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DISTRIBUTION OF BREEDING BIRDS IN BRADFIELD WOODS, SUFFOLK, IN RELATION TO COPPICE MANAGEMENT

by

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SUMMARY

(1) Distribution and abundance of breeding birds were examined in 62ha of mixed coppiced woodland in relation to age of the coppice and vegetation characteristics. The wood was divided into areas (panels) within which the coppice regrowth was at the same age. Panels ranged in age from freshly cut to >30 years.

(2) A total of 516 territories and 43 breeding species were recorded. The five most abundant species were Willow Warbler Phylloscopus trochilus, Robin Erithacus rubecula, Blue Tit Parus caeruleus, Garden Warbler Sylvia borin and Blackbird Turdus merula.

(3) Ordination of panels indicated that three assemblages of birds could be discerned in terms of coppice age: 0-2 years of growth, 3-9 years and more than 9 years. These assemblages broadly corresponded to major stages of structural development particularly to changes in shrubbiness and habitat openness. Ground cover of vegetation was greatest in years 0-3 when the canopy was very open. The field and shrub layers were most developed between 2 and 8 years, reaching a maximum in the 4th year and declining thereafter as the canopy closed. From 9 years the field and shrub layers remained sparse, although the coppice continued to grow in stature.

(4) Warblers, Nightingale Luscinia megarhynchos and Dunnock Prunella modularis strongly selected coppice <10 years. No species selected older coppice. Bird assemblages in coppice of 2 and 8 years were dominated by warblers (Syvlviidae), but as the coppice aged they became increasingly dominated by tits (Paridae) and thrushes (Turdidae). Coppice >20 years was dominated by Robins, Blue Tits and Great Tits Parus major.

(5) Migrant songbird species were almost entirely associated with coppice <10 years. Total densities of resident species also were lowest in very young or very old coppice.

(6) Total density and numbers of species of songbirds were lowest in very young (<3 years) and old coppice (>11 years). However, when corrections were made for the high numbers of individual birds associated with middle aged coppice, no trend was evident in numbers of species.

(7) When panels of all ages were considered, most patterns of bird distribution were best explained by variations in the density of the shrub layer, or by a combination of relatively low canopy height yet high canopy cover. At the scale of the entire wood there was little evidence that tree species composition affected bird distribution. However, within young (3-8 years) and within old (10-30 years) coppice there was evidence of tree species effects, with birch having a negative effect on several measures of bird abundance.

(8) There was no evidence that the density of species was related to the size or shape of panels except for Wren Troglodytes troglodytes which was more abundant in small panels. However,

it is possible that panel size could indirectly affect bird populations because density of the shrub layer was found to be suppressed at the edges of some young panels growing adjacent to old coppice. To avoid such edge effects it is recommended that panels should be at least 0.3ha and preferably more than 0.5ha in size.

(9) To maintain high bird populations in Bradfield Woods, long coppice rotations (>30 years) should be avoided. Populations of breeding migrant species will be enhanced through the operation of a split rotation, with as much as the wood as practicable cut on a short rotation of about 12 years.

(10) Increasing the numbers of standard trees may be beneficial to some hole-nesting species but, if increased too much, would probably reduce the quality of the younger coppice as a habitat for breeding migrants because the height and cover of the coppice is reduced beneath standards. Relationships between density of standards and bird abundance are probably complex.

1. INTRODUCTION

Amongst British woods, Bradfield Woods are probably unique in the continuity of their history of coppicing which has been documented back to 1252 (Rackham 1980). These woods offer a glimpse of how a working medieval coppice might have appeared and they offer an invaluable example of the responses of plant and animal communities to traditional coppice management. At a time when many conservation organisations are attempting to reinstate coppicing in woods with a relic coppice structure, the few surviving examples of long-established coppice such as Bradfield are of special significance.

