, 5 winter wheat). (Error bars are +1se; letters indicate no significant difference between pairs of values in the Duncan multiple range test, $p \geq 0.05$).

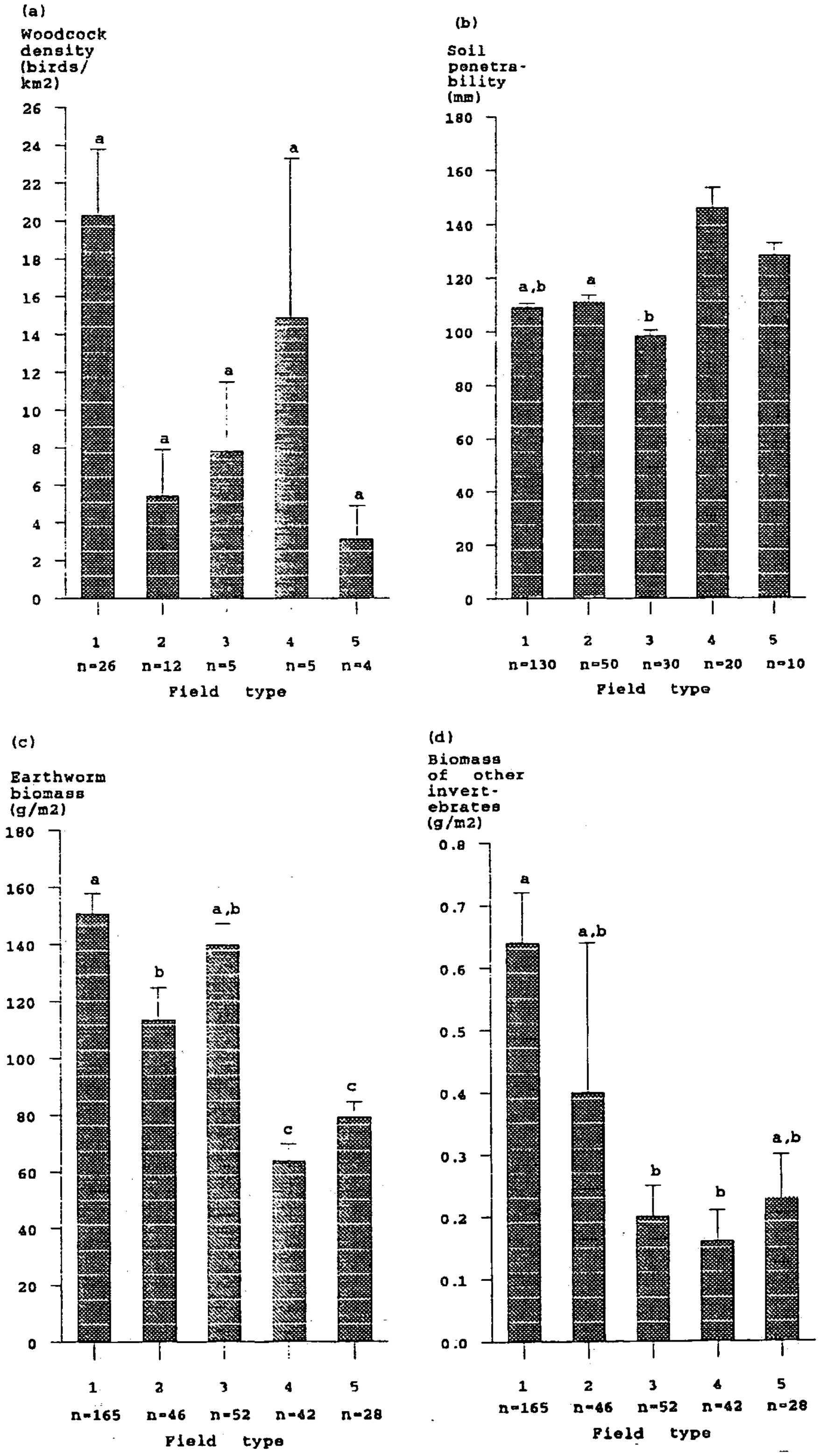


Table 4.4 Preference in the type of fields selected by woodcock for feeding in Cornwall during November 1992.

Field type	Fields searched	Total area (ha)	Mean no. of woodcock	Mean density of woodcock (birds/km^2)
Permanent pasture	11	74.1	19.67	26.5
Ley >2 years old	6	40.7	3.16	7.8
Second-year ley	3	28.7	1.33	4.6
First-year ley	4	16.5	2.50	15.2
Winter wheat	2	28.0	0.67	2.4

statistically significant (one-way ANOVA F=12.99, df=4,328, p<0.001). There was also a significant difference between the five groups of fields with respect to the available biomass of other soil invertebrates (F=3.57, df=4,328, p<0.01). Permanent pasture supported the highest biomass of soil invertebrates other than earthworms and the difference in biomass between permanent pasture and first-year and second-year ley was significant (as revealed by the Duncan multiple range test, Figure 4.4). The first-year leys and winter wheat fields were significantly softer than the other field types. Plots of woodcock density against soil penetrability and available invertebrate density and biomass for 19 grass fields of a range of ages in 1992 revealed that woodcock density was most highly correlated with the density of invertebrates other than earthworms (soil penetrability r=-0.37, df=17, N.S.; earthworm density and biomass respectively r=-0.01, df=17, N.S. and r=0.21, df=17, N.S.; density and biomass of other soil invertebrates r=0.51, df=17, p<0.05 and r=0.37, df=17, N.S.).

4.4.4 Predictability of soil invertebrates within fields

Of the five fields at Trelowarren from which multiple invertebrate samples were taken from the same sites, there were no significant differences in available earthworm density between sampling dates for any of the fields. There was a significant difference between sites within one of the permanent pastures and in the first-year ley and winter wheat fields (Table 4.5). This suggested that earthworms were less patchily distributed within the older grass fields than in the first-year ley and winter wheat fields. The other soil invertebrates occurred at far lower available densities than earthworms and there were no significant differences between sampling sites or dates in any of the fields (Table 4.5). The mean coefficient of variation for earthworm density within the grass fields was significantly lower than that for other soil invertebrates (earthworms 0.50±0.04 (±se), n=19 fields; other invertebrates 1.45±0.16 (±se), n=19 fields; paired t-test t=6.12, df=18, p<0.001). This suggests that there was greater variability in the number of invertebrates other than earthworms between individual samples and that the intensity of sampling was probably not sufficicent to detect any differences in density between the three random sites within fields.

Table 4.5 Spatial and temporal predictability of available soil invertebrate density (no./m^2) within fields, Trelowarren 1992 (one-way ANOVAs).
Three samples were taken at each of the sites within the permanent pastures and the winter wheat field on two dates (30 November and 10 December). Three samples were taken at each site in the two grass leys on three dates (24 November, 30 November and 10 December).

Field type	Random site (+ no. of samples)	Mean density of available earthworms per site (±se)	F	Mean available density of other invertebrates (>2mm) per site (±se)	F
Permanent pasture (field 1)	1(6)	991 ±140	F=4.69	43.8 ±16.2	F=0.18
	2(6)	824 ±155	df=2,15	43.8 ±16.2	df=2,15
	3(6)	465 ± 50	p<0.05	61.4 ±34.4	N.S.
Permanent pasture (field 2)	1(6)	675 ± 75	F=0.26	35.1 ±11.1	F=2.50
	2(6)	622 ± 97	df=2,15	8.8 ± 8.8	df=2,15
	3(6)	596 ± 57	N.S.	8.8 ± 8.8	N.S.
Second-year ley	1(9)	573 ± 60	F=1.16	5.8 ± 5.8	F=0.68
	2(9)	713 ± 63	df=2,24	23.4 ±12.7	df=2,24
	3(9)	812 ±173	N.S.	17.5 ±12.4	N.S.
First-year ley	1(9)	357 ± 34	F=7.80	5.8 ± 5.8	F=0.56
	2(9)	520 ± 75	df=2,24	17.5 ±12.4	df=2,24
	3(9)	234 ± 35	p<0.01	23.4 ±15.5	N.S.
Winter wheat	1(6)	386 ± 78	F=8.10	26.3 ±18.0	F=0.57
	2(6)	517 ± 46	df=2,15	26.3 ±11.8	df=2,15
	3(6)	175 ± 54	p<0.01	8.8 ± 8.8	N.S.
Differences between dates all non-significant, for example:					
Winter wheat	30 Nov(9)	403 ± 68	F=0.85	17.5 ± 8.8	F=0.14
	10 Dec(9)	316 ± 67	df=1,16	23.4 ±12.7	df=1,16
			N.S.		N.S.

4.4.5 Differences between fields selected and avoided by feeding woodcock

During the spot-lamp counts in November and December 1990-1992, woodcock were seen on grass fields ranging from 0.7-22.6ha in size, and there was no suggestion that the small fields (<2.0ha) were avoided. A comparison of the number of woodcock seen on all the grass fields at Trelowarren and Lanarth that were counted at least twice, revealed no significant differences in relation to field size in any year (Table 4.6).

Table 4.6 Use of grass fields by feeding woodcock during November and December 1990-1992 in relation to their size. Each field was counted twice during mid-November to mid-December. The expected number of woodcock is based on the area of the fields searched.

Year	Field size (ha)	Number of fields searched	Total area of fields searched (ha)	Number of woodcock seen during 2 counts of each field	Expected number of woodcock
1990	≤4.0	10	28.5	20	22.2
	4.1-8.0	9	51.7	40	40.3
	>8.0	4	52.0	43	40.5
				χ^2=0.38, df=2, N.S.	
1991	≤4.0	14	42.6	20	13.1
	4.1-8.0	12	65.4	20	20.0
	>8.0	8	110.6	27	33.9
				χ^2=5.04, df=2, N.S.	
1992	≤4.0	10	33.6	11	10.9
	4.1-8.0	7	42.5	14	13.7
	>8.0	8	103.5	33	33.4
				χ^2=0.01, df=2, N.S.	

Comparison of permanent pastures and old leys (>2 years in grass) that were used by woodcock (birds present on 100% and 33-75% of spot-lamp counts) and avoided (woodcock never seen during spot-lamp counts) revealed significant differences in grass length, soil penetrability and the density and biomass of invertebrates other than earthworms that were available to woodcock (Table 4.7). However, apart from the significant one-way ANOVA for grass length (F=4.60, df=2,14, p<0.05), there was no logical pattern to the field use by woodcock in relation to grass length. The Duncan multiple range test revealed that the grass length for fields in the 100% use category was not significantly different from that for the fields that were completely avoided. The soil was significantly softer in the fields that were avoided than in the two sets of fields that were used by woodcock, these having similar softness. The differences in the density and biomass of invertebrates other than earthworms between the three groups of fields were as expected if the woodcock fed on the fields in relation to the availability of this food source.

There was no significant difference in the available earthworm density or biomass between each category of fields, but comparison of the biomass with the density for each of the three groups of fields indicated that the earthworms in the fields used by the woodcock were heavier and therefore larger (Table 4.7). This was confirmed by the weights of individual earthworms from each of the three groups of fields. In fields where woodcock were present on 100% of visits each earthworm averaged 141±8mg (mean wet weight ±se, n=267). In fields where woodcock were present on 33-75% of visits the mean weight was 194±18mg (n=165) and in fields where woodcock were absent the mean weight was 112±5mg (n=369) (one-way ANOVA F=19.68, df=2,798, p<0.001). However, the mean weight of earthworms from fields that were

Table 4.7 Comparison of old leys (>2 years in grass) and permanent pastures used by feeding woodcock with those that were avoided during November and December 1992 (one-way ANOVAs).
Figures are the mean (±se) for each variable. Letters denote values that are not significantly different according to the Duncan multiple range test ($p \geq 0.05$).

Variable	Percent of visits on which woodcock were present			F-value and significance
	100% (n=5 fields)	33-75% (n=5 fields)	0% (n=7 fields)	
Grass length (mm)	9.4 ±0.6 *a,b*	7.9 ±0.6 *a*	11.4 ±1.0 *b*	F=4.60 df=2,14 $p<0.05$
Soil penetrability (mm)	105 ±5 *a*	101 ±3 *a*	120 ±4 *b*	F=6.09 df=2,14 $p<0.05$
Earthworm density (no./m^2)	566 ±72 *a*	525 ±63 *a*	651 ±110 *a*	F=0.51 df=2,14 N.S.
Earthworm biomass (g/m^2)	119 ±12 *a*	150 ±30 *a*	116 ±16 *a*	F=0.84 df=2,14 N.S.
Density of other invertebrates (no./m^2)	35 ±8 *a*	21 ±5 *a,b*	12 ±4 *b*	F=5.14 df=2,14 $p<0.05$
Biomass of other invertebrates (g/m^2)	0.87±0.15 *a*	0.61±0.16 *a,b*	0.29±0.09 *b*	F=5.49 df=2,14 $p<0.05$

used intermittently by the woodcock was greater than that from the fields that were used on all visits, and the Duncan multiple range test revealed that all three mean weights were significantly different from each other. The difference in the mean weight of the earthworms in each of the groups of fields could be attributed to the difference in the density of *Lumbricus terrestris*. The mean density in fields where woodcock were present on 100% of visits was 99±19 *Lumbricus terrestris*/m^2 (±se, n=36 samples); the mean density in fields where woodcock were present on 33-75% of visits was $132\pm25m^{-2}$ (±se, n=30 samples) and in fields where woodcock were absent it was $49\pm8m^{-2}$ (±se, n=45 samples). A one-way ANOVA revealed a significant difference in the density of *Lumbricus terrestris* between the groups of fields (F=6.20, df=2,108, $p<0.01$), but the Duncan multiple range test showed that the densities in the two sets of fields that were visited by woodcock were not significantly different.

Clearly, earthworms were present at far higher available densities than the other soil invertebrates and the relevance to woodcock of the differences in the density of these other invertebrates between fields depends upon their importance in the diet relative to earthworms. Stomachs from woodcock shot during daylight hours in Cornwall suggest that leatherjackets (Tipulidae larvae) are more important in the diet than earthworms, both numerically and in terms of biomass, and that earthworms only comprise a relatively small proportion of the total diet (Table 4.8). The numbers of animals belonging to each prey taxon were not corrected for different rates of digestibility because most of the animals, including some earthworms, were intact. The proportion of earthworms may be underestimated because they are likely to be digested faster than any of the other groups and the number of animals was partly estimated from the number of chaetae.

Table 4.8 Estimated frequencies of invertebrates in the diet of woodcock wintering in Cornwall, assessed by means of stomach analysis (G. Hirons, unpublished data; n=71 stomachs).

Prey taxon	Number of individuals *n*	% of total of *n*	Mean dry weight per taxon (mg)	% of total dry weight
Lumbricidae	83*	17.0	31.4	28.5
Scarabaeidae (adult)	2	0.4	11.6	0.3
Carabidae (adult)	24	4.9	26.9	7.1
Staphylinidae (adult)	21	4.3	4.1	0.9
Other adult Coleoptera	5	1.0	1.0	0.1
Coleoptera larvae	3	0.6	9.0	0.3
Dermaptera	25	5.1	9.0	2.5
Diplopoda & Chilopoda	43	8.8	29.4	13.8
Oniscoidea	2	0.4	8.9	0.2
Tipulidae larvae	261	53.6	16.0	45.7
Other Diptera larvae	18	3.7	3.0	0.6

*The number of earthworms was estimated from the number of intact animals and the number of chaetae on the basis that there were 1080 chaetae per earthworm (the mean of estimates made by Bouche & Gardner (1984) n=966 chaetae per worm, Wroot (1985) n=1080 chaetae per worm and Green & Tyler (1989) n=1191 chaetae per worm).

4.4.6 The relative importance of prey availability and other field parameters in determining the choice of particular fields for feeding by woodcock

The simple correlations between mean woodcock density and the independent field variables for 1991 and 1992 are given in Table 4.9. Among the independent variables, the field perimeter was significantly correlated ($p<0.05$) with field size in both years and the distance to the nearest woodland was significantly correlated with the field perimeter and the percentage of woodland in the field boundary. In 1991, soil moisture was significantly

Table 4.9 Correlation coefficients between woodcock density and the independent field variables (1991, n=12 fields; 1992, n=20 fields).
Critical values ($p<0.05$, two-tailed); 1991 $r=0.576$, 1992 $r=0.444$; * denotes a significant correlation coefficient.

Independent variable	Simple correlation coefficient, r	
	1991	1992
Field size (ha)	0.305	0.302
Length of field perimeter	-0.023	0.230
Percentage hedgerow in boundary	0.122	-0.028
Percentage woodland in boundary	-0.220	0.270
Distance to the nearest wood	-0.175	-0.190
Field type	-0.271	0.299
Grazing intensity	-0.209	-0.201
Grass length (mm)	-	-0.132
Soil moisture	-	0.251
Soil penetrability (mm)	0.282	-0.248
Earthworm density (no./m^2)	0.705*	-0.075
Earthworm biomass (g/m^2)	0.397	0.110
Density of other invertebrates (no./m^2)	0.568	0.459*
Biomass of other invertebrates (g/m^2)	0.349	0.347

positively correlated with soil penetrability and the distance to the nearest woodland and significantly negatively correlated with the percentage woodland in the field boundary. In 1992, soil moisture was significantly positively correlated with field size and field perimeter, implying that larger fields were wetter. Soil penetrability and field type were significantly negatively correlated in 1991 and significantly positively correlated in 1992.

The invertebrate prey availability was both expected and found to be one of the most important factors determining which fields the woodcock visited at night, and the earthworm density and the density of other soil invertebrates were the only two independent variables significantly correlated with woodcock density in either year. The available densities of earthworms and other soil invertebrates were not significantly correlated in either year (1991 r=0.43, df=10, N.S.; 1992 r=0.07, df=18, N.S.) and the selection of one of these variables in the multiple regression analysis would not have had much influence on the possible selection of the other.

The independent variables were entered into the stepwise linear regression with p=0.05 to enter and p=0.10 to remove. The density of woodcock per field was best predicted by available earthworm density in 1991 and the available density of other soil invertebrates in 1992 (Table 4.10). In both years, however, these factors only accounted for a small proportion of the variation in woodcock density between fields, and a large proportion of the variation, particularly in 1992, could not be accounted for by any of the parameters measured in this study. In neither year was more than one factor found to be significant.

Table 4.10 Summary of the results of the stepwise regression analyses of woodcock density (no./km^2) against the independent field variables (PIN=0.05, POUT=0.10).

Variable	Coefficient	se	t	r^2
1991				
Constant	-6.069	8.088	-	-
Earthworm density (no./m^2)	0.047	0.015	3.14	0.497
1992				
Constant	3.589	5.187	-	-
Density of other invertebrates (no./m^2)	0.450	0.206	2.19	0.210

Because the available densities of earthworms and other soil invertebrates in each field were not significantly correlated, fields that had high densities of available earthworms in 1991 were not expected to have high densities of other soil invertebrates in 1992. If the woodcock were selecting different types of invertebrate prey in each year, therefore, they would be expected to visit different fields. The null hypothesis that the woodcock visited the same fields to the same extent in both years was tested by plotting the woodcock density for 16 fields in 1991 against the woodcock density for the same fields in 1992 and comparing the slope of the regression with that expected, allowing for the difference in overall density between the two years. The overall density of woodcock in the study area in 1992 (13.2 birds/km^2) was lower than in 1991 (20.5 birds/km^2), such that the slope expected if the same fields were used in both years was b=0.644. The regression of the woodcock densities in the 16 fields in 1991 against those in 1992 was examined and found to be linear. The slope

(0.302±0.287 ±se) was not significantly different from b=0.644 (t=1.19, df=14, N.S.), but there was no significant correlation between the woodcock densities in the two years (r=0.27, df=14, N.S.). This suggests that some, but not all, of the fields selected by the woodcock were different in each year.

It is possible that the woodcock were not selecting fields solely on the basis of available earthworm density or the available density of other soil invertebrates, but on the combination of their relative abundances. In order to test this, an index of the relative availability of each prey type in each field was derived by expressing the density in each field in terms of the standard error of the mean density for all the fields. Assuming that earthworms and other soil invertebrates were equally important to the woodcock, an index of the availability of the combined prey types was obtained by adding the indices for each. Plotting the three indices against woodcock density in each year revealed that the availability of the combined prey types explained the woodcock distribution between fields slightly better than available earthworm density alone in 1991 (earthworms and other soil invertebrates r=0.75, earthworms alone r=0.71), but explained the woodcock distribution in 1992 no better than the available density of other soil invertebrates (earthworms and other soil invertebrates r=0.26, other soil invertebrates alone r=0.46). A multiple regression equation based on the index of availability of both prey types in 1991 only accounted for an additional 7%

of the variation in woodcock density compared with the equation for available earthworm density.

The most likely explanation for the fact that the choice of fields in which to feed by the woodcock was based on earthworm density in 1991 and on the density of other soil invertebrates in 1992 is the difference in the wetness of fields between years, which caused a difference in the relative abundance of earthworms and other soil invertebrates. The density of available earthworms in grass fields was significantly higher in 1992 (mean earthworm density (no./m^2 ±se); 1991 502±27, n=177; 1992 584±23, n=217; t=2.33, df=392, $p<0.05$) whereas the available density of other soil invertebrates was significantly greater in 1991 (mean density of other invertebrates (no./m^2 ±se); 1991 70±17, n=177; 1992 22±3, n=217; t=3.09, df=392, $p<0.01$).

The rainfall in Cornwall during November and December 1992 was appreciably higher than during November and December 1991 and this resulted in the fields being significantly softer in 1992 (mean soil penetrability (±se) in grass fields; 1991 84±1mm, n=372; 1992 107±2mm, n=130; t=11.0, df=500, $p<0.001$). As a consequence, both earthworm density and the density of other soil invertebrates in the older grass fields (>2 years in grass) were positively correlated with soil penetrability in 1991 (earthworm density r=0.56, df=7, N.S.; density of other invertebrates r=0.73, df=7, $p<0.05$), whereas in 1992 earthworm density was positively correlated with soil penetrability (r=0.49, df=15, $p<0.05$) but the density of other soil invertebrates was negatively correlated with soil penetrability (r=-0.45, df=15, N.S.). In 1991 it would therefore have been more profitable for the woodcock to feed in the wetter fields, whilst in 1992 the availability of soil invertebrates decreased with increased wetness, and it would have been more profitable for the woodcock to feed in the drier fields because earthworms were still available in these fields at as high densities as in the wetter fields in 1991. The simple correlation coefficients between woodcock density and soil penetrability in 1991 (r=0.282, df=10, N.S.) and 1992 (r=-0.248, df=18, N.S.) confirm that the woodcock did feed in the wetter fields in 1991 and the drier fields in 1992.

4.4.7 Choice of feeding site within fields by woodcock

There was no suggestion that woodcock selected particular areas within fields for feeding on the basis of prey availability. Paired t-tests on the data from the 15 pairs of feeding and random sites within permanent pastures and old leys (>2 years in grass) were not significant with respect to earthworm density (feeding locations 579±76m^{-2} (±se), random locations 665±74m^{-2} (±se); t=1.25, df=14, N.S.), the density of other soil invertebrates (feeding locations 55±18m^{-2} (±se), random locations 58±18m^{-2} (±se); t=0.17, df=14, N.S.) or soil penetrability (feeding locations 100±3mm (±se), random locations 100±2mm (±se); t=0.19, df=14, N.S.). Individual t-tests for each of the 15 pairs of sites revealed no more significant differences for any of the three variables than would be expected by chance.

The woodcock exhibited a clear tendency to avoid the edges of fields, particularly the outermost 20m, when feeding at night. Only 4% of the woodcock expected on the basis of area, during spot-lamp counts and radiotracking combined, were recorded in a 10m wide strip around the edge of each field and only 31% of the woodcock expected were recorded 10-20m from the field edge (Table 4.11).

Table 4.11 Avoidance of field edges by woodcock whilst feeding at night.

	Distance from field boundary 0-10m	10-20m	20-30m	Central area of field	
Spot-lamp counts (16 fields, 131ha)					
Woodcock seen	0	7	19	102	$\chi^2=46.8$
Woodcock expected	21.3	20.0	18.7	68.0	df=3 $p<0.001$
% of woodcock expected seen	0	35	102	150	
Radiotracking (16 fields, 109ha)					
Radiolocations	2	6	23	114	$\chi^2=48.7$
Number expected	24.1	22.2	20.4	78.3	df=3 $p<0.001$
% of woodcock expected seen	8	27	113	146	

There are two possible reasons why field edges were avoided by the woodcock. It could have been due to reduced densities of available soil invertebrates near to field boundaries or it could have been a means of avoiding foxes *Vulpes vulpes*, which were numerous at both Trelowarren and Lanarth. Comparison of available invertebrate densities within 20m of field boundaries and in the centre of fields suggested no significant reduction at the edges of fields (Table 4.12).

Table 4.12 Comparison of the available earthworm density and the available density of other soil invertebrates near the centre of fields and within 20m of field boundaries (one-way ANOVAs).
Three fields were examined; fields 1 and 2 were permanent pastures, field 3 was a first-year ley.

Field, position and number of samples	Mean available density of earthworms (no./m^2 ±se)	F-value	Mean available density of other soil invertebrates (no./m^2 ±se)	F-value
1 Centre (n=18)	666 ±52	F=0.26	8.8 ± 4.8	F=9.75
Edge (n=12)	627 ±54	df=1,28	35.1 ± 7.5	df=1,28
		N.S.		p<0.01
2 Centre (n=11)	1090 ±92	F=22.82	47.8 ±15.0	F=0.18
Edge (n=6)	465 ±50	df=1,15	61.4 ±34.4	df=1,15
		p<0.001		N.S.
3 Centre (n=18)	213 ±29	F=14.51	11.7 ± 8.0	F=0.10
Edge (n=24)	419 ±41	df=1,40	8.8 ± 5.2	df=1,40
		p<0.001		N.S.

4.5 DISCUSSION

The radiotagged woodcock in this study behaved similarly to those monitored by Hirons & Bickford-Smith (1983) and only flew short distances to fields to feed at night. Each of the woodcock visited between one and four fields during the 21 day period of radiotracking and they generally remained within an area of 0.5-1.0ha in the chosen field for the entire night (median field size at Trelowarren and Lanarth 4.5ha).

Woodcock may select particular fields at night on the basis of four factors: 1. the size of the field, 2. structural features, such as grass length and the degree to which the field is sheltered by hedgerows or woodland, 3. the type of field and 4. food availability. The absolute field size was shown to be relatively unimportant, although it does determine the importance of the edge effect (section 4.4.7), as the area of the edge strip comprises a smaller proportion of the total field area in large fields. Structural features could not account for the distribution of the woodcock on the Lizard Peninsula, and it was apparent that field type and the difference in the availability of invertebrate food between the fields were the most important factors.

Permanent pastures were clearly preferred by woodcock in Cornwall and this was probably due to the high density of earthworms and other invertebrates that these fields supported. The fact that second-year and older grass leys, which supported similar densities of available earthworms as permanent pastures, were not visited by woodcock as frequently as permanent pastures in 1992 suggests that the available density of soil invertebrates other than earthworms was an important factor influencing the decision to feed on permanent pastures. Soil invertebrates other than earthworms, especially leatherjackets (Tipulidae larvae), comprise an important component of the woodcock's diet in winter and it is possible that these are required to provide the woodcock with proteins that are not present in earthworms. The reduction in earthworm populations following the ploughing of grass fields is well documented (Evans & Guild 1948, Edwards & Lofty 1977, Barnard & Thompson 1985) and it is not surprising that winter wheat fields were avoided, especially as they only comprised a relatively small proportion of the study areas. Hirons (1983) noted that radiotagged woodcock located in fields in Derbyshire in March and early April selected grass fields even though these were outnumbered by arable fields by 18:1.

As well as differentiating between fields of different types, the woodcock selected certain fields within those of the preferred type. Amongst the permanent pastures and old leys (>2 years in grass) in Cornwall, they used fields in relation to the availability of invertebrate prey and there was a suggestion that the distribution of woodcock in these fields was determined by the relative availability of earthworms and other soil invertebrates. Despite the fact that the woodcock returned to the same feeding locations within particular fields each night, there was no evidence that they were exploiting patches of above average density of earthworms or other soil invertebrates. The distribution of available earthworms appeared to be more predictable within permanent pastures than first-year ley or winter wheat fields and the fact that the densities of both earthworms and other soil invertebrates were so similar between the paired feeding and random sites suggests that soil invertebrates were not highly patchily distributed within permanent pastures or old grass leys (>2 years in grass). It seems that any difference in the density of soil invertebrates within fields was far less important than the difference between fields.

The fact that the woodcock did not feed continuously throughout the night and on average were only active for 17 min./h suggests that they had no difficulty in obtaining sufficient food. Presumably an advantage of feeding at night is that birds are less prone to disturbance and species such as the woodcock, which do not require visual cues to locate their prey, are probably able to fulfil their food requirements just as quickly at night as during the day. Support for this idea is provided by the finding that when fields were free of frost and snow, the intake rates of lapwings wintering in Scotland were approximately twice as high at night as those achieved during the day (McLennan 1979). Comparison of the available earthworm densities in the Cornish pastures (300-815 worms/m^2, sample cores 7cm deep) with those from hand-sorted samples in other studies (Heppleston 1971; 418 worms/m^2 (cores 7.6cm deep), Barnard & Thompson 1985; 184-285 worms/m^2 (cores 3cm deep), Tucker 1992; 61-120 worms/m^2 (cores 5cm deep)) suggests that the fields in Cornwall were relatively rich in earthworms. The high earthworm densities combined with the mild, wet winter climate on the Lizard Peninsula probably meant that food limitation was unlikely to ever be a problem for the woodcock. This may explain why some of the radiotagged birds occasionally appeared to forego feeding on certain nights and remained in the woodland.

Of course, the possibility that the woodcock sometimes also fed in the woodland during the day cannot be ruled out. However, it seems unlikely that this occurred regularly as the radiotagged woodcock only moved very short distances (<30m) within the woodland during the day and there is evidence from the stomach volumes of woodcock shot at different times during the daytime and early evening that woodcock feed very little during daylight in winter

(Hirons & Bickford-Smith 1983). Foraging for earthworms in the woodland would have been less productive than in the fields (woodland $112\pm35m^{-2}$ (±se), n=30; fields $560\pm21m^{-2}$ (±se), n=245; F=53.53, df=1,273, $p<0.001$), but foraging for other large invertebrates would have been more productive (woodland $70\pm13m^{-2}$ (±se), n=30; fields $22\pm3m^{-2}$ (±se), n=245; F=33.25, df=1,273, $p<0.001$). As the analysis of woodcock diet in winter was based on stomachs from birds collected during daylight, it is conceivable that the proportion of earthworms consumed was higher at night. Any foraging in the woodland during the day was probably concentrated mainly on invertebrates other than earthworms.

High densities of foxes were present at both Lanarth and Trelowarren and an increase in the perceived risk of predation near field edges would explain why they were avoided by the woodcock. Foxes exhibit a predisposition for hunting along field boundaries (Macdonald 1976, 1979) and usually only venture across fields when foraging for earthworms or when disturbed by man. Brown hares *Lepus europaeus* prefer open ground with short vegetation at night (Fryelstam 1976, Tapper & Barnes 1986) and Holley (1992) concluded that this behaviour reduced the risk of hares being ambushed by foxes. Barnard & Thompson (1985) showed that both lapwings and golden plovers, feeding during the day, preferred large fields and they believed this was because the birds could reduce the risk of surprise attacks from avian predators (kestrels *Falco tinnunculus*, sparrowhawks *Accipiter nisus* and carrion crows *Corvus corone*).

The woodcock on the Lizard Peninsula generally fed within an area of 0.5-1.0ha each night and assuming that a minimum area of 0.5ha is required, it can be estimated that the minimum size of square field likely to be used by woodcock is 1.2ha if the outer 20m strip is avoided. The mean field size at Trelowarren and Lanarth was 6.6ha and it can be estimated that on average 29% of the area of all the fields, assuming that they were approximately square, was not available to the woodcock. This clearly has implications for management, as the importance of the edge effect will be determined by field shape and mean field size. The area of edge will be greater in long, narrow fields than ones which are approximately square. If the fields on a given farm are square but the mean field size is only 3ha, the proportion of the total area not used by woodcock would be 41%, whereas increasing the mean field size to 9ha would reduce the proportion of the area avoided by woodcock to 25%.

When disturbed at night woodcock move to another field within the home range that has been visited before. They appear to have a good spatial knowledge of their home ranges, since in all cases they were found in the same locations within the new fields in which they had been observed on previous nights.

Woodcock appear to prefer diurnal resting places near to a woodland edge. Such sites presumably afford better escape opportunities if birds are disturbed, as escape flights would not be possible in the centre of some woods, such as those dominated by dense *Rhodedendron*. In cases where landowners have an interest in maintaining winter habitat for woodcock, attention should be paid to maintaining rides and small clearings (about 2ha) in large blocks of woodland, *Rhodedendron* or gorse. This form of management used to be practised up to the 1930s on large sporting estates, particularly in Ireland, Wales and Cornwall (Shorten 1974).

5. HABITAT SELECTION AND DIET OF WOODCOCK DURING THE BREEDING SEASON

5.1 INTRODUCTION

Many studies of wild animals have examined habitat use because habitat changes are very often the key to the decline of a species or the reason for a rapid increase in the numbers of a pest species. In the case of the woodcock, woods holding breeding birds in lowland England and Scotland are often managed for pheasants *Phasianus colchicus* or as part of commercial forestry operations, whereas in the uplands suitable breeding areas are subject to grazing pressure from sheep and deer. There is currently little information on the preferred age, species composition and structure of woodland for breeding woodcock and hence on whether woodland managed for pheasants is beneficial for woodcock or on the effect of forestry practices such as thinning. There has been speculation that the decline in breeding woodcock in S England (Marchant *et al.* 1990) has been due to the fragmentation of large deciduous woods and the break-up of sporting estates since about 1930 (Shorten 1974). There is probably some validity in this suggestion because Fuller (1982) has shown that there is a higher incidence of breeding woodcock in large woods (>80ha). Parslow (1967) suggested that numbers of woodcock increased in SW Scotland, N England, N Wales and East Anglia during the early 1960s due to the planting of new conifer forests. This idea is plausible but there is currently very little information on the extent to which coniferous habitat is used by breeding woodcock.

For this study, two sites were chosen which were considered to be representative of the broad categories of habitat used by breeding woodcock in lowland and upland regions of Britain. The lowland site was located in central England and consisted of mixed deciduous woodland, although it was atypical of many lowland deciduous woods in terms of the species composition and the absence of a shrub layer in many parts. The upland woodland site was in E Scotland and consisted primarily of birch *Betula pubescens*, which forms the most abundant class of semi-natural woodland in the Scottish highlands (MacKenzie 1987).

The term habitat has been used frequently in ecological literature to describe the different plant communities within particular study areas but often on vastly different geographical scales. For the purpose of this study, a habitat is defined as a discrete and readily recognizable assemblage of herbs, shrubs and tree species of a particular age within a predefined area of a few square kilometres. Habitat use was assessed as the time spent in each habitat type whilst habitat selection occurred when a particular habitat was used more intensively than expected from its area relative to other habitats.

Radiotracking is the only feasible method of investigating small scale habitat use by a secretive species like the woodcock, simply because direct observation is very seldom possible. A large number of studies have used radiotelemetry to investigate habitat use by wild animals. However, all of the techniques recently reviewed by Alldredge & Ratti (1986) and by White & Garrott (1990) contain at least one of four shortcomings that may affect the validity of the analysis. These are an inappropriate level of sampling and sample size, the non-independence of proportions, differential habitat use by groups of individuals and an arbitrary definition of habitat availability (Aebischer *et al.* 1993). The use of compositional analysis (Aebischer & Robertson 1992, Aebischer *et al.* 1993) or Manly's selectivity index (McDonald *et al.* 1993) avoids the first three of these problems by placing the emphasis on the radiotracked animal as the sampling unit rather than the radiolocation and by circumventing the unit-sum constraint.

Definition of the boundary for a study area and hence the area of available habitat is usually arbitrary (Porter & Church 1987), and the very fact that an animal occurs within the study area is indicative that the animal has already made a selection. The effects of an arbitrary definition can be reduced by considering habitat utilization at two levels (Johnson 1980); first the selection of a home range within the boundary of the study area and then the use of restricted sub-areas within the home range. Clearly, particular habitats may be selected in preference to others for a range of reasons, including an increased availability of food, reduced susceptibility to predators, the number of roost sites or resting places and the availability of areas suitable for breeding and rearing young. Examination of habitat selection in two stages can reveal details about a particular species' habitat use that may be masked by simply comparing the distribution of radiolocations with the overall habitat availability in the study area (Aebischer *et al.* 1993). Radiotracking studies of American woodcock *Scolopax minor* have shown that individuals utilize intensively only small areas of even preferred habitat types (Dunford & Owen 1973, Morgenweck 1977).

Hirons (1983) showed that woodcock are active for a large proportion of the day during the breeding season and the availability of suitable feeding areas is likely to be an important factor governing the choice of particular habitats. However, information concerning the diet of the woodcock in the breeding season is very limited and is mainly based on stomach analyses of birds shot during March and April in Hungary and Rumania (Kiss & Sterbetz 1973, 1978) or the former Czechoslovakia (Koubek 1986). Such analyses are also likely to overestimate the relative proportion of insects with hard elytra in the diet, because earthworms and some insect larvae are rapidly digested. No studies have been conducted on the diet of woodcock chicks and it is not known how this differs from the diet of adults and whether, as speculated by Shorten (1974), insects form an important component during the first few days, as they do for the chicks of other wader species, such as the lapwing *Vanellus vanellus* (Galbraith 1989) and the common sandpiper *Actitis hypoleucos* (Yalden 1986).

5.2 STUDY SITES

Whitwell Wood, NE Derbyshire

Whitwell Wood (grid reference *SK 5278*) lies about 24km south-east of Sheffield and is situated on a plateau at an altitude of 140m a.s.l. within an area of gently undulating agricultural land. It consists of 171ha of mainly deciduous Forestry Commission plantations planted during the period 1932-47, and different blocks of woodland (averaging approximately 15ha in size) have been thinned each winter since 1983/84. The dominant tree species are sycamore *Acer pseudoplatanus* (comprising 55% of the total area) and beech *Fagus sylvaticus* (comprising 37% of the total area), sometimes planted in mixed stands, with smaller areas of Scots and Corsican pine *Pinus sylvestris* and *P. nigra*, ash *Fraxinus excelsior* and birch *Betula* spp. The remaining principal tree species are oak *Quercus robur* and rowan *Sorbus aucuparia*, which are distributed irregularly throughout the wood, and alder *Alnus glutinosa* which dominates the northern boundary of the wood adjoining a small stream.

