Chapter (non-refereed)

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Principles underlying bird numbers in Scottish woodlands

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1 Introduction

In this paper, I will discuss the factors which influence bird numbers in woodland. I will be concerned primarily with generalizations which can be made from previous census work in various parts of the world, but will also mention some aspects, related to commercial forestry, which are especially relevant to the Scottish scene. The original pine and broadleaved forests, which formerly covered most of Scotland, have been so devastated by human impact as to remain only as scattered remnants in a greatly modified state. The bulk of existing woodland was planted in the last 50 years, chiefly in the form of commercial softwood monocultures. Although some native Scots pine (*Pinus sylvestris*) has been used, the plantings have included mainly the introduced spruces (*Picea* spp.) and larches (*Larix* spp.), lodgepole pine (*Pinus contorta*) and Douglas fir (*Pseudotsuga menziesii*).

Associated with its location, forming the cold northern part of an island off a large continental land mass, Scotland has fewer woodland bird species than have nearby parts of Europe. Britain as a whole has 75 woodland bird species, compared with 86 at similar latitudes in Europe. Within Britain, Scotland has about 68 species, but at least 25 of these depend on openings within the forest or on nearby open land. Another 13 species, dependent on water, are not considered here.

In most Scottish woods where censuses have been made, the chaffinch (*Fringilla coelebs*) and wren (*Troglodytes troglodytes*) were the commonest species, together with the goldcrest (*Regulus regulus*) and coal tit (*Parus ater*) in conifer areas and the willow warbler (*Phylloscopus trochilus*) in birch (*Betula* spp.). Total densities in spring have varied from less than 150 pairs km^{-2} in upland pine plantations to more than 1500 pairs km^{-2} in some lowland broadleaved woods with undergrowth (see later). In general, the greater numbers of individuals in a wood are associated with greater numbers of species.

2 Bird census methods

Various methods have been used to count woodland birds, and results are not always comparable between them. Most early work used the *'transect method'*, in which the observer takes a set course and notes all the birds encountered. The abundance of each species is expressed in relation to all the others as a 'relative abundance'. This method is biased towards conspicuous species, and does not readily give densities. It was used in Scottish woods by Yapp (1962) and Simms (1971).

The *area count* entails a line of observers walking through a wood, on a broad front, counting all the birds that fly back through the line. The method is probably biased towards conspicuous species and underestimates densities because some birds leave undetected. It was used in Scottish pinewoods by Watson (1969).

The *point count* entails noting all the birds detected in a set time period, say 10 min, at each of several randomly selected points within a wood. If the counts are restricted to a set radius, say 30 m from the observer, results can be extrapolated to give densities. However, the method is best used for broad comparisons, as it can give results from many woods in a short time. It was used in Scottish woods by Newton *et al.* (1986).

The *mapping method* entails marking on a gridded map the position of all birds encountered on each of 8–10 visits over several weeks to a census plot and, from the distribution of points, estimating the number of territories involved (Enemar 1959; Williamson 1964). This method is most appropriate for song birds, giving approximate densities of each species, as well as their relative abundance. It has been used in Scottish woods by Williamson (1969), Moss (1978a, b) and others. All song bird densities quoted in this paper were obtained by this method, and all trends have been established by methods which are comparable within themselves.

3 The birds

The 68 bird species which breed regularly in Scottish woodland are listed in Table 1. Of the 6 corvids, several are widespread, while magpies (*Pica pica*) and jays (*Garrulus glandarius*) are local, but all would be commoner in certain areas if they were persecuted less by gamekeepers. Among the seed eaters, the chaffinch is common everywhere, the greenfinch (*Carduelis chloris*) near farmland, and the bullfinch (*Pyrrhula pyrrhula*) in areas of young growth and scrub, but the hawfinch (*Coccothraustes coccothraustes*) is extremely local, found only in southern areas of mature broadleaved trees. The numbers of crossbills (*Loxia* spp.) and siskins (*Carduelis spinus*) fluctuate greatly from year to year, according to the size of conifer seed crops, and the numbers of redpolls (*C. flammea*) according to the birch crop in the preceding

