The distribution of breeding songbirds within mixed coppiced woodland in Kent, England, in relation to vegetation age and structure

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The distribution of breeding birds within 30 ha of mixed coppiced woodland in southeast England was determined by territory mapping over five years. During this period all stages of coppice growth from freshly cut to nearly 40 years old were present. Bird species differed greatly in the stages of growth at which they were most abundant and in their habitat amplitude. All species with narrow habitat amplitudes, including all the abundant long-distance migrants, were confined to young coppice; no species was restricted to old coppice. Where migrants did use old coppice they were largely confined to the edges where it adjoined young coppice. Patterns of temporal change in the assemblages of birds closely matched major changes in the structure of the coppice vegetation. Low foliage (within 2 m of the ground) reached its greatest development between 3 and 5 years of growth, subsequently declining as the coppice canopy closed. From 8 years of growth there were no major changes in vegetation structure. Young coppice with few standard oak trees supported higher densities of several migrant species than coppice with many standards. Some areas of old coppice had been thinned with the aim of producing high forest; temporal changes in populations of migrants in such areas were broadly similar to those in coppice.

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1. Introduction

Bird populations in English woodlands are overwhelmingly influenced by human activities. Even the oldest woodland in lowland England has a long history of management. From the early Middle Ages until the nineteenth century much woodland was managed by coppicing, in which the wood was cut on a rotation typically of 10 to 30 years (Rackham 1980, Peterken 1981). The system depended on the ability of many native trees to regrow rapidly from their cut stumps (termed 'stools'). The coppice, or 'underwood', was usually grown with scattered trees (termed 'standards') which were cut on a longer rotation. A massive decline in coppicing started in the late 1800s and by the middle of the present century it had virtually disappeared throughout much of England, except in the extreme south-east. Many formerly coppiced woods survive in a neglected state and an increasing number are being acquired as na-

ture reserves. Such woods present considerable management problems. The options include
1) returning the wood to a coppice regime,
2) thinning the coppice with the aim of changing the structure to high forest,
3) clear-felling and replanting, or
4) leaving the wood as it is.
It is commonly assumed that because coppicing is traditional it must be the best approach for wildlife. However, there are extremely few quantitative studies of the responses of wildlife, including birds, to coppicing. Not only is there a need for more information on the merits of coppicing relative to other forms of management, but also little is known about many aspects of coppice management itself such as the effects of varying the rotation length and the density of standard trees.

This paper presents a case study of the responses of breeding bird populations to the management of a mixed coppiced woodland in south-east England.

Coppice 0 – 4 years
   "   5 – 9   "
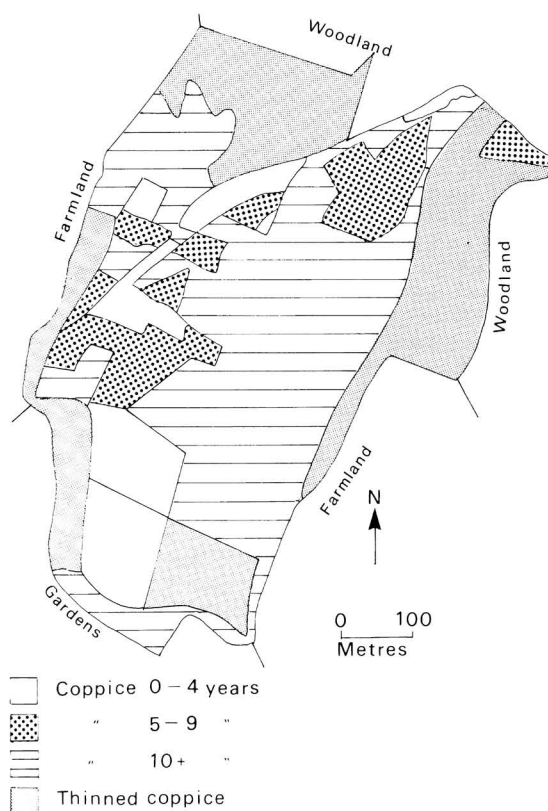   "   10 +   "
Thinned coppice

Fig. 1. The study site at Ham Street Woods, Kent, in 1970 showing the approximate distribution of the main management types.

Special emphasis is given to comparisons of the responses of resident and of migrant species to the coppice cycle because there is a growing body of evidence that these two groups of birds differ appreciably in habitat use (e.g. Haapanen 1965, Ferry & Frochot 1970, Bilcke 1984, O'Connor 1985, Helle & Fuller 1988). The relevance of the results to the management of similar sites in Britain is discussed.