The wood has a reduced shrub layer consisting only of a few scattered patches of hazel *Corylus avellana* and there is little ground vegetation in most areas. In the beech plantations, carpets of ramsons *Allium ursinum* and bluebells *Endymion non-scriptus* are present in April and May whereas in the sycamore stands the ground cover consists of dog's mercury *Mercurialis perennis* and brambles *Rubus* spp. Whitwell Wood has a good network of rides and small tracks which divide it into small blocks and make it relatively easy to determine precise locations.

Millden, Angus

Millden is located about 16km north-west of Brechin, half way along Glen Esk (grid reference *NO 5378*). The entire estate is about 50km^2 with the River North Esk running in a west-east direction through the centre. The valley bottom varies from approximately 400m-1km wide and consists of some narrow strips of pasture fields supporting sheep and fragmented areas of birch woodland. The birch occurs in patches and ranges in age from five year old thickets to mature trees about 50 years old. There is no understorey and the only ground cover is afforded by bracken *Pteridium aquilinum* which is distributed throughout some of the mature areas. The ground to the north and south of the river rises steeply to heights of between 490m and 680m and is dominated by *Calluna* moorland, which comprises approximately 90% of the estate. Fieldwork was restricted to the low-lying birch woodland and the hillsides below about 300m, an area of approximately 9km^2. The vegetation of the lower hillsides consisted of heather *Calluna vulgaris*, bracken, rough grass or *Juncus* spp. flush. There was a single 11.6ha coniferous plantation within the study area comprised of Scots pine about 40 years old.

5.3 METHODS

5.3.1 Ringing and radiotracking

Woodcock were caught at dawn and dusk in a series of mist nets set across the main rides at Whitwell Wood and in small woodland clearings at Millden. In addition, up to 20 drop traps with "lead-in fences" were employed in the main woodcock feeding areas. The drop traps were the primary means of catching female birds because trapping them on the nest invariably causes desertion, even during the latest stages of incubation (Hirons 1983). Catching activities were restricted to a two week period early in the breeding season at Millden but were continued from mid-March until June at Whitwell Wood.

The woodcock were aged according to Clausager (1973*a*) and sexed by means of a discriminant function based on bill length, tail length and weight (Appendix 5.1). Each bird was marked with a BTO ring and 14 birds at Whitwell Wood and ten at Millden were radiotagged. The single-stage radio-transmitters (Biotrack Ltd., Wareham, Dorset) each weighed 4g and were powered by zinc-air cells (giving a potential field life of about 70 days) or by mercury cells (giving a potential life of about 40 days). In 1991 the radios were attached to the skin of the bird's back with cyanoacrylate "superglue" (Raim 1978), but figure-eight harnesses made from 5mm elastic (Amlaner *et al.* 1978, Hirons & Owen 1982) were found to be a more reliable means of attachment and these were used in 1992 and 1993.

The radiotagged birds were located with a portable Mariner Radar M57 receiver and a hand-held three element Yagi antenna. The range of detection varied according to the density of the cover being used by the birds and the height gained by the observer. Typical maximum ranges were 200-500m at Whitwell Wood and 200-1,000m at Millden. Position fixes were determined by triangulation at distances of 30-40m at Whitwell Wood and 50-150m at Millden. Radiotagged birds could not be approached as closely at Millden due to the more open nature of the habitat and the increased risk of flushing the birds. The accuracy of radiolocations at Millden was determined by calculating error triangles from three bearings taken on spare radiotags placed in known locations. The mean size of these error triangles was 0.14±0.14ha (±sd, maximum 0.45ha, n=10). Position fixes were taken at the rate of two per bird per day. They were recorded as X,Y map coordinates using a grid size of 10m x 10m at Whitwell Wood and 50m x 50m at Millden. The radiolocations of 12 woodcock tracked by Dr. G. Hirons at Whitwell Wood in 1986 were included in the analysis of habitat use.

5.3.2 Analysis of habitat utilization

Habitat use by feeding woodcock was determined by means of compositional analysis (Aebischer *et al.* 1993) using diurnal radiolocations from radiotagged woodcock. As Whitwell Wood was surrounded by arable farmland, which was not used by woodcock during the day, the woodland boundary was taken to delimit the study area. In a few cases, radiotagged birds, particularly males, left Whitwell Wood at dusk and remained in nearby copses or other patches of woodland for a few days at a time. The radiolocations for these days were excluded from the analysis. At Millden the study area was defined as the composite minimum convex polygon of all the home ranges of the radiotagged birds. Seven habitat types were defined at each of the study sites. At Whitwell Wood they were based on the dominant tree species and the type of ground cover whereas at Millden they included moorland and pasture as well as woodland categories (Tables 5.1 & 5.2). In each case the habitat types were clearly distinct and readily recognizable. The predominant habitat type within each of the radiotracking grid squares was mapped by means of surveys conducted on foot.

The home ranges of radiotagged woodcock were described by means of minimum convex polygons (Mohr 1947). These were judged to be more appropriate for the analysis of habitats than harmonic mean isopleths (Dixon & Chapman 1980) which tended to "balloon" into areas that were not visited by the birds. For comparison of home range size between individual woodcock, the minimum convex polygon areas were assessed for the first 35 radiolocations for each bird. For those woodcock where fewer than 35 radiolocations were obtained, the home range size at 35 radiolocations was estimated from the increase in range size between ten and 21 radiolocations, which was compared to a regression of the increase between ten and 21 radiolocations against the home range size at 35 radiolocations for the other radiotagged

Table 5.1 Definitions of the different habitats examined with respect to woodcock habitat use in a lowland mixed woodland situation (Whitwell Wood).

	Habitat type	Description
1	Sycamore & bramble	Mature sycamore stand with predominantly bramble or grass ground cover.
2	Sycamore & dog's mercury	Mature sycamore or ash stands with dog's mercury the dominant species of ground cover.
3	Sycamore coppice	Sycamore or hazel areas that were clear-felled since 1984 and consisted entirely of regenerating saplings (mostly 5-7m tall).
4	Beech & bramble	Mature beech areas with bramble ground cover.
5	Beech & ramsons	Mature beech carpeted by ramsons.
6	Beech & bluebells	Mature beech or ash stands with bluebell or occasionally dog's mercury ground cover.
7	Conifer	Mature Scots and Corsican pine plantations and a ten year old Scots pine area.

woodcock (Harris *et al*. 1990). These equations were:

Whitwell Wood $y=33.76+1.46x$

Millden $y=21.33+2.00x$

where y was the home range size at 35 radiolocations and x was the increase in range size between ten and 21 radiolocations.

The proportions of each habitat type within the total study area and within each minimum convex polygon home range were determined using the program RANGES IV (Kenwood 1990).

Table 5.2 Definitions of the different habitats examined with respect to woodcock habitat use in an upland birchwood situation (Millden).

Habitat type	Description
1 Mature birch & bracken	Birch >12m tall with dead or living bracken ground cover.
2 Mature birch & grass	Birch >12m tall with no ground cover except grass (which was sometimes grazed by sheep).
3 Young birch	Intermediate sapling stage birch (6-12m tall), often with no ground cover, and young birch thicket (≤5m tall).
4 Conifer	Mixed areas of 60-70 year old Scots pine with mature beech or ash and a 40 year old Scots pine plantation.
5 *Juncus* flush	Open wet habitat usually characterized by the presence of *Juncus effusus*, *Erica tetralix* and *Sphagnum* spp.
6 Heather	*Calluna*-dominated moorland.
7 Rough & improved grazing	Unmanaged sheep-grazed patches, produced by overgrazing of moorland edges, and managed pasture fields.

Hypothesis testing was conducted by calculating Wilk's Λ by means of a MANOVA applied to the log-ratio differences. With no missing values, any of the habitats can be used as the denominator (Aitchison 1986) and significance can be tested by means of χ^2. Missing values can be used as the denominator (Aitchison 1986) and significance can be tested by means of χ^2. Missing values were treated in two ways during the calculation of log-ratios and mean log-ratio differences. In cases where a particular habitat type was available but not utilized, the proportion of the missing habitat type was set to 0.001 (Aebischer & Robertson 1992). In cases where particular habitat types were not available for use by some of the woodcock (not included within the home ranges when assessing the distribution of radiolocations within the home range) the mean log-ratio differences for each pair of habitat types within the ranking matrix were based only on the home ranges containing both types. By using all possible habitats as the denominator, a separate Wilk's Λ was calculated for each habitat and a mean Λ was then calculated by weighting the Wilk's Λ for each habitat according to its number of non-missing values. Multivariate normality of the residuals could no longer be assumed and significance testing was performed by randomization. Randomization created 999 expected values for Λ and compared the observed value with this expected distribution. It follows that the smallest obtainable level of probability was $p \leq 0.001$.

5.3.3 Measurement of habitat structure

Habitat measurements were recorded from three randomly selected positions at each feeding and random site. At Whitwell Wood these positions were chosen by dividing a 30m x 30m grid, centred over each site, into 36 numbered 5m x

Table 5.3 Habitat parameters measured at woodcock nest sites, adult feeding locations and paired random sites.

Variable	Definition
Mean area per tree	The reciprocal of tree density. Measured in m^2 as the square of the mean of 4 point quarter distances.
Mean basal area	Mean basal area (cm^2) of trees at point quarters.
Sapling density	Number of saplings within 3m radius.
Shrub stem density	Number of shrub stems within 3m radius.
Brushwood density	Number of dead stems or cut branches (>1cm diameter) within 3m radius.
Vegetation cover	Percentage ground surface within quadrat covered by living vegetation.
Height of dominant vegetation	Height (cm) of dominant species of ground cover.
Height of co-dominant vegetation	Height (cm) of second most dominant species of ground cover.
Litter cover	Percentage ground surface within quadrat covered by litter.
Litter depth	Mean depth (cm) of litter within quadrat.
Bare ground	Percentage ground surface visible within quadrat.
Herbaceous species abundance	Percentage ground surface within quadrat covered by a given species. (At Whitwell Wood particular attention was paid to grass, dog's mercury and bramble and at Millden to grass, bracken and *Calluna* heather).

5m squares and selecting three by generating three random numbers on a pocket calculator. Because the trees were more widely spaced at Millden, a larger grid of 40m x 40m, which was divided into 16 numbered 10m x 10m squares, was used. Each set of measurements was centred on a $0.25m^2$ quadrat placed in the centre of each selected square. Details of the parameters measured are given in Table 5.3. The mean area per tree and mean basal area were calculated from point-quarter measurements (Cottam & Curtis 1956). Trees were defined as woody stems >9m high and >10cm diameter at breast height (DBH), saplings as woody stems >9m high and <10cm DBH, and shrubs as woody stems >1m and <9m high. Ground cover was taken to be any vegetative material <1m high. Percentage variables were transformed with arcsin $\sqrt{x}$ prior to analysis.

5.3.4 Invertebrate sampling

Surface-living invertebrates were sampled at each nest site, adult feeding location and paired random site by means of pitfall trapping. Despite the problem of differential susceptibility of invertebrate species to trapping according to their behaviour (e.g. Luff 1978, Williams 1959), pitfall trapping is an adequate means of assessing the relative numbers of a species in different vegetation types (Greenslade 1964). Ten traps were set for a period of ten days at each location during mid-May. The invertebrate catch in each trap was taken to be independent of the catch in the other traps and comparisons between sites were based on the catch in each trap during the ten day period. Earthworms were sampled by taking 11cm diameter ($95cm^2$) soil cores or by digging 25cm square ($625cm^2$) turfs to a depth of 7cm (the average length of the woodcock bill) and handsorting.

5.3.5 Faecal analysis and determination of diet selection

Woodcock faeces were collected from full-grown birds and from chicks at Whitwell Wood in 1991 and 1992 and at Millden in 1992. Samples were stored in 70% alcohol. Before examination, the samples were washed through two sieves, one with a 0.254mm mesh and one with a 0.075mm mesh. This was necessary to remove fine granular particles that otherwise clouded the samples and made the food items difficult to detect. The first sieve retained most of the arthropod fragments and large earthworm chaetae, but the second was required in order to retain small earthworm chaetae.

For analysis the samples were placed in an 89mm diameter Petri dish with a 55mm diameter dish glued in the centre, forming a 17mm annular channel. The underside of the dish was inscribed with radial lines at 22.5° intervals, dividing the annulus into 16 equal sectors. The samples were examined at 30x magnification under a binocular microscope. Because they contained pieces of insect cuticle and other debris that was difficult to attribute to particular taxa, the counts of prey remains were restricted to items that were readily identifiable and were carried in known numbers. Beetles were identified by means of legs, head capsules and mandibles and spiders and harvestmen by leg fragments and chelicerae. For woodlice, both legs and tergites were counted and flies were identified by means of wings. Fragment identification was aided by comparison with reference collections of invertebrates from both study areas and Royal Entomological Society keys to the main insect taxa.

No discrete structures were identified for millipedes and fragments of the characteristically striated posterior margin of the segmental ring exoskeleton were counted (Green & Tyler 1989). Most of these fragments were of fairly uniform size (about 1mm along the ring circumference) and larger pieces were mentally subdivided when accumulating the fragment count. Large numbers of earthworm chaetae were present and were only counted for a quarter of each sample by recording the contents of every fourth sector of the dish. The figure of 1080 chaetae was taken to comprise one earthworm, being the mean of estimates made by Bouche & Gardner (1984); n=966 chaetae per earthworm, Wroot (1985); n=1080 chaetae per worm, and Green & Tyler (1989); n=1191 chaetae per worm.

In order to overcome the problem of different digestion rates of different prey taxa when estimating the relative proportions of prey in the diet from their proportions in the faecal remains, conversion factors based on those obtained from studies on a captive adult stone curlew *Burhinus oedicnemus* (Green & Tyler 1989) and captive lapwing *Vanellus vanellus* chicks (Galbraith 1989) were used (Table 5.4). Because the number of millipede fragments recovered was dependent on the size of the animals ingested, the width of the striated posterior margin (*w*) was measured to 0.05mm with a micrometer eyepiece and the number of fragments comprising a single millipede was estimated using the function given by Green & Tyler (1989): $403.8w^{2.994}$.

The same conversion factors were applied to fragments from samples collected from woodcock adults and chicks because there have been too few studies of differential digestion rates to enable age classes to be treated separately. However, there are bound to be some differences in digestive efficiency between adults and chicks, and the efficiency is also likely to differ from that of stone curlews and lapwings.

Table 5.4 Conversion factors used to correct for the different digestion rates of different prey taxa in the woodcock diet (based on Green & Tyler 1989 and Galbraith 1989).

Prey taxa	Characteristic remain	Conversion factor
Lumbricidae	Chaeta	4.46
Scarabaeidae, Carabidae, Curculionidae and other beetles	Tibia	1.21
	Mandible/head	1.36
Staphylinidae	Tibia	1.47
	Mandible/head	1.69
Coleoptera larvae	Tibia/mandible /head	1.50
Formicidae	Tibia/whole	1.21
Lepidoptera larvae	Mandible/whole	1.50
Araneae, Opiliones	Tarsus/metatarsus /chelicera	2.34
Diplopoda	Exoskeleton fragment	8.93
Oniscoidea	Leg/tergite	10.42
Diptera	Wing	1.50

The number of prey animals in each sample was estimated and the proportion comprised by each taxon was calculated. Estimated prey frequency based on all samples was converted to percentage of prey biomass using mean dry weights for each taxon (Appendix 5.2). These were obtained by oven-drying ten individuals of each group for three days to constant weight and weighing them to the nearest 0.1mg.

The percentage frequencies of carabids, staphylinids, all other adult beetles, beetle larvae, spiders and harvestmen, millipedes and woodlice were used to test for diet preferences in adult woodcock and in chicks. These taxa were considered to be similarly mobile such that their abundance in pitfall traps was approximately representative of their abundance in the study area. Caterpillars, sawfly larvae and flies were excluded because these taxa were likely to have been under-represented in pitfall traps. Similarly, earthworms were not included because they were sampled by a different method and their abundance could not be compared with that of the taxa sampled by pitfall trapping.

The data were examined for diet preferences using two methods; compositional analysis (Aitchison 1986, Aebishcer *et al.* 1993) and Jacobs (1974) preference index. Compositional analysis avoids the unit-sum constraint which is a problem in the use of Jacobs preference index. However, faecal samples were only obtained from a small number of birds in this study and this reduced the power of compositional analysis to determine significant differences in the selection of different prey taxa. Thus the results from both methods were compared. In the compositional analysis spiders and harvestmen were used as the denominator in the calculation of log-ratios. The results of the analysis do not depend on which prey taxon was used as denominator. Jacobs (1974) preference index was calculated as:

$$D=(r-p)/(r+p-2rp)$$

where r was the proportion of each prey taxon in the woodcock diet and p was the proportion of each prey taxon in the study area estimated on the basis of pitfall trapping. The index ranges from -1 to +1 indicating complete avoidance and exclusive use respectively. Zero indicates that the prey taxon was used in proportion to its availability.

5.4 RESULTS

5.4.1 Home range size and movements of woodcock during the breeding season

The size of diurnal minimum convex polygon (MCP) home ranges established by radiotagged woodcock at Whitwell Wood varied considerably between individuals, with home ranges standardized on 35 fixes (Harris *et al.* 1990) varying from 6.6ha to 130ha (Table 5.5).

The variation was not related to the age class (first-year or adult) (t=0.11, df=12, N.S.) or sex (t=1.30, df=12, N.S.) of individuals. The daily ranges (based on eight radiolocations per day) of all individuals were generally much smaller, varying from 0.13ha to 0.67ha (n=5), and the difference in the size of home ranges appeared to be due to differences between individuals in the frequency with which they changed feeding areas.

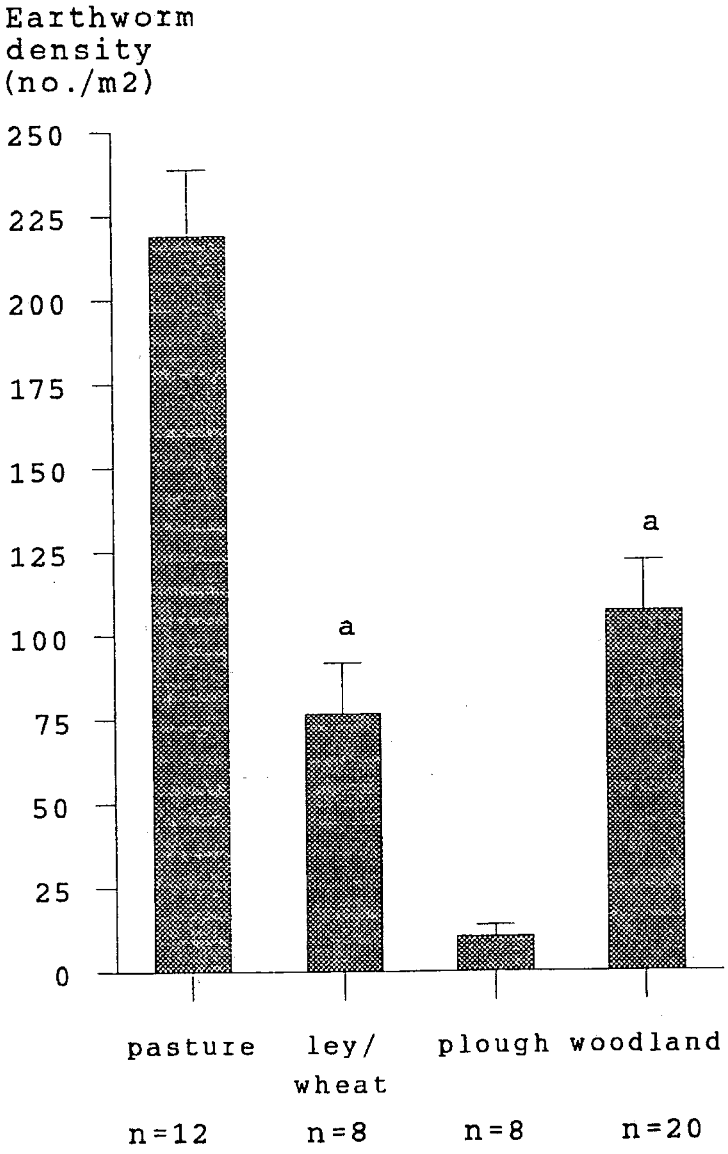
Table 5.5 Diurnal minimum convex polygon (MCP) home range sizes for radiotagged woodcock at Whitwell Wood.

Radio freq.	Age	Sex	Number of days monitored	No. of radio-locations	MCP home range (ha)	
					Total	Standardized on 35 radio-locations
861	Adult	M	38	36	86	86
862	Adult	F	50	37	7	7
863	Adult	M	77	27	68	125*
864	1st-yr	M	22	33	47	70*
865	1st-yr	M	21	25	95	130*
866	1st-yr	M	27	39	15	14
867	Adult	M	26	56	66	58
868	Adult	M	38	99	97	50
869	Adult	M	24	44	54	53
8610	1st-yr	M	32	69	52	34
8611	Adult	M	17	48	54	51
8612	Adult	F	19	36	56	56
220	1st-yr	M	45	17	24	61*
513	Adult	M	29	21	35	51*

*Estimate of home range size at 35 radiolocations derived from the increase in home range size from ten to 21 radiolocations.

During March, April and May, the radiotagged woodcock regularly left Whitwell Wood to feed and roost on the surrounding fields at night (Table 5.6). The flights to fields were made immediately after the dusk roding period and the mean distance travelled was 800±61m (±se, range 70-1,860m, n=58). The birds remained on the fields for the entire night, as in winter. Although the sample of woodcock monitored in this study reflected largely the behaviour of male birds, the two females, plus two others monitored prior to nesting, also visited fields at night when not incubating eggs or rearing chicks. The woodcock regularly used permanent pastures, occasionally used first-year ley and weedy winter wheat fields and completely avoided clean

Figure 5.1 Comparison of available earthworm densities in the top 7cm of soil in woodland and different types of fields in NE Derbyshire in late March. (Error bars are +1se; one-way ANOVA F=22.27, df=3,44, p<0.001; letters indicate no significant difference between pairs of values in the Duncan multiple range test, p≥0.05).



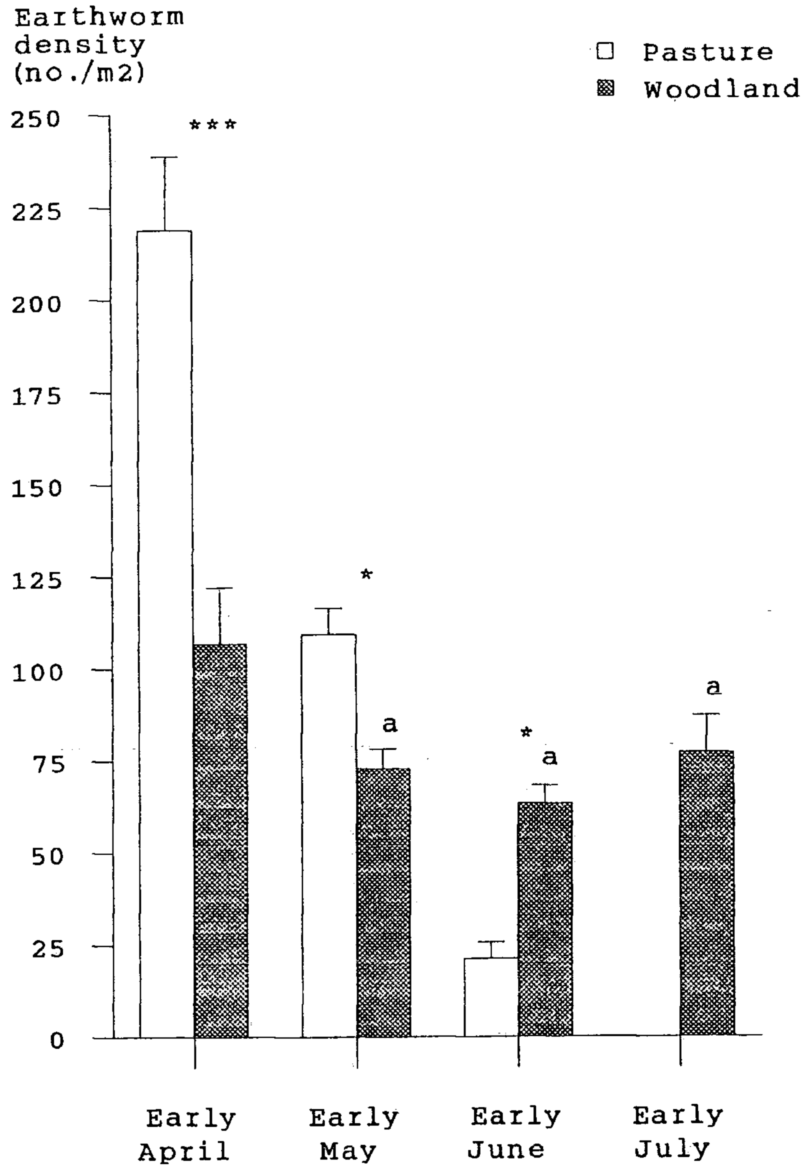
winter wheat and ploughed fields. They were found on permanent pasture and first-year ley on 38 of 61 bird-nights (62%) despite the fact that arable fields outnumbered grass fields by 18:1. The choice of permanent pasture fields was undoubtedly related to the high densities of earthworms that they supported in comparison with first-year ley, winter wheat or ploughed fields (Figure 5.1). Changes in the relative availability of invertebrate prey, particularly that of earthworms, in the fields and woodland during the course of the spring provided the most likely explanation for the change from field to woodland feeding by the woodcock in June. The availability of earthworms in the topsoil declined rapidly in pasture fields from April to June whereas their availability in the woodland remained relatively constant over the same period (Figure 5.2).

Table 5.6 Frequency of use of the fields surrounding Whitwell Wood by woodcock at night during the breeding season.

	March	April	May	June	July
Bird-nights	9	62	61	61	11
Number of bird-nights spent on fields	8	49	50	20	1
Percent of bird-nights spent on fields	89	79	82	33	9

Later in the season when they roosted in the woodland, the radiotagged woodcock exhibited a preference for

Figure 5.2 The change in available earthworm density in pasture fields and in woodland during spring and early summer in NE Derbyshire. (Error bars are +1se; asterisks denote significant one-way ANOVAs between habitats, * $p<0.05$, *** $p<0.01$; letters indicate no significant difference between pairs of values for the same habitat type in the Duncan multiple range test, $p\geq0.05$).



coniferous areas, particularly young (ten year) Scots pine, using these on 48% of 56 occasions even though conifer only comprised 6.8% of the area of Whitwell Wood. The mean distance between diurnal feeding locations and nocturnal roost sites was similar irrespective of where the woodcock roosted; conifer, 320±39m (±se, n=24) as opposed to sycamore or beech, 258±67m (±se, n=20) (t=0.84, df=42, N.S.). Scots pine plantations were frequented significantly more at night (48% of radiolocations) than during the day (16% of radiolocations) (Table 5.7).

Table 5.7 Relative use of conifer, beech and sycamore stands by radiotagged woodcock during the day and night at Whitwell Wood.
Figures are the number of radiolocations from 12 birds. χ^2 tests are based on the percentage use of each habitat by day and by night.

	Conifer	Beech	Sycamore
Day	86 (16%)	164 (30%)	297 (54%)
Night	27 (48%)	12 (22%)	17 (30%)
	χ^2=16.0, df=1, p<0.001	χ^2=1.2, df=1, N.S.	χ^2=6.9, df=1, p<0.05

The standardized (n=35 radiolocations) minimum convex polygon home ranges of ten radiotagged woodcock at Millden varied in size between 9.5ha and 124.8ha (Table 5.8) and did not differ significantly from the size of home ranges used by woodcock at Whitwell Wood (mean±se, 50.5±10.9ha and 60.4±9.3ha respectively; t=0.69, df=22, N.S.). Again, the differences in home range size between individual birds at

Millden were not age class (t=1.87, df=8 N.S.) or sex (t=1.01, df=8, N.S.) related and the size of daily range areas was small; 0.34-0.81ha (n=5 bird-days). Despite the presence of improved pasture in close proximity to the woodland at Millden, the woodcock were not recorded using fields at night as they did at Whitwell Wood. The locations of the radiotagged woodcock following roding revealed that they were roosting in woodland during March and April and no woodcock were seen during spot-lamp searches of improved pastures and areas of rough grazing.

Table 5.8 Diurnal minimum convex polygon (MCP) home range sizes for radiotagged woodcock at Millden.

Radio freq.	Age	Sex	Number of days monitored	No. of radio-locations	MCP home range (ha)	
					Total	Standardized on 35 radio-locations
500	1st-yr	M	105	209	120	65
518	1st-yr	M	61	88	74	12
229	Adult	F	27	32	46	47*
260	1st-yr	F	100	198	240	78
277	Adult	F	21	28	18	42*
299	Adult	F	24	40	10	10
300	1st-yr	F	29	53	68	63
250	Adult	F	54	47	77	40
281	Adult	F	44	33	177	24
301	1st-yr	M	32	31	79	125*

*Estimate of home range size at 35 radiolocations derived from the increase in range size from ten to 21 radiolocations.

5.4.2 Habitat use by woodcock in a mixed deciduous, lowland woodland situation (Whitwell Wood)

Differentiation between stands of different tree species

There was a high degree of overlap amongst the minimum convex polygon home ranges of the different radiotagged woodcock at Whitwell Wood (mean 50.4% overlap between the ranges for all pairs of birds) and most were centred on sycamore stands. The percentage habitat compositions within each of the home ranges and as described by the radiolocation distributions are given in Appendix 5.3. The overall comparison of habitat use from the home ranges compared to habitat availability in the study area gave $\Lambda=0.3315$ ($\chi^2=15.5$, df=6, $p<0.05$), implying that the home ranges were not established at random within the wood. A ranking matrix ordered the habitat types in the sequence conifer > sycamore with dog's mercury > beech with bluebells > sycamore with bramble > sycamore coppice > beech with bramble > beech with ramsons (Table 5.9).

There were no significant differences between the first five habitats, implying that the order of their assigned ranks meant little, but beech with ramsons was used significantly less than any of the habitats except beech with bramble and conifer. Beech with bramble was frequented significantly less than conifer and beech with bluebells (Table 5.10). Together the beech with ramsons and beech with bramble habitats comprised 21% of the available woodland. The implication of this analysis is that diurnal woodcock home ranges were established predominantly in the sycamore areas of Whitwell Wood. The high utilization of

Table 5.9 Matrix of means and standard errors of log-ratio differences averaged over all 14 radiotagged woodcock at Whitwell Wood for comparing habitat use based on minimum convex polygon home ranges with availability in the total study area (top).

The implications for habitat use are revealed by replacement of each element by its sign (bottom) and counting the number of positive values in each row to give a rank. The row with the most positive values (rank 6) corresponds to the most-used habitat type, the one with the most negatives (rank 0) is the least used. Where a mean differs significantly from zero ($p<0.05$, df=12) the sign is tripled.

	Sycam. &bram.	Sycam. &dog's merc.	Sycam. copp.	Beech &bram.	Beech &rams.	Beech &blue-bells	Conifer
Sycamore & bramble		-0.110 ±0.145	0.086 ±0.270	0.609 ±0.403	1.290 ±0.353	-0.003 ±0.341	-0.127 ±0.524
Sycamore & dog's merc.	0.110 ±0.145		0.196 ±0.327	0.718 ±0.431	1.400 ±0.415	0.106 ±0.330	-0.017 ±0.519
Sycamore coppice	-0.086 ±0.270	-0.196 ±0.327		0.522 ±0.246	1.204 ±0.469	-0.090 ±0.232	-0.213 ±0.399
Beech & bramble	-0.609 ±0.403	-0.718 ±0.431	-0.522 ±0.246		0.682 ±0.535	-0.612 ±0.184	-0.735 ±0.330
Beech & ramsons	-1.290 ±0.353	-1.400 ±0.415	-1.204 ±0.469	-0.682 ±0.535		-1.293 ±0.524	-1.417 ±0.685
Beech & bluebells	0.003 ±0.341	-0.106 ±0.330	0.090 ±0.232	0.612 ±0.184	1.293 ±0.524		-0.123 ±0.249
Conifer	0.127 ±0.524	0.017 ±0.519	0.213 ±0.399	0.735 ±0.330	1.417 ±0.685	0.123 ±0.249	

	Sycam. &bram.	Sycam. &dog's merc.	Sycam. copp.	Beech &bram.	Beech &rams.	Beech &blue-bells	Conifer	Rank
Sycamore &bramble		-	+	+	+++	-	-	3
Sycamore & dog's mercury	+		+	+	+++	+	-	5
Sycamore coppice	-	-		+	+++	-	-	2
Beech & bramble	-	-	-		+	---	---	1
Beech & ramsons	---	---	---	-		---	-	0
Beech & bluebells	+	-	+	+++	+++		-	4
Conifer	+	+	+	+++	+	+		6

sycamore stands supports the finding of Hirons & Johnson (1987) that these areas were preferred for feeding. However, the relatively high use of conifer and beech with bluebells is surprising as these habitats supported only low available densities of earthworms (see section 5.4.4).

Table 5.10 Habitat ranking based on the selection of home ranges within Whitwell Wood, showing where differences between ranks are statistically significant. Ranks which do not differ significantly ($p \geq 0.05$) according to the matrices in Table 5.9 are assigned the same letter in the "ranks differ" column.

Rank	Habitat	Ranks differ			
6	Conifer	*a*			*d*
5	Sycamore & dog's mercury	*a*	*b*		
4	Beech & bluebells	*a*			
3	Sycamore & bramble	*a*	*b*		
2	Sycamore coppice	*a*	*b*		
1	Beech & bramble		*b*	*c*	
0	Beech & ramsons			*c*	*d*

There was no further selection of particular habitats by radiotagged woodcock within home ranges (weighted mean $\Lambda=0.4903$, $p=0.432$ by randomization), but this was probably because sycamore areas comprised a large proportion of most of the home ranges. It was, of course, possible that there was a change in the pattern of habitat use by woodcock within home ranges during the course of the breeding season, as changes in the vegetation occurred. In order to test whether this was the case, the habitat compositions of the radiolocations of birds tracked during April and May (861, 862, 863, 864, 865, 866, 867, 8612, 220) were compared with those of birds tracked during June and July (863, 868, 869, 8610, 8611, 220, 513). The herb layer ground flora, consisting predominantly of dog's mercury, wood sorrel *Oxalis acetosella*, bluebells and ramsons, was most profuse during April and May, but died back during June and July when bramble and bracken had started to grow and become more dominant. There was, however, no significant difference in the overall pattern of habitat use between the two time periods; MANOVA F=0.75 (Wilk's Λ=0.5338), df=7,6, N.S., nor in the use of any individual habitat (one-way ANOVAs all not significant).

There were several significant univariate differences between adult woodcock feeding locations and paired random locations within sycamore stands at Whitwell Wood. Feeding locations had a higher percentage of total vegetation cover, comprised largely of dog's mercury and grasses. They also had a higher density of shrubs and relatively little dead wood or leaf litter (Table 5.11). The magnitude of the differences between the feeding and the random sites suggested that the shrub stem density, the percentage cover of dog's mercury and the percentage cover of grass were the most important of these factors.

Stepwise discriminant function analysis between paired feeding and random sites yielded an equation which correctly classified 92% of sites on the basis of eight variables. The standardized discriminant function coefficients are given in Table 5.12, the magnitude of each conveying their relative importance and the signs indicating whether each variable was weighted towards feeding (+) or random (-) sites. Clearly the percentage covers of dog's mercury and grass were the most important factors in determining whether or not a particular area was likely to be used for feeding by woodcock.

Table 5.11 Means and standard deviations of habitat variables that were significantly different between woodcock feeding locations and paired random sites within sycamore stands at Whitwell Wood (Mann-Whitney U-test).

Variable	Feeding sites (n=24 quadrats)	Random sites (n=24 quadrats)	U	Sig.
Shrub stem density (stems in 3m radius)	14.6 ±11.0	3.8 ± 6.9	89.0	$p<0.001$
Brushwood density (dead stems in 3m radius)	46.5 ±16.3	64.7 ±22.6	147.5	$p<0.01$
Vegetation cover (%)	72.9 ±18.2	49.9 ±23.9	127.5	$p<0.001$
Litter cover (%)	38.4 ±31.8	79.0 ±20.8	90.0	$p<0.001$
Litter depth (cm)	2.58 ±1.55	4.78 ±1.32	86.5	$p<0.001$
Dog's mercury (% cover)	48.7 ±33.4	11.3 ±19.4	104.0	$p<0.001$
Grass (% cover)	14.6 ±22.5	2.3 ± 5.9	152.5	$p<0.01$

Table 5.12 Standardized discriminant function coefficients for discriminating between woodcock feeding locations and paired random sites within sycamore stands at Whitwell Wood.

Importance rank	Variable	Standardized coefficient
1	Dog's mercury (% cover)	1.400
2	Grass (% cover)	0.874
3	Vegetation cover (%)	-0.706
4	Brushwood density	-0.388
5	Sapling density	0.312
6	Bramble (% cover)	0.300
7	Shrub stem density	0.279
8	Litter cover (%)	-0.269

Differentiation between woodland edges and the centre of stands

Comparison of the proportions of woodland edge and non-edge habitats within minimum convex polygon home ranges with those in the study area (Appendix 5.4), gave a mean difference in log-ratios for all 14 birds of -0.041±0.113 (±se). This value does not differ significantly from zero (t=0.37, df=12 N.S.), indicating that the two habitats were used at random. However, the use of edge habitat based on the radiolocation distributions was significantly greater than expected from the habitat distribution within the minimum convex polygon home ranges: the mean log-ratio difference was 0.362±0.153 (±se) (t=2.37, df=12, p<0.05).

The reason that the woodcock at Whitwell Wood made greater use of the edges of woodland blocks within their home ranges appeared to be because the edges contained twice as many shrub stems, affording better cover, and because they only had approximately two-thirds the cover and depth of leaf litter found in the centre of woodland blocks, which presumably made foraging easier (Table 5.13).

Table 5.13 Means and standard deviations of habitat variables that differed significantly between the edge (40m) and the centre of woodland blocks at Whitwell Wood (Mann-Whitney U-test).