Table 1. Breeding birds of Scottish woodlands
O – dependent on openings or nearby open land; B – dependent on broadleaved trees; C – dependent on conifers; N – found only in the north; S – found only in the south; E – found only in the east

Corvids (6)	Raven (*Corvus corax*) (O), carrion/hooded crow (*C. corone*) (O), rook (*C. frugilegus*) (O), jackdaw (*C. monedula*) (O), magpie (*Pica pica*) (O), jay (*Garrulus glandarius*)
Seed-eating song birds (8)	Hawfinch (*Coccothraustes coccothraustes*) (B,S), common crossbill (*Loxia curvirostra*) (C), Scottish crossbill (*L.c. scotica*) (C,N), greenfinch (*Carduelis chloris*) (O,S), siskin (*C. spinus*) (C), redpoll (*C. flammea*) (B), bullfinch (*Pyrrhula pyrrhula*), chaffinch (*Fringilla coelebs*)
Insect-eating song birds (30)	Tree pipit (*Anthus trivialis*) (O), nuthatch (*Sitta sitta*) (B,S), tree creeper (*Certhia familiaris*), wren (*Troglodytes troglodytes*), mistle thrush (*Turdus viscivorus*) (O), fieldfare (*T. pilaris*) (O,N), song thrush (*T. philomelos*), redwing (*T. musicus*) (N), blackbird (*T. merula*), redstart (*Phoenicurus phoenicurus*), robin (*Erithacus rubecula*), goldcrest (*Regulus regulus*) (C), blackcap (*Sylvia atricapilla*) (B), garden warbler (*Sylvia borin*) (B), whitethroat (*Sylvia communis*) (B), lesser whitethroat (*S. curruca*) (B,S), willow warbler (*Phylloscopus trochilus*), chiffchaff (*P. collybita*) (B), wood warbler (*P. sibilatrix*) (B), spotted flycatcher (*Muscicapa striata*) (B), pied flycatcher (*Ficedula hypoleuca*) (B), dunnock (*Prunella modularis*), starling (*Sturnus vulgaris*) (O), great tit (*Parus major*) (B), blue tit (*P. caeruleus*) (B), coal tit (*P. ater*) (C), crested tit (*P. cristatus*) (C,N), marsh tit (*P. palustris*) (B,S,E), willow tit (*P. montanus*) (S), long-tailed tit (*Aegithalos caudatus*) (B)
Near passerines (5)	Green woodpecker (*Picus viridis*) (B,O), great-spotted woodpecker (*Dendrocopus major*), wryneck (*Jynx torquilla*) (B,E), nightjar (*Caprimulgus europaeus*) (O), cuckoo (*Cuculus canorus*) (O)
Doves and game birds (6)	Wood pigeon (*Columba palumbus*) (O), stock dove (*C. oenas*) (O,E), turtle dove (*Streptopelia turtur*) (O,S), red grouse (*Lagopus lagopus*) (O), black grouse (*Tetrao tetrix*) (O), capercaillie (*Tetrao urogallus*) (N,C)
Owls and raptors (10)	Long-eared owl (*Asio otus*), tawny owl (*Strix aluco*), golden eagle (*Aquila chrysaetos*) (O), sparrowhawk (*Accipiter nisus*), goshawk (*A. gentilis*), buzzard (*Buteo buteo*) (O), honey buzzard (*Pernis apivorus*), kestrel (*Falco tinnunculus*) (O), merlin (*F. columbarius*) (O)
Waders (3)	Woodcock (*Scolopax rusticola*), wood sandpiper (*Tringa glareola*) (O,N), greenshank (*T. nebularia*) (O,N)

Of the above, Scottish crossbill, crested tit, wood sandpiper, greenshank and golden eagle do not breed in southern England, whereas woodlark (*Lullula arborea*), golden oriole (*Oriolus oriolus*), nightingale (*Luscinia megarhynchos*), firecrest (*Regulus ignicapillus*) and lesser-spotted woodpecker (*Dendrocopos minor*) breed in England, but not Scotland

winter (Newton 1972). In years when seeds are locally plentiful, any of these 3 species can outnumber all the other birds in a wood. The crossbills of northern Scotland form a distinct race (*L. c. scotica*), feeding primarily on seeds from pine cones; they are larger, with heavier bills, than the nominate *L. c. curvirostra* of northern Europe, which feeds largely on seeds from softer spruce cones. This crossbill is now found over most of Scotland, following the widespread planting of spruce.