2. The study site

The study site (Fig. 1) formed part of Ham Street Woods National Nature Reserve, Kent (national grid reference TR006339). The site was situated in the south-west corner of the Reserve. To the north-east, the site was bounded by woodland and elsewhere by farmland and gardens. The wood contained two main management types: (a) coppice ranging in age from freshly cut to nearly 40 years old, and (b) stands of 'overstood' coppice which had been thinned for eventual promotion to high

forest. We term these two management types 'coppice' and 'thinned coppice' respectively. The coppice formed a central continuous block of woodland (forming some 75% of the study area) while the thinned coppice was largely confined to the edges of the study site (Fig. 1). The wood was divided into a large number of compartments, each containing even-aged coppice or thinned coppice. During the study period the exact numbers and distribution of compartments changed with the coppicing and thinning.

The coppice compartments were generally small. In 1970 there were 52 compartments of median size 0.3 ha with 41 (79%) of the compartments 0.5 ha or less and only 6 (12%) exceeded 1 ha. The coppice was grown with oak *Quercus robur* standards. Parts of the wood carried a very high density of standards, exceeding 50 oaks per hectare, but other parts carried less than 25 per hectare. Although rich in shrub species, the underwood was dominated by hornbeam *Carpinus betulus*. In July 1987, 200 coppice stools were examined at 10 locations spread throughout the site giving the following breakdown by species: hornbeam 121 stools (60.5%), sweet chestnut *Castanea sativa* 36 (18%), hazel *Corylus avellana* 29 (14.5%), birch *Betula* spp. 11 (5.5%), ash *Fraxinus excelsior* 2 (1%), field maple *Acer campestre* 1 (0.5%). Based on the numbers of coppice stools lying entirely within three 300 m² plots examined in July 1987, the average density of live stools was 790/ha (910/ha including stools touching the boundaries). For further details of the coppice at Ham Street Woods see Ford & Newbould (1970, 1977).

Throughout the paper the age of the coppice is given as the number of full summers of growth. Hence, freshly cut coppice in the spring or summer immediately following the winter in which it was cut was treated as year 0, but the following spring or summer it was treated as year 1. The same system was applied to thinned coppice.

3. Methods

Songbirds are defined here as all passerines excluding starling *Sturnus vulgaris*, Hirundinidae and Corvidae. Birds were counted by one of us (P.S.) using a territory mapping method over a 5 year period from 1969 to 1973. Each year 23 to 25 visits were made, spread throughout the breeding season from late March to early July. Each year the entire site was covered evenly and the coverage was consistent between years. The extreme complexity of the site made it impossible to assign most of the 'territories' to one compartment or another. We decided, therefore, to use the densities of registrations recorded in compartments of different ages as indices of abundance. This approach had been adopted in a previous study of nightingales at Ham Street Woods (Stuttard & Williamson 1971).

Fuller & Whittington (1987) found that density of registrations was a reasonable index of bird density as measured by territories. To assess the validity of us-

ing registrations in the context of the present study, the study site was divided into nine sub-plots which were broadly internally homogeneous with respect to management and age of coppice. The mean area of the sub-plots was 3.2 ha, range 2.8 to 3.9 ha. The densities of registrations and of territories in 1970 were calculated for each sub-plot for 14 of the most abundant species on the site. For most species there were strong associations between the two measures of density. Spearman rank correlations between the densities of registrations and of territories were as follows: wren *Troglodytes troglodytes* r=0.80, dunnock *Prunella modularis* r=0.91, robin *Erithacus rubecula* r=0.90, nightingale *Luscinia megarhynchos* r=0.98, blackbird *Turdus merula* r=0.78, song thrush *Turdus philomelos* r=0.90, whitethroat *Sylvia communis* r=0.93, garden warbler *Sylvia borin* r=1.00, blackcap *Sylvia atricapilla* r=0.97, chiffchaff *Phylloscopus collybita* r=0.93, willow warbler *Phylloscopus trochilus* r=0.98, blue tit *Parus caeruleus* r=0.83, great tit *Parus major* r=0.68, chaffinch *Fringilla coelebs* r=0.73. We conclude, therefore, that use of registrations should give a realistic indication of intra-specific patterns of bird distribution within the site. No attempt has been made to use registrations to compare the relative abundance of different species.

It has been assumed that the detectability of birds did not differ sufficiently between vegetation of different ages to obscure the real patterns of bird distribution within the coppice. This is a reasonable assumption because the growth of the vegetation was so rapid that only in the first two years was the habitat sufficiently open to aid observation of birds.

The pattern of management was such that not all ages of coppice were present within the site each year. Furthermore, the areas of individual year-classes were often too small to allow adequate comparisons within individual years. This situation is typical of most coppiced woods in England. To produce a general picture of the response of each species to the coppice cycle, results were combined from the 5 years of the study by the method adopted by Fuller & Moreton (1987) in a 10 year study of sweet chestnut coppice. For each year-class the total number of registrations recorded in that year-class was divided by the total area. The resulting index was expressed as the number of registrations per hectare. This procedure gave a sample of at least 3 ha (range 3.0–6.4 ha) for each year-class up to 15 summers of growth. Beyond this age, samples were too small to treat years separately so they were combined into four groups (16–20 years, 21–25 years, 26–30 years and >30 years). The

median ages of these four groups were used in the analyses.