Variable	Edge (n=18 quadrats)	Centre (n=30 quadrats)	U	Sig.
Sapling density (saplings in 3m radius)	0.11 ±0.32	1.47 ±2.40	173.0	p<0.05
Shrub stem density (stems in 3m radius)	13.5 ±11.7	6.6 ± 9.0	156.5	p<0.05
Vegetation cover (%)	69.7 ±24.8	56.4 ±22.5	166.0	p<0.05
Litter cover (%)	42.2 ±31.7	68.6 ±31.1	141.0	p<0.01
Litter depth (cm)	2.90 ±2.02	4.15 ±1.51	173.5	p<0.05

5.4.3 Diet of woodcock and prey selection in mixed deciduous, lowland woodland

Faecal analysis revealed that in addition to earthworms, the woodcock at Whitwell Wood consumed a range of arthropod prey in spring, including adult and larval beetles (Coleoptera), millipedes (Diplopoda), woodlice (Isopoda, Oniscoidea), spiders (Araneae), harvestmen (Opiliones), caterpillars (Lepidoptera) and sawfly larvae (Hymenoptera), and flies (Diptera). Oribatid mites and plant fragments were also present in the faecal samples, but were not recorded as prey items as they were probably ingested accidentally as a consequence of probing through leaf litter. The absence of molluscs from the diet of adult woodcock is interesting and unexpected. Slugs would have been relatively difficult to detect in the faecal analysis as only the radula would have remained intact, but if snails were eaten there would have been many fragments of shell. Earthworms comprised 22% of prey items taken by adult woodcock and only 7% of those taken by chicks but were relatively more important in terms of total prey biomass, comprising 43% and 13% of adult and chick diets respectively (Table 5.14). Millipedes clearly comprised an important component of the woodcock chick diet at Whitwell Wood.

Table 5.14 Estimated frequencies of invertebrates in the diet of woodcock at Whitwell Wood based on faecal analysis.

	Adult (23 samples from 11 birds)			Chick (7 samples from 7 birds)		
Prey taxon	*n*	% of total *n*	% of total dry wt.	*n*	% of total *n*	% of total dry wt.
Lumbricidae	57	22.1	43.2	3	7.0	13.2
Carabidae (adult)	6	2.3	3.9	3	7.0	11.3
Curculionidae (adult)	3	1.2	0.2	2	4.7	0.7
Staphylinidae (adult)	20	7.8	2.0	2	4.7	1.1
Other adult Coleoptera*	1	0.4	<0.1	-		
Coleoptera larvae	19	7.4	4.1	2	4.7	2.5
Lepidoptera larvae#	6	2.3	1.1	-		
Araneae & Opiliones	78	30.2	6.4	10	23.3	4.8
Diplopoda	50	19.4	35.5	14	32.6	57.6
Oniscoidea	16	6.2	3.4	7	16.3	8.7
Diptera	2	0.8	<0.1	-		

*Mainly Elateridae.

#Includes sawfly larvae (Hymenoptera, Symphyta).

Comparison of the percentage biomass of each prey taxon in the diet of adults and chicks revealed that earthworms comprised a significantly larger component of the diet of adult woodcock (χ^2=16.0, df=1, $p<0.001$) but that millipedes comprised a significantly smaller proportion (χ^2=5.2, df=1, $p<0.05$). Spiders and harvestmen comprised an important numerical component of the diet of both adult woodcock and chicks but were relatively unimportant in terms of biomass. Harvestmen comprised a small proportion (<10%) of the total number of animals identified for the combined group. Caterpillars, sawfly larvae and flies were only taken by adult birds and then comprised only a very small proportion of the diet in terms of prey frequency and biomass.

The mean frequency in the diet and the availability in the study area of the mobile prey taxa considered equally likely to be caught in pitfall traps are given in Table 5.15. The proportions of spiders and harvestmen and staphylinids taken by both adult woodcock and chicks were clearly greater than the proportions of these two taxa available in the study area. The proportion of beetle larvae in the diet of adult woodcock was also appreciably greater than the available proportion and the proportion of adult carabids appreciably lower.

Table 5.15 The relative proportions of available prey taxa at Whitwell Wood and their mean proportions in the diet of adult woodcock and chicks.

Prey taxon	Availability in study area (%)*	Mean percent frequency in the diet (±se)	
		Adults (n=11 birds)	Chicks (n=7 birds)
Carabidae (adult)	8.7	3.3 ± 1.4	10.2 ± 6.1
Staphylinidae (adult)	12.9	19.5 ± 7.5	20.7 ±16.3
Other adult Coleoptera	31.1	1.5 ± 0.9	1.2 ± 1.2
Coleoptera larvae	2.1	15.4 ± 5.7	1.0 ± 1.0
Araneae & Opiliones	30.6	41.2 ± 6.4	52.4 ±16.9
Diplopoda	9.0	11.8 ± 4.5	8.7 ± 8.7
Oniscoidea	5.6	7.3 ± 3.1	4.3 ± 4.3

*Based on the pitfall catch for 1580 trap-days in all habitats.

For the compositional analysis of adult woodcock prey selection the "other adult beetle" category was excluded because beetles other than carabids and staphylinids only comprised a very small proportion of the diet and were not present in the faecal samples from some of the birds. The data from only five adult woodcock were used because those from the other birds contained several missing prey types. The comparison of prey selection based on these five birds with prey availability in Whitwell Wood gave $\Lambda=0.0069$ ($\chi^2=24.9$, df=5, $p<0.001$) suggesting that prey types were not taken at random. A ranking matrix (Appendix 5.5) ordered the prey taxa from most preferred to least preferred in the sequence beetle larvae > woodlice > spiders and harvestmen > millipedes > staphylinids > carabids. However, there were no significant differences between any of the six prey types, implying that the order of their assigned ranks meant little.

Ranking the prey types according to their Jacobs (1974) preference index values (Appendix 5.5) gave a similar sequence to that for the compositonal analysis: beetle larvae > staphylinids > spiders and harvestmen = millipedes > woodlice > carabids, the only difference being that the relative preferences for woodlice and staphylinids were reversed. The preference index values indicate that beetle larvae were clearly preferred by adult woodcock and that adult carabids were largely avoided whilst the other four prey taxa were taken in proportion to their availability at Whitwell Wood. It seems likely that other adult beetles were avoided more than carabids (Table 5.15) and that flies were rarely taken (Table 5.14).

The compositional analysis of prey selection by woodcock chicks was restricted to carabids, staphylinids, spiders and harvestmen, millipedes and woodlice using the data from four birds. Comparison of woodcock chick diet with prey availability at Whitwell Wood revealed that prey selection was significantly different from random (Wilk's $\Lambda=0.0006$, $\chi^2=29.7$, df=4, $p<0.001$). A ranking matrix ordered the prey taxa in the sequence spiders and harvestmen > carabids > woodlice > staphylinids > millipedes (Appendix 5.6), but again there were no significant differences between any of the prey types, implying that the ranking meant little. The Jacobs (1974) preference index values (Appendix 5.6) suggested that spiders and harvestmen comprised the group most preferred by woodcock chicks and that woodlice were the least preferred.

The difficulty of interpretation of the results of the compositional analyses arose due to the small numbers of woodcock involved, which meant there were very few degrees of freedom with which to test differences between pairs of prey taxa. However, the fact that the Wilk's Λ values were significant for both adult woodcock and chicks in the comparison of log-ratio differences and that the most preferred groups suggested by the compositional analyses and the Jacobs (1974) preference indices were the same, implies that adult woodcock at Whitwell Wood actively selected beetle larvae and that chicks selected spiders and harvestmen.

5.4.4 Habitat selection in relation to the availability of invertebrate prey in mixed deciduous, lowland woodland

Not surprisingly, the available density of earthworms in sycamore stands (mean±se, $152\pm13m^{-2}$, n=63) was significantly higher than that in areas comprised of beech (mean±se, $95\pm24m^{-2}$, n=21); one-way ANOVA F=4.66, df=1,82, $p<0.05$. Insufficient samples were obtained from coniferous areas to provide a reliable estimate of available earthworm density (mean±se, $69\pm35m^{-2}$, n=3), but the density in such areas was also likely to have been significantly lower than the density in sycamore stands. There were differences in the total catch of other invertebrates (excluding caterpillars, sawfly larvae and flies) in pitfall traps between the habitats, with sycamore again supporting the highest numbers (Table 5.16).

Table 5.16 Differences in the total numbers of invertebrates caught in pitfall traps in different habitats at Whitwell Wood, May 1991 (one-way ANOVA).
The sampling unit was one trap set for a period of ten days. The invertebrate catch in each trap was assumed to be independent of the catch in the other traps.
Letters indicate no significant difference between pairs of values in the Duncan multiple range test ($p \geq 0.05$).

Habitat	Trap-periods	Invertebrates per trap-period (mean ±se)	Between habitat difference
Sycamore	129	120 ± 5	
Beech	19	82 ± 6	*a*
Conifer	10	73 ± 9	*a*
		F=8.58, df=2,155, p<0.001	

Comparison of the availability of invertebrate prey at adult woodcock feeding sites and paired random sites within the same habitat type revealed a significantly higher density of earthworms at feeding sites (168 earthworms/m^2 compared to 118 earthworms/m^2 at random sites) (Table 5.17). Differences in the pitfall catch at eight paired sites (seven in sycamore and one in beech) revealed that significantly higher numbers of staphylinids and spiders were present in woodcock feeding areas but that numbers of woodlice were significantly lower (Table 5.17). It seems likely that available earthworm density was an important factor in the selection of feeding sites because earthworms comprised approximately one fifth of the prey items ingested. Of the differences in the other prey taxa, the differences in the number of staphylinids and spiders between woodcock feeding and random sites may be important but it is surprising that there was no significant difference in the number of beetle larvae, the most preferred taxon.

Table 5.17 Means and standard deviations of available earthworm density and of invertebrate numbers caught per ten day trap-period for taxa that differed significantly between woodcock feeding locations and paired random sites at Whitwell Wood, May 1991 (Mann-Whitney U-test). Earthworms were sampled by means of soil cores (n=39 feeding, 39 random); data presented as number/m^2.

Taxon	Feeding sites (n=80 trap-periods)	Random sites (n=78 trap-periods)	U	Sig.
Lumbricidae	168 ± 99	118 ±113	528.5	$p<0.05$
Staphylinidae	31 ± 12	25 ± 17	2269.5	$p<0.01$
Other beetles	35 ± 36	24 ± 20	2544.0	$p<0.05$
Araneae	31 ± 14	25 ± 26	2087.0	$p<0.001$
Oniscoidea	4 ± 3	7 ± 6	2413.5	$p<0.05$

5.4.5 Habitat use by woodcock in an upland birchwood situation (Millden)

All of the woodcock home ranges at Millden were centred on the birchwood component of the study area, which comprised 25%-68% of each range (Appendix 5.7), and there was an average overlap between all the pairs of home ranges of 40.4%. The comparison of habitat use from home ranges with habitat availability in the study area gave $\Lambda=0.1070$ ($\chi^2=22.3$, df=6, $p<0.01$) suggesting that the woodcock did not establish home ranges at random. A ranking matrix ordered the habitats in the sequence young birch > mature birch

Table 5.18 Matrix of means and standard errors of log-ratio differences averaged over all 10 radiotagged woodcock at Millden for comparing habitat use within minimum convex polygon home ranges with availability in the total study area (top).
The implications for habitat use are shown by replacement of each element by its sign (bottom). The sign is tripled for means differing significantly from zero ($p<0.05$, df=8).

	Mature birch & bracken	Mature birch& grass	Young birch	Conifer	*Juncus* flush	Heather	Rough & improved grazing
Mature birch & bracken		0.566 ±0.213	-0.506 ±0.436	2.195 ±0.654	0.797 ±0.299	0.784 ±0.536	0.874 ±0.269
Mature birch & grass	-0.566 ±0.213		-1.072 ±0.320	1.629 ±0.728	0.231 ±0.155	1.218 ±0.590	0.308 ±0.236
Young birch	0.506 ±0.436	1.072 ±0.320		2.701 ±0.993	1.303 ±0.249	2.290 ±0.698	1.379 ±0.499
Conifer	-2.195 ±0.654	-1.629 ±0.728	-2.701 ±0.993		-1.398 ±0.851	-0.411 ±0.770	-1.322 ±0.557
Juncus flush	-0.797 ±0.299	-0.231 ±0.155	-1.303 ±0.249	1.398 ±0.851		0.987 ±0.597	0.077 ±0.339
Heather	-0.784 ±0.536	-1.218 ±0.590	-2.290 ±0.698	0.411 ±0.770	-0.987 ±0.597		-0.910 ±0.590
Rough & improved grazing	-0.874 ±0.269	-0.308 ±0.236	-1.379 ±0.499	1.322 ±0.557	-0.077 ±0.339	0.910 ±0.590	

	Mature birch& brack.	Mature birch& grass	Young birch	Conifer	*Juncus* flush	Heather	Rough& improved grazing	Rank
Mature birch & brack.		+++	-	+++	+++	+++	+++	5
Mature birch & grass	---		---	+	+	+	+	4
Young birch	+	+++		+++	+++	+++	+++	6
Conifer	---	-	---		-	-	---	0
Juncus flush	---	-	---	+		+	+	3
Heather	---	-	---	+	-		-	1
Rough & improv. grazing	---	-	---	+++	-	+		2

with bracken > mature birch with grass > *Juncus* flush > rough and improved grazing > heather > conifer (Table 5.18). There was no detectable difference in the use of young birch and mature birch with bracken, implying that the order of their assigned ranks meant little (Table 5.19). These top two habitats were, however, used significantly more than any of the others. There was also a significant difference between the use of rough and improved grazing and conifer.

Table 5.19 Habitat ranking based on the selection of home ranges by woodcock within the study area, showing where the differences between ranks are statistically significant. Ranks which do not differ significantly ($p \geq 0.05$) according to the matrices in Table 5.18 are assigned the same letter in the "ranks differ" column.

Rank	Habitat	Ranks differ
6	Young birch	*a*
5	Mature birch & bracken	*a*
4	Mature birch & grass	*b c*
3	*Juncus* flush	*b c*
2	Rough & improved grazing	*c*
1	Heather	*b c*
0	Conifer	*b*

All of the habitats were present in most of the home ranges and so all were retained for the comparison of radiolocation distributions with habitat availability in the home ranges. This gave a weighted mean $\Lambda = 0.0414$ ($p = 0.016$ by randomization) indicating that particular habitats within the home ranges were used more intensively than others. The ranking matrix gave the order of habitat

Table 5.20 Matrix of means and standard errors of log-ratio differences for all woodcock at Millden for comparing the distribution of radiolocations with habitat availability within minimum convex polygon home ranges (top). The degrees of freedom for each comparison are given in parentheses. Habitat use is revealed by replacement of each element by its sign (bottom). The sign is tripled where a mean differs significantly from zero (p<0.05).

	Mature birch & bracken	Mature birch& grass	Young birch	Conifer	*Juncus* flush	Heather	Rough & improved grazing
Mature birch & bracken		-1.114 ±0.808 (df=8)	-1.561 ±0.953 (df=8)	1.459 ±0.824 (df=3)	2.012 ±0.717 (df=8)	2.153 ±1.170 (df=7)	3.881 ±0.884 (df=8)
Mature birch & grass	1.114 ±0.808 (df=8)		-0.447 ±0.540 (df=8)	1.079 ±0.798 (df=3)	3.125 ±0.605 (df=8)	2.934 ±0.847 (df=7)	4.995 ±0.490 (df=8)
Young birch	1.561 ±0.953 (df=8)	0.447 ±0.540 (df=8)		1.023 ±1.183 (df=3)	3.572 ±0.537 (df=8)	3.250 ±1.020 (df=7)	5.442 ±0.813 (df=8)
Conifer	-1.459 ±0.824 (df=3)	-1.079 ±0.798 (df=3)	-1.023 ±1.183 (df=3)		1.881 ±1.166 (df=3)	3.087 ±1.170 (df=3)	3.633 ±1.612 (df=3)
Juncus flush	-2.012 ±0.717 (df=8)	-3.125 ±0.605 (df=8)	-3.572 ±0.537 (df=8)	-1.881 ±1.166 (df=3)		-0.079 ±0.937 (df=7)	1.869 ±0.713 (df=8)
Heather	-2.153 ±1.170 (df=7)	-2.934 ±0.847 (df=7)	-3.250 ±1.020 (df=7)	-3.087 ±1.170 (df=3)	0.079 ±0.937 (df=7)		2.056 ±0.853 (df=7)
Rough & improved grazing	-3.881 ±0.884 (df=8)	-4.995 ±0.490 (df=8)	-5.442 ±0.813 (df=8)	-3.633 ±1.612 (df=3)	-1.869 ±0.713 (df=8)	-2.056 ±0.853 (df=7)	

	Mature birch& brack.	Mature birch& grass	Young birch	Conifer	*Juncus* flush	Heather	Rough& improved grazing	Rank
Mature birch & brack.		-	-	+	+++	+	+++	4
Mature birch & grass	+		-	+	+++	+++	+++	5
Young birch	+	+		+	+++	+++	+++	6
Conifer	-	-	-		+	+	+	3
Juncus flush	---	---	---	-		-	+++	1
Heather	-	---	---	-	+		+++	2
Rough & improv. grazing	---	---	---	-	---	---		0

preference as young birch > mature birch with grass > mature birch with bracken > conifer > heather > *Juncus* flush > rough and improved grazing (Table 5.20). The three birch habitats were clearly favoured, each being used significantly more than *Juncus* flush or rough and improved grazing (Table 5.21).

Table 5.21 Habitat types ranked according to relative utilization by woodcock within home ranges, showing where the differences between ranks are statistically significant.

Rank	Habitat	Ranks differ
6	Young birch	*a*
5	Mature birch & grass	*a*
4	Mature birch & bracken	*a b*
3	Conifer	*a b c d*
2	Heather	*b c*
1	*Juncus* flush	*c*
0	Rough & improved grazing	*d*

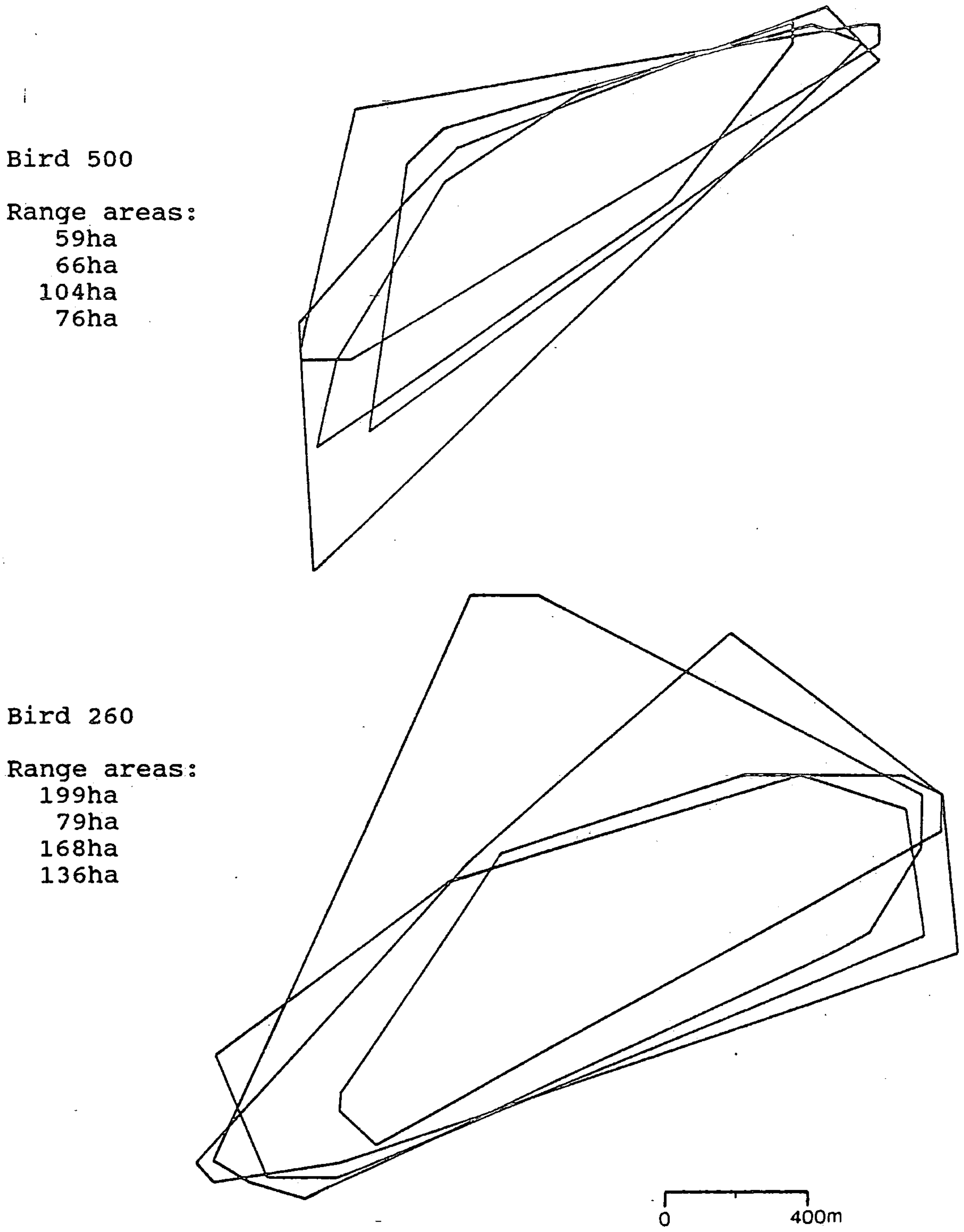
A test for a change in the pattern of habitat use during the course of the breeding season was performed by splitting the radiotagged woodcock into two groups; those tracked during April and May (500, 518, 229, 260, 277, 299) and those tracked during June and July (500, 260, 300, 250, 281, 301). There was no significant overall difference in habitat use between the two time periods; MANOVA F=0.40 (Wilk's Λ=0.5880), df=7,4, N.S., nor were there any significant differences in the use of individual habitats (one-way ANOVAs). Further evidence that the woodcock did not shift their home ranges and hence alter their pattern of habitat use comes from the radiolocation data for birds

500 and 260, which was re-analysed for four equal time periods during the spring and summer. The four separate home ranges of both birds remained concentric despite small changes in range size, and the average overlap between the ranges was 79% for bird 500 and 77% for bird 260 (Figure 5.3).

Due to their apparent importance, the woodland habitats were sub-divided and the pattern of habitat utilization within the home ranges was re-examined with respect to the woodland habitats alone. Habitat use, however, did not differ significantly from random (weighted mean $\Lambda=0.1305$, $p=0.055$ by randomization) and the construction of another ranking matrix based on the woodland habitats alone was not justified.

There were no significant univariate differences in particular habitat variables between adult woodcock feeding locations and paired random locations within the same habitat types at Millden on the basis of Mann-Whitney U-tests, and stepwise discriminant function analysis could only classify 53% of sites correctly. Despite open habitats being largely avoided by feeding woodcock, there was some evidence to suggest that they were used more frequently by nesting females. The number of adult woodcock seen and the number of nests or broods of chicks less than 3 days old were recorded during the course of twelve 500m transect walks through woodland (young, intermediate and mature birch and conifer) or open (bracken, heather and flush) habitats and approximately similar periods of nest searching in each. Twenty-one adult woodcock were flushed,

Figure 5.3 Seasonal change in the size and location of the home ranges (minimum convex polygons) of two radiotagged woodcock at Millden monitored for four 47 day periods during early April to mid-July.



of which 19 (91%) were seen in woodland, whereas ten nests and young broods were located, of which five were found in each habitat type. Six of the nests and young broods were found in bracken, three on the open hill and three under mature birch. Habitat measurements taken from 11 adult feeding sites and seven of the nest sites revealed five significant univariate differences (Table 5.22). Nests were located in areas with relatively fewer, but larger, birch trees than feeding locations and they had a significantly greater percentage cover of bracken and heather.

Table 5.22 Means and standard deviations of habitat variables that were significantly different between woodcock nest sites and adult feeding locations at Millden (Mann-Whitney U-test).

Variable	Nest sites (n=21 quadrats)	Adult feeding sites (n=33 quadrats)	U	Sig.
Mean area per tree (m^2)	4.04 ±1.36	2.95 ±1.45	185.0	$p<0.01$
Basal area per tree (cm^2)	12.5 ± 3.0	11.5 ± 2.0	224.0	$p<0.05$
Brushwood density (dead stems in 3m radius)	7.1 ±12.4	14.4 ±17.4	224.0	$p<0.05$
Bracken (% cover)	29.1 ±34.0	17.7 ±30.6	228.0	$p<0.05$
Calluna (% cover)	6.3 ±13.6	0.0 ± 0.0	231.0	$p<0.001$

Stepwise discriminant function analysis correctly classified 80% of the sites into feeding or nesting locations on the basis of five variables, of which the percentage cover of bracken and heather were the most important (Table 5.23). The signs of the standardized discriminant function coefficients indicate their weighting towards nesting (+) or feeding (-) sites.

Table 5.23 Standardized discriminant function coefficients for discriminating between woodcock nest sites and adult feeding sites at Millden.

Importance rank	Variable	Standardized coefficient
1	Bracken (% cover)	0.900
2	*Calluna* (% cover)	0.614
3	Height of dominant vegetation (cm)	-0.603
4	Mean area per tree (m^2)	0.401
5	Percentage bare ground	-0.294

5.4.6 Diet of woodcock and prey selection in upland birchwood during the breeding season

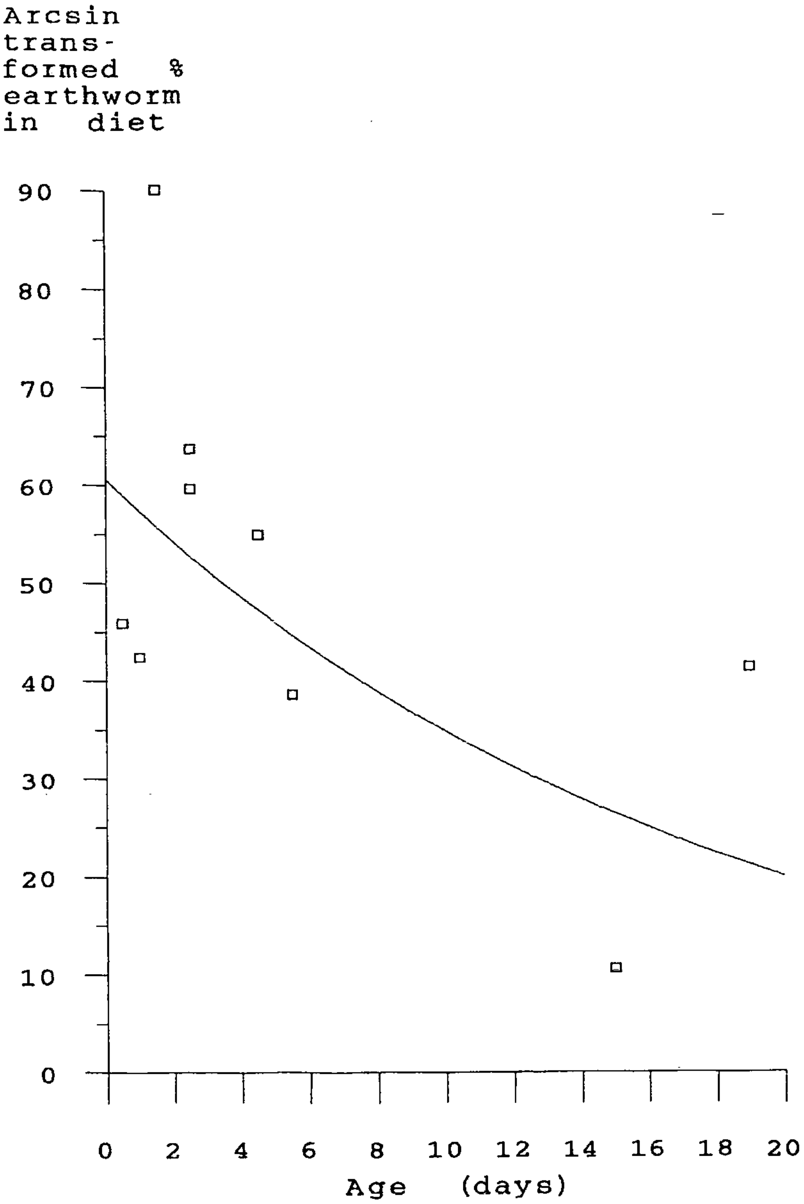
A greater range of prey items was found in the faecal samples from the woodcock at Millden than in those from Whitwell Wood, with dung beetles (Scarabaeidae) included in the adult diet, ants (Hymenoptera, Formicidae) in the chick diet and weevils (Curculionidae) in the diet of adults and chicks. At this site, the diet of adult woodcock and chicks was largely similar, with earthworms comprising 71-76% in terms of biomass (Table 5.24). Spiders were again a relatively important component of the diet in terms of the numbers of individuals ingested although they were far less important in terms of prey biomass. As at Whitwell Wood, caterpillars, sawfly larvae and flies were only taken by adult birds. Carabids comprised a significantly larger component of the diet of adult woodcock in terms of biomass ($\chi^2=5.3$, df=1, $p<0.05$).

Table 5.24 Estimated frequencies of invertebrates in the diet of woodcock at Millden based on faecal analysis.
+ indicates that a small number of prey fragments equal to less than one animal of a particular taxon were identified.

	Adult (9 samples from 4 birds)			Chick (25 samples from 9 birds)		
Prey taxon	*n*	% of total *n*	% of total dry wt.	*n*	% of total *n*	% of total dry wt.
Lumbricidae	34	33.0	70.9	27	42.2	75.6
Scarabaeidae (adult)	2	1.9	1.5	-		
Carabidae (adult)	6	5.8	10.7	1	1.5	2.4
Curculionidae (adult)	6	5.8	1.0	2	3.1	0.4
Staphylinidae (adult)	6	5.8	1.6	4	6.3	1.0
Other adult Coleoptera	3	2.9	0.2	1	1.5	0.1
Coleoptera larvae	4	3.9	2.4	8	12.5	6.4
Formicidae	-			5	7.8	0.8
Lepidoptera larvae	10	9.7	5.1	-		
Araneae & Opiliones	27	26.2	6.1	11	17.2	3.3
Diplopoda	+	<0.1		3	4.7	7.9
Oniscoidea	-			2	3.1	1.6
Diptera	5	4.9	0.4	-		

Changes in the diet of woodcock chicks with age were examined by means of regressions against arcsin transformed percentage frequencies of the different prey taxa. There were no significant relationships between the age of chicks and the proportions of adult and larval beetles, spiders and harvestmen, millipedes and woodlice, or ants in the diet. However, the proportion of earthworms declined as the chicks grew older (Figure 5.4), refuting the hypothesis, at least at this site, that the chicks were likely to be more

Figure 5.4 Change in the proportion of earthworm in the diet of woodcock chicks at Millden with age. (Relationship described by the equation $y=60.61 \times 10^{(0.024x)}$; r=0.62, df=7, N.S.).



dependent on prey that could be obtained without probing during their first few days of life.

Comparison of the mean percentage frequency of the prey taxa sampled by pitfall trapping in adult woodcock and chick diets with their availability in the study area revealed that spiders and harvestmen, beetle larvae and staphylinids were selected in greater proportion than their availability (Table 5.25). Millipedes were largely avoided by adult woodcock and chicks despite being the single most abundant taxon in the pitfall catch.

Table 5.25 The relative proportions of available prey taxa at Millden and their mean proportions in the diet of adult woodcock and chicks.

Prey taxon	Availability in study area (%)*	Mean percent frequency in the diet (±se)	
		Adults (n=4 birds)	Chicks (n=9 birds)
Carabidae (adult)	4.8	7.0 ± 3.0	4.5 ± 3.8
Staphylinidae (adult)	6.0	16.7 ± 5.5	14.8 ± 6.9
Other adult Coleoptera	8.8	20.9 ± 4.6	11.0 ± 5.3
Coleoptera larvae	3.4	11.3 ± 6.5	10.2 ± 6.7
Araneae & Opiliones	17.4	43.8 ± 7.3	53.5 ±14.6
Diplopoda	56.2	0.4 ± 0.4	2.5 ± 2.5
Oniscoidea	3.4	0.0 ± 0.0	3.5 ± 2.4

*Based on the pitfall catch for 1760 trap-days in all habitats.

Millipedes and woodlice were excluded from the comparison of adult woodcock diet with availability at Millden. Compositional analysis based on the other prey taxa gave $\Lambda=0.5837$ ($\chi^2=2.15$, df=4, N.S.) suggesting that they were selected at random. Jacobs (1974) preference index suggested that spiders and harvestmen, staphylinids and other adult beetles were taken by adult woodcock in proportion to their availability, but that there was a preference for beetle larvae and some avoidance of carabids. This result is in agreement with the prey preferences shown by adult woodcock at Whitwell Wood.

The comparison of prey selection for six woodcock chicks and all seven prey taxa with prey availability at Millden gave $\Lambda=0.0175$ ($\chi^2=24.27$, df=6, $p<0.001$), implying that prey selection was not random. A ranking matrix ordered the prey taxa from most preferred to least preferred as spiders and harvestmen > other adult beetles > staphylinids > beetle larvae > woodlice > carabids > millipedes (Appendix 5.8). There were significant differences between millipedes and all the other prey taxa and between spiders and harvestmen and carabids (Appendix 5.8). The Jacobs (1974) preference index values indicated clear preferences for spiders and harvestmen, beetle larvae and staphylinids in that order and a strong avoidance of millipedes (Appendix 5.8). The preference for spiders and harvestmen is in agreement with that shown by woodcock chicks at Whitwell Wood.

5.4.7 Habitat selection in relation to the availability of invertebrate prey in an upland situation

There were significant differences between habitats at Millden in terms of both earthworm density and the availability of soil-surface invertebrates. Earthworms tended to be more abundant in the woodland habitats, but the surface invertebrates were more abundant in the open habitats (Table 5.26). The magnitude of the difference between the woodland and open habitats was greater for earthworms (approximately 2-3x) than for the surface invertebrates (approximately 1.5x) and this probably explains why the woodland habitats were favoured by adult woodcock.

Table 5.26 Differences in the relative abundance of earthworms and soil-surface invertebrates in different habitat types at Millden (one-way ANOVAs).
Letters indicate no significant difference between pairs of values in the Duncan multiple range test ($p \geq 0.05$).

	Earthworm density (no./m^2)			Numbers of invertebrates caught per trap-period		
Habitat	No. of cores	Mean ±se		Trap-periods	Mean ±se	
Mature birch & grass	20	200 ±40	*a*	20	48 ± 6	*a*
Mature birch & bracken	20	116 ±26	*ab*	60	53 ± 3	*ab*
Young & inter-mediate birch	40	111 ±28	*ab*	10	62 ±11	*abc*
Juncus flush	20	111 ±35	*ab*	30	70 ± 7	*bcd*
Calluna	20	74 ±27	*b*	20	83 ±10	*cd*
Conifer	20	47 ±21	*b*		-	
Bracken	20	37 ±20	*b*	36	88 ± 6	*d*
	F=2.96, df=6,153, p<0.01			F=8.02, df=5,170, p<0.001		

There were four significant differences in the availability of invertebrate taxa between adult woodcock feeding sites and random sites within the same habitats, of which a two-fold increase in the number of beetle larvae and a ten-fold increase in the number of adult tipulids at feeding sites were probably of most importance to the woodcock (Table 5.27).

Table 5.27 Means and standard deviations of invertebrate numbers caught per ten day trap-period for taxa that differed significantly between adult woodcock feeding locations and paired random sites at Millden (Mann-Whitney U-test).

Taxon	Feeding sites (n=30 trap-periods)	Random sites (n=30 trap-periods)	U	Sig.
Coleoptera larvae	2.4 ± 2.4	1.2 ± 3.5	215.5	p<0.001
Opiliones	8.0 ± 0.6	15.2 ±11.1	235.0	p<0.01
Oniscoidea	0.1 ± 0.3	0.8 ± 1.4	322.5	p<0.05
Tipulidae (adults)	2.3 ± 6.6	0.2 ± 0.7	315.0	p<0.01

Similar differences in the abundance of beetle larvae and adult tipulids were present between adult woodcock feeding sites and nest sites, whilst significantly higher numbers of caterpillars, spiders, harvestmen and millipedes were present at nest sites (Table 5.28). The differences in the abundances of beetle larvae and spiders and harvestmen between adult feeding sites and nest sites reflect the respective prey preferences of adults and chicks.

Table 5.28 Means and standard deviations of invertebrate numbers caught per ten day trap-period for taxa that differed significantly between woodcock nest sites and adult feeding sites at Millden (Mann-Whitney U-test).

Taxon	Nest sites (n=69 trap periods)	Adult feeding (n=30 trap periods)	U	Sig.
Coleoptera larvae	1.5 ± 2.0	2.4 ± 2.4	764.0	$p<0.05$
Lepidoptera larvae	0.5 ± 1.0	0.1 ± 0.4	763.5	$p<0.01$
Araneae	33.7 ±33.0	16.0 ±13.4	721.5	$p<0.05$
Opiliones	15.9 ±17.4	8.0 ±10.6	657.0	$p<0.01$
Diplopoda	3.0 ± 2.9	0.3 ± 0.8	285.5	$p<0.001$
Tipulidae (adults)	0.4 ± 1.0	2.3 ± 6.6	777.5	$p<0.01$

5.5 DISCUSSION

5.5.1 Habitat use and management in lowland areas

Clearly the nocturnal pattern of feeding activity seen in woodcock in the winter does not end abruptly in early spring as soon as males start searching for mates, but appears to be sustained until late May. By this time most females will have attempted to breed and the peak of roding activity will have been reached (Hirons 1983). The preference for pasture fields at night during the spring was consistent with the finding that woodcock in winter selected particular fields according to their available densities of earthworms and other soil invertebrates and avoided winter cereals (Chapter 4). The fact that earthworm availability in pasture fields declines in summer due to progressive dessication of the topsoil is well documented (Edwards & Lofty 1977) and the relative stability of earthworm densities in the woodland provides a convincing reason for the change in behaviour by the woodcock in June.

A secondary consideration may be that the relatively sparse vegetation cover in woodland during early spring prevents the woodcock from feeding here because of their vulnerability to avian predators (Chapter 6).

The use of sycamore stands by feeding adult woodcock and, in particular, the preference for areas with a high percentage cover of dog's mercury at Whitwell Wood, agrees well with the findings of Hirons & Johnson (1987). The current study shows that the woodcock were able to differentiate between subtle differences in the amount of herbaceous species cover and the amount of leaf litter and dead wood within the same sycamore stands. The reduced leaf litter and dead wood at feeding sites presumably made probing easier, but the sites chosen by the birds also had higher densities of earthworms and soil surface invertebrates than random sites.

The hypothesis that woodland edges were important to woodcock was first inspired by studies of American woodcock that suggested that nests were invariably located close to edges (Coon *et al.* 1977, Gregg 1984). However, Hirons & Johnson (1987) concluded that European woodcock nests at Whitwell Wood were located further from edges than random sites. The pattern of habitat use in relation to woodland edges by feeding birds has not been previously examined. It is conceivable that the increased use of edge strips for feeding by the woodcock at Whitwell Wood was related to the increased shrubby cover which probably reduced the risk of detection by avian predators. Aebischer & Robertson (1992) have shown that pheasants also make greater use of woodland edge habitats within their home ranges than expected by chance. Shrubs are important for pheasants, which intensively use woodland edges rich in cover 30-200cm tall (Robertson *et al.* 1993, Lachlan & Bray 1976). Woodland management for pheasants involves maintaining open rides and shrubby woodland edges (Woodburn & Robertson 1990) and this should also benefit breeding woodcock because as well as preferring to feed in edge habitat, rides are an essential feature for roding males in large woods. This is important because pheasants are a species of considerable economic value and as such they influence the ways in which many landowners plant and manage their woodlands (Cobham Resource Consultants 1992).