Of 30 insectivorous song birds, the commonest are the wren, willow warbler (a summer visitor), goldcrest and coal tit. In general, the coal tit outnumbers the crested tit (*Parus cristatus*) in pinewoods by 3–4 to one (Nethersole-Thompson & Watson 1974) and, while the former can nest in holes in the ground, the latter requires soft, rotten tree stumps, and is thus largely absent from plantations which lack dead trees. In Britain, the crested tit is found only in north-east Scotland, but it has a wide distribution in conifer woods abroad. Great tits (*Parus major*) and blue tits (*P. caeruleus*) are found only near deciduous trees, while long-tailed tits (*Aegithalos caudatus*) and dunnocks (*Prunella modularis*) nest chiefly in low bushes. The pied flycatcher (*Ficedula hypoleuca*), which breeds in pinewoods in northern Europe, is scarce in such woods in Britain, but breeds locally in broadleaved woods. The willow warbler is the commonest warbler, followed by the chiffchaff (*Phylloscopus collybita*), while the various *Sylvia* species are all rather scarce.

Redwings (*Turdus musicus*) and fieldfares (*T. pilaris*) have colonized Scotland in recent years, and breed in a wide variety of sites, chiefly in association with birch. Wrynecks (*Jynx torquilla*) have also bred regularly in small numbers since about 1950, and in the same period the green woodpecker (*Picus viridis*) has spread into south and central Scotland from England. The great-spotted woodpecker (*Dendrocopus major*) became almost extinct during the last century, but has since re-established itself widely. The nightjar (*Caprimulgus europaeus*) has declined in the last 100 years, and is now extremely scarce in many of its former haunts. The cuckoo (*Cuculus canorus*) is common in openings and lays its eggs mainly in the nests of pipits. Wood pigeons (*Columba palumbus*) and stock doves (*C. oenas*) use woodland mainly for nesting, and are commonest close to farmland where they feed.

Broadly speaking, the 3 game birds occupy different stages of forest succession: the red grouse (*Lagopus lagopus*) occurs in large openings, where heather (*Calluna vulgaris*) prevails; the black grouse (*Tetrao*

tetrix) is most numerous in young forests, with some birch and pine, and the capercaillie (*Tetrao urogallus*) prefers mature forests. This last species was extinct in Britain by 1770, but, after abortive attempts to reintroduce it from Sweden to Deeside in 1827–29, it was successfully re-established near Taymouth in 1837–38. Twenty-five years later there were thought to be 1000–2000 birds in the area (Ritchie 1920). Birds from Taymouth and fresh importations from Sweden were then released in various parts of Scotland from where birds spread naturally to other areas, though they are still absent from the south and west.

The woodcock (*Scolopax rusticola*) occurs in damp woodland throughout Scotland, but the other forest waders depend on extensive bogs, and are found only in the north. The wood sandpiper (*Tringa glareola*) may have colonized Scotland only in recent decades, and is still extremely scarce. Among the predators, the tawny (*Strix aluco*) and long-eared owls (*Asio otus*), sparrowhawk (*Accipiter nisus*), kestrel (*Falco tinnunculus*) and buzzard (*Buteo buteo*) are widespread; the golden eagle (*Aquila chrysaetos*) and merlin (*Falco columbarius*) breed only near the altitudinal tree limit (or lower on deforested ground), while the red kite (*Milvus milvus*) and honey buzzard (*Pernis apivorus*) were exterminated last century. The goshawk (*Accipiter gentilis*) was similarly exterminated, but has re-established itself in recent years, as a result of falconry escapes, and now breeds in some of the largest forests.