The derived patterns of bird distribution in relation to coppice age must be treated with some caution for two reasons. First, it is conceivable that individual compartment effects (for example, coppice composition, soil type) could be confounded with year-class effects. This seems unlikely, however, given the rather small size of the study area and the fact that, over the five years, compartments contributing to many of the year-classes were not confined to one part of the study area. Second, it is not possible to test statistically that the patterns are not purely random, because the registrations upon which they are based are not independant samples; in many cases they will represent repeated observations of the same individual. We avoid, therefore, drawing detailed inferences from the patterns.

Most bird populations in southern England were reasonably stable during the period 1969–73 (Batten & Marchant 1976). With the exception of wren, most resident birds had largely recovered from the effects of the severe 1962–63 winter and there was no severe winter during the study period itself. Although whitethroat numbers crashed between 1968 and 1969 (Winstanley, Spencer & Williamson 1974) they remained stable during the study period. Hence, results from the five years of the study can be combined with little risk of national population changes confounding patterns of habitat distribution.

Vegetation structure was measured in various ages of coppice within the study area in July 1987. There was no reason to suppose that vegetation structure would have been any different to that during 1969–73. Vegetation was sampled within ten year-classes. Four sampling stations were selected at random in each year-class. At each station the following were measured:

1) *coppice cover* was estimated visually for a 10 m radius,
2) *coppice height* was measured as the maximum height of the five nearest stools,
3) *low foliage density* was measured at 0.5 m above ground,
4) *mid foliage density* was measured at 1.5 m above ground.

The low foliage included both the coppice growth itself and vegetation such as willowherb *Epilobium* spp. and bramble *Rubus fruticosus* growing between the stools, whereas the mid foliage was predominantly composed of coppice shrubs. Foliage density was measured using a 30 cm × 50 cm chequerboard

Table 1. The development of coppice at Ham Street Woods; mean values and range.

Age of coppice (summers growth)	Height[1] (m)		Canopy cover[2] (%)		Low foliage density index		Mid foliage density index	
0	0.6	(0.3–1.1)	<5	(all <5)	2	(all 2)	2	(all 2)
1	1.6	(0.8–2.5)	18	(10–25)	17	(8–50)	2	(2–3)
3	3.1	(1.0–5.0)	66	(55–75)	20	(11–33)	15	(4–25)
5	4.3	(2.5–6.0)	75	(65–85)	33	(20–50)	12	(6–20)
8	6.5	(2.5–11.0)	96	(85–100)	5	(3–20)	5	(3–6)
11	9.2	(6.0–12.0)	99	(95–100)	3	(2–4)	3	(2–6)
15	10.8	(8.0–14.0)	99	(95–100)	2	(all 2)	2	(all 2)
18	11.5	(8.0–13.0)	98	(95–100)	2	(all 2)	2	(all 2)
24	11.0	(7.0–17.0)	100	(all 100)	2	(all 2)	2	(all 2)
30	10.5	(3.0–15.0)	99	(95–100)	2	(all 2)	2	(all 2)

1. Heights of stools were measured directly in year-classes 0 and 1, but thereafter were estimated to the nearest 0.5 m.
2. Coppice canopy cover was estimated to the nearest 5%.

(Fuller & Whittington 1987). At each station the distance at which half the board was obscured by foliage was measured on two random bearings given the constraint that the entire distance measured had to lie within the same coppice compartment. An index was derived from the reciprocal of this distance multiplied by 100 so that a distance of 5 m equated with an index of 20 and 25 m with an index of 4. Values exceeding approximately 10 represent very dense foliage. Very open habitats, where the distance measured would have often extended beyond 30 m, were given an index value of 2.

4. Results

4.1. Vegetation development

The main changes in vegetation structure occurred in the first 10 years (Table 1). After the first summer of growth the low foliage rapidly thickened and both the low and mid foliage reached their maximum development at about 3 to 5 years. The coppice canopy closed rapidly between years 1 and 3 but only became fully closed between years 5 and 8 and this was associated with loss of the foliage close to the ground. Height of the coppice continued to increase until approximately 15 years.

Thinned coppice underwent vegetation changes superficially similar to those that followed coppicing but no directly comparable vegetation measurements were made. Immediately after thinning the ground was largely bare but some areas became rapidly cov-

ered by bramble. Regrowth from cut stumps appeared to be highly variable with some stands thinned 4 years previously having a very sparse shrub layer unlike coppice of the same age.

4.2. Responses of bird species to the coppice cycle

The distributions of 14 of the most abundant songbirds are shown in relation to the age of coppice in Figs. 2 and 3 for resident and migrant species respectively. The species selected are those for which a density of more than 5 registrations/ha was recorded in at least two year classes. With the exception of whitethroat these species were the most abundant songbirds on the study area. Dunnock reached peak abundance in years 2–4. Wren and robin were relatively scarce in the earliest years before canopy closure. Song thrush, blackbird, the tits and chaffinch showed no striking preference for one particular stage of growth.