The coniferous habitat at Whitwell was probably used relatively intensively during the day because the canopy within the favoured patches was still relatively open such that the habitat provided a shrub layer and dense ground cover. There was no evidence that the woodcock fed in the conifer areas and they would have been relatively unprofitable compared to the stands of sycamore and even beech. For this reason it is more likely that the conifer was simply used as resting sites. The relative safety afforded by the dense cover probably also explains why the young Scots pine was regularly used for roosting. Clearly, if large conifer plantations are to be of value to woodcock, some effort must be made to ensure that blocks are maintained at a range of ages because coniferous areas are likely to be avoided as soon as the canopy closes and the vegetation below is shaded out.

5.5.2 Habitat use and management in the uplands

The home ranges of woodcock at Millden were clearly established in areas of young birch or mature birch with bracken and these habitats were used more intensively within the home ranges. Mature birch with grass as the dominant herb species was probably used less because it afforded very little cover and the woodcock's plumage would have offered it less effective camouflage than in other areas. Woodcock are also more likely to be disturbed by sheep in the patches of woodland with grass. Not surprisingly, rough and improved grazing and heather were largely avoided, although some of the radiotagged birds did occasionally feed in these habitats by day. It seems strange that the woodcock at Millden were not nocturnally active and did not use the nearby pasture fields (section 5.4.1); at present no explanation can be offered for this difference in behaviour between the birds at Whitwell Wood and Millden.

The woodcock did not restrict feeding to particular patches of a certain vegetation structure within the preferred habitats as at Whitwell Wood. The reason for this was probably because there were greater differences between the habitats at Millden, but within each habitat type the vegetational structure was relatively uniform compared to Whitwell Wood. Earthworms, which were relatively more important in the diet at Millden than at Whitwell Wood, occurred at higher densities in the birchwood than the open habitat types. *Juncus* flush was the exception, supporting good numbers of both earthworms and soil-surface invertebrates, but it was used relatively little by the woodcock, presumably because of the relatively poor cover afforded. However, the spring and summer of 1993, when the earthworm samples were taken, remained relatively wet and it is conceivable that these flushes become more important in dry years.

Obviously only limited confidence can be placed on any conclusions about the distribution of nests at Millden because the sample was small. Nevertheless, it was clear that nests were not located exclusively in the woodland. In addition, roding males did not restrict their flights to the wooded areas but regularly displayed for up to 1km over areas of bracken and heather moorland. Hirons (1988*a*) showed that the woodcock at Whitwell Wood roded most intensively over the patches of habitat that were most frequently used for nesting. Assuming the same was true at Millden, the behaviour of the males would suggest that nests were located in open areas as often as in the woodland. Studies of the American woodcock in naturally regenerating alder and aspen woodland showed that the birds nest in relatively open areas whereas broods and solitary birds use heavier cover (Rabe 1977). It is possible that the bracken and heather were used for nesting at Millden because the birds were less likely to be disturbed by sheep and deer than in the woodland.

The encroachment of bracken has become a problem in the uplands during the last decade due to increased grazing pressure from sheep on marginal hill ground which was formerly comprised mainly of heather (Hudson & Newborn

1989). In some areas bracken harbours the tick *Ixodes ricinus* which carries the louping ill virus and this is beginning to worry grouse moor owners. It seems likely that large areas of bracken will be sprayed out in many areas in the next few years, removing nesting habitat for woodcock. The extent of the impact on local populations of breeding woodcock cannot be gauged at this stage, but will obviously depend on the relative success of nesting attempts in the remaining habitats.

5.5.3 The effect on breeding woodcock of changes in the area and types of woodland in Britain during the last 50 years

There has been a 76% increase in the total area of woodland in Britain during the last 50 years (Warren & Key 1991) which might be expected to have provided more habitat for breeding woodcock. However, there has been a major change in the abundance of different types of woodland with the result that there is currently a larger proportion of conifer habitat. There has been a 199% increase in coniferous woodland in the last 50 years, but managed coppice has declined by 82% (Warren & Key 1991) and coppicing has virtually ceased throughout the country (Rackham 1980). Between 30% and 50% of Britain's ancient semi-natural woodland has also been lost. These changes may have reduced the size of the British breeding woodcock population.

Although some of the conifer areas at Whitwell Wood were highly utilized, these consisted of young Scots pine (ten years old) which was still relatively open and supported dense ground vegetation. The mature Scots pine areas at Millden comprised the least preferred habitat type. While it seems likely therefore that woodcock benefitted from the large-scale planting of conifer forests in S Scotland and N Wales in the 1960s, as supposed by Parslow (1967), the value of this habitat to woodcock for breeding is probably now much reduced due to closing of the forest canopy.

Under traditional coppice management, rotations were usually every 7-25 years, which produced a mosaic of coppice patches at different stages within the same wood. Such coppices were characterized by a dense understorey and an open tree canopy and would probably have provided good habitat for woodcock during the breeding season. The loss of coppice habitat has therefore undoubtedly contributed to the decline in the size of the British breeding woodcock population. The woods that have replaced the former coppices consist of tall, mature woodland which is heavily shaded, a good example being the beechwoods of the Chilterns. There is also an increasing trend towards reafforestation of parts of broadleaved woods with conifers (Fuller 1982, Warren & Key 1991). In such woods, the maintenance of rides will enhance their value to woodcock by promoting more woodland edge habitat, which is preferred by woodcock whilst feeding (section 5.4.2).

Intense grazing in unenclosed woodland reduces natural regeneration, and the shrub layer and most of the ground vegetation may be absent. This is currently the case in the New Forest and many western sessile oakwoods, which consequently are unlikely to provide good habitat for woodcock in spring. It is conceivable that the increased grazing pressure exerted by sheep and deer in upland Britain may reduce the suitability of some woods for woodcock due to removal of the understorey.

5.5.4 The diet of woodcock

The range of prey items found in the diets of the woodcock at Whitwell Wood and Millden was similar to that found by Bettmann (1961) based on the examination of 88 gut contents, with the exception that he also found the remains of earwigs *Forficula auricularia* and snails. Rundle (1982) suggested that the gizzard contents of waders were biased towards the remains of large, hard prey and that only the oesophagus, which is frequently empty, could provide a reliable indication of the diet. This explains why Koubek (1986) found beetle remains in 63.5% of woodcock stomachs from birds shot during mid-March to mid-April (n=55) but evidence that earthworms had been eaten in only 6.6%. Green & Tyler (1989) concluded that the relative frequencies of prey items in the diet can be more accurately assessed from analysis of faecal samples than stomachs, provided that estimates of the relative rates of digestion of different prey items can be obtained from calibration experiments on captive birds. The results of the present study, based on faecal analysis, should therefore be more reliable than those of previous studies and suggest that earthworms are more important than beetles in the diet of adult woodcock, comprising 22-33% of the prey items ingested.

The absence of dipteran larvae in the diet was surprising as they comprised 12.8% of the prey items identified in stomachs by Koubek (1986) and were known to comprise an important component of the woodcock diet in winter (Chapter 4). Galbraith (1989) found that tipulid larvae comprised 6.2% of prey items in the diet of lapwing chicks feeding on areas of rough grazing in central Scotland, compared to earthworms which comprised only 3.9%. It is unlikely that tipulid larvae were overlooked in the present study because their distinctive mandibles remain intact in the faeces and I had previously identified them in faecal samples taken from woodcock in winter. The density of dipteran larvae in soil cores at Whitwell Wood (approximately $20m^{-2}$) and Millden (birch $44.7\pm7.9m^{-2}$ (±se), n=80 and bracken, flush and heather $22.8\pm8.3m^{-2}$ (±se), n=60) was relatively low, such that it was probably more profitable for the woodcock to take alternative prey items at these sites. The fact that adult carabids were largely avoided by adult woodcock and chicks at both sites is probably because many carabids exude a pungent chemical when handled (Crowson 1981) which makes them distasteful to birds.

Earthworms only comprised a relatively small proportion of the diet of woodcock chicks at Whitwell Wood and spiders and harvestmen comprised the most important prey taxon. This was in contrast to the situation at Millden where earthworms were a very important component of the chick diet during the first five days of life. Here, rather than increasing as the chicks grew and their bills became better suited to probing, the proportion of earthworms in the diet decreased. The reason for this difference is not clear as the mean ages of the chicks from which the faecal samples were taken were similar at both sites; 5.7 days at Millden and 5.4 days at Whitwell Wood.

This begs the question as to whether the chicks at Millden were fed by the female during the first few days. In general, young waders, with the exception of oystercatchers *Haematopus ostralegus* are not fed by their parents, although young common snipe *Gallinago gallinago* may be fed from the parent's bill at first (Tuck 1972). Broods of young woodcock chicks are very difficult to observe in the wild and there has only been one description of an adult in the wild feeding offspring bill to bill (Workman 1954). Marcström & Sundgren (1977), however, concluded that captive chicks were unable to recognize and collect their own food for the first few days. In the American woodcock, young chicks are said to crowd around the feeding female and take earthworms from her bill (Gregg 1984). They are believed to be dependent on the hen for food until they are at least a week old. Varga (1968) reported that female European woodcock would scrape leaf litter aside so that the chicks could feed, but this behaviour has not been confirmed by other workers. Nevertheless, the clear preference for spiders and harvestmen, a prey type not strongly selected by adult woodcock, at both sites suggests that the chicks also attempted to forage for themselves. There was a suggestion at Millden that woodcock nest sites and adult feeding sites were located in areas supporting the greatest abundance of the preferred prey types of chicks and adults respectively.

Plant material was considered unimportant in the diet of woodcock in this study because the items found consisted solely of small amounts of leaf material, presumed to have been ingested incidentally during probing. However, Koubek (1986) reported the presence of seeds of six species plus pine needles, with plant fragments comprising 20.5% of all the items (excluding grit) identified in stomachs. The American woodcock is also considered to take some plant material as food (Gregg 1984).

6. WOODCOCK BREEDING SUCCESS AND A SIMULATION MODEL FOR BREEDING WOODCOCK POPULATIONS

6.1 INTRODUCTION

There is presently some concern that the resident British breeding woodcock population is declining, particularly in S England (Marchant *et al.* 1990, Lewis & Roberts 1993). In order to devise a means of correcting this trend it is necessary to have an understanding of the rate of mortality at different stages in the breeding process and during the winter. Basic breeding data are limited for the woodcock and there has been no substantial contribution to our understanding of woodcock breeding success in Britain since the Woodcock Inquiry of 1934-35 (Alexander 1945-47). Morgan & Shorten (1974) examined the BTO nest record cards for 1945-71 but only estimated the proportion of nests that were successful and did not attempt to calculate clutch survival. There have been no attempts to measure chick survival or growth in the woodcock probably because the chicks cannot be observed and are difficult to relocate once they have left the nest. Information on chick survival is clearly important because it is at this stage that extrinsic factors such as weather and food availability are likely to have the most impact on overall breeding success.

In addition to an understanding of the relative importance of the different mortality factors in the life-cycle of the woodcock, a reliable method of counting breeding woodcock is required so that populations can be more accurately monitored. Because woodcock are at their most conspicuous when the males are roding, this is the obvious time at which to attempt to census the species. Both the period in which roding males can be observed (the duration of roding) and the number of flights observed per roding period (the intensity of roding) increase through the season, peaking in May and June (Hirons 1983, Ferrand 1989). Hirons (1983) found that the intensity of roding each night was reduced by low daily temperatures early in the breeding season (March) and May and June would appear to be the best months to census roding males. However, the main drawback with a census based on the number of roding males is that it is not possible to recognize individuals by sight and thus a given number of observations may represent different individuals on each occasion or may represent several observations each for a relatively small number of individuals. An attempt was made to quantify this on the basis of sightings of radiotagged males in the present study, in order to determine whether roding counts could be corrected for the number of times the same individuals were seen.

Models are being increasingly used to examine various ecological processes and systems and to assess the relative merits of different management options for particular species. Models are of value in this respect because they enable the effects of different mortality factors to be examined in combination. They can only ever be as reliable as the data on which they are founded, but in cases where large rigorously-collected data sets are available they can be used to produce predictions for subsequent independent testing.

In this chapter an attempt has been made to construct a simple deterministic model for a breeding woodcock population on the basis of 15 years of field data and additional information from national woodcock bags. The data are insufficient for a robust model to be built but the present model has been used to tentatively examine the effect of different levels of harvesting on the equilibrium density of breeding female woodcock, maintained by probable density-dependent overwinter loss, and to estimate the maximum sustainable yield. It has also been used to determine the effect of imposing a cold weather ban on shooting, to show the value of a robust model built on a larger dataset.

Mortality in woodcock is thought to increase in severe winters (Baillie *et al.* 1986) and there is evidence that some woodcock, probably mainly Continental migrants, move south-west in response to cold weather (Tapper & Hirons 1983, Chapter 3). Current legislation enables the Secretary of State to impose wildfowling bans in exceptionally cold winters to offset the extra mortality caused by the freezing of wetland areas, and these apply also to the shooting of woodcock. It is usually considered, though not proven, that some of the additional mortality is attributable to shooting itself, especially where birds are concentrated in ice or snow free areas.

6.2 STUDY SITES

Data were collected from the two woodcock breeding sites, Whitwell Wood, NE Derbyshire (grid reference *SK 5278*) and Millden, Angus (grid reference *NO 5378*), described in Chapter 5.

6.3 METHODS

6.3.1 Estimation of recapture rates and adult survival of woodcock during the breeding season

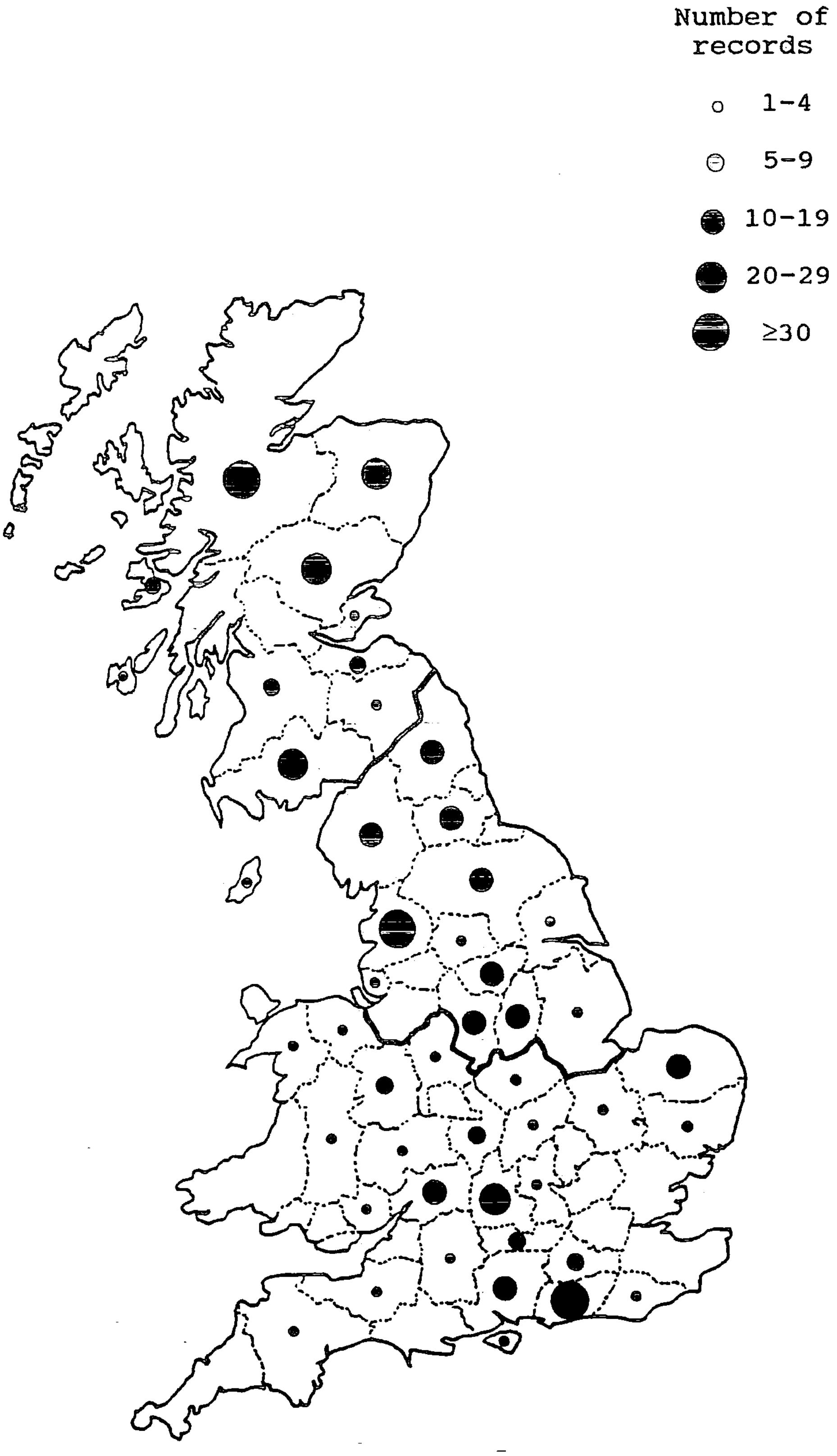
A continuous effort with mist nets and drop traps was employed to catch and ring full-grown woodcock at Whitwell Wood during March-June in 1978-81 and 1985-92. Estimates of the rates of recapture of ringed birds during the same breeding season were weighted according to the days of exposure from the time of ringing. Adult survival during the breeding season was determined from 20 male woodcock and four female woodcock radiotracked during 1986, 1991 and 1992. A finite daily survival rate was calculated by means of the Bart & Robson (1982) estimator, which was then used to estimate survival during the breeding season (taken as 1 March-31 July). This method assumes that each survival event (one bird surviving one day) is independent and has a constant probability over all the birds and all days. It was used in preference to the Kaplan-Meier (1958) or product limit estimator described by Pollock *et al.* (1989) because the woodcock were not all radiotagged and released at the same time; one of the requirements of the product limit estimator. In addition only one bird was found dead, which would have rendered the latter method relatively inaccurate.

6.3.2 Analysis of nest record cards

A total of 539 nest record cards collected by the British Trust for Ornithology during the period 1945-1989 were analyzed. The nests were encountered during the course of general nest finding by observers throughout Britain. Seventy-nine cards were excluded because they related only to hatched young, as were 11 nests that were recorded as predated or abandoned when first found. The distribution of records was biased towards N England and Scotland and there were particularly few records from Wales (n=6) or SW England (n=3) (Figure 6.1). This is in agreement with the distribution of breeding woodcock given by Sharrock (1976) and Lewis & Roberts (1993). At least two visits were made to 328 of the nests, enabling the records for these to be used to calculate daily rates of nest loss.

The incubation period was taken as beginning on the day the last egg was laid and finishing on the day the last chick hatched. Records of clutch size were only accepted on two conditions. First, if two visits to the nest more than 48 hours apart showed no increase in the number of eggs laid, or second, if nests where hatching was recorded were visited during the 15 days prior to the hatch. First egg dates were determined from nests found during laying by subtracting one day for each egg laid, or from nests for which the hatch date was known by subtracting 22 days plus one day for each egg. Records where the date of hatching

Figure 6.1 The distribution of records for woodcock nests from the BTO Nest Record Scheme for 1945-1989 (n=449) and the division of Britain into central and S England, N England and Scotland for the purpose of determining regional differences in first egg dates.



could be determined to within ±5 days were included. Regional differences in the onset of egg laying were studied by splitting Britain into three areas; central and S England, N England and Scotland (Figure 6.1).

Rates of nest loss were calculated using the Mayfield method (Mayfield 1961, 1975) in a revised form which allowed statistical comparisons (Hensler & Nichols 1981, Sokal & Rohlf 1981). This method assumes that the daily survival probability (S) during a given stage of nesting is constant and that the probability of a nest surviving throughout a stage lasting x days is S^x. Loss rates were estimated from the number of days during which nests were observed and from the number of losses occurring during that period. If the date of nest failure could not be ascertained it was assumed to have been half-way between visits, except in cases where the parent bird was flushed during a visit and the nest was subsequently found to be deserted. In these cases, the date of nest failure was taken as the date on which the parent bird was last present. In order to test whether nest searching influenced clutch survival during incubation, separate rates of nest loss were calculated for the five days immediately after the nest was found and for the period 6-22 days after finding.

6.3.3 Nest and brood location at Whitwell Wood

Nests were located by performing systematic searches of Whitwell Wood throughout the breeding season using trained dogs. They were then checked from a distance through binoculars every day until hatching. Broods from known nests were usually located on the day they hatched but a number of additional broods were found when searching with dogs. In each case measurements were taken and the chicks were ringed. As far as possible, broods were recaptured at three day intervals and further measurements were obtained.

Daily rates of chick mortality were calculated on the basis of chick-days, with losses assumed to have occurred midway between brood captures, using the revised Mayfield method (Hensler & Nichols 1981). It was assumed that all of the chicks were found each time a brood was located, although in a few cases this may not have been the case. The calculated chick survival is therefore likely to be a minimum estimate. The period from hatching to flying was taken as 20 days (Hirons 1983).

6.3.4 Counts of roding male woodcock

Counts of roding male woodcock were made at dusk during May and June 1991 at Whitwell Wood and during May and June 1992 at Millden. The same location was used on all nights and the intensity of roding each night was recorded as the number of times that a woodcock flew within 100m of the observer. The duration of the roding period was recorded as the time between the first and last sightings. The last sighting was judged to have been made if more than 30 min. elapsed during which no further birds were seen. The air temperature at 20.00 BST was recorded each evening in order to examine its effect on the roding intensity.

Data on the duration of roding periods and the number of sightings per evening of six radiotagged male woodcock during May and June 1986, supplied by Dr. G. Hirons, have been examined to determine the degree to which individual male woodcock differ in their roding behaviour.

6.3.5 Key and *k* factor analyses

Data collected at Whitwell Wood during the period 1978-1992 were used to investigate the strength of the different mortality factors acting on the woodcock there. As male woodcock are polygynous (Hirons 1979, 1980, 1981), the viability of breeding populations is determined by the number of females and so the key factor analysis was restricted to females. It had to be assumed that there was no difference in the mortality of female woodcock with age, because there is currently no evidence to suggest otherwise. Survival after the first year of life is not age dependent in the lapwing *Vanellus vanellus* (Peach *et al.* 1994). Mortalities were calculated as *k* values (Varley & Gradwell 1960) and five mortality factors were examined, four of which were included in the analysis:

Egg mortality k_1

The total number of eggs laid each year was estimated from the eggs counted in active nests and from the number of nests found freshly predated and the number of broods located (Appendix 6.1). The number of eggs that hatched from the nests found during incubation was known. Each nest found predated and each additional brood was assumed to have originally consisted of a nest containing four eggs. In these cases, it was assumed that all the eggs hatched for each brood found and that all the eggs were lost for nests found predated. The estimated total number of eggs laid (E) and the number hatched (H) were corrected for the nest searching effort each year and were converted to densities km^{-2} by dividing by 1.71 (Whitwell Wood covers an area of $1.71km^2$). The correction for nest searching effort (Appendix 6.1) was an imprecise subjective estimate which might cause substantial error in the key and k factor analyses. Estimates of egg mortality k_1 for 1978-81 and 1985-92 were calculated as $\log E - \log H$. Egg mortality k_1 could not be calculated for 1982-84 because the fates of the nests found were not known.

Female mortality k_2

Insufficient data were obtained to enable individual values to be calculated for each year and this mortality factor was not included in the key and k factor analyses. An estimate of the proportion of nest failures that resulted in death of the female was determined from the outcomes for active nests found during 1978-81 and 1985-92.

Chick mortality k_3

The number of woodcock chicks fledging from every brood could not be determined and thus chick mortality k_3 was estimated from chick survival (S) calculated on the basis of chick-days of observation (Hensler & Nichols 1981). Chick mortality k_3 was determined as $-\log S$ for the six years (1986, 1988-1992) where more than 40 chick-days of data were obtained.

Shooting mortality k_4

Shooting mortality k_4 each year was estimated from the proportion of the woodcock ringed at Whitwell Wood in spring and known to be alive, that were recovered each winter (P) (Appendix 6.2). The number of ringed birds at risk each winter was estimated using a constant annual adult survival rate of 0.58 (Chapter 2) and it was assumed that all the recoveries due to shooting were reported. Shooting mortality k_4 was then calculated as $-\log(1-P)$. It was assumed that both sexes were equally susceptible to being shot.

Overwinter loss k_5

Overwinter loss k_5 due to natural factors was determined from the total overwinter loss (k_4+k_5) minus the shooting mortality k_4. It included all the unknown natural mortality occurring between the end of the breeding season and the onset of nesting the following spring, as well as immigration and emigration (hence the term overwinter loss as opposed to mortality).

Total overwinter loss due to shooting and natural losses (k_4+k_5) was calculated as the difference between the estimated density of females in autumn (A_a+Y) each year (n) and the known spring female density (A_s) the following year ($n+1$): $\log(A_a+Y)-\log(A_s)$. The density of adult females in the autumn of year n was estimated from the spring female density in year n, using a female survival rate during the breeding season of 0.68 (Hirons 1983), to which was added half the number of young woodcock fledged (assuming that equal proportions of male and female young were fledged).

The number of woodcock chicks at hatching was known for 1978-81 and 1985-92 and was estimated for 1982-84 using a constant clutch survival (including hatching rate) of 0.692. The number of young woodcock fledged was estimated as the number at hatching multiplied by the known rates of chick survival for 1986 and 1988-92 and by a constant survival of 0.451 for the remaining years. In some years, immigration exceeded natural mortality and emigration, and negative k values were used in these cases.

The total annual mortality K was determined as the sum of the individual mortalities during each year. The key factor analysis was performed by plotting each of the k values as the dependent variable against the total mortality K (Podoler & Rogers 1975). The relationships between the individual mortality factors and the log of density before the mortality occurred were examined, although there were insufficient data for chick mortality k_3 to enable the regressions to be used to test for density dependence as described by Southwood (1966) and Ito (1972). Errors in the estimation of density dependence from plots of k values against log initial densities arise because there is serial correlation between the population sizes in a series of years and so k and log initial density are not independent variables. In addition, the population size is estimated and the errors of estimation are not equal for all stages of the life cycle (Kuno 1971).

As a check on the relationship between the density of woodcock at Whitwell Wood in spring and the production of young, bag data and age ratios from birds that were shot throughout N England were employed to examine the relationship. These were obtained from the Game Conservancy Trust's National Game Census (regions 7+8) and the British Association for Shooting and Conservation's Woodcock Production Survey respectively for the years 1975-85. Data for N England were used because these were likely to be mostly resident woodcock (Chapter 2). National data could not be used because of the high proportion of Continental woodcock wintering throughout S England and Wales.

The figures for the proportion of ringed woodcock from Whitwell Wood shot during the winters of 1978/79-1985/86 were used to represent the proportion of woodcock shot each winter throughout N England. A mean value of 4% was used for the winters of 1975/76-1977/78, and in those years when no ringed woodcock from Whitwell Wood were shot the proportion for N England was taken as 2%. As shooting takes place on approximately 62.5% of the land surface of the UK (Piddington 1981), it was estimated that the proportion of woodcock shot on the area on which shooting took place in N England was equivalent to 16%. The density of woodcock during the autumn prior to shooting was then calculated by dividing the bag/km^2 by 0.16. The density in the spring following shooting was equivalent to the autumn density less the woodcock bag/km^2. The densities of adult and young woodcock in the autumn were estimated by multiplying their proportions in the bag by the total autumn density. The log spring density calculated from the woodcock bag each year was then plotted against the log of the density of young in autumn calculated from the woodcock bag and young: old ratio in the following year.

There were several difficulties and possible sources of error in the key and *k* factor analyses. The estimate of the number of eggs laid each year was dependent on assumptions about the number of eggs in nests found already predated and the number of eggs and their hatching success for broods where the nest was not found. Because the location of woodcock nests and broods was not a primary concern during 1978-1987, corrections were required for the reduced searching effort during these years. These corrections were subjective estimates and hence there is scope for substantial error in the estimate of the number of eggs laid each year. Another problem was in estimating chick mortality k_3, because relatively few broods were retrapped each year and sufficient data for an annual chick survival rate estimate were only obtained in six years. The fact that annual estimates of chick mortality k_3 were not obtained for 1978-85 and 1987 meant that a constant mean value had to be used. As the value of k_3 was used in calculating the number of young in the autumn, this will also have produced an error in the estimated size of the autumn population and hence in the value for overwinter loss k_5 for these years. During 1983-85, very few ringed woodcock were at risk from shooting (Appendix 6.2) and the estimates of shooting mortality k_4 for these years are relatively inaccurate. These inadequacies in the data mean that the results of the key and *k* factor analyses should be treated with caution. The present analyses are best viewed as a means of identifying the areas requiring additional data for reliable future analyses.

6.3.6 Construction of a population model

A simple deterministic model of the breeding woodcock population at Whitwell Wood was constructed on the basis of those relationships between mortality factors and the log of density prior to the mortality that were significant. In the cases where the relationships were not significant, mean values for the mortality factors were used. The approach was to start the first year with an arbitrary density of breeding female woodcock and to estimate successively the number of eggs they laid and hatched, and the number of young that survived to flying. Half the number of young were added to the females that survived the breeding season and shooting and winter losses were subtracted to give the density of females the following spring.

The number of breeding females each spring was estimated from the number of nests and additional broods located each year (Appendix 6.1). Nests found freshly predated were included because 80% of the females whose first nesting attempt fails move to a different wood to re-nest (Hirons 1983) and there was therefore little chance of finding two nests laid by the same female. Nests initiated after 15 May or broods estimated to have been from nests started after this date were excluded, because they were likely to have constituted re-nesting attempts by additional females whose first clutches had failed in other woods. Intensive nest searches were conducted throughout the breeding season in 1988-92 and it was assumed that all the woodcock nests in Whitwell Wood were found in these years. The number of nests and additional broods found in the earlier years was corrected according to an approximate estimate of the search effort employed (Appendix 6.1).

Each female was given two opportunities to rear a brood, but because most of the females that lost their first clutches were likely to leave the wood (Hirons 1983), it was assumed that the females that left were replaced by an equal number of females whose first clutches had failed in other woods. There was no evidence for any age dependent effects in female mortality k_2, shooting mortality k_4 or overwinter loss k_5 and differential mortality with respect to age has not been considered in the model. The mean annual total female mortality was such that each bird only survived for two years in the model, so that age dependent effects would not be important.

The model was first run to equilibrium and was then used to predict the size of the spring woodcock population at Whitwell Wood each year when given values for the overwinter loss k_5. As immigration occurred at Whitwell Wood in some years, it was simulated by using negative values of overwinter loss k_5. Validation, the quantitative comparison of output from the model with independent observed results

(Jeffers 1978, Carter *et al.* 1982), was not possible with the woodcock model because no further data were obtained. Hence model testing only involved checking the equations and mean values used in each step of the calculation of the new spring population. The model was used to determine the maximum sustainable yield for the woodcock population at Whitwell Wood. Immigration could not be allowed to maintain the sustainable yield and the overwinter loss k_5 was constrained to a minimum value of zero. The maximum sustainable yield was estimated from the spring density of females and the yield (shooting bag) after the model was run for 20 generations with a range of shooting mortality k_4 values between 0% and 50%. A fixed period of 20 generations was used in the simulations because approximately 60 generations were required to reach equilibrium once more than 25% of the autumn female population was harvested.

The effect of a cold weather ban on shooting was investigated using the model by imposing a high overwinter loss for one year and determining the time to recovery to the equilibrium density. The annual survival rate during the year which included the 1962/63 winter, the coldest in England for 223 years, was 0.34 (Potts & Hirons 1983) and thus the overwinter loss k_5 was set to 50% (68% female survival during the breeding season). The spring female density following the severe winter was determined with and without shooting during the winter. The two most extreme outcomes were simulated by assuming that no bag was taken when the simulated ban was imposed and that all the shooting had taken place before the severe winter weather when shooting was permitted. The model was run to equilibrium spring female density before and after the year of the severe winter with shooting mortality k_4 set to 4%. The simulation was repeated with the shooting mortality set to 10% and then 20%.

It is possible that the proportion of woodcock shot might increase as a result of cold weather, but this effect was not considered in the simulations because Potts & Hirons (1983) showed it to be small and not statistically significant. It is unlikely that the proportion of birds shot increases in woodcock in the same manner as for wildfowl because woodcock are solitary birds and do not occur in large concentrations on frost-free patches except very occasionally at night. Unlike wildfowl, woodcock cannot be attracted to particular areas by the provision of supplementary food.

6.4 RESULTS

6.4.1 Adult fidelity to the breeding site

During 1978-1991, a total of 226 full-grown woodcock were ringed at Whitwell Wood between 25 February and 30 June. Of these, 20 (9%) were recovered dead during the breeding season (1 March-31 July), 16 (80% of those recovered) within Whitwell Wood. Two of the four other birds were recovered 8km and 9km away during June and July of the same season and probably represented females that moved after losing their first clutches at Whitwell Wood. The remaining two birds were recovered in Sweden and

Estonia later in the same year. Both were ringed early in the season (16 March and 26 March) and were clearly migrant birds passing through Whitwell Wood on their way back to their Continental breeding areas.

Ninety-three of the woodcock marked at Whitwell Wood during 1978-1991 were ringed during 25 February-31 March and 133 were ringed during 1 April-30 June. Twenty-one of these ringed birds were recovered during the same season, nine (10%) of which had been ringed prior to 1 April and 12 (equivalent to 12% when corrected for exposure time) of which had been ringed on or after 1 April. The difference in the proportions of each group recaptured was not significant (d=0.43). Forty-two of the woodcock were recaptured in subsequent breeding seasons, 15 (16%) and 27 (20%) respectively from the birds ringed before and after 1 April. The difference in the proportion recaptured in later years was not significant (d=0.80). These results suggest that there were only relatively small numbers of Continental woodcock passing through Whitwell Wood during March.

Eighteen of the woodcock ringed as full-grown birds at Whitwell Wood during the breeding season were recovered in winter (1 October-28 February). Of these 15 (83%) were within 15km of Whitwell Wood. The three others were recovered in N Yorkshire (54km) and S Ireland (330km and 530km), but there was no suggestion that these movements were caused by cold weather. All except one of the birds were shot.

6.4.2 Adult survival during the breeding season

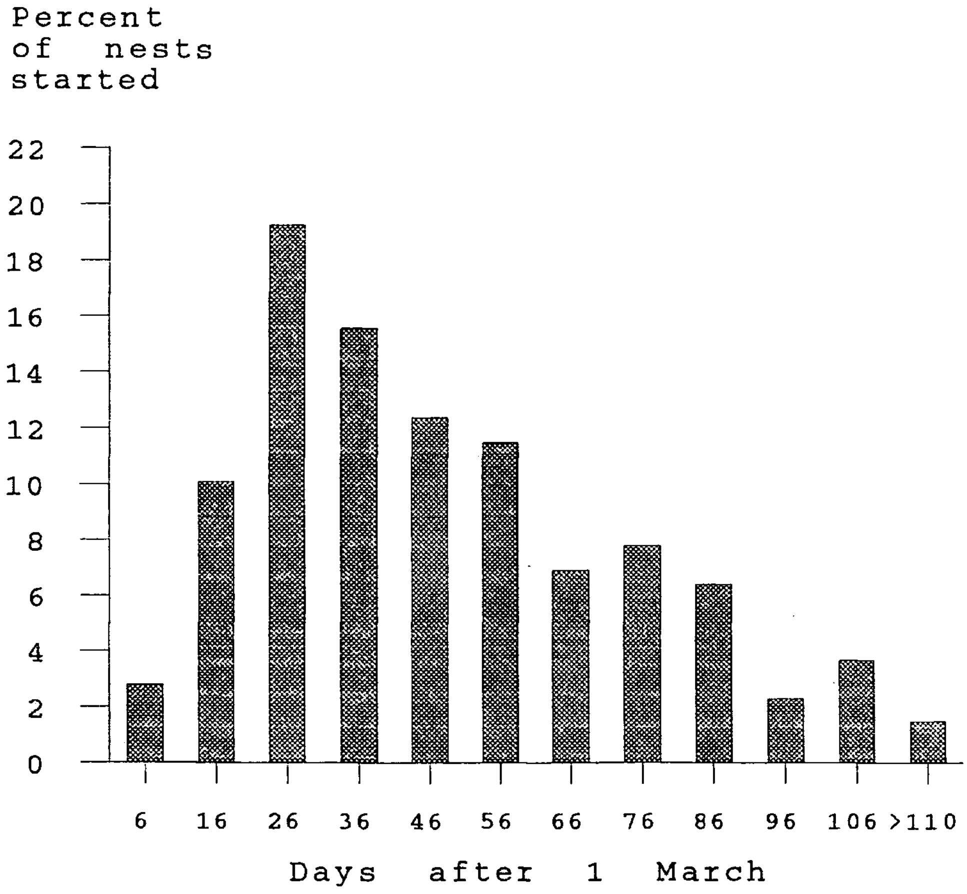
Survival data were obtained for a total of 24 radiotagged woodcock at Whitwell Wood during 1986 and 1992. During 535 bird-days one bird died, giving a daily survival rate of 0.9981 (0.9927-1.0000 95% cl) by the Bart & Robson (1982) estimator. Taking the breeding season as 1 March to 31 July, this is equivalent to an adult survival of 0.751 (0.325-1.000 95%cl) during breeding. Considering that the sample of radiotagged woodcock consisted largely of males, this estimate is similar to those of 0.76 male survival and 0.68 female survival during the breeding season calculated by Hirons (1983).

Of the 16 ringed woodcock recovered at Whitwell Wood and the two recovered within 10km during the breeding season, the cause of death was established for 11 birds. One was hit by a car, and the ten other birds were predated, three by foxes *Vulpes vulpes*, two by stoats *Mustela erminea*, three by sparrowhawks *Accipiter nisus* and two by tawny owls *Strix aluco*.

6.4.3 Timing of breeding and duration of the incubation period

First egg dates (n=218) from the BTO nest record cards ranged from 8 March to 21 July, with a peak in egg laying during early April (Figure 6.2). The mean first egg date was 18 April and there was no evidence of a bimodal distribution in egg laying. Egg laying commenced later in N England than in central and S England and later still in Scotland, as revealed by a significant Kruskal-Wallis test

Figure 6.2 Distribution of first egg dates in the woodcock, based on BTO nest record cards for 1945-1989 (n=218), presented as the frequency during ten day intervals after 1 March.