At least 4 of the species mentioned, the Scottish crossbill, siskin, crested tit and capercaillie, were formerly more or less restricted to northern Scotland, but all have spread with the planting of conifers. The Scottish crossbill and crested tit have spread only within the north, whereas the others have spread further, and the siskin now breeds in all parts of Britain with large plantations of conifers.

4 Factors influencing bird numbers

The importance of the dominant tree species in influencing the numbers and variety of birds in a forest is at once apparent to any ornithologist. But the same type of forest may grow in one region or another, on high or low ground, on rich or poor soil, and may vary in structure according to age and management. All these factors affect the bird life. The main questions are what determines, for any one forest: (i) the number of species, (ii) which species they will be, and (iii) at what densities they will occur. These aspects are best considered together, because the same factors influence all 3. Most bird censuses have been done in birch and oak (*Quercus* spp.), or in spruce and pine. Discussion will be limited to these types, as the main types available in Scotland. Reference will also be made to Finnish forests, where spruce, pine and birch dominate, and where much more census work has been done than in Scotland (Palmgren 1930; Merikallio 1946; Haapanen 1965, 1966).

4.1 Tree species

The obvious division is between broadleaved and coniferous trees. Most woodland birds in Britain live in both types, but a few species are almost entirely restricted to one or other type (Table 1). Thus, hawfinch, marsh tit (*Parus palustris*), garden warbler (*Sylvia borin*), blackcap (*Sylvia atricapilla*), wood warbler (*Phylloscopus sibilatrix*), chiffchaff, pied flycatcher and green woodpecker are more or less confined to broadleaved woods in Scotland, while capercaillie, crested tit and crossbill are restricted to conifers; in addition, goldcrest, coal tit and siskin are much commoner in conifers than in broadleaved woods. The tree species also influence bird density. Comparing forests with similar soils and field layers, breeding birds are more abundant in birch/oak than in spruce, and more abundant in spruce than in pine. Among mixed forests, bird densities in spruce/pine are nearer to pine than to spruce, whereas densities in birch/spruce are as high, or higher, than those in birch, and much higher than in spruce (Palmgren 1930; Merikallio 1946; Haapanen 1965). It is not clear why pine supports only low densities, but it has less foliage per unit area than the other trees, and hence less habitat for insects. It also offers less good nesting sites for birds than does spruce (von Haartman 1971), and has cones which are difficult for most birds to open. It is less clear whether consistent differences in song bird densities occur between different types of broadleaved woods, but few censuses have yet been made and further work is needed (see Massey 1974 for Wales). In Deeside woods, oak held more species and individuals than birch, which in this area held fewer birds even than conifers (French *et al.* 1986).

Mixtures of conifer and broadleaved trees increase bird species partly by improving structural diversity, but mainly by providing habitat for species tied to one or other tree type. Maximum bird densities are achieved if the ratio of conifer to broadleaf species lies between 1:3 and 1:5 in either direction, and if the subdominant tree type is present as clumps up to 1 ha in area, rather than intermixed. This was the conclusion of French *et al.* (1986) who compared bird life in various woods in north-east Scotland. The advantage of having the secondary tree type in clumps was that it then formed a discrete habitat, able to hold complete territories of type-specific birds which might be lacking in uniform mixtures.

4.2 Regional trends

In Europe as a whole, the numbers of bird species found in woodlands decrease from south to north, and from east to west across the continent. Similar trends are found in other animals and in plants. The reasons are not clear, but may depend on rates of spread from glacial refuges. Within Scotland, 8 species are found only in the south; 5 species are found only in the north; and 3 species are found in the east but not the west (Table 1). In addition, several other species become more local in the north and west, compared

with the south and east (Sharrock 1976). Fuller (1983) presented a map showing the number of bird species which could be found in a standard '50 ha wood' in different parts of Scotland. This number varied from 45–55 in the south-east to 15–25 in the north-west. As a result of this and other survey work organized by the British Trust for Ornithology, regional aspects of bird distribution have been well studied, and no longer form a major research need.