In general, the migrant species showed very different patterns of distribution to the residents (Fig. 3). Without exception they reached highest densities in the first 10 years of growth. Whitethroat strongly colonised very young coppice but, unlike all the other migrants, had virtually disappeared once canopy cover exceeded 50%. Garden warbler reached a peak just after whitethroat but remained abundant until just after canopy-closure. Willow warbler strongly colonised just after garden warbler and remained one of the most characteristic species of the coppice until year 9. Nightingale, chiffchaff and blackcap in-
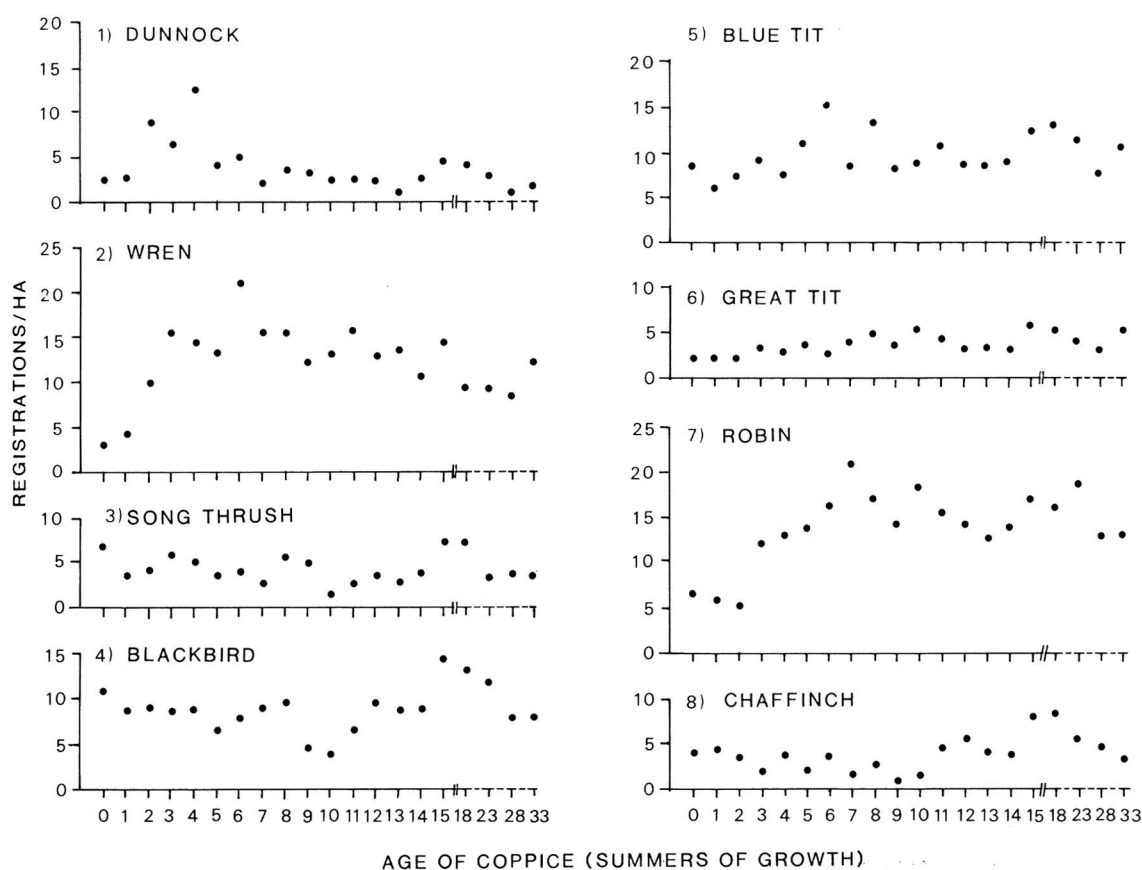
Fig. 2. Registrations/ha of eight resident species in relation to age of the coppice. The species are numbered approximately in order of habitat selection with species preferring the youngest coppice first.

creased more gradually and each of these species peaked in year 6.

It is clear from Figs. 2 and 3 that species differed greatly in their responses to the coppice cycle. These differences were quantified for 22 species in terms of peak abundance (i.e. the stage of coppice growth supporting the greatest numbers) and of habitat amplitude (i.e. how widely a species was distributed across the coppice cycle). All species of songbirds recorded on the site during the 5 years were used in the analysis, with the exception of those for which very small (<20) numbers of registrations were available. The 'peak year' was assessed in two ways:

1) by taking the year with the highest running 3-year mean density,
2) by taking the median of the 5 years with the highest densities of registrations.