This report presents the results of a detailed census of the breeding birds in Bradfield Woods conducted by the British Trust for Ornithology in 1987. This exercise involved mapping the distribution of birds throughout the woods in relation to variations in structure and composition of the vegetation. The main aims were:

1. To document relationships between the age of the coppice and the structure and composition of the breeding bird community.
2. To assess factors influencing the abundance of selected species within coppice panels. The factors examined included vegetation structure, underwood composition, density of standard trees and panel size.
3. To compare breeding bird communities in Bradfield with those documented for coppice woods elsewhere.
4. To make predictions and, where appropriate, recommendations concerning the effects on birds of future coppice rotations in Bradfield Woods; in particular the effects of manipulating rotation length and panel size.

It is hoped that the results of this study will be of practical conservation value not just at Bradfield, but also in other woods where mixed coppice is being managed for conservation reasons. Perhaps the greatest advantage of Bradfield for research of this nature is that it contains large areas of coppice at all stages of growth. We know of no other mixed coppice site in Britain where this study could have been carried out in a single year.

2. THE WOODS

2.1 The main features of the study area

It is the combination of biological and historical interests that gives Bradfield Woods its celebrated reputation. Much has been written on the subject (Rackham 1976, 1980) so it is unnecessary to give a detailed account here. It is sufficient to say that the ground vegetation is one of the richest known for any English woodland. The diversity of the tree and shrub species is high: the dominant species are alder *Alnus glutinosa*, ash *Fraxinus excelsior*, birch *Betula* spp. and hazel *Corylus avellana*, with oak *Quercus robur* and ash the commonest standard trees. There are many ancient earthworks including fine boundary ditches and banks complete with their traditional pollarded trees.

The area studied was the 62ha of Bradfield Woods under the management of the Suffolk Wildlife Trust. This area includes all but a small part of the Woods at the extreme western edge, known as Hannah's Close or Annis Close Fell, which is privately owned. The main physical features of the Woods and the names of the compartments, traditionally known as 'fells', are illustrated in Fig.1. The fells each contain several areas of coppice at different stages of growth. To avoid confusion we use the term "panel" to describe any such area within which the regrowth of underwood is at the same age; hence each fell was comprised of several panels.

2.2 The coppice regime

Although coppiced more or less continuously since at least the early Middle Ages there was an interlude of several years without cutting in the late 1960s and early 1970s. This accounts for the absence of coppice between 15 and 20 years growth. Otherwise, there was excellent representation of all age classes during 1987 (Fig.2). Throughout this report, coppice is aged according to the number of complete summers of growth, so that underwood in its first year of growth (i.e. in the spring and summer following cutting) is year class 0, in its second summer of growth year class 1 etc. The locations of the panels and their ages of growth are shown in Fig.3. In recent years, underwood on some of the boundary banks has been cut in narrow linear strips; edges treated in this way are marked on Fig.3 and these strips have been excluded from the analyses.

There were few problems in identifying the boundaries between coppice of different ages where at least one of the panels was less than 15 years of growth. However, within the blocks of coppice of 20 years and older in Pear Tree Fell, Strawberry Bank and Plantation Fell it proved impossible to detect the original panel boundaries. For analytical purposes, therefore, these blocks of old coppice were subdivided into areas similar to the average size of the other panels; these "pseudo-panels" are distinguished by dotted lines in Fig.3. A total of 40 coppice panels was available, all in ancient woodland.