4.3 Altitude

Within similar types of woodland, bird densities generally decline with increasing elevation (Newton *et al.* 1986). The reasons are not clear, but may link with climate (as in the south–north trend mentioned above) or with soil productivity, discussed below. Species changes with altitude usually link with vegetation changes.

4.4 Soil fertility

Soil productivity can be judged directly, or more readily from the ground vegetation. Arranged according to decreasing productivity, the following main vegetation types are distinguished in north European woods: grass/herb (several types), *Oxalis/Myrtilus*, *Myrtilus*, *Vaccinium* and *Calluna* (Cajander 1925). When other factors are constant, birds in Finnish woods were 3–6 times more numerous on the most productive than on the least productive soils (von Haartman 1971). In those species that were examined individually, this variation resulted from birds taking smaller territories in the good than in the poor areas (von Haartman 1971; Newton 1972). This trend is explicable in terms of organic production, for all types of productivity are better on better soils, including not only wood and foliage, but also various other crops, from flowers and fruits to earthworms (von Haartman 1971). Our knowledge of this aspect is based mainly on findings in Fennoscandia, and some similar work in Scotland is desirable.

4.5 Area

Another pattern found repeatedly is that the larger the area of uniform woodland, the lower the overall density of birds (Oelke 1968). This rule is mysterious but widespread; oceanic islands often have astonishingly high densities of birds, as do small islands of habitat in mainland situations (MacArthur 1971). It is unlikely that this effect can be explained in terms of productivity. One factor involved in woodland is the so-called 'edge effect' (Odum 1959), in which birds are found at much greater density at the boundary between 2 habitats than within either one of them. As small woods have relatively more edge than large ones, this effect contributes to increased bird densities. The edge effect is apparent at the junction between different tree communities, but especially where a wood adjoins an open area. In this last situtation, some species nest on the forest edge, but do not penetrate the forest interior. They may obtain part (or all) of their food from nearby open land, so that the density of birds that nest in the wood is greater than could be sustained by the wood itself. Such species include crow (*Corvus corone*), wood pigeon and kestrel.

While the overall density of birds is greater in a small wood than in an equivalent area of a large wood, the number of species in a small wood is often less. Comparing various British woods, Moore and Hooper (1975) found that the number of species became fewer with decreasing area and also with increasing distance from other woods. This situation presents another parallel with oceanic islands, where size and degree of isolation influence the numbers of bird species present. One reason for this relationship in woodlands is that the smallest woods may be too small to accommodate even a single territory of certain bird species. Another reason is that larger woods tend to be more diverse, with rides and other openings which provide habitat for extra species. There may also be a chance element, with rare species more likely to be encountered in a large wood than in a small one.

The relationship between the area and isolation of a wood and its bird fauna needs further quantification in the British context. This aspect forms one of the most obvious research needs at present.

4.6 Structure

As a forest grows, its bird fauna changes from an initial predominance of field-dwelling species, through scrub and thicket species, to woodland species proper (Lack 1933; Moss *et al.* 1979). The overall density of birds may also increase, as may be expected from the increase in structural complexity of the habitat. In a well-grown forest, a many-layered stand containing trees and shrubs of varying height holds more bird species than a uniform stand in which all the trees are the same height. In a mature forest, structural diversity is apparently more important than the number of tree species in influencing the number of bird species present (MacArthur & MacArthur 1961; Moss 1978b; O'Connor 1981; Orians 1969; Recher 1969). Scottish pinewoods with a shrub layer hold slightly more species, and about double the density of birds, as do even-age stands with no shrub layer (Newton & Moss 1977).

The main reason why the complexity of the habitat has such a great influence on the bird community is that many woodland birds show a distinct vertical zonation in their feeding. Long ago, Colquhoun and Morley (1943) distinguished 3 separate classes: the upper canopy birds, the tree and shrub species, and the ground feeders. Among the tits, for example, in oakwoods, the blue tit feeds mainly in the canopy, the marsh tit on the lower branches and the shrub layer, and the great tit largely on the ground. If the shrub layer is lacking, then so too is a whole element of the bird fauna.