(χ^2=7.75, df=2, $p<0.05$). The mean first-egg dates were; central and S England, 14 April ±2.8 days (±se, n=86), N England, 18 April ±3.4 days (±se, n=67) and Scotland, 25 April ±3.2 days (±se, n=65).

Clutch size in the nest record card data ranged from two to five eggs and averaged 3.89 eggs (n=277 nests). Eggs were usually laid on consecutive days or, less frequently, on alternate days. The mean laying interval for eight nests for which the entire laying period was observed was 1.37 days, giving an average laying period of 4.1 days for a clutch of four eggs. There were 15 accurate records of the incubation period; one of 17 days, one of 19 days, three of 21 days, three of 22 days, five of 23 days and two of 24 days, giving a mean of 21.9 days.

6.4.4 Daily rate of nest loss

The daily rates of nest loss during egg laying and during incubation were 0.035±0.030 (±95% cl, n=144 nest-days) and 0.031±0.006 (±95% cl, n=2,906 nest-days) respectively. These rates were not significantly different (z=0.26 N.S.). Daily rates of nest loss due to desertion and predation during egg laying and incubation combined were similar; 0.013±0.004 (±95% cl) and 0.018±0.005 (±95% cl) respectively, z=1.76 N.S. Nest searching did not appear to affect clutch survival, as there was no evidence of an increased rate of nest desertion or total nest loss immediately after nests were found (Table 6.1).

Table 6.1 Estimated daily rates of nest loss (±95% cl) in relation to days after which nests were found during the incubation period.

	1-5 days	6-22 days	
No. of nest-days	1,386	942	
Rate of desertion	0.010 ±0.005	0.013 ±0.007	z=0.66 N.S.
Rate of other loss	0.017 ±0.007	0.024 ±0.010	z=1.15 N.S.
Total rate of loss	0.027 ±0.008	0.037 ±0.012	z=1.33 N.S.

Losses due to desertion were largely attributable to man, either through accidental flushing of sitting birds or through disturbance caused by forestry activities. It is likely that some of the losses recorded as desertion were due to predation of the female away from the nest. Other losses were mainly caused by predation, although the identity of the predator was rarely recorded. Of the predators that were reported, jays *Garrulus garrulus*, crows *Corvus corone*, woodmice *Apodemus sylvaticus*, and hedgehogs *Erinaceus europaeus* were responsible for egg predation, foxes and stoats for taking both the parent bird and eggs, and tawny owls for killing the female.

Insufficient nests were found during egg-laying at Whitwell Wood to enable estimates of mortality and survival rate to be calculated, but of the five nests that were found during this stage, three were deserted and one was predated. Sixty-one nests were monitored during incubation at Whitwell Wood and the daily rate of nest loss was 0.025±0.011 (±95% cl) (Table 6.2). This rate is slightly lower but not significantly different (z=0.93) from that calculated for Britain as a whole from the BTO nest record cards. There was no difference in the daily rate of nest loss between 1978-1988 and 1989-1992 (Table 6.2).

Table 6.2 Daily rates of nest loss in woodcock at Whitwell Wood during 1978-1992.

Years	Nest-days	Daily rate of nest loss (±95% cl)	Significance
1978-1988	494.5	0.026 ±0.014	z=0.29 N.S.
1989-1992	304	0.023 ±0.017	
Total	798.5	0.025 ±0.011	

Ten nest losses at Whitwell Wood could be attributed to particular predators due to the manner in which the eggs were broken or the locations where radiotagged hens were recovered. Four clutches plus one hen were lost to foxes, one clutch plus hen to a stoat or rat *Rattus norvegicus*, one clutch to a grey squirrel *Sciurus carolinensis* and two clutches to corvids (probably jays). Two hens were killed, one by a sparrowhawk and the other by a tawny owl. The female taken by the sparrowhawk was killed a short distance from the nest whilst feeding. In the case of the bird killed by the tawny owl, the female was taken off the nest and later found in an owl box.

Daily rates of nest loss from the nest record card data were examined with respect to region and time period, using the data for egg laying and incubation combined. The rates in central and S England, N England and Scotland were similar (Table 6.3). The rate of nest loss was lower during the period 1980-89 than during 1970-79 or 1945-69, the difference between 1980-89 and 1970-79 being statistically significant (Table 6.3).

Table 6.3 Regional and temporal differences in daily rates of woodcock nest loss during the nesting period, calculated from BTO nest record cards for 1945-1989.

	Nest-days	Daily rate of nest loss (±95% cl)	Significance	
Central & S England	1358	0.029 ±0.009		
			z=0.53 N.S.	
N England	902	0.033 ±0.012		z=0.39 N.S.
			z=0.12 N.S.	
Scotland	790	0.032 ±0.012		
1945-69	1072.5	0.034 ±0.011		
			z=0.48 N.S.	
1970-79	923.5	0.038 ±0.012		z=1.83 N.S.
			z=2.22 $p<0.05$	
1980-89	1054	0.021 ±0.009		

6.4.5 Annual rate of chick production

The daily rate of loss during egg laying suggests that a clutch of four eggs taking four days to complete (section 6.4.3) would have a probability of 0.87 of surviving the laying period. During the 22 day incubation period the daily rate of nest loss from the nest record cards suggests that 0.50 nests survived to hatch and that from the nests observed at Whitwell Wood that 0.57 nests survived to hatch. The probability of an average clutch surviving from the day the first egg was laid until hatching is therefore 0.44 for the nest record card data and 0.50 for Whitwell Wood. Many woodcock will re-nest after the loss of a clutch, but probably only attempt to do so once. Assuming that each hen can make two nesting attempts but that each will only raise a single brood per year, it is possible to calculate the proportion of hens hatching a brood of chicks per year by considering the breeding season as two consecutive 30 day periods, the first commencing on 18 April (the mean first egg date). Taking the daily survival of woodcock hens as 0.9975, based on Hirons' (1983) estimate of survival during the breeding season (1 March-31 July) of 0.68, and assuming that the rate of nest loss remained constant throughout the breeding season, it can be estimated that between 65% (nest record cards) and 71% (Whitwell Wood) of the hens alive on 18 April would have produced a brood of chicks (Table 6.4). This is equivalent to 75%-83% of the hens surviving the 60 day breeding period.

Table 6.4 Annual brood production by woodcock hens, based on data from BTO nest record cards and from Whitwell Wood.

Days after 1 March	Number of hens alive	Percentage of hens attempting to nest		Percentage of hens producing a brood	
		BTO	Whitwell Wood	BTO	Whitwell Wood
48-78	100	100	100	43.5	49.7
79-109	92.8	49.3	43.1	21.4	21.4
Number of hens surviving	86.1	Percentage producing a brood		64.9	71.1

Previous studies of nesting woodcock (Morgan & Shorten 1974) have simply recorded the proportion of the nests found which produced a brood, regardless of the stage of laying or incubation when first found. With the nest record card data, the proportion of nests hatching from the 317 nests for which the outcomes were known gave a misleadingly high estimate of clutch survival (Table 6.5). However, the table again shows that desertion was an important cause of nest failure, accounting for 46% of all nest losses.

Table 6.5 Fates of woodcock nests from BTO nest record cards for which the outcomes were known.

Fate of nest	Number of nests		% of nests for which outcome known
Deserted	58		18.3%
Predated/nest empty	68	(41+27)	21.4%
Hatched ≥1 young	191		60.3%

The fates of 933 eggs were known from the 277 nests where the clutch size was determined accurately. In all, 74.1% of the eggs survived incubation and of these 7.2% were addled or damaged by the parent bird (equivalent to 5.4% of the eggs at the start of incubation). At Whitwell Wood, 20 broods were found within a day of hatching such that the number of chicks and the number of hatched egg-shells could be counted. 79 eggs yielded 73 chicks: three eggs were infertile, two chicks were found dead in their shells and one egg was damaged by the parent bird. Mortality at this stage was therefore 7.6%; a figure very similar to that calculated from the BTO nest record cards.

6.4.6 Chick survival and annual production of fledged young

No information was available on the survival of woodcock chicks from the nest record card data but a total of 37 broods were recaptured at Whitwell Wood. This yielded data for 1211 chick-days and suggested a daily rate of chick mortality of 0.039±0.011 (±95% cl) (Table 6.6). This figure should be treated with caution because it is likely that chick mortality was higher during the first 3-4 days until the chicks were able to thermoregulate. If true, this violates the assumption of a constant mortality rate during the period from hatching to fledging required for the calculation of chick mortality by the Mayfield (1961, 1975) method. Chick mortality was significantly higher during 1978-1988 than during 1989-1992, but the data for 1978-1988 were only based on ten broods and probably do not provide a reliable estimate of chick mortality. Examination of the 1989-1992 data with respect to summers of normal rainfall (1989 and 1990) and very low rainfall (1991 and 1992) suggested that chick mortality was relatively high during dry summers, although the difference was not significant: 1989+1990, 0.025±0.011 (±95% cl, n=766.5 chick days) and 1991+1992, 0.056±0.040 (±95% cl, n=125.5 chick days); z=1.46 N.S. The overall daily rate of chick mortality suggests that the mean chick survival during the 20 day period until fledging was 0.451.

Table 6.6 Daily rates of woodcock chick loss at Whitwell Wood during 1978-1992.

Years	Chick -days	Daily rate of chick loss (±95% cl)	Significance
1978-1988	319	0.066 ±0.029	z=2.45 $p<0.05$
1989-1992	892	0.029 ±0.011	
Total	1211	0.039 ±0.011	

The mean production of fledged young per breeding female according to the BTO nest record card data and the data from Whitwell Wood was determined by multiplying the probabilities of survival at each of the component stages (Table 6.7). This gave values for the mean number of fledged young per female of 1.14 and 1.23 for the data from the nest record cards and from Whitwell Wood respectively. These figures were equivalent to mean flying brood sizes for the nest record card data and for Whitwell Wood respectively of 1.74 young and 1.71 young per female that successfully produced a brood.

Table 6.7 Annual production of fledged young per breeding female woodcock.

	Mean clutch size	Survival during incubation*	Egg fertility	Chick survival	Mean no. of fledged young
Nest record cards	3.89	0.701	0.928	0.451	1.14
Whitwell Wood	3.95	0.747	0.924	0.451	1.23

*Allowing for one re-nesting attempt.

6.4.7 Growth of woodcock chicks

A total of 162 woodcock chicks were observed at hatching and 59 of these were ringed during their first 12 hours. Ninety-six chicks were recaptured on 144 occasions 2-30 days later. The mean bill length on the day of hatching was 16.2±0.1mm (±se, n=51) and the mean weight was 19.2±0.3g (±se, n=51). Both bill length and weight decreased significantly between day 0 and day 1 and increased significantly between day 1 and day 2 (Table 6.8).

Table 6.8 Changes in the bill length and weight of woodcock chicks during the first three days of life.
Differences between days tested by one-way ANOVAs. None of the chicks measured on the three days were the same individuals.

	Day 0 (n=51)		Day 1 (n=6)		Day 2 (n=22)
Bill length (mm) (mean±se)	16.2 ±0.1	F=8.30 df=1,55 p<0.01	15.2 ±0.2	F=10.95 df=1,26 p<0.01	18.4 ±0.5
Weight (g) (mean±se)	19.2 ±0.3	F=5.34 df=1,55 p<0.05	17.2 ±0.6	F=17.93 df=1,26 p<0.01	26.5 ±1.1

These observations were as expected from studies of the growth of other wader chicks, such as those of common snipe *Gallinago gallinago* (Green 1985), with the exception that the bill length could not have decreased from day 0 to day 1. This anomaly is probably due to the fact that only a small number of woodcock chicks (n=6) were measured when one day old. It is also unlikely that the value for the mean bill length on day 0 represented the bill length at hatching because most of the chicks were not ringed until at least six hours after hatching.

Both bill length and weight were good indicators of the age of woodcock chicks (Figures 6.3 & 6.4) and the growth for chicks aged 2-15 days could be described by linear relationships. These suggested that the bill increased daily by 1.7mm and that the daily increase in weight was 7.9g. The relationships were used to derive the following equations for ageing young woodcock chicks:

$$\text{Age (days)} = -4.32+0.41\ \text{bill length (mm)}$$

$$\text{Age (days)} = 0.95+0.09\ \text{weight (g)}$$

The correlation coefficients for both equations were highly significant; bill length $r=0.83$, $df=70$, $p<0.001$ and weight $r=0.85$, $df=91$, $p<0.001$. Weight is probably the better indicator of chick age as the mean error in ageing was lower for chick weight (1.30 days) than for bill length (1.56 days). The growth curve could not be determined for chicks older than 20 days because most were able to fly at this age and hence only a few were caught after this stage. However, the chicks that were caught at the age of 30 days had attained approximately 80% of the adult body weight (280g) and their bills were 93% of the mean adult length (70mm). Woodcock chicks were usually led from the nest by the female within two hours of hatching, but on average

Figure 6.3 The relationship between bill length and age for woodcock chicks at Whitwell Wood, Derbyshire measured during 1989-1992. (Mean bill lengths plotted for days 0-2; 95% confidence limits too small to show).

Bill length (mm)=17.46+1.69 age (days)

$r=0.83$, $df=70$, $p<0.001$

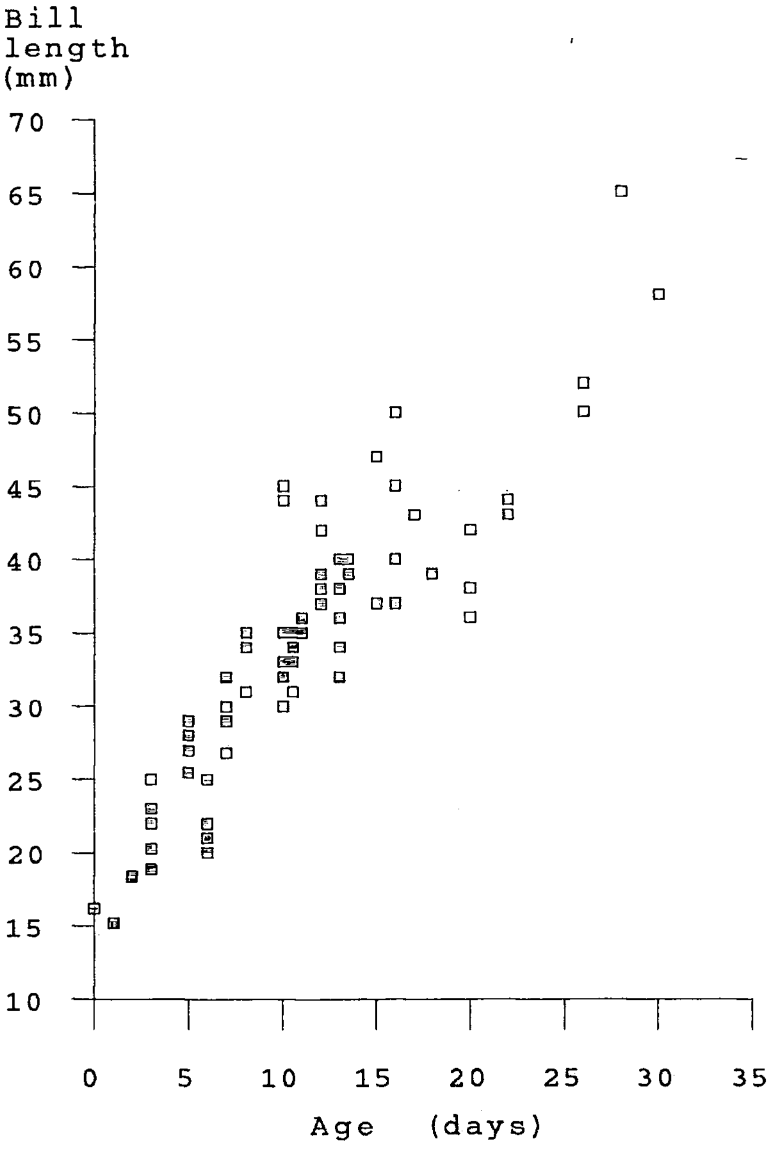
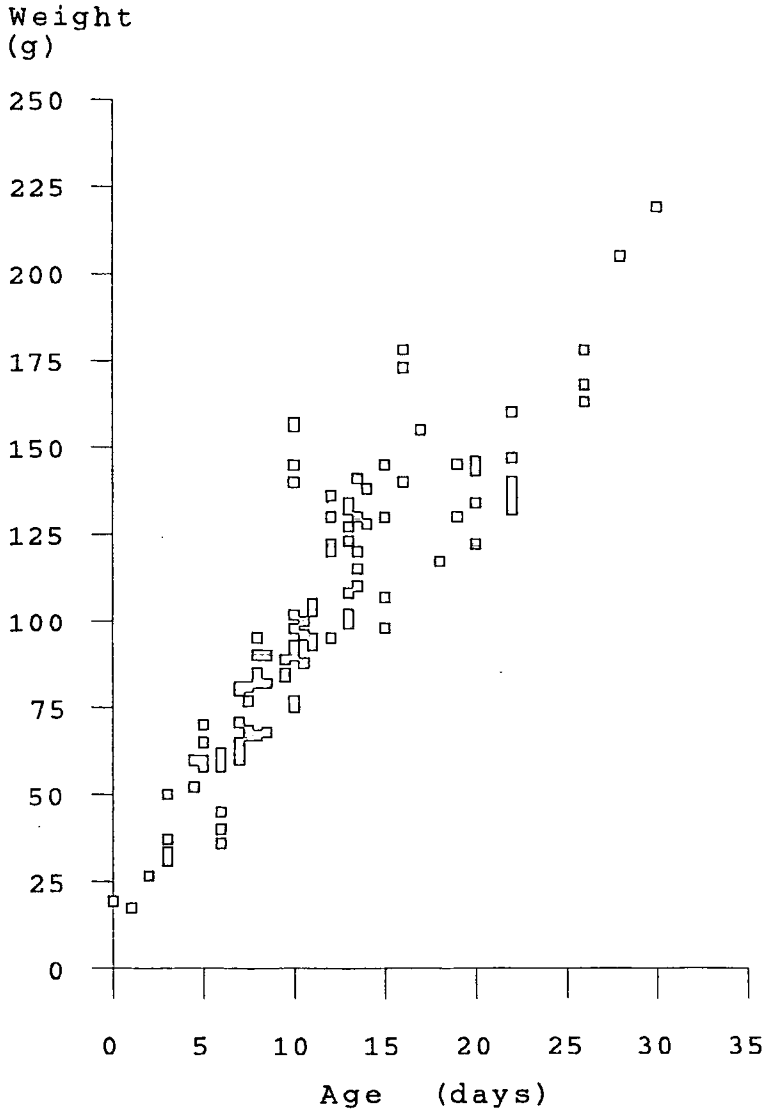


Figure 6.4 The relationship between weight and age for woodcock chicks at Whitwell Wood, Derbyshire measured during 1989-1992. (Mean weights plotted for days 0-2; 95% confidence limits too small to show).

Weight (g)=16.48+7.94 age (days)

$r=0.85$, $df=91$, $p<0.001$



broods only moved a straight line distance of 39m per day upto the age of ten days (115 brood days from 19 broods), although one brood of day-old chicks travelled 137m.

6.4.8 Roding counts as a measure of population density

There was no relationship between the number of roding male woodcock seen each night and the evening air temperature during May and June in this study; Whitwell Wood (1991) r=0.23, df=16, N.S. and Millden (1992) r=0.05, df=22, N.S. There was, however, considerable variation between individual radiotagged birds in the time spent roding each night, the mean number of times each bird was seen and the mean percentage of the total observations for all the birds that these comprised (Table 6.9). The coefficients of variation for the time spent roding on consecutive nights by each bird ranged from 0.46 to 0.72, indicating that there was relatively high variation in the roding behaviour exhibited by each individual. Contrary to expectation, the two first-year birds were the ones that roded most actively. These data indicate that no general correction can be made to convert the number of sightings of roding males into an estimate of the number of individuals.

Table 6.9 The roding behaviour of six radiotagged male woodcock at Whitwell Wood during May and June 1986. Differences in the mean duration of roding (min.) and the mean number of sightings tested by one-way ANOVAs.

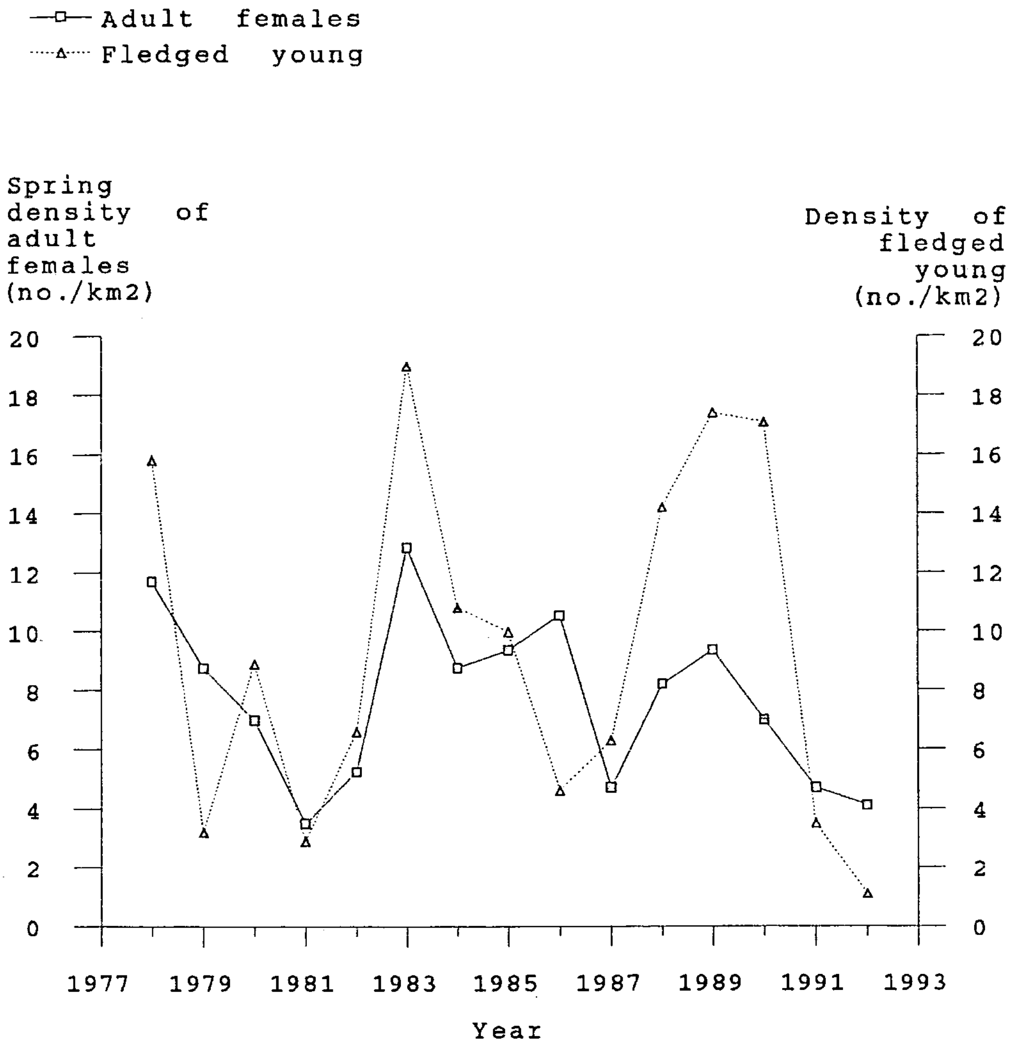
Age	Mean duration of roding per night (±se) (min.)	Mean number of sightings per night (±se)	Mean % (±se) of total sightings
Adult	8.1 ±1.8 (n=11)	1.7 ±0.7 (n=3)	5.7 ±1.9 (n=3)
Adult	10.9 ±2.1 (n=9)	2.0 ±1.0 (n=3)	7.4 ±3.2 (n=3)
Adult	10.5 ±1.3 (n=18)	2.8 ±0.4 (n=16)	10.1 ±1.6 (n=16)
Adult	18.0 ±2.2 (n=17)	4.2 ±0.7 (n=13)	18.2 ±3.8 (n=13)
1st-yr	19.3 ±3.6 (n=11)	6.7 ±1.7 (n=12)	23.6 ±4.3 (n=12)
1st-yr	27.7 ±3.4 (n=14)	11.0 ±2.0 (n=11)	38.3 ±3.3 (n=11)
	F=8.83 df=5,74 p<0.001	F=6.17 df=5,52 p<0.001	

6.4.9 Key and *k* factor analyses

There was no obvious trend in the density of breeding female woodcock at Whitwell Wood during the years 1978-1992 (Figure 6.5), but there were appreciable fluctuations from year to year. The population dropped to its lowest density in the spring of 1981 and was low in the springs of 1987, 1991 and 1992. Relatively high numbers of young woodcock were fledged in 1978, 1983, 1989 and 1990.

Annual individual and total mortalities are given in Figure 6.6. Total mortality was high in 1979, 1980, 1986 and 1992 and relatively low in 1982, 1987 and 1988. Chick mortality k_3 appeared to have the largest influence on the total annual mortality K in those years for which there were data. Shooting mortality k_4 was the mortality factor showing the least variability. The regressions of the individual k factors on K (Figure 6.7) confirmed that chick

Figure 6.5 The trend in the density of female woodcock in spring and the density of young woodcock fledged at Whitwell Wood during 1978-1992.



mortality k_3 was the key factor ($r=0.83$, $p<0.05$; slope(±se)=0.677±0.225; df=4). Egg mortality k_1 and overwinter loss k_5 were also significantly related to the total mortality K ($r=0.59$, $p<0.05$; slope(±se)=0.374±0.161; df=10 and $r=0.58$, $p<0.05$; slope(±se)=0.482±0.198; df=12 respectively), but there was no relationship between shooting mortality k_4 and the total annual mortality K ($r=0.29$, N.S.; slope(±se)=-0.018±0.106; df=13).

The regression of egg mortality k_1 on log egg density was not significant ($r=0.02$, N.S.; slope(±se)=-0.016±0.315; df=10) and neither was that of chick mortality k_3 on log density of hatched chicks ($r=0.62$, N.S.; slope(±se)=-0.620±0.379; df=4) (Figure 6.8). These data are clearly too limited to enable a conclusion to be drawn on whether egg and chick mortality at Whitwell Wood are density-dependent. There was no relationship between the log density of young woodcock in autumn and the log spring density of adult woodcock calculated using the bag and age ratio data from shoots throughout N England ($r=0.22$, N.S.; slope=0.172; df=8), but only eight years of data were available.

Shooting mortality k_4 was not related to log autumn female density ($r=0.00$, N.S.; slope(±se)=-0.000±0.023; df=13) but there was a positive correlation between overwinter loss k_5 and log post-shooting density (Figure 6.8), such that with an increase in post-shooting density the proportion of female woodcock which were lost over the winter increased ($r=0.69$, $p<0.01$; slope(±se)=0.775±0.234; df=12). Two-way regression analysis

Figure 6.6 Annual individual and total mortalities for the female woodcock at Whitwell Wood during 1978-1992. Egg mortality data only obtained for 1978-81 and 1985-92, chick mortality data only obtained for 1986 and 1988-92. (Note scale of axis for shooting mortality ten times greater than for other mortality factors.)

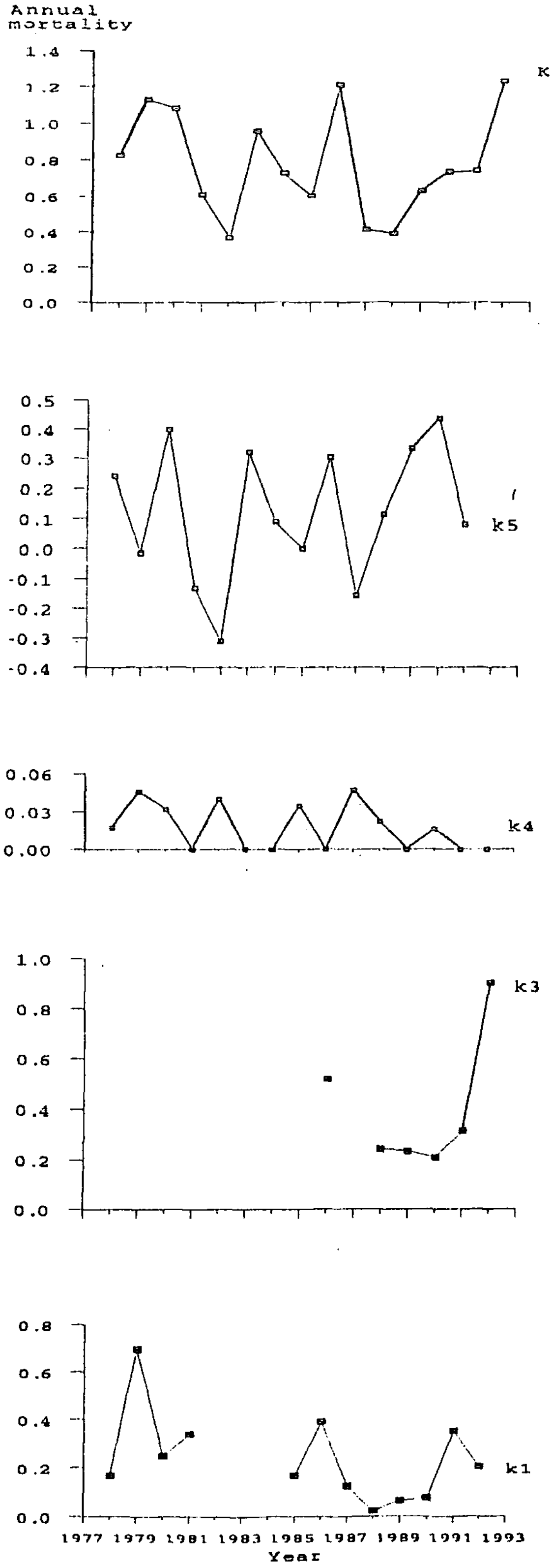


Figure 6.7 Regressions of the individual mortality factors against the total mortality K for the woodcock at Whitwell Wood, Derbyshire during 1978-1992.

(a) Egg mortality k_1 slope(±se)=0.374±0.161 $p<0.05$

$r=0.59$, $df=10$

(b) Chick mortality k_3 slope(±se)=0.677±0.225 $p<0.05$

$r=0.83$, $df=4$

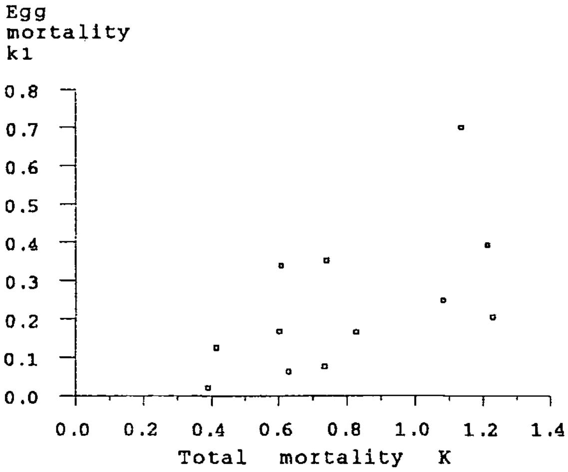
(c) Shooting mortality k_4 slope(±se)=-0.018±0.106 N.S.

$r=0.29$, $df=13$

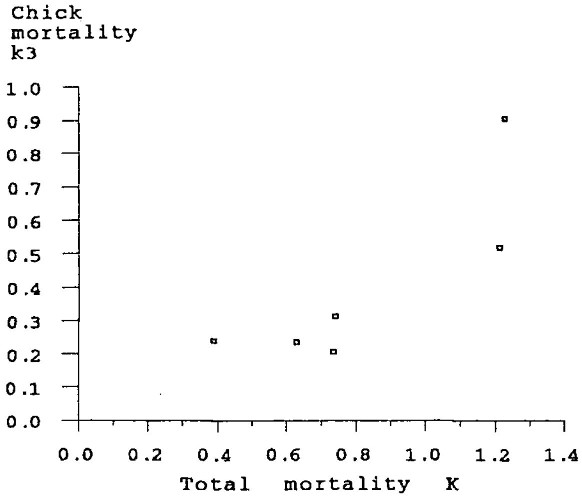
(d) Overwinter loss k_5 slope(±se)=0.482±0.198 $p<0.05$

$r=0.58$, $df=12$

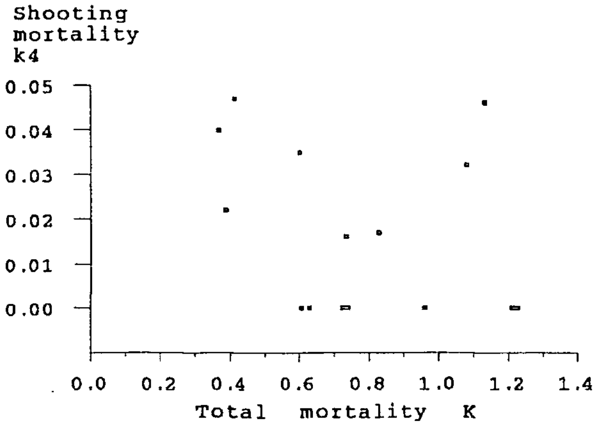
(a)


Egg mortality k1
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
Total mortality K

(b)


Chick mortality k3
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
Total mortality K

(c)


Shooting mortality k4
0.05
0.04
0.03
0.02
0.01
0.00
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
Total mortality K

(d)

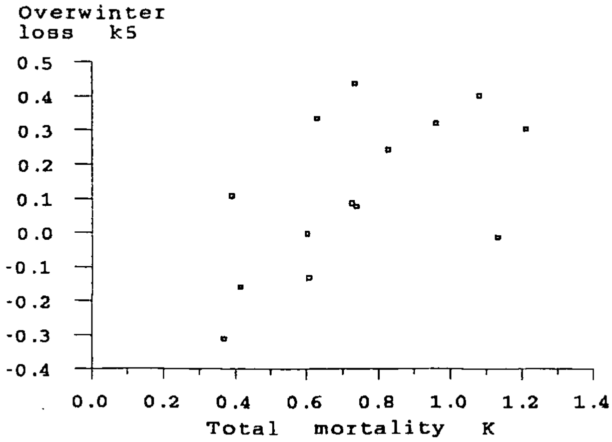

Overwinter loss k5
0.5
0.4
0.3
0.2
0.1
0.0
-0.1
-0.2
-0.3
-0.4
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
Total mortality K

Figure 6.8 Regressions of the individual mortality factors on the log density prior to each mortality at Whitwell Wood, Derbyshire during 1978-1992.

(a) Egg mortality k_1 vs. log egg density

slope(±se)=-0.016±0.315 N.S.

r=0.016, df=10

(b) Chick mortality k_3 vs. log density of hatched chicks

slope(±se)=-0.620±0.397 N.S.

r=0.62, df=4

(c) Shooting mortality k_4 vs. log autumn density of female woodcock

slope(±se)=0.000±0.023 N.S.