Habitat amplitude was assessed in two ways:
1) by calculating 'niche-breadth' from the Simpson index (Southwood 1978),
2) by calculating 'year-span' from the total number of years spanned by the five with the highest densities of registrations.

Because there may have been a bias towards increased detectability of some species in very open young coppice, all measures of peak year and habitat amplitude were calculated with and without the data for year 0. This had little effect so the results are presented here for all years of growth.

There were no differences (Mann-Whitney U tests) between residents and migrants in terms of peak year or of niche-breadth. However, year-span of residents was significantly larger than that of migrants ($P<0.01$). A possible bias is that one might expect an
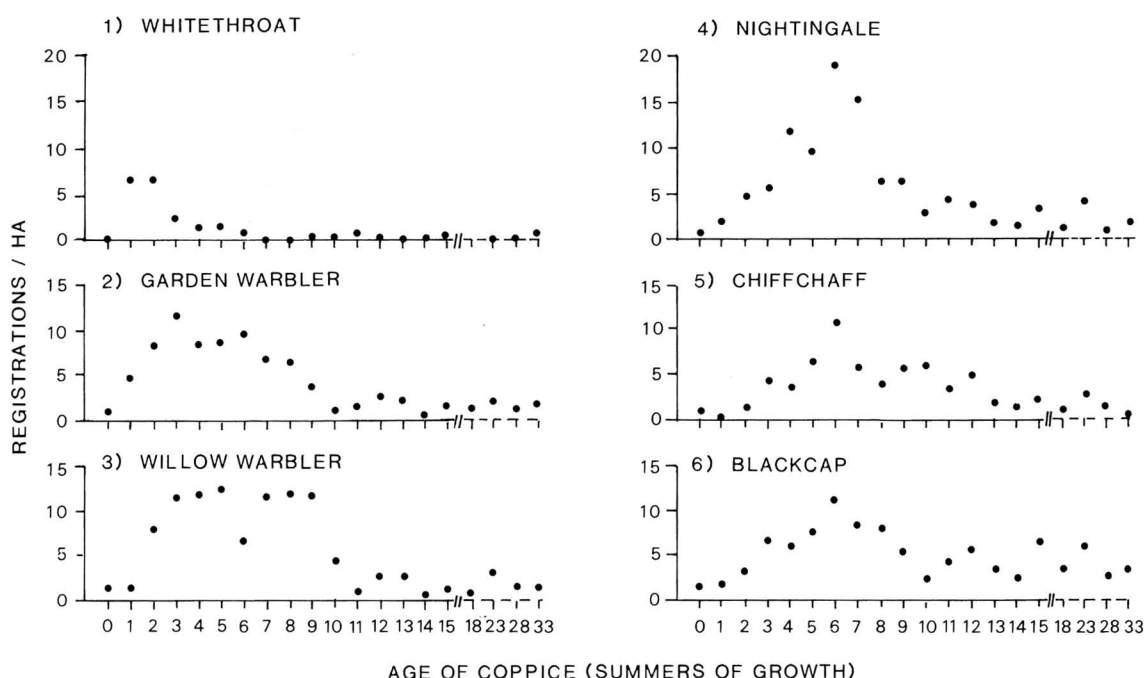
Fig. 3. Registrations/ha of six migrant species in relation to age of the coppice. The species are numbered approximately in order of habitat selection with species preferring the youngest coppice first.

abundant species to have a higher amplitude than a relatively scarce species. However, when the analyses were repeated, for the 14 relatively abundant species listed in Figs. 2 and 3, the residents were found to have not only significantly larger year spans ($P<0.01$), but also higher niche-breadths ($P<0.01$) and higher peak years (both measures, $P<0.05$). Migrants and residents differed in the distribution of their peak years with respect to canopy-closure. The proportion of migrant species peaking before canopy-closure, defined as occurring at 7 years of growth (Table 1), was significantly higher than that of residents ($P=0.02$, Fisher Exact Test); this was the case for both the entire suite of species and the 14 most abundant. This significant result was obtained only with method (2) of calculating peak year.

All measures of peak year were strongly correlated with all the measures of habitat amplitude (all Spearman rank correlations significant at least $P<0.01$). Hence, the species which peaked in young coppice were tightly confined to that stage of growth, unlike the species which reached greatest abundance in the later stages. No species was restricted to old

coppice but, in contrast, several were largely restricted to young coppice, none more so than the migrants (Fig. 4).