Complexity in structure has a horizontal, as well as a vertical, component, and many typical woodland birds are associated with openings of one sort or another. Some species, such as willow warbler, prefer a broken canopy, while others, such as tree pipit (*Anthus trivialis*), prefer glades devoid of trees, while yet others, such as whitethroats (*Sylvia communis*), require areas of low scrub. As a wood opens out, other bird species, more typical of open land, move in, and no clear boundary between communities can be drawn.

In a range of Deeside woods, bird species diversity was greatest where gaps occupied some 10–35% of the total woodland area, and had a mean diameter of 20–35 m (French *et al.* 1986). The distribution of gap sizes was skewed, however, and, with a mean of 20–35 m, some gaps exceeded 100 m. These areas still excluded certain species, such as short-eared owl (*Asio flammeus*), which require even larger open areas.

4.7 Micro-habitat

An important aspect of forest structure concerns the availability of nest sites. In managed forests, where dead timber and scrub may be absent, the densities of hole- and shrub-nesting birds may be limited by shortage of nest sites. This has been shown repeatedly by experiments in which the provision of nest boxes or bunches of branches (tied and stuck up to look like bushes) in managed woods was followed by marked increases (up to 10 times or more) in the density of hole-nesting and shrub-nesting birds (Pfeifer 1953, 1963). The main hole-nesting species involved were various tits, pied flycatchers and redstarts (*Phoenicurus phoenicurus*). The increase in breeding density usually followed immediately, but in some woods pied flycatchers invaded only after several years. In certain places in Europe, provision of nest boxes has resulted in densities of pied flycatchers equivalent to 2000 pairs km^{-2}, more than the total density of all birds so far found in any forest in Europe without nest boxes (Udvardy 1957; von Haartman 1971). Moreover, such increases were achieved over areas up to 25 ha (Pfeifer 1963). Given nest boxes, pied flycatchers will breed in pure conifer woods, lacking natural holes, if these woods also have an open structure.

Dead trees also provide feeding sites for woodpeckers, which extract insects from the rotten wood. Almost absent in commercial plantations, these birds can form a dominant element of the bird fauna in neglected woods, where large numbers of dead trees occur. One has to travel abroad to appreciate the devastating impact of forestry procedures on woodpeckers in Britain.

To summarize, the number of bird species breeding in a wood may be influenced by tree species, geographical location, altitude, forest structure and area; the type of bird species by tree species, geographical location, altitude, forest structure and area; and bird density by tree species, altitude, forest structure, area and soil fertility. In any one region, irregular forests on good soil with a mixture of hardwoods and conifers contain significantly more bird species at a higher density than do regular, intensively managed, uniform stands on poor soil. Thus stated, it is clear that the planting of trees on open ground leads to an increase in the number and diversity of birds, but modern forestry practice, involving even-age monocultures, acts against high density and variety of birds in the mature wood.

5 Bird communities in winter

These generalizations apply to summer communities of breeding birds. They probably hold in winter too, but at this season high-altitude woods may be largely deserted, nest sites are no longer constraining, and the actual species of tree is of greater significance, especially to seed eaters. Thus, redpolls are dependent on birch seed, siskins on birch, alder (*Alnus glutinosa*) and conifers, while chaffinches, bramblings (*Fringilla montifringilla*) and several tit species gather in beechwoods (*Fagus sylvatica*) in years when mast is plentiful. In Swedish woods, Ulfstrand (1975) found a general correlation between the number of tree and shrub species present and the number of song bird species in winter feeding flocks, because the birds showed different preferences for feeding in certain trees. Little work of this type has been done in Scottish woods and the winter bird communities are in need of study.