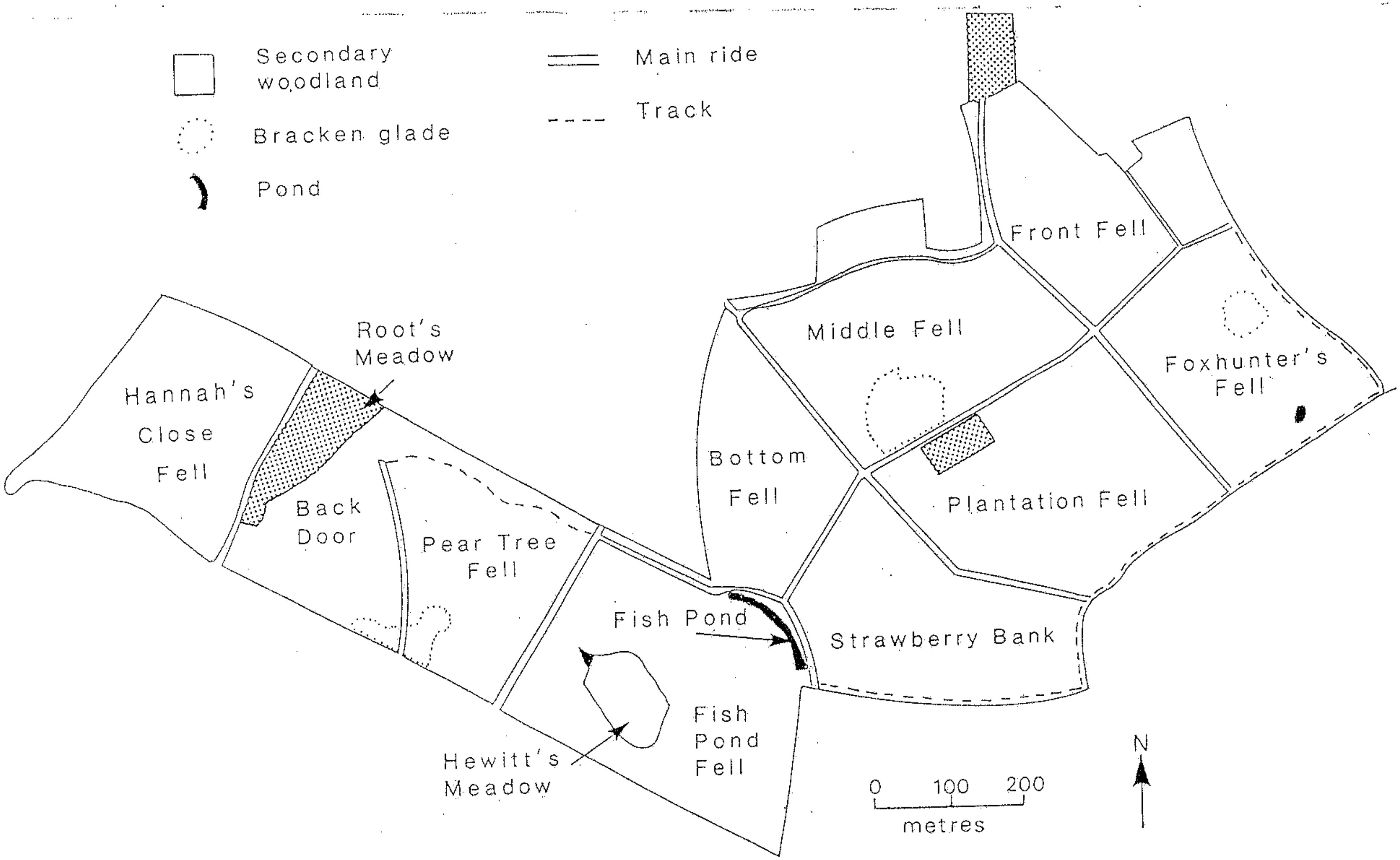


FIGURE 1. Bradfield Woods showing the main rides, ponds, glades and areas of secondary woodland. Most of the fells have more than one name; see Rackham (1976). Figure 14 for alternatives. That part of the woods to the west of the Fish Pond is called Monks' Park, that to the east, Felsham Hall Wood.