4.3. Spatial distribution of migrants

Although the migrants were strongly associated with younger stages of coppice growth, each species showed differences in its response to the coppice cycle. The distributions of the six most abundant migrant passerine species in 1970 are shown in Fig. 5 in relation to the age of coppice. Management details are shown in Fig. 1, which may help to interpret some of the distribution patterns. All migrant species were associated with that half of the plot containing the young coppice (<10 years growth). Chiffchaff was apparently associated more with the edges of the young coppice than was willow warbler. The three *Sylvia* species also differed in distribution. Whitethroat was concentrated into an area of very young coppice in the south. Garden warbler was more widely distributed through the young coppice. Blackcap,
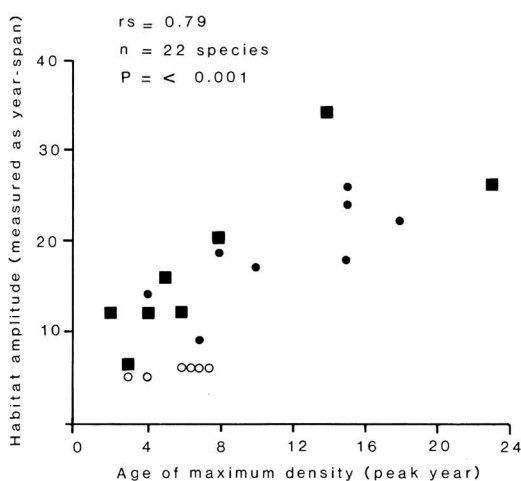
Fig. 4. The relationship between habitat amplitude (year span) and the age of coppice at which maximum density (peak year) was reached for 22 species. Year-span is the number of years spanned by the 5 years with the greatest densities of registrations; peak year is the median of these 5 years. Those species shown in Figs. 2 and 3 are shown as circles (open for migrants, closed for residents); all the other species are residents.

however, was perhaps most strongly associated with the edges of the young coppice. Nightingale made particularly heavy use of coppice compartments aged 5–9 years. The thinned coppice in the north of the site was heavily used by nightingales and, to a lesser extent, by warblers. This area was in its fourth summer after thinning, unlike the other areas of thinned coppice which had been thinned more recently.

Where migrants did use old coppice they were largely confined to its edges (Fig. 5). In 1969 and 1970 a large block of old coppice occurred in the eastern half of the site and analysis of bird distribution within this area confirmed that the centre of old coppice was a very poor habitat for migrants (Fig. 6). Within this old coppice, all species showed strong edge effects, being most abundant within 25 m of the young coppice. Blackcap penetrated deeper into the old coppice than the other species. The same analyses for the most abundant resident species showed no such striking edge effects within old coppice.

4.4. Bird distribution in relation to density of standard trees

Densities of registrations were calculated for selected species both in relation to the age of the cop-

pice (five age classes were used) and the density of standards (two density classes were used). The samples of coppice with low densities of standards (<25 per ha) were similar to those with high densities of standards (>50 per ha) in terms of distribution in relation to the edge of the plot and plant species composition. The five age classes are defined in Figs. 7 and 8. A sample of at least 7 ha was available for each age class in each of the two density classes of standards.

For resident species there were few clear differences in abundance between areas with few and many standards (Fig. 7). In the youngest age class of coppice, most migrants reached higher densities in coppice with few standards but this difference in density was most striking for whitethroat (Fig. 8). Nightingale was appreciably more abundant in coppice of 3–7 years with a high density of standards.

4.5. Comparison of short-term responses of bird species to coppicing and to thinning

During the study period adequate samples of thinned coppice were available only for the first 7 year-classes. Dunnock, wren and all the migrant species strongly increased during the first 7 years after thinning but blackbird and chaffinch apparently decreased while there was no obvious trend for blue tit, great tit and robin. The similarity of the responses to the two managements was assessed by using Spearman rank correlation (Table 2). Of the residents, only wren and blackbird showed the same trends in coppice and thinned coppice. Most of the migrant species, however, experienced similar trends following coppicing and thinning. This similarity is not suprising because broadly similar changes occurred in the structure of the vegetation in the two managements. Wilcoxon matched-pairs signed-ranks tests were used to assess whether species were consistently more abundant in one management type than another (Table 2). Over the first 7 year- classes wren, chaffinch and blackcap were more abundant in thinned coppice while blackbird, whitethroat and willow warbler were more abundant in coppice.

5. Discussion

Migrants strongly selected the early stages of coppice growth at Ham Street. This phenomenon appears to be characteristic of most coppice cycles in

Fig. 5. The distribution of registrations of six species of breeding migrants in 1970. The location of young coppice (<10 years of growth) is shown in relation to the boundary of the study site. See Fig. 1 for more details of the site and distribution of different management types.

England (Fuller & Warren in press) and provides further evidence that habitat selection by migrants and residents is fundamentally different. The present results are broadly consistent with Bilcke's (1984) finding in Belgium that migrant passerines were primarily associated with early successional stages while residents preferred more mature habitats. In coppice, however, several resident species seem to be widely distributed across all stages of growth with a few, notably dunnock, associated with the early stages. Canopy-closure in coppice was associated with the loss of much of the vegetation within 2 m or so of the ground (Table 1). It seems likely that the migrants were responding to this major change in vegetation profile rather than to the increasing height of the vegetation. Further support for this hypothesis

comes from the fact that most of the migrants showed similar trends in the early stages of thinned coppice where the canopy was much higher.