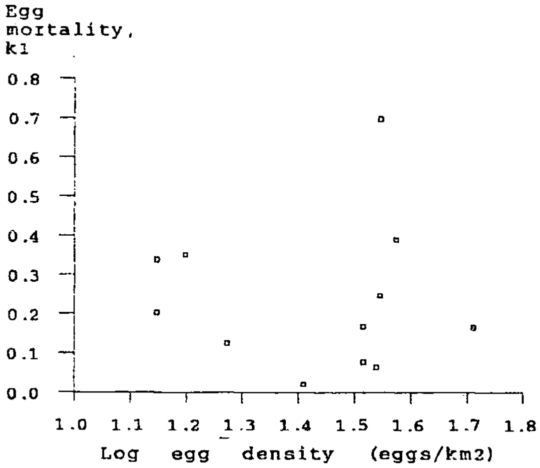
r=0.00, df=13

(d) Overwinter loss k_5 vs. log post-shooting density of female woodcock

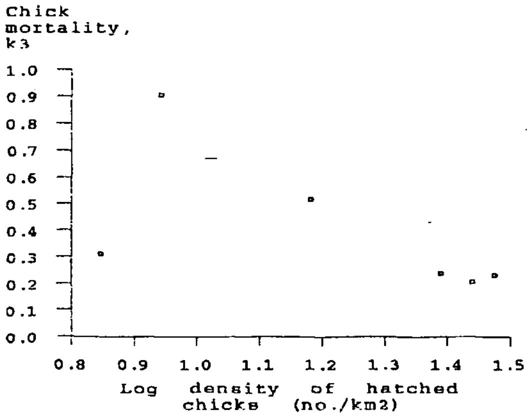
slope(±se)=0.775±0.234 $p<0.01$

r=0.69, df=12

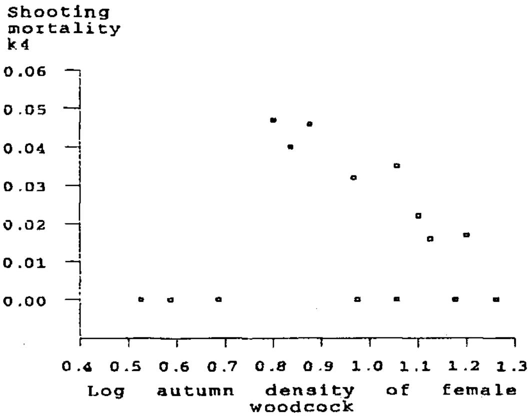
(a)


Egg mortality, k1
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
1.0 1.1 1.2 1.3 1.4 1.5 1.6 1.7 1.8
Log egg density (eggs/km2)

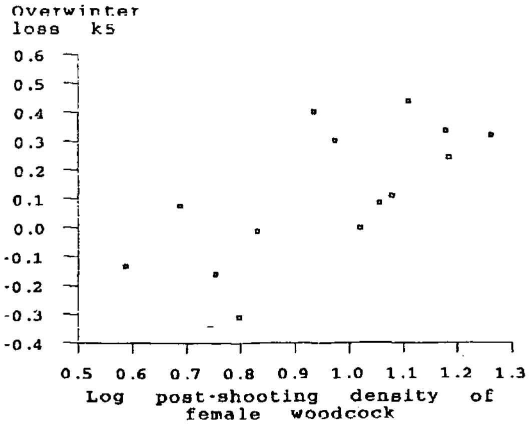
(b)


Chick mortality, k3
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0.8 0.9 1.0 1.1 1.2 1.3 1.4 1.5
Log density of hatched chicks (no./km2)

(c)


Shooting mortality k4
0.06
0.05
0.04
0.03
0.02
0.01
0.00
0.4 0.5 0.6 0.7 0.8 0.9 1.0 1.1 1.2 1.3
Log autumn density of female woodcock

(d)


Overwinter loss k5
0.6
0.5
0.4
0.3
0.2
0.1
0.0
-0.1
-0.2
-0.3
-0.4
0.5 0.6 0.7 0.8 0.9 1.0 1.1 1.2 1.3
Log post-shooting density of female woodcock

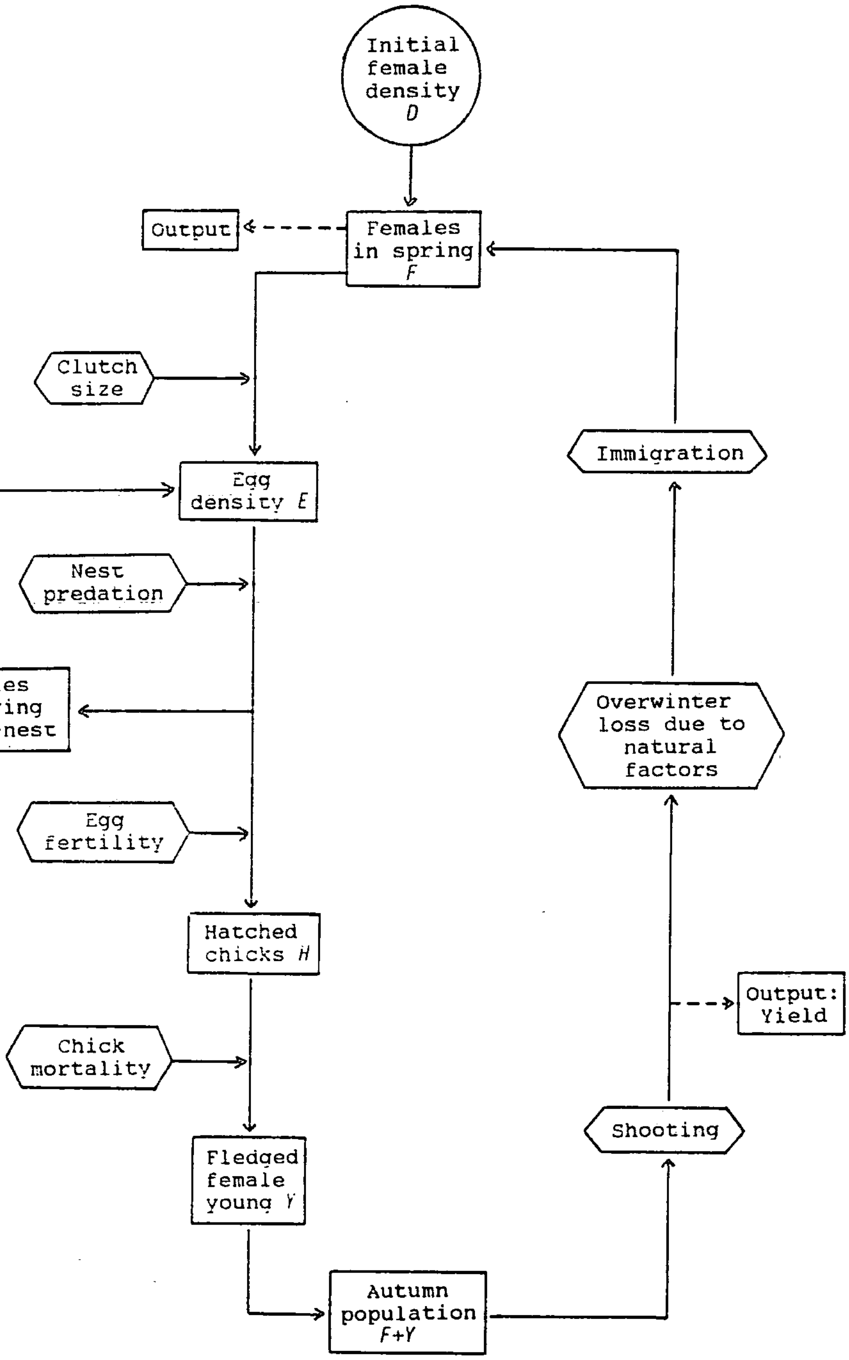
(Varley & Gradwell 1968) suggested a possible density-dependent relationship between overwinter loss k_5 and log post-shooting density, because the slopes of log post-shooting density on log spring density and log spring density on log post-shooting density were both significantly different from unity and were on the same side of a slope of b=1; b=0.224 and b=0.321 respectively. The slope of the regression of the *k* value on log initial density was highest for overwinter loss (=0.775), which was clearly the main regulatory, or *k*, factor. As such, overwinter loss was the factor best able to compensate for additional sources of mortality.

It is apparent from the trends in the spring density of breeding females and the annual production of young woodcock at Whitwell Wood during 1978-1992 (Figure 6.5), that density independent factors had an important influence on the variation in the size of the breeding woodcock population. The two low spring densities of female woodcock in 1981 and 1987 followed relatively cold winters in 1980/81 and 1986/87, and low numbers of young woodcock were fledged in 1991 and 1992, when there were dry summers.

6.4.10 Modelling the breeding woodcock population at Whitwell Wood

A schematic diagram of the processes simulated in the woodcock model is given in Figure 6.9. Because none of the relationships between egg mortality k_1, chick mortality k_3 and shooting mortality k_4 and the log densities prior to the mortalities were significant, mean values for these

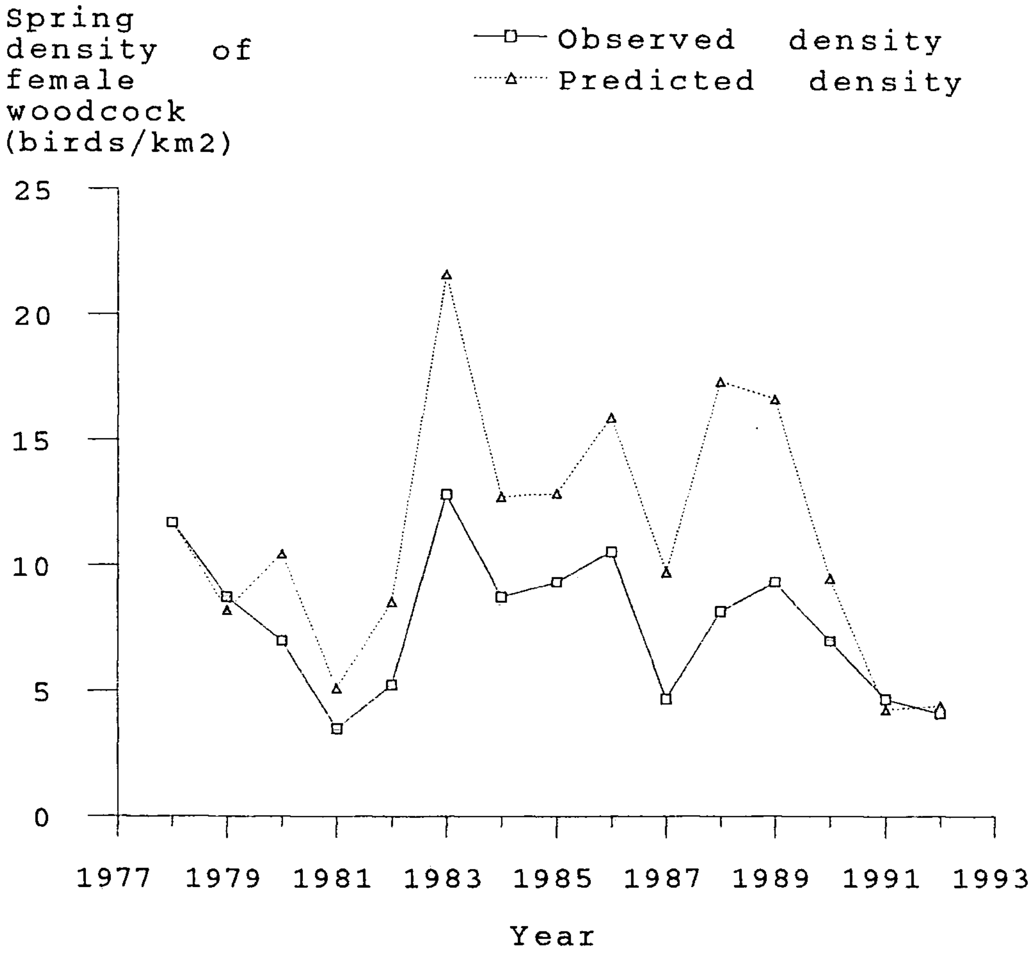
Figure 6.9 A schematic diagram of the processes simulated in the deterministic model for the population of breeding female woodcock at Whitwell Wood, Derbyshire.
Annual data were obtained for the variables in the hexagonal boxes. When the model was run to equilibrium, the number of females in spring (*F*) was the only annually variable input. When used to predict the trend in the female woodcock population at Whitwell Wood, the relationship between post-shooting female density and overwinter loss was replaced by the annual values for overwinter loss.



mortality factors were used in the model (k_1 0.238, k_3 0.402, k_4 0.017). Death of the female was estimated to occur on 23% of the occasions that nests were predated, on the basis that the female was killed in three instances out of 13 cases where active nests were predated at Whitwell Wood. This figure was used to determine the number of females attempting to re-nest following the loss of the first nest, but the value of 0.68 was used for the female mortality k_2 during the breeding season. The mean clutch size was taken as 3.95 eggs. Overwinter loss k_5 was determined according to the relationship with the log female density after shooting derived previously. A program listing for the model is given in Appendix 6.3.

The model was run to equilibrium from starting densities of one female/km^2 and 20 females/km^2. The equilibrium spring density was 6.80 females/km^2 and was reached after five and seven generations respectively. This equilibrium density approximated the mean of the observed spring densities of 7.72 females/km^2 (geometric mean 7.19 females/km^2) at Whitwell Wood. The model was then run using the observed overwinter loss k_5 each year as input. The predictions from the deterministic model of breeding female woodcock at Whitwell Wood over time are compared with the observed data in Figure 6.10. The two trends are similar but the model clearly overestimated the density of female woodcock in spring during 1980-1990. This was due to the relatively high levels of immigration following the winters of 1981/82 (k_5=-0.133) and 1982/83 (k_5=-0.311), which caused the model to overestimate the size of the

Figure 6.10 Comparison of the predicted spring density of female woodcock, from the deterministic population model, with the observed spring density at Whitwell Wood, Derbyshire during 1978–1992. Annual estimates of overwinter loss k_5 have been used to drive the simulation.

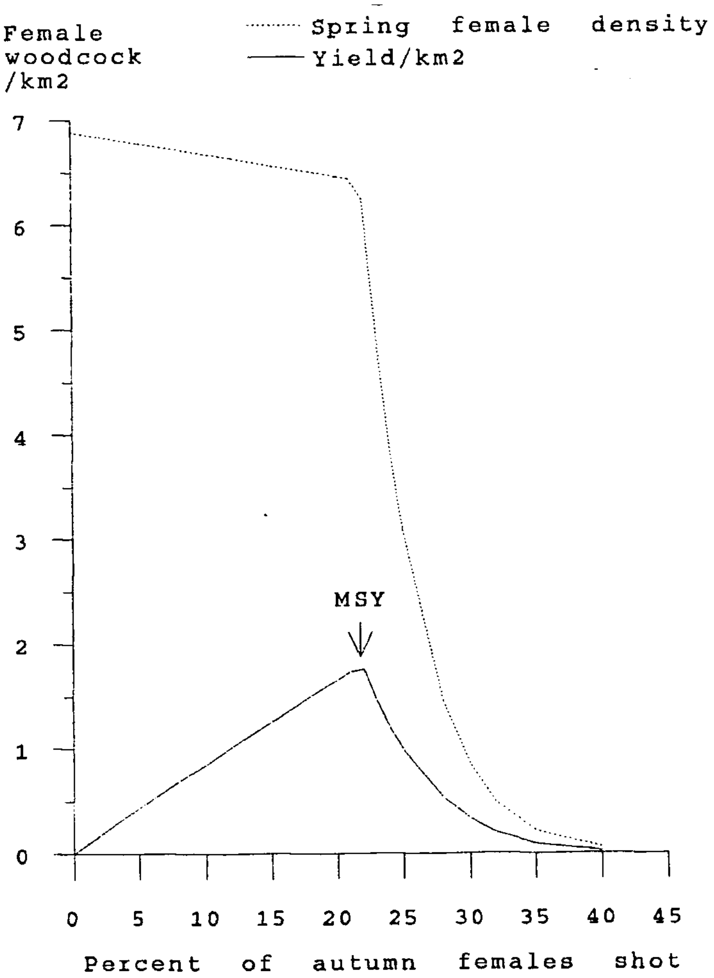


spring population for eight years afterwards. The main shortcoming of the model is that overwinter loss k_5 is the only annually variable parameter, which means that the model cannot adjust for errors in the estimation of overwinter loss k_5 at later stages in the life cycle.

Adult woodcock were highly faithful to Whitwell Wood (section 6.4.1) and it seems likely that any immigration must be of first-year birds. Ringing recoveries show woodcock to be philopatric to the extent that 76% of birds were found within 10km of the natal site (Chapter 2). It is therefore possible that there is a local redistribution of first-year birds in some years, although this is unlikely after widespread cold winter weather because the woodcock in all areas will be affected. It is also possible that there is an error in the data for the size of the breeding population at Whitwell Wood in 1981 and 1982 as very few nests or broods were found in these years (Appendix 6.1). This is a problem of using a correction for nest searching efficiency.

Simulations of the spring density of female woodcock and the yield of female woodcock with varying rates of shooting mortality suggested a maximum sustainable yield of 22% of the post-breeding population, which was equivalent to a shooting bag of 1.79 female woodcock/km^2 woodland (Figure 6.11). The curve for spring female density indicates that overwinter loss compensates well for shooting mortality up to the maximum sustainable yield. Once this rate of harvesting is exceeded, however, the number of female woodcock in spring declines sharply

Figure 6.11 Estimation of the maximum sustainable yield for the female woodcock at Whitwell Wood, Derbyshire on the basis of simulations run for 20 generations with different levels of shooting mortality.
The figure illustrates the manner in which the female woodcock population is likely to withstand levels of shooting mortality up to the maximum sustainable yield, but the value of 22% for the maximum sustainable yield should be treated with extreme caution given the limitations of the data upon which the model is based.



without immigration. The error of this estimate of the maximum sustainable yield cannot easily be calculated, but it will be a function of the error associated with the mean values of egg mortality k_1, female mortality k_2 and chick mortality k_3 used in the model. The estimate of the maximum sustainable yield should be treated with extreme caution given the inadequacies of the data used to build the model and should not be used as a management recommendation to hunters. The estimated mean annual mortality of woodcock from Whitwell Wood due to shooting was very low (4%), well below the estimated maximum sustainable yield and is likely to have reduced the spring breeding density by a negligible amount.

The effect of the severe winter in the simulation was to reduce the spring female density for three years afterwards. With shooting mortality k_4 at 4% the spring female density was reduced by 39% in the year of the severe winter when shooting occurred and was reduced by 36% with a shooting ban imposed. With shooting mortalities of 10% and 20% the spring female density was reduced by 42% and 49% respectively in the year of the severe winter. Considering the year of the severe winter and the three years of recovery together, the effect of the simulated shooting ban was to reduce the overall bag by 17% for a 1% increase in spring female density when the shooting mortality was 4%. With a shooting mortality of 10%, the overall bag was reduced by 16% for a 3% increase in spring female density, and with 20% shooting mortality, the bag was reduced by 14% for a 5% increase in spring female density. Clearly the benefit of the simulated shooting ban during cold weather was only small.

6.5 DISCUSSION

Evidence from Whitwell Wood suggests that adult woodcock are highly faithful to the breeding site, both during the breeding season and in winter. However, the chances of recovery elsewhere during the breeding season were undoubtedly low and the true degree of fidelity to Whitwell Wood was probably exaggerated by the intensive effort employed there. It seems likely from the degree of overwinter loss in certain years that emigration sometimes took place. There was some evidence that Continental woodcock passed through Whitwell Wood in March on their return migration, although the number of birds doing so was apparently only small. The adult survival rate of 0.75 during the breeding season on the basis of 20 radiotagged males and four radiotagged females was similar to the estimate of 0.76 male survival made by Hirons (1983) and is of the correct order to give an annual adult survival rate of 0.58, provided that the rate of mortality is slightly lower during the winter ($0.9981^{365}=0.50$). The main predators of adult woodcock during the breeding season appear to be foxes, stoats, sparrowhawks and tawny owls. Incubating females are most likely to be killed by mammalian predators, particularly foxes, whereas foraging males and females are susceptible to sparrowhawks. Only the hen sparrowhawk is likely to kill birds as large as woodcock

(Newton 1986) and the woodcock are probably most vulnerable during the pre-laying period of the sparrowhawk when the hen is putting on weight and the vegetative cover in the woodland is still relatively sparse. Woodcock are also at risk to predation by sparrowhawks if there is a fall of snow (Potts pers. comm.). The most surprising predator was the tawny owl and it is conceivable that Whitwell Wood represented an atypical situation because tawny owls were present at high density (upto 4.7 pairs/km^2) due to the provision of nest boxes. However, tawny owls also kill lapwings (Thompson pers. comm.).

All of these predators are generalists and woodcock can only comprise a small proportion of their diets. In S Scotland woodcock comprised only 0.7% of the prey items in the diet of sparrowhawks, equivalent to 3.5% by weight (Newton 1986). Similarly, Zomerdijk (1983) reported that woodcock remains comprised upto 3.3% of the bird component in tawny owl pellets in Holland. The fact that they are generalists means that the impact of these predators on the woodcock population is likely to be density-dependent. This is because given a relatively constant density of predators, changes in woodcock density will make them more or less vulnerable to predation. Of course, individual predators may specialize on particular types of prey, a good example being individual foxes that may specialize on nesting grey partridges *Perdix perdix* (Potts 1986).

There was no suggestion that clutch or chick predation at Whitwell Wood was density-dependent, but the data were probably too limited to enable such an effect to be detected. It is possible that the changes in the density of woodcock were never of sufficient magnitude to significantly alter their relative abundance compared to the other types of more numerous prey, such as rodents and songbirds, that were available. It is likely that any density-dependent adult predation acted early in the breeding season when the woodcock became more numerous and more active in the woodland than in winter, and when the vegetation was still relatively sparse compared to during late spring and summer. Such an effect would not have been detected at Whitwell Wood because predation was not measured until the females started nesting and it is likely that the overwinter loss measured at Whitwell Wood included density-dependent predation of adults early in the breeding season which reduced the potential nest density.

In most cases, desertion due to disturbance by man or to adverse weather conditions cannot be separated from predation of the female away from the nest. Nevertheless, apparent desertion seems to be an important cause of nest failure in the woodcock, accounting for almost half the nest losses. Other authors (Shorten 1974, Kalchreuter 1983) have also commented that woodcock appear to be particularly prone to desertion. In the pheasant *Phasianus colchicus*, another ground nesting species of woodland, the daily rate of nest loss due to desertion was also high, being approximately equal to the rate of loss to predation and other failure (Robertson 1991). Pheasants were more prone to desertion on the day when the nest was first found during both egg-laying and incubation (Robertson 1991), but there was no evidence for this in the woodcock. The total daily rate of nest loss was similar throughout egg-laying and incubation in the woodcock whereas in the pheasant it was found to be significantly higher during egg-laying than during incubation. This is probably because the pheasant has a considerably longer laying period (16 days for an average clutch of 11.4 eggs). Clutch survival during egg-laying and incubation was better in the woodcock (0.453-0.497) than the pheasant (0.071 from BTO nest record cards and 0.214 from records from keepered sporting estates, Robertson 1991), although pheasants often make three nesting attempts. The fact that the daily rate of woodcock nest loss was lower during 1980-89 than during 1945-79 could be due to increased predation pressure if nest loss is density-dependent. At a given nest density, increased predation pressure would produce a lower nest density and hence a lower rate of nest predation.

Again, the explanation for the fact that the daily rate of woodcock chick loss at Whitwell Wood was lower during 1989-92 than during 1978-88 could be increased predation pressure if chick mortality is density-dependent. However, woodcock chick loss is likely to be more affected by density-independent effects than clutch loss and the difference in the rates of chick loss between 1978-88 and 1989-92 might be due to inaccuracy of the 1978-88 estimate which was only based on a small sample of chicks. Comparison of chick mortality in the dry summers of 1991 and 1992 with that during the relatively normal summers of 1989 and 1990 suggested that mortality was higher during years with dry summers. Earthworms, which comprise an important component of woodcock chick diets (Chapter 5), are less available in dry conditions and Hirons (1988*b*) has shown that the proportion of young woodcock in the shooting bag for N England increased with the June rainfall during the previous summer. Jackson & Jackson (1980) found that in drought conditions lapwing chick growth rates were significantly reduced, that the chicks took longer to fledge and that mortality was higher. The same may be true in woodcock chicks.

The estimated national production of fledged young from the BTO nest record cards (1.14 per breeding female) was not sufficient to match the requirement (1.78 fledged young per breeding female) calculated on the basis of an annual adult survival rate of 0.58 from British ring recoveries (Chapter 2) unless a proportion of the woodcock were double-brooded. However, the calculation was dependent on the single estimate of chick survival of 0.45 from Whitwell Wood which was low relative to the previous estimates of 0.78 (Alexander 1946) and of 0.67 for the American woodcock *Scolopax minor* (Sheldon 1971). It is possible that the actual rate of chick survival at Whitwell Wood was slightly higher than 0.45 because a few chicks may have been missed when broods were recaptured. At present the only direct evidence of a second brood in the woodcock comes from two descriptions of woodcock incubating eggs whilst surrounded by a brood of chicks (von Zedlitz 1927, cited by Glutz von Blotzheim *et al.* 1977, Jensen, cited by Pay 1937). Alexander (1946) reported six cases of woodcock laying into the same nest and two cases of displaying or mating following a successful brood but in these instances there was no proof that only one female was involved. Clausager (1972) noted that 90% of *Scolopax rusticola* nests in Denmark were found over a period of 15 weeks, while the same proportion of *Scolopax minor* nests were found in only 5-6 weeks. Kalchreuter (1983) believed that this was suggestive of double-brooding in *Scolopax rusticola* and concluded that the number of broods per year probably fluctuates regionally and annually.

The failure of chicks to gain weight in the first few days after hatching is a typical phenomenon in precocial birds (Ricklefs 1973, Aulie 1976), because the chicks can survive for a few hours on the lipids absorbed from the egg yolk and because their foraging ability and digestive efficiency are poor during the first few days. The weight changes of woodcock chicks during the first three days were similar to those observed in common snipe by Green (1985). It is possible that some of the error in ageing the woodcock chicks from the linear regression of weight on age was caused by diurnal variation in the weight of the chicks. Diurnal variation was not examined in this study but Green (1985) showed that the effect was not significant in common snipe. Wader chicks are known to be susceptible to cold weather during their first few days until they are able to thermoregulate (Chappell 1980, Beintema & Visser 1989), and the survival of woodcock chicks also appears to be related to earthworm availability which is determined by summer rainfall. For these reasons it is not surprising that chick mortality was shown to be the key mortality factor. The number of breeding female woodcock did not fluctuate in relation to chick mortality between years because overwinter loss, the main regulatory factor, was able to buffer between-year fluctuations in the production of young.

The results of the present key and *k* factor analyses obviously need to be treated with caution, but if overwinter loss is density-dependent it could be due to a proportional increase in winter mortality or to dispersal as the density of woodcock left after shooting increases. Emigration of birds from their natal area prior to breeding offers a plausible explanation for overwinter loss and Taylor & Taylor (1977) suggest that dispersal plays a fundamental role in the regulation of many animal species. Density-dependent breeding dispersal of females during early spring has been clearly demonstrated in the grey partridge (Potts 1986). Further data are required to substantiate the interesting possibility that woodcock populations may be regulated by overwinter loss.

A factor not considered in the present analysis was the presence of Continental woodcock during the winter. The arrival of migrant woodcock in autumn obviously increases the density of birds in winter and if overwinter loss is density-dependent, then this would be expected to increase the rate of overwinter loss among the resident birds. This effect is likely to have been small at Whitwell Wood because the proportion of foreign to resident birds in winter is relatively low in this part of the country

(Chapter 2). The low density of woodcock in the vicinity of Whitwell Wood in winter (Chapter 3) confirms this. However, the increase in density may be important in S England and Wales, and may explain why no woodcock breed in most parts of SW England and W Wales (Lewis & Roberts 1993) where the highest densities of woodcock are found in winter (Chapter 3). Potts & Hirons (1983) estimated that the rate of predation of woodcock on the Lizard Peninsula, Cornwall during December-February 1980 and 1981 was about 40%.

The construction of the deterministic model for the woodcock population at Whitwell Wood illustrates the potential value of a modelling approach to understanding woodcock populations given a reliable data set. The present model, however, is flawed by the undetermined error in the estimates of female density in spring, caused by the fact that the number of nests and broods found each year had to be corrected using crude estimates of the nest searching effort. The model is also specific to this given situation and has not been validated using an independent data set. Construction of the model highlighted the difficulties in determining population parameters for the woodcock, whose spring breeding density and annual production cannot be readily assessed from counts in the spring and autumn as for gamebirds. The density of breeding females in spring has to be determined by intensive nest searching because there is no evidence that the number of roding males is related to the number of breeding females. In general, only a small proportion of first-year males rode (Hirons 1980) whereas females breed in their first year (Ostermeyer &

Ferrand 1979, Hirons 1980), and, in any case, there is no means of determining the number of individuals from a given number of sightings of roding males. In this study there is an unknown error in the estimates of female density in spring because the number of nests and broods found each year had to be corrected using crude estimates of the nest searching effort. The fact that the daily rate of nest loss at Whitwell Wood (0.025) for the years 1978-1992 was very similar to the national value based on the BTO nest record cards (0.021) for 1980-1989 suggests that Whitwell Wood was subject to rates of predation and disturbance similar to the averages for Britain as a whole.

The estimated maximum sustainable yield for the woodcock population at Whitwell Wood (22%, section 6.4.10) was very similar to that estimated at the national level (24%) in an early model by Potts & Hirons (1983). If the maximum sustainable yield is equal to 24% in most parts of Britain it is likely that the current rates of harvesting in a few areas, assuming that they affect the resident breeding woodcock and the Continental migrants similarly, will lead to declines in the size of local breeding populations. This may explain why woodcock do not breed in Cornwall and parts of W Wales where the highest densities of wintering woodcock are found. The harvest rate in these regions is often as high as 40% (Chapter 3) and this would prevent a breeding population from becoming established. The data from Whitwell Wood suggest that immigration was necessary following cold winters to counteract the effect of the increased density-independent mortality. Immigration cannot occur if cold weather effects are widespread, as in the winter of 1962/63, and this explains why the winter woodcock population indicated by the size of shooting bags took three years to return to its former level (Chapter 3).

The benefit of a ban on shooting during cold winters appears to be only small provided that a series of cold winters do not follow each other. The present model gave similar results to the one devised by Potts & Hirons (1983), but should be more robust because it is based on field data for different stages of the life cycle and examined the likelihood of density dependence in the production of young woodcock and in overwinter loss. Potts & Hirons (1983) used national woodcock bags and age ratios to assess the strength of density dependence in adult survival because at the time it was not known how Continental woodcock were distributed in Britain in winter in relation to British birds.

Ferrand (1989) has proposed a system for counting roding male woodcock in France for use as an index of the size of breeding populations. However, the fact that males are polygynous, combined with the variability in the roding behaviour of each individual and between different birds observed in this study, means that counts of roding males are unlikely to be reliable. Hirons (1988*a*) showed that male woodcock spent longer roding over areas of good nesting habitat and that, consequently, counts of roding males at different locations within the same wood varied according to the habitat in which observations were made. In order to stand any chance of obtaining a representative estimate of a breeding woodcock population from a census based on counts of roding males, the census would have to include a large number of observation points scattered throughout all possible types of breeding habitat.

7. GENERAL DISCUSSION

7.1 The British breeding woodcock population

British woodcock are typically sedentary and exhibit a high degree of philopatry. Ring recovery data suggest that they also winter close to their breeding areas, although it seems likely that a small component, unlike in Continental woodcock, of the British woodcock population (about 4%) is truly migratory. The estimated annual adult survival rate of woodcock ringed in Britain and Ireland (58%) is slightly lower than the adult survival rates for other waders, e.g. the lapwing *Vanellus vanellus* 66% and the redshank *Tringa totanus* 68%, and this may be because they are more frequently shot in winter or because they utilize a different type of habitat.

The British breeding woodcock population is believed to be declining (Marchant *et al.* 1990, Lewis & Roberts 1993). The present study also suggests that this is likely and that the reason is because the current annual rate of production of young woodcock is not sufficient to compensate for adult mortality each year. Most woodcock ringing recoveries, however, are of shot birds and the overall adult survival rate in the British Isles may be higher than estimated in this study due to appreciable areas where woodcock are not shot. There was no evidence for a significant change in the annual adult survival rate this century. Woodcock chick survival at a site in

NE Derbyshire was found to be highly variable from year to year and the mean chick survival rate used for comparison with the annual adult survival rate may be an underestimate, due to the inclusion of data from the two dry summers of 1991 and 1992. In any case, the chick survival data are from a single breeding site and should be treated with caution.

Unlike in many nesting gamebirds, e.g. the grey partridge *Perdix perdix* (Potts 1986) and the red grouse *Lagopus lagopus scoticus* (Hudson 1992), and waterfowl, e.g. the mallard *Anas platyrhynchos* (Hill 1984), the production of young woodcock did not appear to be density-dependent in this study. The only evidence that nest loss may be density-dependent comes from BTO nest record cards which suggest that the rate of nest loss was lower during 1980-89 than during 1945-1979. This would be expected if nest loss was density-dependent and predation pressure has increased. The sharp reduction in gamekeepering effort in Britain since the 1950s has been described by Potts (1980). There was no evidence for regional differences in the rate of nest loss between S England, N England and Scotland. Variable weather, in particular the amount of rainfall in early summer (Hirons 1988*b*), seems to have a greater influence on chick survival because it determines the availability of earthworms to growing and recently fledged young. However, few data were obtained on annual chick survival rates and variation in relation to chick density is clearly an area that merits further investigation.

The data collected for the breeding woodcock population at Whitwell Wood, Derbyshire were insufficient to enable any firm conclusions to be drawn about the manner in which population regulation operated. Overwinter loss (excluding shooting) appeared to be density-dependent and was the factor most likely to have regulated the number of breeding woodcock at Whitwell Wood. If overwinter loss acts as the main regulatory factor throughout Britain, there are important implications for the British breeding woodcock population. It seems likely that the increased density of woodcock in winter, caused by the large influx of Continental migrants, will increase overwinter loss among resident British woodcock. The reason why woodcock do not breed in most parts of SW England and W Wales (Lewis & Roberts 1993) may be because very high densities of Continental woodcock winter in these areas, resulting in high rates of winter loss. In addition, the largest annual woodcock bags in Britain are shot in these areas and the proportion of the birds present that are shot is such that the maximum sustainable yield for the resident population (estimated at 22-24%) is likely to be exceeded.

7.2 The wintering woodcock population in the British Isles

Continental woodcock originating from Fennoscandia and the former USSR outnumber British woodcock by approximately 10:1 in winter (Hirons & Linsley 1989, Lewis & Roberts 1993). Most of these foreign birds probably return to the British Isles in successive winters because the adult survival rate of foreign-ringed woodcock recovered in

Britain and Ireland is similar to that of British woodcock. If they did not return the survival rate of Continental-ringed woodcock would be lower owing to the shortage of older birds reported in Britain and Ireland. Nevertheless, it is possible that the proportion of woodcock of each year class returning to Britain varies annually and that older birds do not return every year. This would produce a similar age distribution in the ring recoveries provided the birds in each age class had the same probability of returning to Britain.

Evidence from ring recoveries and winter density estimates indicate that relatively few foreign woodcock overwinter in Scotland (3% of ringing recoveries were of foreign birds) and that the largest proportion and largest number of foreign woodcock winter in SW England and Wales (57% of ringing recoveries were of foreign birds), further south than many British woodcock. The birds shot in these main wintering areas must therefore be almost exclusively foreign woodcock because British woodcock do not breed in SW England or W Wales (Lewis & Roberts 1993) and a large proportion of all the woodcock killed in Britain and Ireland each winter are undoubtedly foreign migrants.

The increase in pheasant *Phasianus colchicus* shooting in the UK since 1980 has probably led to more woodcock being shot. This has had the greatest impact in N England and Scotland, because although the total number of pheasants shot in these regions is still relatively low compared to S England, these are the regions where the largest percentage increase in the pheasant bag has occurred. The increase in pheasant shooting has probably therefore had as great an impact on the British woodcock population as on the Continental migrants. Henderson *et al.* (1993), however, have suggested that the overall hunting rate on ringed woodcock throughout Britain has declined since the early 1960s. It is important to remember that the large numbers of Continental woodcock that winter in Britain may also be harvested on migration in other countries, although Henderson *et al.* (1993) provide evidence for a decline in the hunting rate in most other European countries.

Data obtained from the Lizard Peninsula, Cornwall suggest that the wintering site fidelity of Continental woodcock is high (about 69%). There is evidence from the difference in the distribution of woodcock bags in mild and cold winters to suggest that there is a net movement of woodcock south and west in Britain in cold weather (Tapper & Hirons 1983). The ring recoveries showed that British woodcock remained just as faithful to the breeding site in cold winters as in mild ones, implying that only Continental woodcock move. It is plausible that different strategies are employed by British and Continental woodcock. The former probably benefit from remaining in an area with which they are familiar and where they may have experience of locating unfrozen feeding sites, whereas, provided the severe weather is not widespead, the Continental woodcock are likely to find better feeding opportunities more quickly if they move. Woodcock experience increased mortality in very severe winters, such as that of 1962/63, and the subsequent population recovery may take about three years. Simulation results suggest that shooting bans only lead to a small reduction in the mortality during cold winters.

7.3 Habitat use by woodcock during the breeding season and the influence of woodland management

Whitwell Wood, Derbyshire was atypical of many lowland mixed deciduous woods because it was comprised largely of sycamore *Acer pseudoplanatus* and beech *Fagus sylvaticus*. Sycamore is not rated highly by foresters because it is not a native species to Britain and is particularly susceptible to bark stripping by grey squirrels *Sciurus carolinensis* (Shorten 1957, Corbet & Southern 1977). However, the sycamore areas were clearly preferred by the woodcock in this study and the reason for this is likely to be that sycamore leaves are highly palatable to earthworms, resulting in high earthworm densities in the soil beneath sycamore trees (Edwards & Lofty 1977).

Radiotagged woodcock monitored in lowland mixed deciduous woodland were able to select feeding sites with higher available densities of earthworms and other soil invertebrates than paired random locations, but the preferred sites were also within areas with dense ground cover, often comprised of dog's mercury *Mercurialis perennis*. The woodcock favoured the edges of stands for feeding, probably because they supported a higher density of shrubs which afforded protection from avian predators, in particular sparrowhawks *Accipiter nisus*. This information is important in determining the likely effects of woodland management. The decline in managed coppice in Britain (82% since 1950, Warren & Key 1991) has undoubtedly been an important factor in the decline of breeding woodcock because traditional coppice management produced an open canopy and dense understorey; the type of structure typical of woodland edges. Because the pheasant has become a species of considerable economic value, its habitat requirements currently influence the way in which many woodlands are planted and managed throughout lowland Britain (Avery & Leslie 1990, Cobham Resource Consultants 1992). Woodland management for pheasants involves the maintenance of open rides and shrubby woodland edges (Woodburn & Robertson 1990) and should therefore benefit breeding woodcock. Woodland rides are probably important for roding males in large woods.

The use of upland woodland habitats by breeding woodcock has not previously been studied and a basic understanding of woodcock ecology in woods of birch *Betula pubescens* is important because these form the most abundant class of semi-natural woodland in the Scottish highlands (MacKenzie 1987) and are likely to support an appreciable proportion of the breeding woodcock population in Scotland. Cover was clearly important for feeding birds during the daytime in this situation and activity was restricted almost exclusively to patches of dense young birch or to mature birch with bracken *Pteridium aquilinum* cover. This was probably because the woodcock would have been vulnerable to predation by sparrowhawks, which were regularly seen in the area, had they fed in the more open habitats. Some woodcock nests were located in relatively open areas including *Calluna* heath and dead bracken was again clearly important. The high use of bracken-dominated areas means that there is likely to be a conflict of interest for private landowners with an interest in red grouse shooting, because one of the options for controlling louping ill virus on grouse moors is to remove bracken, which harbours the tick *Ixodes ricinus* that carries the virus.

The other type of habitat important to woodcock in Britain is conifer plantation, which comprises 41% of the woodland in England, 70% of the woodland in Wales and 83% of all Scottish woodland (Avery & Leslie 1990). The ecology of woodcock in conifer plantations was not examined in detail in this study, but evidence from Whitwell Wood, Derbyshire and Millden, Angus suggests that only relatively young (<15 year old), open plantations are likely to be used intensively and that mature Scots pine *Pinus sylvestris* is largely avoided. There is usually no understorey or ground vegetation in mature conifer plantations and the available earthworm and soil surface invertebrate densities are much reduced compared with deciduous woodland. In England, where in general conifer has replaced existing broadleaved woodland in many areas, the increase in the area of coniferous woodland during the last 40 years is likely to have been detrimental, but in Scotland where conifer plantations represent the creation of new woodland, the change is likely to have increased woodcock habitat.

The woodcock was originally a species that was thought would not benefit from afforestation in Scotland (Thom 1986), but it is believed to be currently abundant in the conifer plantations of SW Scotland (Avery & Leslie 1990) and has been recorded breeding in plantations as far north as the north coast of Sutherland (Stroud *et al.* 1987). Clearly more information is required concerning the densities at which woodcock occur in conifer plantations and the ages of preferred stands. In 1980, 77% of the conifer forests in Britain were less than 30 years old (Avery & Leslie 1990), but they have now have reached the age where they are likely to be less attractive to woodcock (Lewis & Roberts 1993).

7.4 Habitat use by woodcock in winter and the influence of agricultural practices

Several authors have noted that woodcock are less specific with respect to their diurnal woodland habitat requirements in winter (Shorten 1974, Kalchreuter 1983, Cramp & Simmons 1983) and it is clearly the nature of nearby farmland that determines the suitability of wintering areas. In this study, the woodcock in a predominantly grassland area in Cornwall mainly avoided winter cereal fields and short-term leys, exhibiting a strong preference for permanent pastures, which supported the highest densities of earthworms and other soil invertebrates. They even selected between different permanent pastures, apparently on the basis of the relative availability of these two types of prey. There was no evidence that the woodcock differentiated between patches within certain fields, as has been demonstrated for lapwings and golden plovers (Barnard & Thompson 1985). This is probably because the older grass fields in Cornwall supported very high densities of available earthworms and there was relatively little variation in prey availability within these fields.