6 Commercial forests

New forests have usually been planted on open land, which for hundreds of years previously has been grazed by sheep or burned for grouse. Each forest passes through a number of stages during its growth (Ratcliffe & Petty 1986). Ornithologically, the important divisions are as follows.

i. The establishment stage, a grassy or heathery landscape with young trees dotted through it. At this stage, the habitat is at once more structurally diverse than the sheepwalk, and not surprisingly holds more bird species.
ii. The pre-thicket stage, at which stage the open country birds have gone and the scrub-dwelling birds move in.
iii. The thicket stage, when most woodland species move in.
iv. Relatively mature-looking woodland, which develops as the trees grow, and the forest is thinned out.

These trends are illustrated in Table 2 from counts in south Scotland (Moss 1978b; Moss *et al.* 1979). The open land in this region holds only 2–3 species of song birds, mostly at densities of less than 100 pairs km^{-2}, but the well-grown plantation holds about 5 times as

Table 2. Numbers of breeding song birds in open upland and forests at different stages of growth, from counts in south Scotland

	Number of sites (and censuses)	Number of species	Number of pairs (range) km^{-2}
Unplanted heather moor	2 (3)	2	51 (38–72)
Unplanted grassland	3 (7)	4	93 (72–130)
Establishment	5 (8)	10	115 (54–203)
Pre-thicket	2 (3)	11	257 (231–289)
Thicket	3 (7)	15	347 (302–443)
Post-thinned	4 (8)	15	377 (318–425)

many species and 5 times as many individual birds. The same changes occur in birds other than song birds, but are less marked. So, at least in terms of species numbers and densities, the forests are considerably richer in birds than the open sheepwalk they replace. This finding reflects a general trend, found elsewhere, for both density and species numbers to increase with maturity of woodland (Jones 1972; Rose 1979; Yapp 1955).

Commercial forestry, by providing new habitat, has also led to a spread in the distribution of certain birds. Notable examples are the crossbill and siskin, 2 small finches which eat conifer seeds. Earlier this century, these species bred in only a small part of Britain, but they are now common throughout the uplands of Scotland, northern England and Wales, wherever large-scale areas of conifers are grown.

Other birds have spread with commercial forestry, but for different reasons. They include some raptors, such as the hen harrier (*Circus cyaneus*). For these species, afforestation has provided large areas free from gamekeeper predation. Owing to persecution, the hen harrier at the turn of the century was restricted to islands of north and western Scotland, and its return to the mainland from the 1930s coincided with the expansion of forestry, and with its being allowed to nest undisturbed in the young forests. The species now breeds regularly again in the uplands of the north and west. For such species, it is not the trees themselves which are important, but the sanctuary that the trees provide.

The early stages of tree growth are especially interesting to the naturalist, mainly because of the short-tailed vole (*Microtus agrestis*). The removal of sheep from grassland allows the grass to grow tall. This grass provides food and cover for other herbivores, including voles, which in 2–3 years reach densities that can be 100–200 times greater than on the original sheepwalk. The voles undergo cycles of abundance, with peaks about every 4 years. The initial increase usually leads to an influx of vole predators, particularly various kinds of owl. The short-eared owl, being a ground nester, can best exploit this situation in the open hills (Goddard 1935; Lockie 1955). At peak vole densities, these owls can reach densities of 7 pairs km^{-2}. They start breeding in early spring, lay 7–9 eggs, and raise up to 2 broods in a year. At lower vole densities, they breed in lesser numbers and produce fewer young per pair. This abundance of voles lasts only 10–12 years, however, by which time the young trees have grown to shade out the grass on which the voles depend. At that stage, the owls leave.

Other avian predators benefit from high vole numbers, but, as they are not ground nesters, in the open hills they are often limited by a shortage of nest sites. They include barn owls (*Tyto alba*), which breed in abandoned buildings, long-eared owls, occupying any shelterbelts which already exist when the land is planted, and kestrels, which nest in tree holes, old crow nests or crag ledges (Village 1981, 1982, 1983). During peak vole conditions, all these species reach densities higher than those recorded anywhere else in Britain, but all must move on as the trees grow, and the grass which supports the voles disappears. These events are not repeated so spectacularly at the next rotation, in the gap between the felling of one tree crop and the growth of the next. A clearfelled area is covered initially by branches from the preceding crop, but vegetation soon grows through. This vegetation differs from that on the original sheepwalk, however, and voles occur but in unknown numbers. Vole predators also occur, but much less numerously. Tawny owls and kestrels frequently hunt on clearfelled areas, but short-eared owls occur only on the larger ones. So the extreme abundance of voles and vole predators is a once-only event in the history of any commercial forest.