This study, because it is based solely on counts of birds, reveals little about how birds actually use the habitat. Some species, such as certain finches, may use coppice mainly for feeding. Others may prefer to nest in one age of coppice but feed in another. There is considerable scope for detailed studies of avian habitat use in structurally complex environments such as coppiced woods.

A study of chestnut coppice by Fuller & Moreton (1987) was conducted less than 20 km north of Ham Street. Despite the proximity of these two sites there were several marked differences between their bird communities. These differences were so great they
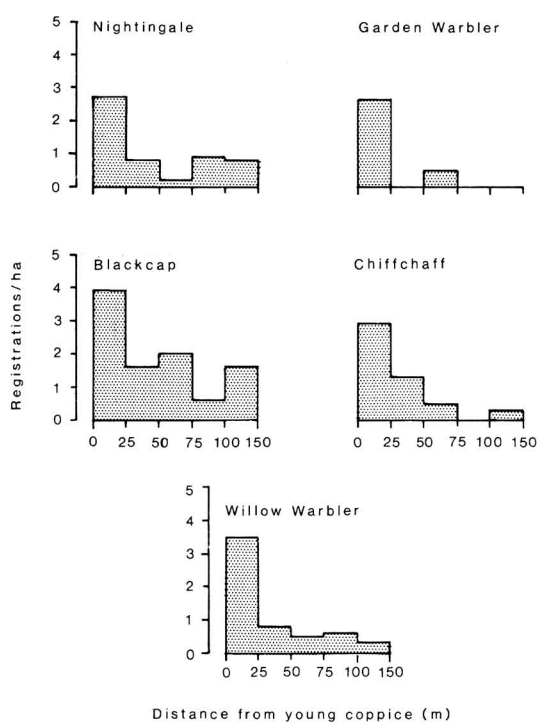
Fig. 6. Distribution of migrant species within a large block of old coppice (>20 years growth) in relation to distance from young coppice (<10 years growth). Data have been combined from 1969 and 1970 for the large area of old coppice in the eastern half of the site (see Fig. 1).

were most unlikely to be accounted for by sampling error. First, two of the most abundant species in the young chestnut, tree pipit *Anthus trivialis* and yellowhammer *Emberiza citrinella*, were virtually absent at Ham Street. The reasons for this difference are by no means clear. Second, several of the most abundant species — nightingale, wren and chaffinch — at Ham Street were scarce or virtually absent in the chestnut. This may have been related to differences in vegetation composition and structure because the chestnut, which was grown as a monoculture, may have lacked the dense low vegetation that was so characteristic of the early stages of growth at Ham Street. Also, the chestnut was virtually devoid of standards which may have been critical in the case of chaffinch which is primarily a canopy feeder.

Where standard trees are present in coppice they create an entirely separate stratum of vegetation from the underwood. One might expect, therefore, that
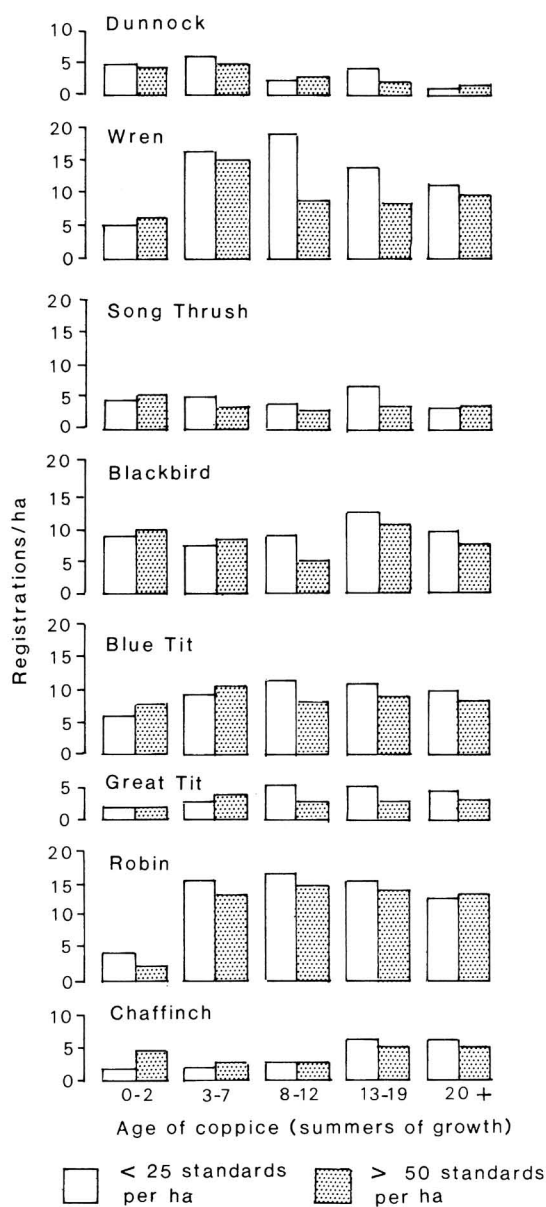