Equally interesting was the fact that the woodcock in a predominantly arable area in Derbyshire showed similar preferences between fields, even though they had to fly longer distances to reach the grass fields. It seems possible that local densities of woodcock in winter are determined by the relative proportions of grass to arable fields and that winter cereal monocultures may only support very low densities irrespective of the quality of the woodland habitat. Further evidence for this was the finding that the winter density of woodcock in Teesdale, Co. Durham was consistently higher throughout 1991/92 than the density in NE Derbyshire. Both sites experienced similar winter weather and, if anything, the minimum temperatures in Teesdale were lower, so the difference in density was probably because most of the fields at the Teesdale site were grass.

Woodcock exhibited a clear avoidance of field edges (the outer 20m) on the Lizard Peninsula, Cornwall where there were high densities of foxes *Vulpes vulpes*. If this behaviour is typical of woodcock in other areas throughout

Britain, it clearly has important implications for farmland management. This is because the edge strip will comprise a higher proportion of small fields (e.g. 41% in a 3ha field) than large fields (e.g 25% in a 9ha field) and long, narrow fields will have a higher proportion of field edge (e.g. 39% in a rectangular 6ha field measuring 500m x 120m) than approximately square fields of the same size (e.g. 30% in a 6ha field measuring 245m x 245m).

7.5 Failings in the current understanding of woodcock populations

Present estimates of the number of breeding woodcock in Britain and Ireland and the population trend are still largely unreliable because the BTO Breeding Bird Atlas and Common Birds Census methodologies are not suited to this species (Marchant *et al.* 1990, Lewis & Roberts 1993). The present study has shown that even counts of roding males cannot provide an estimate of the number of breeding woodcock in a given location, although they may be sufficient for detecting changes in woodcock numbers at a national level.

There are no obvious alternatives for censusing breeding woodcock because nests are difficult to find, even with trained dogs, and the efficiency of nest finding is likely to vary in relation to the search effort employed within a given area. Transect walks might be a possibility but woodcock are only flushed infrequently and a large number of walks would be required in order to obtain a reliable density estimate. The flushing efficiency is bound to differ between different types of habitat and this would have to be quantified. The best time for a transect-based census would be in March, before most females started nesting, but an error would then be caused by the proportion of Continental migrants that were still present.

Further information is needed on woodcock chick survival from a larger number of breeding sites to determine whether the British woodcock population is indeed falling short of the required annual production of young and, if so, to what extent. The ecology of breeding woodcock in conifer plantations also merits further investigation so that a favourable management strategy can be determined.

It seems extraordinary that an effective means of sexing the European woodcock on the basis of external morphology has eluded biologists for so long. In the present study, a method of sexing woodcock during the breeding season on the basis of bill length, tail length and weight has been proposed, but this requires further validation. Until a reliable method that can be employed all year round is devised, population studies of the European woodcock will continue to be hindered by a lack of information concerning the sex ratio amongst different groups of individuals.

7.6 Contribution of the present study to the understanding of woodcock populations

The present study implied that the British breeding woodcock population is probably declining, although the errors involved in determining the trend were such that little confidence can be placed in it. The size of the Continental population, gauged from the trend in the number of woodcock wintering in Britain that were shot, has probably increased slightly over the period 1961-1992. This was the case even allowing for the increase in pheasant shooting in Britain during the 1980s. The effect of the increased hunting pressure on woodcock due to the increase in pheasant shooting is difficult to quantify because it depends on the proportional increase in the pheasant bag and the density of woodcock present in a given area. As the highest densities of wintering woodcock occur in S England and Wales and the proportion of foreign woodcock there is greater than in N England and Scotland, it is likely that the proportion of woodcock shot that were foreign birds increased during the 1980s.

Yeatman-Berthelot (1991) found that the size of the wintering population in France had declined during 1970-1990, but a higher proportion of the woodcock wintering in France undoubtedly originate from areas further south and east than birds wintering in Britain. Evidence for this comes from ringing recoveries of woodcock ringed in "eastern" Europe (the former Czechoslovakia, Estonia, Hungary, Lithuania and Poland), 38% of which were recovered in France whereas none were recovered in Britain

(Henderson *et al.* 1993). Clausager (1972) believed there had been a decline in the breeding woodcock populations in Poland and the former Czechoslovakia.

Henderson *et al.* (1993) demonstrated a decline in the hunting rate of woodcock in most European countries since the early 1960s, suggesting that the possible increase in the size of the Continental breeding populations that visit Britain in winter and the probable decline in the breeding populations that winter in France are due to changes in the availability of suitable habitat and predation pressure on the different breeding grounds. France has the highest hunting rate of all European countries and is the country where the hunting rate has probably declined least since 1960 (Henderson *et al.* 1993). It is therefore possible that there has been selection for Continental woodcock to winter in Britain instead of France. Such a shift from the Continent, and particularly from the Netherlands, to Britain has been described for "wintering" common snipe *Gallinago gallinago* (Beintema & Müskens 1983), attributed to drainage and the loss of moulting grounds in the Netherlands.

Density dependence is important in many animal populations because it regulates the number of individuals in a given population. The present study suggested that overwinter loss was the factor most likely to operate in a density-dependent manner in British woodcock populations although this needs substantiating. If true, it is interesting because it means that a large wintering population may decrease the size of the local resident population through winter density-dependent effects. The presence of Continental woodcock in winter may increase overwinter mortality among British woodcock and is a possible factor explaining why the British woodcock population has declined at a time when the Scandinavian and Finnish populations appear to have increased.

SUMMARY

1. The constant annual adult survival rate for British-ringed woodcock is 0.579±0.018 (±se, n=342 ring recoveries) and that for foreign-ringed woodcock recovered in Britain and Ireland is 0.539±0.035 (n=113). The rates do not differ significantly.

2. First-year survival of British woodcock is 0.472±0.024 (n=426 ring recoveries).

3. There has been no significant change in the annual adult survival rate over three time periods since 1909: 1909-1939, 0.606±0.023 (n=185 recoveries); 1940-1969, 0.561±0.064 (n=31); 1970-1990, 0.546±0.037 (n=126).

4. The mean first egg date for woodcock in Britain is 18 April (n=218 records) and egg laying commences on average 11 days later in Scotland than in S England and seven days later than in N England. The difference between the regions is significant.

5. National data suggest that clutch survival during the 26 day period of egg-laying and incubation is 44%. Data from Derbyshire gave an estimate of 50%. In both datasets 7% of the eggs surviving the incubation period were infertile. Mean woodcock chick survival during the 20 day period from hatching to flying was estimated at 45% in Derbyshire.

6. The current annual production of young woodcock, estimated at 1.14 fledged young per female, is probably not sufficient to meet the requirement of 1.78 fledged young per female needed to balance the annual adult survival rate of 58%. The error associated with the present estimate of the annual production of young, however, is such that this result requires confirmation.

7. British woodcock are highly philopatric, with 76% of recoveries (n=45) of ringed British chicks during March-September in later years within 10km of the place of ringing.

8. British woodcock are faithful to the natal or breeding site in winter, even during cold winters and cold spells within winters, with 68% (n=388 ring recoveries) recovered within 30km of the place of ringing. A small component of the British breeding population (*c*.4%) is believed to be truly migratory, moving southwards to mainland Europe.

9. Continental woodcock outnumber British woodcock by about 10:1 in winter and originate from the former USSR (*c*.36% of the British wintering population), Finland (*c*.25%), Sweden (*c*.12%) and Norway (*c*.10%).

10. Continental migrants start to arrive in N Britain during the second week of October (earliest foreign ring recovery = 12 October) and about ten days later in S Britain. A few Continental woodcock are still present in Britain as late as 15 April, by which time resident British woodcock have started breeding.

11. About 11% of ringed British young woodcock were recovered on the Continent in the breeding season (March-July) and, despite the fact that the shooting of roding birds on the Continent may have exaggerated the proportion, this suggests that some British woodcock breed in Continental Europe. There is no evidence that Continental woodcock breed in Britain.

12. The wintering site fidelity of Continental woodcock returning to the Lizard Peninsula, Cornwall was estimated as 69%, on the basis that the adult survival rate from British recoveries of woodcock ringed in winter (measuring survival only) was 0.55±0.04 (n=105) and that the adult survival rate of woodcock ringed and recovered on the Lizard Peninsula (measuring both survival and wintering site fidelity) was 0.38±0.10 (n=29).

13. The proportion of first-year males on the Lizard Peninsula (65%) was higher than expected and there was some evidence of long-distance movements (>100km) involving mainly this age and sex class. A significantly higher proportion (74%) of female birds was found amongst the adult woodcock wintering on the Lizard Peninsula, Cornwall, due to the shooting of roding males in the former USSR or to differential migration of the sexes.

14. The areas of Britain with the highest proportion of shoots killing woodcock during 1988/89-1992/93 were SW England (90%, mean number of shoots=31) and Wales (100%, mean number of shoots=9). The largest mean annual woodcock bags (birds killed/km^2) during 1988/89-1992/93 were taken in SW England (2.21 birds/km^2) and E Anglia (2.07 birds/km^2).

15. Approximately 3-5 times as many pheasants *Phasianus colchicus* are shot per woodcock in S England and Wales (147-250) as in N England and Scotland (40-84). The large increase in the number of pheasants shot per annum since 1980 has had a greater effect on the woodcock in N England and Scotland, because the proportional increase in the annual pheasant bag has been greater in these regions than in S England.

16. The size of the British wintering woodcock population appears to have remained stable during the period 1961 to 1992.

17. Larger than average woodcock bags were taken in cold winters in central and S England, and recovery of numbers following the severe winter of 1962/63 took three years. The results of simulating a cold weather shooting ban, however, revealed that the increase in the number of woodcock alive at the end of the winter was only small (=3% with shooting mortality equal to 10%).

18. Woodcock wintering on the Lizard Peninsula, Cornwall flew a mean distance of 322±175m (±sd, maximum 620m) to fields to feed at night. Eight radiotagged woodcock each visited between one and four fields only during 21 days of observation and only used areas of 0.5-1.0ha within each field (median field size 4.5ha).

19. On average, radiotagged woodcock were only active for 17±5 min./h (±se) each night and were least active between 02.00 GMT and 06.00 GMT. On 13% of all bird-nights, individuals did not feed, implying that the woodcock had no difficulty obtaining sufficient food.

20. Woodcock wintering in Cornwall (where grass fields outnumber arable by about 4:1) selected permanent pastures (mean density 26.5 birds/km^2) in preference to grass leys (mean density 4.6 to 15.2 birds/km^2) and winter wheat fields (mean density 2.4 birds/km^2) for feeding. This was probably because of the significant difference between field types in terms of available earthworm biomass and available biomass of other soil invertebrates. Woodcock in Derbyshire (where arable fields outnumbered grass fields by about 18:1) selected grass fields in preference to winter cereal and ploughed fields, and an appreciable proportion of resident birds continued to visit fields at night as late into the breeding season as June.

21. Woodcock in Cornwall probably selected between permanent pastures and old leys (>2 years in grass) on the basis of the relative availability of earthworms and other soil invertebrates. During November and December 1991, when rainfall was low, fields were selected according to available earthworm density (multiple regression analysis r^2=0.50), whereas in November and December 1992, when rainfall was high, fields were selected according to the available density of other soil invertebrates (multiple regression analysis r^2=0.21).

22. There was no evidence for the selection of patches with above average soil invertebrate density within the preferred fields, but the outer 20m zone of fields was avoided, probably due to a high perceived risk of predation from foxes *Vulpes vulpes*.

23. In lowland mixed deciduous woodland (Derbyshire) during the breeding season (March-July), woodcock used sycamore *Acer psuedoplanatus* areas significantly more during the day (54% of all radiolocations from 12 radiotagged birds) than at night (30% of radiolocations), whereas conifer areas (mainly Scots pine *Pinus sylvestris*) were used significantly more at night (48% of radiolocations) than during the day (16% of radiolocations).

24. Compositional analysis (Aebischer *et al.* 1993) of diurnal habitat use by woodcock in lowland mixed deciduous woodland showed that home ranges were not established at random and that sycamore habitat classes were preferred to the categories of beech *Fagus sylvaticus*. There was no selection of particular habitats within home ranges, but the edges of stands were utilized significantly more than the central areas.

25. Woodcock feeding sites within sycamore stands at the study site in Derbyshire were characterized by a higher density of shrubs (measured as the number of shrub stems within a 3m radius of each feeding site) than paired random sites and a higher percentage cover of dog's mercury *Mercurialis perennis* than paired random sites. The preference for shrubby cover probably explains why the edges of stands were preferred by woodcock when feeding.

26. Compositional analysis of diurnal habitat use by woodcock in the breeding season in an area of scattered birch *Betula pubescens* woodland in Angus revealed that home ranges were not established at random within the study area. Young birch (≤12m tall) and mature birch with bracken *Pteridium aquilinum* were ranked significantly higher than the other available open habitat types and conifer in terms of preference by woodcock. Habitat use within home ranges was not random and again young birch was most strongly selected.

27. There was some evidence that the woodcock in Angus nested in more open habitat than that selected by feeding birds. The mean area per tree (= the reciprocal of tree density) was significantly higher at nest sites and there was a significantly higher percentage cover of bracken and heather *Calluna vulgaris*.

28. Earthworms formed an important component of the diet of adult woodcock and chicks in Angus (71% and 76% in terms of biomass respectively), but were relatively less important in the diet of woodcock in Derbyshire (43% of the total biomass of prey items in the adult diet and 13% of the total biomass in the chick diet). Among soil surface invertebrates, adult woodcock at both sites exhibited a preference for beetle larvae whilst woodcock chicks exhibited a preference for spiders and harvestmen.

29. Key and *k* factor analyses using data for four mortality factors (egg mortality k_1, chick mortality k_3, shooting mortality k_4 and overwinter loss k_5) from Derbyshire for 1978-1992 revealed that chick mortality was the key factor and that overwinter loss was the main regulatory, or *k*, factor. There was no evidence to suggest that the annual production of young was density-dependent, but the increase in overwinter loss with increased woodcock density following shooting was significant. The results of these analyses must, however, be treated with caution due to the difficulty in estimating the number of breeding females each year and the use of a subjective estimate of relative nest searching effort.

30. The maximum sustainable yield for the woodcock breeding in the Derbyshire study area was estimated at 22% using a simulation model based on the data collected during 1978-1992. This figure must be treated with caution but the current rate of harvesting of the woodcock in this locality is low (4%) and is likely to be well below the maximum sustainable yield.

REFERENCES

Aebischer,N.J. & Robertson,P.A. (1992) Practical aspects of compositional analysis as applied to pheasant habitat utilization. In: *Wildlife telemetry: remote monitoring and tracking of animals* (Eds. I.G.Priede & S.M.Swift). Ellis Horwood, Chichester. pp.285-293.

Aebischer,N.J., Robertson,P.A. & Kenwood,R.E. (1993) Compositional analysis of habitat use from animal radio-tracking data. *Ecology* **74**, 1313-1325.

Aitchison,J. (1986) *The statistical analysis of compositional data*. Chapman & Hall, London.

Alexander,W.B. (1945) The woodcock in the British Isles. *Ibis* **87**, 512-550.

Alexander,W.B. (1946) The woodcock in the British Isles. *Ibis* **88**, 1-24, 159-179, 271-286, 427-444.

Alexander,W.B. (1947) The woodcock in the British Isles. *Ibis* **89**, 1-2.

Alexander,W.B. & Lack,D. (1944) Changes in status among British breeding birds. *British Birds* **38**, 42-45, 62-69, 82-88.

Alldredge,J.R. & Ratti,J.T. (1986) Comparison of some statistical techniques for analysis of resource selection. *J.Wildl.Manage*. **50**, 157-165.

Amlaner,C.J.Jr., Sibley,R. & McCleery,R. (1978) Effects of telemetry transmitter weight on breeding success in herring gulls. *Biotelemetry* **5**, 154-163.

Anderson,D.R. & Burnham,K.P. (1976) Population ecology of the mallard VI. The effect of exploitation on survival. *U.S. Fish and Wildlife Service Resource Publication* **128**. 66pp.

Ash,J.S. (1964) Observations in Hampshire and Dorset during the 1963 cold spell. *British Birds* **57**, 221-241.

Aulie,A. (1976) The pectoral muscles and the development of thermoregulation in chicks of willow Ptarmigan (*Lagopus lagopus*). *Biochem.Physiol*. **56A**, 343-346.

Avery,M. & Leslie,R. (1990) *Birds and forestry*. Poyser, London.

Bailey,N.T.J. (1952) Improvements in the interpretation of recapture data. *J.Anim.Ecol*. **21**, 120-127.

Baillie,S.R., Clark,N.A. & Ogilvie,M.A. (1986) *Cold weather movements of waterfowl and waders: an analysis of ringing recoveries*. CSD Report No.650. NCC, Peterborough.

Barnard,C.J. & Thompson,D.B.A. (1985) *Gulls and plovers: the ecology and behaviour of mixed species feeding groups*. Croom Helm, London.

Barnes,R.F.W. & Tapper,S.C. (1985) A method for counting hares by spotlight. *J.Zool.*, Lond. **206**, 273-276.

Bart,J. & Robson,D.S. (1982) Estimating survivorship when the subjects are visited periodically. *Ecology* **63**, 1078-1090.

Beintema,A.J. & Visser,G.H. (1989) The effect of weather on time budgets and development of chicks of meadow birds. *Ardea* **77**, 181-192.

Beintema,A.J. & Müskens,G.J.D.M. (1983) Changes in the migration pattern of the common snipe. In: *Proc. 2nd European Woodcock and Snipe Workshop* (Ed. H.Kalchreuter). IWRB, Slimbridge, UK. pp.146-160.

Bettman,H. (1961) *Die Waldschnepfe*. F.C. Mayer Verlag Munchen-Solln. 112pp.

Bickford-Smith,P. (1980) Wintering woodcock studies in Cornwall. *Woodcock and Snipe Research Group Newsletter* No.6, pp.43-46.

Bouche,M.B. & Gardner,R.H. (1984) Earthworm functions. VII. Population estimation techniques. *Rev.écol.biol.sol.*, **21**, 37-63.

Boyd,H. (1962) Mortality and fertility of European Charadrii. *Ibis* **104**, 368-387.

Brownie,C., Anderson,D.R., Burnham,K.P. & Robson,D.S. (1985) Statistical inference from band recovery data - a handbook, 2nd Edn. *U.S. Fish and Wildlife Service Resource Publication* **131.** 305pp.

Carter,N., Dixon,A.F.G. & Rabbinge,R. (1982) *Cereal aphid populations: biology, simulation and prediction*. Simulation Monographs. Pudoc, Wageningen, The Netherlands. 94pp.

Chappell,M.A. (1980) Thermal energetics of chicks of arctic-breeding shorebirds. *Comp.Biochem.Physiol.* **65A**, 311-317.

Clausager,I. (1972) *Skovsneppen (Scolopax rusticola) som ynglefugl i Danmark*. Danske Vildtundersogelser, hefte 19. 39pp.

Clausager, I. (1973*a*) Age and sex determination of the woodcock (*Scolopax rusticola*). *Dan.Rev.Game Biol.* **8**, 1-18.

Clausager, I. (1973*b*) Skovsneppens *Scolopax rusticola* yngletid i Danmark. *Dansk orn.Foren.Tidsskr.* **67**, 129-137.

Clausager, I. (1974) Migration of Scandinavian woodcock (*Scolopax rusticola*) with special reference to Denmark. *Dan.Rev.Game Biol.* **8**, 1-38.

Cobham Resource Consultants (1992) *Countryside sports: their economic and conservation significance.* The Standing Conference on Countryside Sports, Reading. 69pp.

Coon, R.A., Williams, B.K. & George, J.L. (1977) Examination of woodcock nest sites in central Pennsylvania. In: *Woodcock ecology and management* (Eds. T.J.Dyer & G.L.Storm). Wildl.Res.Report 14, US Dept. of the Interior, Washington D.C. pp.55-62.

Corbet, G.B. & Southern, H.W., Eds. (1977) *The handbook of British mammals.* 2nd edn. Blackwell, Oxford.

Cottam, G. & Curtis, J.T. (1956) The use of distance measures in phytosociological sampling. *Ecology* **37**, 451-460.

Cramp, S. & Simmons, K.E.L., Eds. (1983) *Handbook of the birds of Europe, the Middle East and North Africa. The birds of the Western Palearctic.* Vol.III. Oxford University Press.

Crowson, R.A. (1981) *The biology of the Coleoptera.* Academic Press, London.

Dixon, K.R. & Chapman, J.A. (1980) Harmonic mean measure of animal activity areas. *Ecology* **61**, 1040-1044.

Dobell, J.V. (1977) Determination of woodcock habitat changes from aerial photography in New Brunswick. In: *Proc. 6th Woodcock Symp.* Fredericton. pp.73-81.

Dobinson, H.M. & Richards, A.J. (1964) The effects of the severe winter of 1962/63 on birds in Britain. *British Birds* **57**, 373-434.

Dugan, P.J. (1981) The importance of nocturnal foraging in shorebirds: a consequence of increased invertebrate prey activity. In: *Feeding and survival strategies of estuarine organisms* (Eds. N.V.Jones & W.J.Wolff). Plenum Press, New York. pp.251-260.

Dunford, R.D. & Owen, R.B.Jr. (1973) Summer behavior of immature radio-tagged woodcock in central Maine. *J.Wildl.Manage.* **37**, 462-469.

Edwards,C.A. & Lofty,J.R. (1977) *The biology of earthworms.* Chapman & Hall, London.

Evans,A.C. & Guild,W.J.Mc.L. (1948) Studies on the relationships between earthworms and soil fertility. V. Field populations. *Ann.appl.Biol.* **35**, 485-493.

Fadat,C. (1968) A propos du sexe chez la bécasse. *La Mordorée* **88**.

Fadat,C. (1972) Existence de deux groupes de bécasses des bois. Consequénces sur la législation de sa chasse en France. *La Mordorée* **101**, 21-25.

Fadat,C. (1973) Mâle ou femelle? *La Mordorée* **107**, 9-18.

Ferrand,Y. (1989) *Contribution a l'étude du comportement du mâle de Bécasse des bois, Scolopax rusticola L., en période de reproduction. Méthode de dénombrement.* These de Doctorat, Academie de Montpellier, Universite Montpellier 3.

Ferrand,Y. & Gossman,F. (1988) Répartition spatiale des bécasses des bois sur leurs habitats nocturnes en Bretagne. In: *Proc. 3rd European Woodcock and Snipe Workshop* (Eds. P.Havet & G.Hirons) IWRB, Slimbridge, UK. pp.48-52.

Fryelstam,B. (1976) Effect of cattlegrazing and harvesting of hay on density and distribution of a European hare population. In: *Ecology and management of European hare populations* (Eds. Z.Pielowski & Z.Pucek). Polish Hunting Association, Warsaw. pp.199-203.

Fuller,R.J. (1982) *Bird habitats in Britain.* Poyser, Calton.

Galbraith,H. (1989) The diet of lapwing, *Vanellus vanellus*, chicks on Scottish farmland. *Ibis* **131**, 80-85.

Glutz von Blotzheim,U.N., Bauer,K.M. & Bezzel,E. (1977) *Handbuch der Vogel Mitteleuropas.* Vol.7. Akademische Verlagsgesellschaft. Weisbaden.

Gossman,F., Ferrand,Y., Loidon,Y. & Sardet,G. (1988) Méthodes et résultats de baguages des bécasses des bois en Bretagne. In: *Proc. 3rd European Woodcock and Snipe Workshop* (Eds. P.Havet & G.Hirons). IWRB, Slimbridge, UK. pp.34-41.

Granval,P. (1988) Influence de la disponsibilité et de l'accessibilité des lombriciens sur le choix des milieux fréquentés par la bécasse des bois (*Scolopax rusticola* L.). In: *Proc. 3rd European Woodcock and Snipe Workshop.* (Eds. P.Havet & G.Hirons). IWRB, Slimbridge, UK. pp.60-66.

Granval,P. & Muys,B. (1992) Management of forest soils and earthworms to improve woodcock (*Scolopax* sp.) habitats: a literature survey. *Gibier Faune Sauvage* **9**, 243-255.

Green,R.E. (1985) Growth of snipe chicks, *Gallinago gallinago. Ringing & Migration* **6**, 1-5.

Green,R.E. & Tyler,G.A. (1989) Determination of the diet of the stone curlew (*Burhinus oedicnemus*) by faecal analysis. *J.Zool.,* Lond. **217**, 311-320.

Greenslade,P.J.M. (1964) Pitfall trapping as a method for studying populations of Carabidae (Coleoptera). *J.Anim.Ecol.* **33**, 301-310.

Gregg,L. (1984) *Population ecology of woodcock in Wisconsin.* Technical Bulletin No.144, Dept. of Natural Resources, Madison, Wisconsin.

Haldane,J.B.S. (1955) The calculation of mortality rates from ringing data. In: *Proc. XI Int.Ornithol.Congr., 1954.* pp.454-458.

Harradine,J. (1988) The woodcock production survey in the United Kingdom and Ireland. In: *Proc. 3rd European Woodcock and Snipe Workshop* (Eds. P.Havet & G.Hirons). IWRB, Slimbridge, UK. pp.87-91.

Harris,S., Cresswell,W.J., Forde,P.G., Trewella,W.J., Wollard,T. & Wray,S. (1990) Home-range analysis using radio-tracking data: a review of problems and techniques particularly as applied to the study of mammals. *Mammal Review* **20**, 97-123.

Hawes,M.L. (1977) Home range, territoriality, and ecological separation in sympatric shrews, *Sorex vagrans* and *Sorex obscurus. Journal of Mammalogy* **58**, 354-367.

Henderson,I.G., Peach,W.J. & Baillie,S.R. (1993) *The hunting of Snipe and Woodcock in Europe: a ringing recovery analysis.* BTO Research Report No.115. Thetford.

Hensler,G.L. & Nichols,J. (1981) The Mayfield method of estimating nest success: a model, estimators and simulation results. *Wilson Bulletin* **93**, 42-53.

Hepp,G.R., Blohm,R.J., Reynolds,R.E., Hines,J.E. & Nichols,J.D. (1986) Physiological condition of autumn banded mallards and its relation to hunting vulnerability. *J.Wildl.Manage.* **50**, 177-183.

Hepp,G.R., Hoppe,R.T. & Kennamer,R.A. (1987) Population parameters and philopatry of breeding female wood ducks. *J.Wildl.Manage.* **51**, 401-404.

Heppleston,P.B. (1971) The feeding ecology of oystercatchers (*Haematopus ostralegus* L.) in winter in Northern Scotland. *J.Anim.Ecol.* **40**, 651-672.

Hestbeck,J.B., Nichols,J.D. & Malecki,R.A. (1991) Estimates of movement and site fidelity using mark-resight data of wintering Canada geese. *Ecology* **72**, 523-533.

Hill,D.A. (1984) Population regulation in the mallard (*Anas platyrhnchos*). *J.Anim.Ecol.* **53**, 191-202.

Hirons,G. (1979) The roding behaviour of the European woodcock *Scolopax rusticola* - an alternative hypothesis. In: *Proc. 1st European Woodcock and Snipe Workshop* (Ed. H.J.Wilson). Woodcock and Snipe Research Group Newsletter, No.5.

Hirons,G. (1980) The significance of roding by woodcock, *Scolopax rusticola*: an alternative explanation based on observation of marked birds. *Ibis* **122**, 350-354.

Hirons,G. (1981) Sex and discrimination in the woodcock. *Game Conservancy Annual Review* **12**, 67-72.

Hirons,G. (1983) A five-year study of the breeding behaviour and biology of the woodcock in England - a first report. In: *Proc. 2nd European Woodcock and Snipe Workshop* (Ed. H.Kalchreuter) IWRB, Slimbridge, UK. pp.51-67.

Hirons,G. (1988*a*) Habitat use by woodcock (*Scolopax rusticola*) during the breeding season. In: *Proc. 3rd European Woodcock and Snipe Workshop* (Eds. P.Havet & G.Hirons). IWRB, Slimbridge, UK. pp.42-47.

Hirons,G. (1988*b*) Some factors affecting the age ratios among Woodcock wings collected from hunters in Britain. In: *Proc. 3rd European Woodcock and Snipe Workshop* (Eds. P.Havet & G.Hirons). IWRB, Slimbridge, UK. pp.92-95.

Hirons,G. & Bickford-Smith,P. (1983) The diet and behaviour of Eurasian woodcock wintering in Cornwall. In: *Proc. 2nd European Woodcock and Snipe Workshop* (Ed. H.Kalchreuter). IWRB, Slimbridge, UK. pp.11-17.

Hirons,G. & Johnson,T.H. (1987) A quantitative analysis of habitat preferences of woodcock, *Scolopax rusticola*, in the breeding season. *Ibis* **129**, 371-381.

Hirons,G. & Linsley,M. (1989) Counting woodcock. *Game Conservancy Annual Review* **20**, 47-48.

Hirons,G.J.M. & Owen,R.B.Jr. (1982) Radio-tagging as an aid to the study of woodcock. *Symp.Zool.Soc.Lond.* **49**, 139-152.

Holley,A.J.F. (1992) *Studies on the biology of the brown hare (Lepus europaeus), with particular reference to behaviour*. Unpubl. Ph.D. thesis, University of Durham.

Hudson,P. (1992) Grouse in space and time. Game Conservancy Ltd., Fordingbridge, Hampshire.

Hudson,P.J. & Newborn,D.N. (1989) The environmental impact of bracken. *Game Conservancy Annual Review* **20**, 117-119.

Hulscher,J.B. (1976) Localization of cockles (*Cardium edule* L.) by the oystercatcher (*Haematopus ostralegus* L.) in darkness and daylight. *Ardea* **64**, 292-310.

Hutchinson,C.D. (1989) *Birds in Ireland*. Poyser, Calton.

Ito,Y. (1972) On the methods for determining density dependence by means of regression. *Oecologia* **10**, 347-372.

Jackson,R. & Jackson,J. (1980) A study of lapwing breeding population changes in the New Forest, Hampshire. *Bird Study* **27**, 27-34.

Jacobs,J. (1974) Quantitative measurement of food selection. *Oecologia* **14**, 413-417.

Jeffers,J.N.R. (1978) *An introduction to systems analysis: with ecological applications*. Edward Arnold, London. 198pp.

Jespersen,P. (1946) *The breeding birds of Denmark*. Copenhagen.

Johnson,D.H. (1980) The comparison of usage and availability measurements for evaluating resource preference. *Ecology* **61**, 65-71.

Kalchreuter,H. (1983) *The woodcock*. Verlag Dieter Hoffmann, Mainz. 119pp.

Kaplan,E.L. & Meier,P. (1958) Nonparametric estimation from incomplete observations. *Journal of the American Statistical Association* **53**, 457-481.

Kenward,R.E. (1982) Techniques for monitoring the behaviour of grey squirrels by radio. *Symp.zool.Soc.Lond.* **49**, 175-196.

Kenward,R. (1987) *Wildlife radio tagging: equipment, field techniques and data analysis*. Academic Press, London.

Kenward,R.E. (1990) *Software for analysing animal location data (RANGES IV)*. Institute of Terrestrial Ecology, Wareham, UK.

Kiss,J.B. & Sterbetz,I. (1973) Beitrage zur ernahrung der waldschnepfe. *Vogel der Heimat* **43**, 69-73.

Kiss,J.B. & Sterbetz,I. (1978) Data on the feeding of the woodcock (*Scolopax rusticola*). *Aquila* **85**, 107-112.

Koubek,P. (1986) The spring diet of the woodcock (*Scolopax rusticola*). *Folia Zoologica* **35**, 289-297.

Kozlova,E.V. (1961, 1962) *Fauna of SSR* **80**, **81** (in Russian, trans. at British Museum, Tring).

Kuno,E. (1971) Sampling error as a misleading artefact in key-factor analysis. *Res.Popul.Ecol.* **13**, 28-45.

Lachlan,C. & Bray,R.P. (1976) Habitat selection by cock pheasants in spring. *J.Appl.Ecol.* **13**, 691-704.

Lack,D. (1943) The age of some more British birds. *British Birds* **36**, 193-197, 214-221.

Lack,P. (1986) *The atlas of wintering birds in Britain and Ireland.* Poyser, Calton.

Lewis,J. & Roberts,S.J. (1993) Woodcock *Scolopax rusticola.* In: *The New Atlas of Breeding Birds in Britain and Ireland 1988-91* (Eds. D.W.Gibbons, J.B.Reid & R.A.Chapman). Poyser, London.

Lofaldli,L., Kalas,J.A. & Fiske,P. (1992) Habitat selection and diet of great snipe, *Gallinago media,* during breeding. *Ibis* **134**, 35-43.

Luff,M.L. (1978) Diel activity patterns of some field Carabidae. *Ecol.Ent.* **3**, 53-62.

Macdonald,D.W. (1976) Food caching by red foxes and some other carnivores. *Z.Tierpschol.* **42**, 170-185.

Macdonald,D.W. (1979) Some observations and field experiments on the urine marking behaviour of the red fox, *Vulpes vulpes* L. *Z.Tierpschol.* **51**, 1-22.

MacKenzie,N. (1987) *The native woodlands of Scotland.* Friends of the Earth (Scotland), Edinburgh.

Madsen,M., Overgaard Nielsen,B., Holter,P., Pedersen,O.C., Brochner Jespersen,J., Vagn Jensen, K-M., Nansen,P. & Gronvold,J. (1990) Treating cattle with ivermectin: Effects on the fauna and decomposition of dung pats. *J.Appl.Ecol.* **27**, 1-15.

Manley,G. (1974) Central England temperatures: monthly means 1659 to 1973. *Quarterly Journal of the Royal Meteorological Society* **100**, 389-405.

Marchant,J.H. (1982) Waders. In: *Wildfowl and wader counts 1981/82* (Ed. D.G.Salmon). Wildfowl Trust, Slimbridge. pp.32-48.

Marchant,J.H., Hudson,R., Carter,S.P. & Whittington,P.A. (1990) *Population trends in British breeding birds.* BTO, Tring.

Marcström,V. (1988) A study on display activities of woodcock in Sweden. In: *Proc. 3rd European Woodcock and Snipe Workshop* (Eds. P.Havet & G.Hirons). IWRB, Slimbridge, UK. pp.83-85.

Marcström,V. & Sundgren,F. (1977) On the reproduction of the European woodcock. *Viltrevy* **10**, 27-40.

Martin,G. (1990) *Birds by night*. Poyser, London.

Mayfield,H.F. (1961) Nesting success calculated from exposure. *Wilson Bull.* **73**, 255-261.

Mayfield,H.F. (1975) Suggestions for calculating nest success. *Wilson Bull.* **87**, 456-466.

McCabe,R.A. & Brackbill,I.M. (1973) Problems in determining sex and age of European woodcock. In: *Proc.Int.Un.Game Biol. 10th Congress 1971, Paris*: 619-637.

McDonald,L.L., Manly,B.F.J. & Raley,C.M. (1990) Analysing foraging and habitat use through selection functions. *Stud.Avian Biol.* **13**, 325-331.

McLennan,J.A. (1979) *The formation and function of mixed-species wader flocks in fields*. Unpubl. Ph.D. thesis, University of Aberdeen.

McNeil,R., Drapeau,P. & Goss-Custard,J.D. (1992) The occurrence and adaptive significance of nocturnal habits in waterfowl. *Biol.Rev.* **67**, 381-419.

Mohr,C.O. (1947) Table of equivalent populations of North American small mammals. *American Midland Naturalist* **37**, 223-249.

Morgan,R. & Shorten,M. (1974) Breeding of the woodcock in Britain. *Bird Study* **21**, 193-199.

Morgenweck,R.O. (1977) Diurnal high use areas of hatching-year female woodcock. In: *Proc. 6th Woodcock Symp.* Fredericton. pp.155-160.

Newton,I. (1986) *The sparrowhawk*. Poyser, Calton.

Nichols,J.D., Reinecke,K.J. & Hines,J.E. (1983) Factors affecting the distribution of mallards wintering in the Mississippi alluvial valley. *Auk* **100**, 932-946.

Norusis,M.J. (1988) SPSS-X advanced statistics guide. 2nd edn. SPSS Inc., Chicago.

Ostermeyer,R. & Ferrand,Y. (1979) *Approche du comportement de la bécasse des bois (Scolopax rusticola L.) en période de reproduction en fôret domaniale de Compiegne (Oise-France)*. Off.natn.Chasse, Paris.

Parker,D.E., Legg,T.P. & Folland,C.K. (1991) A new daily central England temperature series, 1772-1991. *Climate Research Technical Note*, No.11. Met.Office, Bracknell.

Parslow,J.L.F. (1967) Changes in status among breeding birds in Britain and Ireland. *British Birds* **60**, 97-123.

Pay,L.M. (1973) *Die waldschnepfe*. Munchen.

Peach,W.J., Thompson,P.S. & Coulson,J.C. (1994) Annual and long-term variation in the survival rates of British lapwings *Vanellus vanellus*. *J.Anim.Ecol.* **63**, 60-70.

Pettigrew,J.D. & Frost,B.J. (1985) A tactile fovea in the Scolopacidae? *Brain Behaviour and Evolution* **26**, 185-195.

Piddington,H.R. (1981) *Land management for shooting and fishing*. Occasional Paper No.13, Department of Land Economy, University of Cambridge.

Pienkowski,M.W. (1983) Changes in the foraging pattern of plovers in relation to environmental factors. *Anim.Behav.* **31**, 244-264.

Piersma,T., Ed. (1986) Breeding waders in Europe: a review of population size estimates and a bibliography of information sources. *Wader Study Group Bulletin* **48**, Supplement.

Podoler,H. & Rogers,D. (1975) A new method for the identification of key factors from life table data. *J.Anim.Ecol.* **44**, 85-114.

Pollock,K.H., Winterstein,S.R. & Conroy,M.J. (1989) Estimation and analysis of survival distributions for radio-tagged animals. *Biometrics* **45**, 99-109.

Porter,W.F. & Church,K.E. (1987) Effects of environmental pattern on habitat preference analysis. *J.Wildl.Manage.* **51**, 681-685.

Potts,G.R. (1980) The effects of modern agriculture, nest predation and game management on the population ecology of partridges *Perdix perdix* and *Alectoris rufa*. *Advances in Ecological Research* **11**, 2-79.

Potts,G.R. (1986) *The partridge. Pesticides, predation and conservation*. Collins, London. 274pp.

Potts,G.R. & Hirons,G. (1983) Towards a realistic simulation model for woodcock populations. In: *Proc. 2nd European Woodcock and Snipe Workshop* (Ed. H.Kalchreuter). IWRB, Slimbridge, UK. pp.83-91.

Rabe,D. (1977) Structural analysis of woodcock diurnal habitat in northern Michigan. In: *Proc. 6th Woodcock Symp.* Fredericton. pp.125-134.

Rackham,O. (1980) *Ancient woodland*. Edward Arnold, London.

Raim,A. (1978) A radio transmitter attachment for small passerine birds. *Bird Banding* **49**, 326-332.

Ralph,C.L. (1957) Persistent rhythms of activity and energy consumption in the earthworm. *Physiol.Zool.* **30**, 41-55.