The vegetation that prevails between the felling of one crop and the growth of the next depends on soil type, deer grazing and seed availability from birch and other non-commercial trees. In north Wales, in the absence of deer, rich soils were soon colonized by broadleaved seedlings and forbs, which in turn supported a diverse scrub-dwelling bird fauna, including blackcap, whitethroat and garden warbler (Currie & Bamford 1981). In Northumbria, on the other hand, where deer grazing resulted in grassy vegetation, the bird community was similar to that on newly planted land, with the meadow pipit (*Anthus pratensis*) the most abundant species (Leslie 1981).

The main conservation problems associated with commercial forestry have resulted from the sheer scale of planting in certain areas, such as Galloway. This afforestation has led to marked regional declines in open country birds, particularly certain predators such as ravens (*Corvus corax*), which are considered of high conservation value (Marquiss *et al.* 1978). In other parts of Scotland, populations of rare wading birds have also been affected, either by the trees themselves or by the lowering of water tables which precedes planting. As these aspects are considered by D A Ratcliffe in this volume, they will not be discussed further here.

Another problem, which has only recently come to the fore, is the enhanced acidification of soils and waters, which widespread conifer planting promotes (Harriman & Morrison 1982; Stoner *et al.* 1984). The effect is most marked in areas, such as Galloway, which are of mainly low base status anyway. It may have contributed to the recent decline (or disappearance) of fish and certain birds (such as dippers (*Cinclus cinclus*)) in many waters (eg Ormerod *et al.* 1985).

These broader problems can only be tackled by greater planning control over forestry, or by changes in incentive schemes. However, from what is known of birds in woodland, guidelines are readily available for foresters who wish to improve their individual holdings for wildlife. In a nutshell, the best advice would be to diversify, and in particular to grow more native hardwoods such as birch. The maintenance of long rotations, of ponds and other features, a varied age structure, islands of broadleaved shrubs and trees, and a tolerance of scrub and dead timber would all help to enhance the local bird fauna. Many of the procedures which foresters regard as good, clean silvicultural practice are, in fact, highly inimical to wildlife. Parallels occur in agriculture.

7 Summary

7.1 At least 68 bird species breed regularly in Scottish forests, but 24 depend on openings within the forest or on nearby open land. The bird fauna is distinctive and contains the crested tit, Scottish crossbill and capercaillie, which are absent elsewhere in Britain. The siskin was also formerly restricted to northern Scotland, but has recently spread, following the widespread planting of conifers. The common crossbill has also become widespread.

7.2 Within Scotland, 7 woodland bird species are found only in the south, 6 species only in the north, and 3 in the east but not the west.

7.3 The commonest birds in Scottish woods include the chaffinch and wren, together with the goldcrest and coal tit in conifers, and the willow warbler in broadleaved areas.

7.4 In any one region, the variety of birds is greater in woods (i) of birch and other broadleaved trees than of conifers, (ii) which are large rather than small, (iii) which have much rather than little undergrowth, and (iv) which have many rather than few nest holes. The same is true for bird densities, except that these tend to be highest in small woods, especially adjoining farmland. Densities also tend to be higher in woods on rich rather than poor soils.

7.5 A new forest passes through a number of stages during its growth, each of which has a distinct bird fauna. Because commercial forests are grown as single-aged monocultures, they are poor in birds compared with more natural woods, which contain a greater range of tree species, especially hardwoods, and a greater variety of structure. An interesting feature of young forests planted on grassland is the high densities of short-eared owls and other vole predators, which occur in response to temporary increases in the numbers of field voles.

7.6 Main research needs include further study of the relationship between woodland area, isolation and bird population, and study of winter bird communities and factors influencing them.

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