Fig. 7. Registrations/ha of eight resident species in relation to age of coppice and density of oak standard trees.

their presence should have an important effect on the avifauna by providing nesting and feeding sites for arboreal species. Hole-nesters, such as tits, have very few suitable nest sites in young coppice which lacks standard trees. There is a need to assess the effects of presence or absence of standards within coppice that is botanically comparable in the composition of its
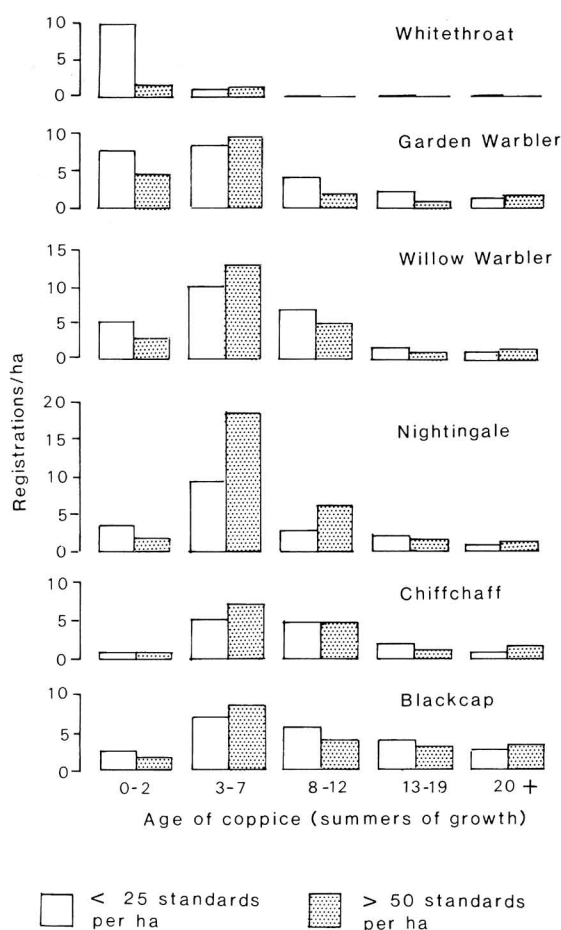
Fig. 8. Registrations/ha of six migrant species in relation to age of coppice and density of oak standard trees.

Table 2. The responses of selected species to coppicing (CO) and to thinning (TH) as shown by densities of registrations during the first seven year-classes. Significance levels are * $P<0.05$, ** $P<0.01$, *** $P<0.001$.

| Species | Modal year-class | | Comparison of | |
	CO	TH	trends[1]	abundance[2]
Resident				
Wren	6	6	0.89 **	0 * (TH>CO)
Dunnock	4	6	0.57	13
Robin	7	3	–0.14	13
Blackbird	0	0	0.96 ***	0 * (CO>TH)
Song thrush	0	1&3	0.44	6
Blue tit	6	5	0.53	6
Great tit	3&5	4	–0.12	6
Chaffinch	1	3	–0.29	2 * (TH>CO)
Migrant				
Nightingale	6	5	0.89 **	11
Whitethroat	1	2	0.75	0 * (CO>TH)
Garden warbler	3	5	0.67	5
Blackcap	6	5	0.93 **	0 * (TH>CO)
Chiffchaff	6	6	0.96 ***	2
Willow warbler	5	5	0.88 **	0 * (CO>TH)

[1] (Spearman correlation coefficient r)
[2] (Wilcoxon tests T)

opposite pattern to nightingale is unclear for one would have expected it to have also benefitted from a well developed field layer.

Species with narrow habitat amplitudes were confined to early stages of coppice growth; no species was strongly confined to old coppice. This was also the case in chestnut coppice (Fuller & Moreton 1987). These results suggest that bird species with very specialised habitat requirements are associated with the early stages of coppice growth while the most abundant species in the old coppice are more catholic in their requirements. Long rotations, therefore, will not benefit the species with special habitat needs. Where a management objective of coppicing is to maximise the 'conservation interest' of the bird community, the rotation should be designed such that substantial areas of young (pre canopy-closure) coppice are always present.

underwood. Underwood grows more vigorously in areas with low numbers of standards (Rackham 1980, Fuller & Ray 1989). This may be the reason why migrants in Ham Street Woods appeared to be more abundant in young coppice with relatively few standard trees. As the coppice grows, bramble and low shrubs often persist longer in the immediate proximity of standard trees probably because there is a phase of coppice development when light penetration is greater under the standards than through the underwood canopy itself. This could explain the relatively high abundance of nightingales in middle aged coppice with many standards. Why wren should show the

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