Rands,M. & Tapper,S. (1986) The National Game Census: 1985/86 season. *Game Conservancy Annual Review* **17**, 145-150.

Raynsford,L.J. (1959) Early roding of woodcock. *British Birds* **52**, 268.

Ricklefs,R.E. (1973) Patterns of growth in birds II. Growth rate and mode of development. *Ibis* **115**, 117-201.

Ridgill,S.C. & Fox,A.D. (1990) *Cold weather movements of waterfowl in Western Europe*. IWRB Special Publication 13, Slimbridge, UK. 87pp.

Robertson,P.A. (1991) Estimating the nest success and productivity of British pheasants *Phasianus colchicus* from nest-record schemes. *Bird Study* **38**, 73-79.

Robertson,P.A. & Rosenberg,A.A. (1988) Harvesting gamebirds. In: *Ecology and management of gamebirds* (Eds. P.J.Hudson & M.R.W.Rands). Blackwell, Oxford. pp.177-201.

Robertson,P.A., Woodburn,M.I.A., Neutel,W. & Bealey,C.E. (1993) Effects of land use on breeding pheasant density. *J.Appl.Ecol.* **30**, 465-477.

Rochford,J.M. (1982) *The structure of the western European population of the woodcock, Scolopax rusticola L.* Unpubl. Ph.D. thesis, University of Dublin.

Rochford,J.M. & Wilson,H.J. (1982) Value of biometric data in the determination of age and sex in the woodcock (*Scolopax rusticola*). In: *Woodcock ecology and management. Proc. 7th Woodcock Symposium*. Pennsylvania. pp.158-167.

Rundle,W.D. (1982) A case for oesophageal analysis in shorebird food studies. *J.Fld.Ornith.* **53**, 249-257.

Salomonsen,F. (1968) The moult migration. *Wildfowl* **19**, 5-24.

Sanderson,G.C. (1977) *Management of migratory shore and upland game birds in North America*. Int.Ass.Fish & Wildl.Agencies. Washington, D.C.

Satchell,J.E. (1967) Lumbricidae. In: *Soil Biology*. (Eds. A.Burges & F.Raw) Academic Press, London. pp.259-322.

Sharrock,J.T.R. (1976) *The atlas of breeding birds in Britain and Ireland.* Poyser, Calton.

Sheldon,W.G. (1971) *The book of the American woodcock.* Univ.Mass.Press, Amherst.

Shorten,M. (1957) Damage caused by squirrels in Forestry Commission areas 1954-6. *Forestry* **30**, 151-72.

Shorten,M. (1974) *The European Woodcock (Scolopax rusticola). A search of the literature since 1940.* Game Conservancy Report No.21. 95pp.

Snedecor,G.W. & Cochran,W.G. (1980) *Statistical methods.* 7th edn. Iowa St.Univ.Press, Amersham.

Sokal,R.R. & Rohlf,F.J. (1981) *Biometry.* 2nd edn. W.H.Freeman & Co., New York.

Southwood,T.R.E. (1966) *Ecological methods, with particular reference to the study of insect populations.* Chapman & Hall, London.

Spaans,A.L. (1977) Are starlings faithful to their individual winter quarters? *Ardea* **65**, 83-87.

Spencer,W.D. & Barrett,R.H. (1984) An evaluation of the harmonic mean measure for defining carnivore activity areas. *Acta Zoologica Fennica* **171**, 255-259.

Stickel,L.F. (1954) A comparison of certain methods of measuring ranges of small mammals. *Journal of Mammalogy* **35**, 1-15.

Stickel,W.H., Dodge,W.E., Sheldon,W.G., Dewitt,J.B. & Stickel,L.F. (1965*a*) Body condition and response to pesticides in woodcocks. *J.Wildl.Manage.* **29**, 147-155.

Stickel,W.H., Hayne,D.W. & Stickel,L.F. (1965*b*) Effects of heptachlor-contaminated earthworms on woodcocks. *J.Wildl.Manage.* **29**, 132-146.

Strandgaard,H. (1964) The Danish bag record I. Studies in game geography based on the Danish bag record for the years 1956-57 and 1957-58. *Dan.Rev.Game Biol.* **4**, 1-116.

Strandgaard,H. & Asferg,T. (1980) The Danish bag record II. Fluctuations and trends in the Game Bag Record in the years 1941-1976 and the geographical distribution of the bag in 1976. *Dan.Rev.Game Biol.* **11**, 1-112.

Stronach,B. (1983) A report concerning the reproductive organs of the woodcock in the month of February. In: *Proc. 2nd European Woodcock and Snipe Workshop* (Ed. H.Kalchreuter). IWRB, Slimbridge, UK. pp.43-50.

Stronach,B. Harrington,D. & Wilkens,N. (1974) An analysis of Irish woodcock data. In: *Proc. 5th American Woodcock Workshop*. Athens, Georgia.

Stroud,D.A., Reed,T.M., Pienkowski,M.W. & Lindsay,R.A. (1987) *Birds, bogs and forestry. The peatlands of Caithness and Sutherland*. NCC, Peterborough.

Swihart,R.K. & Slade,N.A. (1985) Testing for independence of observations in animal movements. *Ecology* **66**, 1176-1184.

Tapper,S.C. (1988) Population changes in gamebirds. In: *Ecology and management of gamebirds* (Eds. P.J.Hudson & M.R.W.Rands). Blackwell, Oxford. pp.18-47.

Tapper,S. (1992) *Game heritage - An ecological review from shooting and gamekeeping records*. Game Conservancy Ltd., Fordingbridge, Hampshire.

Tapper,S.C. & Barnes,R.W.F. (1986) Influence of farming practice on the ecology of the brown hare (*Lepus europaeus*). *J.Appl.Ecol*. **23**, 39-52.

Tapper,S. & Hirons,G. (1983) Recent trends in woodcock bags in Britain. In: *Proc. 2nd European Woodcock and Snipe Workshop* (Ed. H.Kalchreuter). IWRB, Slimbridge, UK. pp.132-137.

Taylor,L.R. & Taylor,R.A.J. (1977) Aggregation, migration and population mechanics. *Nature* (Lond.) **265**, 415-421.

Teixeira,R.M., Ed. (1979) *Atlas van de Netherlandse broedvogels*. Deventer.

Tester,J.R. & Watson,A. (1973) Spacing and territoriality of woodcock (*Scolopax rusticola*) based on roding behaviour. *Ibis* **115**, 135-138.

Thom,V.M. (1986) *Birds in Scotland*. Poyser, Calton.

Tuck,L.M. (1972) *The Snipes*. Canadian Wildlife Service, Monograph 5. Ottawa.

Tucker,G.M. (1992) Effects of agricultural practices on field use by invertebrate-feeding birds in winter. *J.Appl.Ecol*. **29**, 779-790.

Varga,F. (1968) Nesting and hatching of the woodcock in the neighbourhood of Zagyvaróna and Mátraszele in 1965 and 1966. *Aquila* **75**, 297-298.

Varley,G.C. & Gradwell,G.R. (1960) Key factors in population studies. *J.Anim.Ecol*. **29**, 399-401.

Varley,G.C. & Gradwell,G.R. (1968) Population models for the winter moth. In: *Insect Abundance* (Ed. T.R.E. Southwood) Symposium of the Royal Entomological Society of London. pp.132-142.

Vaurie,C. (1965) *The birds of the Palearctic fauna; non-passeriformes*. Witherby, London. 763pp.

von Zedlitz,O. (1927) Contributions a l'étude biologique de la bécasse. *Rev.franc.Orn.* **11**, 74-81.

Voous,K.H. (1960) *Atlas of European birds*. Nelson, London. 284pp.

Warren,M.S. & Key,R.S. (1991) Woodlands: past, present and potential for insects. In: *The conservation of insects and their habitats* (Eds. N.M.Collins & J.A.Thomas). Academic Press, London.

Watson,A. (1985) Social class, socially induced loss, recruitment and breeding of red grouse. *Oecologia* **67**, 493-498.

Watson,A. & Jenkins,D (1968) Experiments on population control by territorial behaviour in red grouse. *J.Anim.Ecol.* **37**, 595-614.

White,G.C. & Garrott,R.A. (1990) *Analysis of wildlife radiotracking data*. Academic Press, San Diego, California, USA.

Williams,G. (1959) The seasonal and diurnal activity of the fauna sampled by pitfall traps in different habitats. *J.Anim.Ecol.* **28**, 1-13.

Williamson,K., Ed. (1958-1962) Reports from bird observatories, autumn migration. *Bird Migration* **1**(1), 2-27; **1**(3), 97-147; **1**(5), 249-272; **2**(2), 121-131.

Wilson,J. (1983) Wintering site fidelity of woodcock in Ireland. In: *Proc. 2nd European Woodcock and Snipe Workshop* (Ed. H.Kalchreuter). IWRB, Slimbridge, UK. pp.18-27.

Wiltshire,C.W. & Glen,D.M. (1989) Effects of molluscicide on slugs and soil arthropods in winter cereal crops. In: *Slugs and snails in world agriculture* (Ed. I.Henderson). Proc.Symp.Brit.Crop Protect.Council, BCPC Monograph 41. British Crop Protection Council, Guildford. pp.399-406.

Witherby,H.F., Jourdain,F.C.R., Ticehurst,C.B. & Tucker,B.W. (1940) *The handbook of British birds*. Vol.4, 184-192.

Woodburn,M.I.A. & Robertson,P.A. (1990) Woodland management for pheasants. In: *The future of wild Galliforms in the Netherlands* (Eds. J.T.Lumeij & Y.R.Hoogeveen). Gegevens Koninklijke Bibliotheek, The Hague. pp.185-198.

Workman (1954) On hen woodcock feeding chicks. *Irish Naturalists' Journal* **11**, 232.

Wroot,A.J. (1985) A quantitative method for estimating the amount of earthworm (*Lumbricus terrestris*) in animal diets. *Oikos* **44**, 239-242.

Yalden,D.W. (1986) Diet, food availability and habitat selection of breeding common sandpipers *Actitis hypoleucos*. *Ibis* **128**, 23-36.

Yeatman-Berthelot,D. (1991) *Atlas des oiseaux de France en hiver*. Société Ornithologique de France. pp.575.

Zomerdijk,P. (1983) De houtsnip (*Scolopax rusticola*), deelI. *De Graspieper*, October 1983. Pp.107-121.

Plant names were taken from:

Clapham,A.R., Tutin,T.G. & Moore,D.M. (1987) *Flora of the British Isles*. Cambridge University Press, Cambridge.

APPENDICES

(Numbered by chapter)

Appendix 2.1 Recovery distributions of ringed British woodcock and foreign-ringed woodcock recovered in Britain, with goodness-of-fit tests.

Goodness-of-fit tests were performed on each set of data to check for any age-related survival effects. The only departure from the expected distributions was for British woodcock ringed as chicks, of which the number surviving their first year after fledging was lower than expected. The adult survival rate was therefore calculated from 1 April in the year following ringing, after which time there were no age-related effects. As most of the woodcock ringed as adults were caught in autumn and winter, adult survival rate for these birds was also calculated from 1 April in the year following ringing.

The maximum lifespan of any British-ringed adult or foreign-ringed adult or chick recovered in Britain was eight years from 1 April following ringing. There are five British woodcock ringed as chicks which lived longer than eight years. All five were shot and it seems likely that in areas of Britain where no shooting takes place there might be a greater proportion of woodcock living more than eight years.

(Appendix 2.1, continued)

	Before 1 April in year following ringing	Year of recovery														
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
British-ringed chicks (n=426)																
Obs.	225	81	48	33	12	14	5	2	1	0	1	2	1	0	0	1
Exp.	194.9	105.7	57.4	31.1	16.9	9.2	5.0	2.7	1.5	0.8	0.4	0.2	0.1	0.1	0	0
											$\chi^2=18.69$, df=7, $p<0.01$					
Exp.		80.0	48.2	29.0	17.5	10.5	6.3	3.8	2.3	1.4	0.8	0.5	0.3	0.2	0.1	0.1
												$\chi^2=10.58$, df=7, N.S.				
British-ringed adults (n=240)																
Obs.	99	65	35	24	11	3	1	1	0	1						
Exp.		69.0	35.2	18.0	9.2	4.7	2.4	1.2	0.6	0.3						
						$\chi^2=4.12$, df=5, N.S.										
British-ringed adults+chicks (n=666)																
Obs.	324	146	83	57	23	17	6	3	1	1	1	2	1	0	0	1
Exp.		147.5	83.9	47.7	27.1	15.4	8.8	5.0	2.8	1.6	0.9	0.5	0.3	0.2	0.1	0.1
												$\chi^2=9.52$, df=7, N.S.				
Foreign-ringed adults+chicks (n=226)																
Obs.	113	54	31	11	7	5	3	0	1	1						
Exp.		53.9	28.2	14.7	7.7	4.0	2.1	1.1	0.6	0.3						
						$\chi^2=1.95$, df=3, N.S.										

Data for goodness-of-fit tests were pooled to ensure expected values >5.

Appendix 3.1 Mean numbers of woodcock seen per field and per night during spot-lamp counts on the Lizard Peninsula, Cornwall in 1990/91 and 1991/92.

	Trelowarren				Lanarth (main area)			
Field/ night	Field code	Mean birds/ field	Date	Mean birds/ field/ night	Field code	Mean birds/ field	Date	Mean birds/ field/ night
Pre-shoot 1990/91								
1	B	2.60	28 Nov	1.43	B	12.40	3 Dec	2.57
2	C	0	29 Nov	3.00	D	2.40	4 Dec	3.57
3	D	0	30 Nov	2.50	E	0.20	5 Dec	2.86
4	E	2.00	1 Dec	3.25	F	0	6 Dec	2.71
5	J	1.80	10 Dec	0.57	J	0.80	7 Dec	2.83
6	K	5.00			P	3.00		
7	Q	6.00			BA	1.25		
8	T	0.60						
Post-shoot 1990/91								
1	A	1.00	5 Feb	2.17	B	3.50	2 Jan	1.00
2	B	1.75	6 Feb	2.00	D	0	10 Feb	1.00
3	C	0	7 Feb	1.17	J	0		
4	J	1.00	8 Feb	0.33	P	0.50		
5	K	1.25						
6	Q	3.25						
Pre-shoot 1991/92								
1	B	1.17	5 Nov	0.29	B	7.50	6 Nov	1.60
2	C	0	8 Nov	0.14	D	0.25	1 Dec	1.75
3	D	0.33	11 Nov	1.00	J	0.50	6 Dec	2.00
4	E	0.33	12 Nov	0.43	P	1.00	11 Dec	2.60
5	K	1.00	1 Dec	0.14	Z	0.33		
6	M	0	2 Dec	0.67				
7	T	0.17						
Post-shoot 1991/92								
1	C	0	10 Feb	0.83	B	5.00	5 Feb	3.75
2	D	2.00	11 Feb	0.71	AB	4.00	7 Feb	1.75
3	E	1.00	12 Feb	0.67	AC	0	13 Feb	2.50
4	J	0.33			AD	3.33		
5	L	0						
6	M	0						
7	P	1.67						

Appendix 3.2(a) Recovery table for woodcock ringed at Trelowarren and Lanarth, Cornwall and shot at Trelowarren and Lanarth in winters subsequent to the winter of ringing. Data for χ^2 goodness-of-fit test pooled to ensure expected values >2 (Snedecor & Cochran 1980).

Year of ringing	Year of recovery				
	1	2	3	4	5
1978/79	2	2	0	0	0
1979/80	3	0	0	0	1
1980/81	0	0	0	0	0
1986/87	0	1	0	0	0
1987/88	5	1	1	0	0
1988/89	3	1	0	0	
1990/91	2	1			
1991/92	6				
Total	21	6	1	0	1
			=2		
Expected distribution	20.6	6.0	1.8	0.5	0.2
			=2.5		
Goodness-of-fit test	χ^2=0.11, df=2, N.S.				

Appendix 3.2(b) Recovery distribution with goodness-of-fit test for woodcock ringed throughout Britain in winter and recovered in years subsequent to the winter of ringing. Data for χ^2 goodness-of-fit test pooled to ensure expected values >5.

	Year of recovery								
	1	2	3	4	5	6	7	8	9
Observed distribution	40	37	16	7	2	1	1	0	1
							=5		
Expected distribution	49.7	26.2	13.8	7.3	3.8	2.0	1.1	0.6	0.3
							=7.8		
Goodness-of-fit test						χ^2=7.70, df=4, N.S.			

Appendix 4.1 Summary of the data obtained for the woodcock radiotracked in Cornwall during 1992.

Radio freq.	Age of bird	Dates of tracking, 1992	Total days	Nocturnal radio-locations	Diurnal radio-locations	Fate of bird
Lanarth						
218	Adult	21 Nov.- 12 Dec.	22	29	7	
228	1st-yr	21 Nov. 12 Dec.	22	22	6	Recaptured 12 Dec.
247	1st-yr	19 Nov.- 8 Dec.	20	13	6	Signal lost 8 Dec.
319	1st-yr	24 Nov.- 12 Dec.	19	27	4	
349	1st-yr	21 Nov.- 12 Dec.	22	30	7	Shot 31 Dec.
Trelowarren						
298	1st-yr	23 Nov.- 2 Dec.	10	10	2	Died 4 Dec.
309	1st-yr	26 Nov.- 12 Dec.	17	31	5	
336	1st-yr	23 Nov.- 12 Dec.	20	25	5	Shot mid-Jan. 1993

Appendix 5.1 Sexing woodcock during the breeding season.

The sexes in woodcock are morphologically similar and there are no obvious differences in plumage. A number of studies have examined ways of distinguishing the sexes on the basis of biometrics (Clausager 1973*a*, McCabe & Brackbill 1973, Stronach *et al.* 1974, Rochford 1982), but all have met with limited success. In the present study, a small sample (n=25) of birds shot in winter and sexed by dissection yielded a discriminant function based on tarsus length and wing length which correctly classified 72% of cases:

$$Y = 0.444(\mathrm{TARSUS}) - 0.113(\mathrm{WING}) + 4.186$$

where tarsus length was taken as the distance from the tibio-tarsal joint to the first scale before the separation of the first toe, measured to 0.05mm with dial calipers, and wing length was the maximum flattened chord, measured to the nearest mm.

During the breeding season, however, woodcock could be sexed with greater certainty on the basis of measurements from a sample of 47 radiotagged birds that were sexed according to their subsequent behaviour (i.e. roding or incubating eggs and rearing chicks). The birds were all captured during March-June and yielded a discriminant function that correctly classified 94% of cases on the basis of three measurements:

$$Y = 0.083(\mathrm{BILL}) - 0.091(\mathrm{TAIL}) + 0.040(\mathrm{WEIGHT}) - 9.607$$

where bill length was taken as the distance from the bill tip to the feather margin, measured to the nearest mm, and tail length was measured to the nearest mm, weight to the nearest gram.

Weight was clearly the most important of the factors, as shown by the standardized discriminant function coefficients (WEIGHT 0.929, TAIL 0.405, BILL 0.326). This was because females were heavier prior to egg-laying and maintained a relatively constant weight after incubation, whereas males were initially lighter and continued to lose weight during the course of the breeding season in relation to their roding activity.

The classification of cases was as follows:

	Predicted sex	
Actual sex	Male	Female
Male (n=33)	31 (93.9%)	2 (6.1%)
Female (n=14)	1 (7.1%)	13 (92.9%)

This discriminant function cannot be used throughout the year because the weights of both sexes are very variable in winter.

Appendix 5.2 Mean dry weights (mg) of individual prey invertebrates used to estimate composition of the woodcock diet in terms of biomass.

Invertebrate taxon	Dry weight (mg)
Lumbricidae	31.4
Scarabaeidae (adult)	11.6
Carabidae (adult)	26.9
Curculionidae (adult)	2.5
Staphylinidae (adult)	4.1
Other adult Coleoptera	1.0
Coleoptera larvae	9.0
Formicidae	1.7
Lepidoptera larvae	7.7
Araneae & Opiliones	3.4
Diplopoda	29.4
Oniscoidea	8.9
Diptera	1.2

Appendix 5.3 Percentage habitat composition within the total study area, within each woodcock minimum convex polygon (MCP) home range and as defined by the distribution of radiolocations for each bird at Whitwell Wood.

Bird no.	Sycamore &bramble	Sycamore & dog's mercury	Sycamore coppice	Beech &bram.	Beech &rams.	Beech &blue-bells	Conifer
Study area							
	26.1	25.1	2.7	8.4	12.6	18.3	6.8
MCP home range							
1	31.8	23.9	3.0	2.4	11.6	17.8	9.5
2	27.1	63.6	0.0	0.0	8.1	1.2	0.0
3	23.6	20.0	2.2	10.1	4.0	23.4	16.7
4	43.2	25.8	6.3	4.3	14.6	5.6	0.2
5	36.7	29.0	4.0	3.1	7.0	12.4	7.8
6	15.1	28.0	1.9	8.1	0.0	35.8	11.0
7	29.1	17.1	3.6	6.3	6.0	23.6	14.3
8	26.5	21.3	2.7	9.6	6.0	22.4	11.6
9	12.3	23.3	1.9	13.2	2.4	27.7	19.5
10	26.2	25.1	2.1	3.4	4.5	18.2	20.5
11	12.7	10.2	2.0	18.9	10.6	32.5	12.9
12	47.2	31.3	3.9	2.1	0.6	8.5	6.4
13	8.8	27.3	3.2	3.4	0.8	34.9	21.5
14	20.0	29.0	2.0	3.4	0.9	29.1	15.6
Radiolocations							
1	30.6	30.6	0.0	13.9	5.6	5.6	13.9
2	5.6	80.6	0.0	0.0	5.6	8.3	0.0
3	26.9	30.8	3.8	0.0	0.0	7.7	30.8
4	48.5	33.3	3.0	3.0	0.0	12.1	0.0
5	40.0	40.0	0.0	0.0	8.0	12.0	0.0
6	2.6	7.7	2.6	5.1	0.0	35.9	46.2
7	23.2	14.3	12.5	3.6	8.9	1.8	35.7
8	24.2	15.2	4.0	8.1	2.0	40.4	6.1
9	6.8	52.3	0.0	2.3	6.8	20.5	11.4
10	14.5	59.4	1.4	2.9	5.8	10.1	5.8
11	8.3	8.3	0.0	12.5	4.2	39.6	27.1
12	19.4	25.0	5.6	0.0	8.3	22.2	19.4
13	11.8	17.6	0.0	0.0	5.9	29.4	35.3
14	66.7	0.0	0.0	9.5	0.0	14.3	9.5

Appendix 5.4 Percentage of edge and non-edge habitats within Whitwell Wood, within each woodcock minimum convex polygon (MCP) home range and as represented by the distribution of radiolocations for each bird.

Bird number	MCP home range		Radiolocations	
	Edge	Non-edge	Edge	Non-edge
1	52.5	47.5	41.7	58.3
2	22.9	77.1	47.2	52.8
3	58.6	41.4	70.4	29.6
4	49.4	50.6	60.6	39.4
5	47.8	52.2	56.0	44.0
6	45.9	54.1	33.3	66.7
7	64.1	35.9	75.0	25.0
8	51.8	48.2	44.4	55.6
9	55.0	45.0	65.9	34.1
10	57.4	42.6	82.6	17.4
11	59.6	40.4	75.0	25.0
12	47.7	52.3	72.2	27.8
13	51.8	48.2	47.1	52.9
14	44.7	55.3	47.6	52.4
Study area	51.5	48.5		

Appendix 5.5(a) Matrix of means and standard errors of log-ratio differences averaged over all five adult woodcock at Whitwell Wood for comparing prey occurrence in the diet with availability in the study area (top). The implications for prey preference are given by replacement of each element by its sign and ranking the prey taxa according to the number of positive values (bottom). None of the means differ significantly from zero (df=3).

	Carabidae	Staphylinidae	Coleoptera larvae	Araneae & Opiliones	Diplopoda	Oniscoidea
Carabidae		-1.062 ±0.718	-3.013 ±1.382	-1.968 ±1.060	-1.795 ±2.013	-2.154 ±2.002
Staphylinidae	1.062 ±0.718		-1.951 ±2.236	-0.905 ±1.059	-0.733 ±1.758	-1.092 ±1.811
Coleoptera larvae	3.013 ±1.382	1.951 ±2.236		1.046 ±1.159	1.218 ±1.860	0.859 ±1.750
Araneae & Opiliones	1.968 ±1.060	0.905 ±1.059	-1.046 ±1.159		0.172 ±1.057	-0.186 ±1.025
Diplopoda	1.795 ±2.013	0.733 ±1.758	-1.218 ±1.860	-0.172 ±1.057		-0.359 ±0.215
Oniscoidea	2.154 ±2.002	1.092 ±1.811	-0.859 ±1.750	0.186 ±1.025	0.359 ±0.215	

	Carabidae	Staphylinidae	Coleoptera larvae	Araneae & Opiliones	Diplopoda	Oniscoidea	Rank
Carabidae		-	-	-	-	-	0
Staphylinidae	+		-	-	-	-	1
Coleoptera larvae	+	+		+	+	+	5
Araneae & Opiliones	+	+	-		+	-	3
Diplopoda	+	+	-	-		-	2
Oniscoidea	+	+	-	+	+		4

Appendix 5.5(b) Jacobs (1974) preference index values based on prey selection in the diet of adult woodcock at Whitwell Wood.

Definitions of *p*, *r* and the method of calculating *D* are given in the methods of Chapter 5. The index ranges from -1 to +1 indicating complete avoidance and exclusive choice respectively. Zero indicates that a prey type was used in proportion to its abundance in the study area. The prey taxa have been ordered from most preferred (5) to least preferred (0) for comparison with the ranking produced by the compositional analysis.

Prey taxon	Availability in study area (%) *p*	% frequency in diet *r*	Preference index *D*	Rank
Carabidae (adult)	12.6	3.4	-0.61	0
Staphylinidae (adult)	18.7	19.8	0.04	4
Coleoptera larvae	3.0	15.6	0.71	5
Araneae & Opiliones	44.4	41.8	-0.05	2=
Diplopoda	13.1	12.0	-0.05	2=
Oniscoidea	8.1	7.2	-0.06	1

Appendix 5.6(a) Matrix of means and standard errors of log-ratio differences averaged over four woodcock chicks at Whitwell Wood for comparing prey occurrence in the diet with availability in the study area (top). The implications for prey preference are given by replacement of each element by its sign and ranking the prey taxa according to the number of positive values (bottom). None of the means differ significantly from zero (df=2).

	Carabidae	Staphylinidae	Araneae & Opiliones	Diplopoda	Oniscoidea
Carabidae		2.182 ±2.686	-0.749 ±1.550	2.251 ±1.998	-1.957 ±1.867
Staphylinidae	-2.182 ±2.686		-2.931 ±1.611	0.069 ±2.036	-0.225 ±1.907
Araneae & Opiliones	0.749 ±1.550	2.931 ±1.611		2.999 ±2.327	0.303 ±2.650
Diplopoda	-2.251 ±1.998	-0.069 ±2.036	-2.999 ±2.327		-0.294 ±0.180
Oniscoidea	1.957 ±1.867	0.225 ±1.907	-0.303 ±2.650	0.294 ±0.180	

	Carabidae	Staphylinidae	Araneae & Opiliones	Diplopoda	Oniscoidea	Rank
Carabidae		+	-	+	+	3
Staphylinidae	-		-	+	-	1
Araneae & Opiliones	+	+		+	+	4
Diplopoda	-	-	-		-	0
Oniscoidea	-	-	-	+		2

Appendix 5.6(b) Jacobs (1974) preference index values based on prey selection in the diet of woodcock chicks at Whitwell Wood.
Definitions of *p*, *r* and the method of calculating *D* are given in the methods of Chapter 5. The index ranges from -1 to +1 indicating complete avoidance and exclusive choice respectively. Zero indicates that a prey type was used in proportion to its abundance in the study area. The prey taxa have been ordered from most preferred (4) to least preferred (0) for comparison with the ranking produced by the compositional analysis.

Prey taxon	Availability in study area (%) *p*	% frequency in diet *r*	Preference index *D*	Rank
Carabidae (adult)	13.0	10.6	-0.12	2
Staphylinidae (adult)	19.3	21.5	0.07	3
Araneae & Opiliones	45.8	54.4	0.17	4
Diplopoda	13.5	9.0	-0.22	1
Oniscoidea	8.4	4.5	-0.32	0

Appendix 5.7 Percentage habitat composition within the total study area, within each woodcock minimum convex polygon (MCP) home range and as defined by the distribution of radiolocations for each bird at Millden.

Bird no.	Mature birch & bracken	Mature birch& grass	Young birch	Conifer	*Juncus* flush	Heather	Rough & improved grazing
Study area							
	8.2	9.4	3.6	3.4	9.5	23.8	42.0
MCP home range							
1	19.3	6.8	10.5	4.3	4.5	20.7	33.9
2	7.8	9.3	16.0	0.0	15.7	8.2	43.0
3	33.2	11.4	13.6	0.0	11.6	20.3	9.9
4	15.7	6.2	3.7	6.3	5.4	23.5	39.2
5	15.4	11.1	41.2	0.0	11.4	4.0	16.9
6	11.4	14.0	34.2	0.0	11.7	0.0	28.8
7	12.3	8.9	16.4	1.3	4.3	20.8	36.0
8	12.5	8.7	16.8	0.0	12.0	24.9	24.9
9	8.1	17.1	7.0	2.9	10.2	8.3	46.4
10	19.2	4.9	0.6	14.2	1.6	1.8	57.5
Radiolocations							
1	75.6	7.1	14.1	2.4	0.5	0.0	0.0
2	0.0	2.3	95.5	0.0	1.1	1.1	0.0
3	40.6	15.6	15.7	0.0	0.0	28.1	0.0
4	58.5	14.2	18.6	6.6	1.0	1.0	0.0
5	0.0	46.4	53.6	0.0	0.0	0.0	0.0
6	0.0	7.5	92.5	0.0	0.0	0.0	0.0
7	30.2	11.4	54.7	3.8	0.0	0.0	0.0
8	17.0	6.4	44.7	0.0	10.6	21.3	0.0
9	21.3	33.3	33.3	0.0	3.0	0.0	9.1
10	32.2	19.4	0.0	25.8	0.0	3.2	19.4

Appendix 5.8 Jacobs (1974) preference index values based on prey selection in the diet of adult woodcock at Millden. Definitions of *p*, *r* and the method of calculating *D* are given in the methods of Chapter 5. The index ranges from -1 to +1 indicating complete avoidance and exclusive choice respectively. Zero indicates that a prey type was used in proportion to its abundance in the study area. The prey taxa have been ordered from most preferred (4) to least preferred (0) for comparison with the ranking produced by the compositional analysis.

Prey taxon	Availability in study area (%) *p*	% frequency in diet *r*	Preference index *D*	Rank
Carabidae (adult)	11.9	7.0	-0.28	0
Staphylinidae (adult)	14.9	16.8	0.07	3
Other adult Coleoptera	21.8	21.0	-0.02	1
Coleoptera larvae	8.4	11.3	0.16	4
Araneae & Opiliones	43.1	43.9	0.02	2

Appendix 5.9(a) Matrix of means and standard errors of log-ratio differences averaged over six woodcock chicks at Millden for comparing prey occurrence in the diet with availability in the study area (top). The implications for prey preference are given by replacement of each element by its sign and ranking the prey taxa according to the number of positive values (bottom).

	Carabidae	Staphy-linidae	Other Coleoptera	Coleoptera larvae	Araneae & Opiliones	Diplo-poda	Onisc-oidea
Carabidae		-1.779 ±1.065	-1.780 ±0.919	-0.855 ±1.437	-3.365 ±1.148	3.051 ±0.889	-0.479 ±1.289
Staphy-linidae	1.779 ±1.065		-0.001 ±1.625	0.924 ±1.868	-1.586 ±1.276	4.830 ±1.180	1.300 ±1.204
Other Coleoptera	1.780 ±0.919	0.001 ±1.625		0.925 ±1.196	-1.585 ±0.907	4.831 ±1.071	1.301 ±1.167
Coleoptera larvae	0.855 ±1.437	-0.924 ±1.868	-0.925 ±1.196		-2.510 ±1.493	3.906 ±0.978	0.376 ±1.438
Araneae & Opiliones	3.365 ±1.148	1.586 ±1.276	1.585 ±0.907	2.510 ±1.493		6.416 ±1.171	2.886 ±1.190
Diplopoda	-3.051 ±0.889	-4.830 ±1.180	-4.831 ±1.071	-3.906 ±0.978	-6.416 ±1.171		-3.530 ±0.874
Oniscoidea	0.479 ±1.289	-1.300 ±1.204	-1.301 ±1.167	-0.376 ±1.438	-2.886 ±1.190	3.530 ±0.874	

	Carabidae	Staphy-linidae	Other Coleoptera	Coleoptera larvae	Araneae & Opiliones	Diplo-poda	Onisc-oidea	Rank
Carabidae		-	-	-	-	+	-	1
Staphy-linidae	+		-	+	-	+	+	4
Other Coleop.	+	+		+	-	+	+	5
Coleop. larvae	+	-	-		-	+	+	3
Araneae & Opil.	+	+	+	+		+	+	6
Diplopoda	-	-	-	-	-		-	0
Onisc-oidea	+	-	-	-	-	+		2

Appendix 5.9(b) Prey taxa ranked according to their selection by woodcock chicks at Millden, showing where differences between ranks are significant. Ranks which do not differ significantly ($p \geq 0.05$) according to the matrices in Appendix 5.9(a) are assigned the same letter in the "ranks differ" column.

Rank	Prey taxon	Ranks differ
6	Araneae & Opiliones	*a*
5	Other adult Coleoptera	*a b*
4	Staphylinidae (adult)	*a b*
3	Coleoptera larvae	*a b*
2	Oniscoidea	*a b*
1	Carabidae (adult)	*b*
0	Diplopoda	

Appendix 5.9(c) Jacobs (1974) preference index values based on prey selection in the diet of adult woodcock at Whitwell Wood.

Definitions of *p*, *r* and the method of calculating *D* are given in the methods of Chapter 5. The index ranges from -1 to +1 indicating complete avoidance and exclusive choice respectively. Zero indicates that a prey type was used in proportion to its abundance in the study area. The prey taxa have been ordered from most preferred (6) to least preferred (0) for comparison with the ranking produced by the compositional analysis.

Prey taxon	Availability in study area (%) *p*	% frequency in diet *r*	Preference index *D*	Rank
Carabidae (adult)	4.8	4.5	-0.03	1
Staphylinidae (adult)	6.0	14.8	0.46	4
Other adult Coleoptera	8.8	11.0	0.12	3
Coleoptera larvae	3.4	10.2	0.53	5
Araneae & Opiliones	17.4	53.5	0.69	6
Diplopoda	56.2	2.5	-0.96	0
Oniscoidea	3.4	3.5	0.02	2

Appendix 6.1 The total number of woodcock nests and broods found at Whitwell Wood, Derbyshire prior to 15 May during 1978-1992 and the estimated number of breeding females each year.

Year	Number of nests found during incubation	Number of nests found predated	Number of broods located	Correction for nest searching effort	Estimated number of breeding females
1978	6	1	3	x2	20
1979	4	1	0	x3	15
1980	2	0	2	x3	12
1981	1	0	1	x3	6
1982	2	0	1	x3	9
1983	10	0	1	x2	22
1984	3	0	2	x3	15
1985	6	1	1	x2	16
1986	8	1	0	x2	18
1987	2	0	2	x2	8
1988	9	0	5	x1	14
1989	12	0	4	x1	16
1990	4	0	8	x1	12
1991	4	2	2	x1	8
1992	5	1	1	x1	7

Appendix 6.2 Numbers of full-grown woodcock ringed at Whitwell Wood, Derbyshire each spring during 1978-1992 and annual estimates of the proportion shot during the winter. The number of ringed birds at risk each year has been calculated using a constant annual survival rate of 0.58 and the assumption has been made that all recoveries were reported.

Year	Number of full-grown woodcock ringed	Number of ringed birds at risk	Number of ringed woodcock shot	% of birds at risk that were shot
1978	26	26	1	3.8
1979	15	30	3	10.0
1980	24	42	3	7.1
1981	25	44	0	0
1982	0	23	2	8.7
1983	0	9	0	0
1984	5	5	0	0
1985	10	13	1	7.7
1986	27	35	0	0
1987	20	39	4	10.3
1988	19	40	2	5.0
1989	7	25	0	0
1990	17	27	1	3.7
1991	19	31	0	0
1992	10	27	0	0
Means	14.9	27.7	1.13	3.75

Appendix 6.3 Program listing for the deterministic woodcock population model, written in Borland Turbo Pascal v.7.0.

```
program Woodcock (input, output, Results);
  const
    Clutch = 3.95;
    K1 = 0.2375;
    K3 = 0.4018;
    K4 = 0.017;
  var
    Year,X: Integer;
    Sprpop,Autpop,Eggs,Chicks,Pshoot: Real;
    K2,K5,Leggs,Lchicks,Laut,Lps: Real;
    K1surv,K2surv,K3surv,K4surv,K5surv: Real;
    Y1,Y2,F1,F2: Real;
    Fem,Young,Autfem,Sprfem: Real;
    Femsurv,Femsucc,Femfail: Real;
    Results: Text;
  begin
    Write('Enter initial population size ');
    Readln(Sprpop);
    Fem := Sprpop;
    Year := 1;
    Assign(Results,'LPT1');
    Rewrite(Results);
  while Year < 21 do
    begin
      Writeln(Results,'Year ',Year);
      Writeln(Results,'Spring population ',Sprpop:5:2);
      Y2 := 0;
      X := 1;
      while X < 3 do
        begin {Calculation of the production of young}
          Eggs := Fem*Clutch;
          K1surv := Exp(-2.303*K1);
          K2 := (1-K1surv)*0.231;
          K2surv := 1-K2;
          Chicks := Eggs*K1surv;
          K3surv := Exp(-2.303*K3);
          Y1 := Chicks*K3surv; {Young produced}
          Young := Y1+Y2;
          Y2 := Y1;
          Y1 := 0;
          Femsucc := Fem*K1surv;
          Femsurv := Fem*K2surv;
          Femfail := Femsurv-Femsucc; {Females re-nesting}
          Fem := Femfail;
          X := X+1;
        end;
      Autfem := 0.68*Sprpop;
      Autpop := (Young/2)+Autfem; {Autumn population}
      K4surv := Exp(-2.303*K4);
      Pshoot := Autpop*K4surv;
      Lps := Ln(Pshoot)/2.303;
      K5 := -0.625+(0.775*Lps);
      K5surv := Exp(-2.303*K5);
```

```
    Sprpop := Pshoot*K5surv; {New spring population}
    Fem := Sprpop;
    Year := Year+1;
    Writeln(Results,'Autumn population ',Autpop:4:1);
    Writeln(Results,' ':10);
  end;
  Close(Results);
end.
```