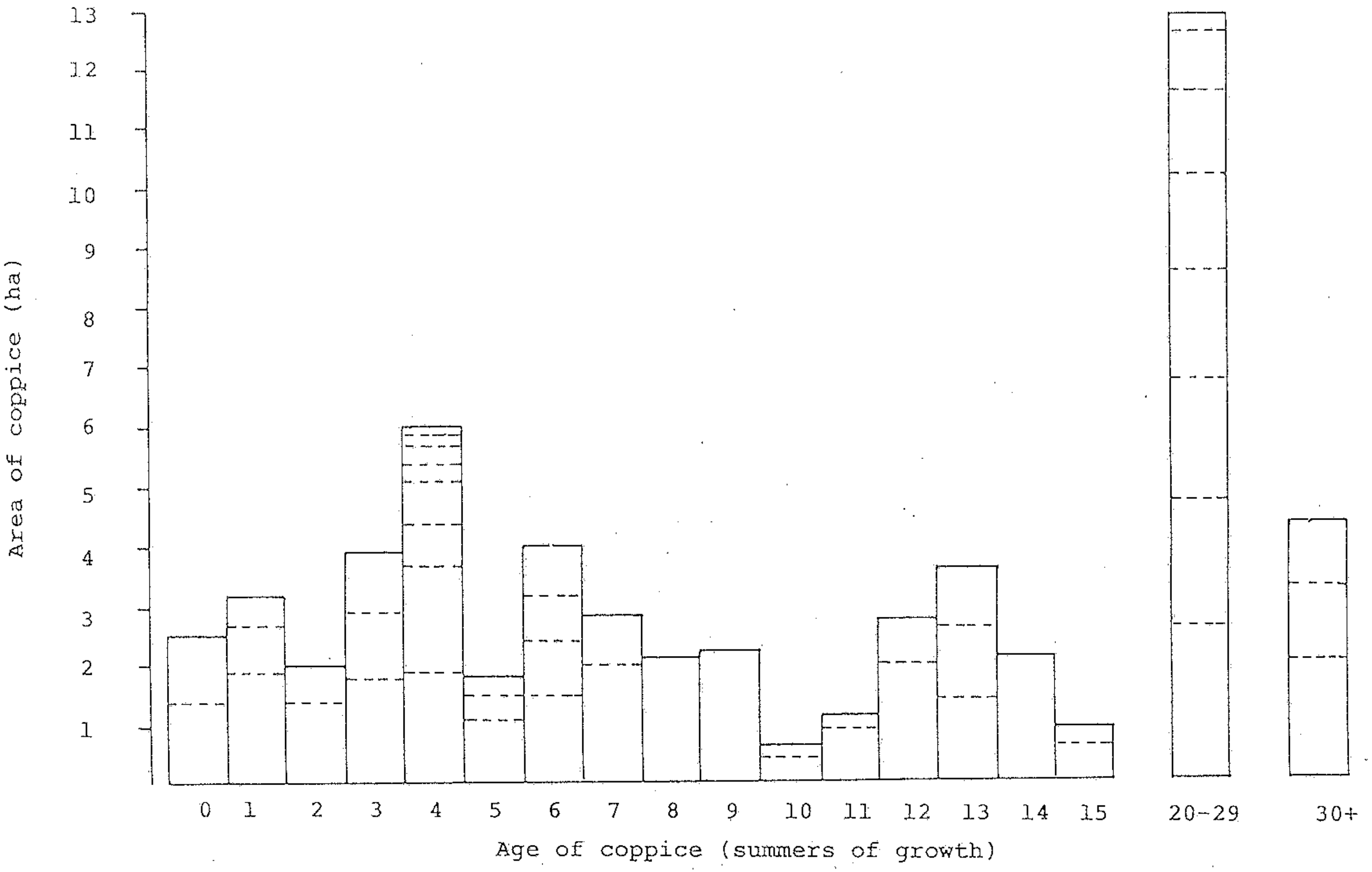


FIGURE 2. The total areas of each year-class of coppice in Bradfield Woods in 1987. Individual panels within each year-class are distinguished by broken lines with the smallest panels at the top and the largest at the bottom.

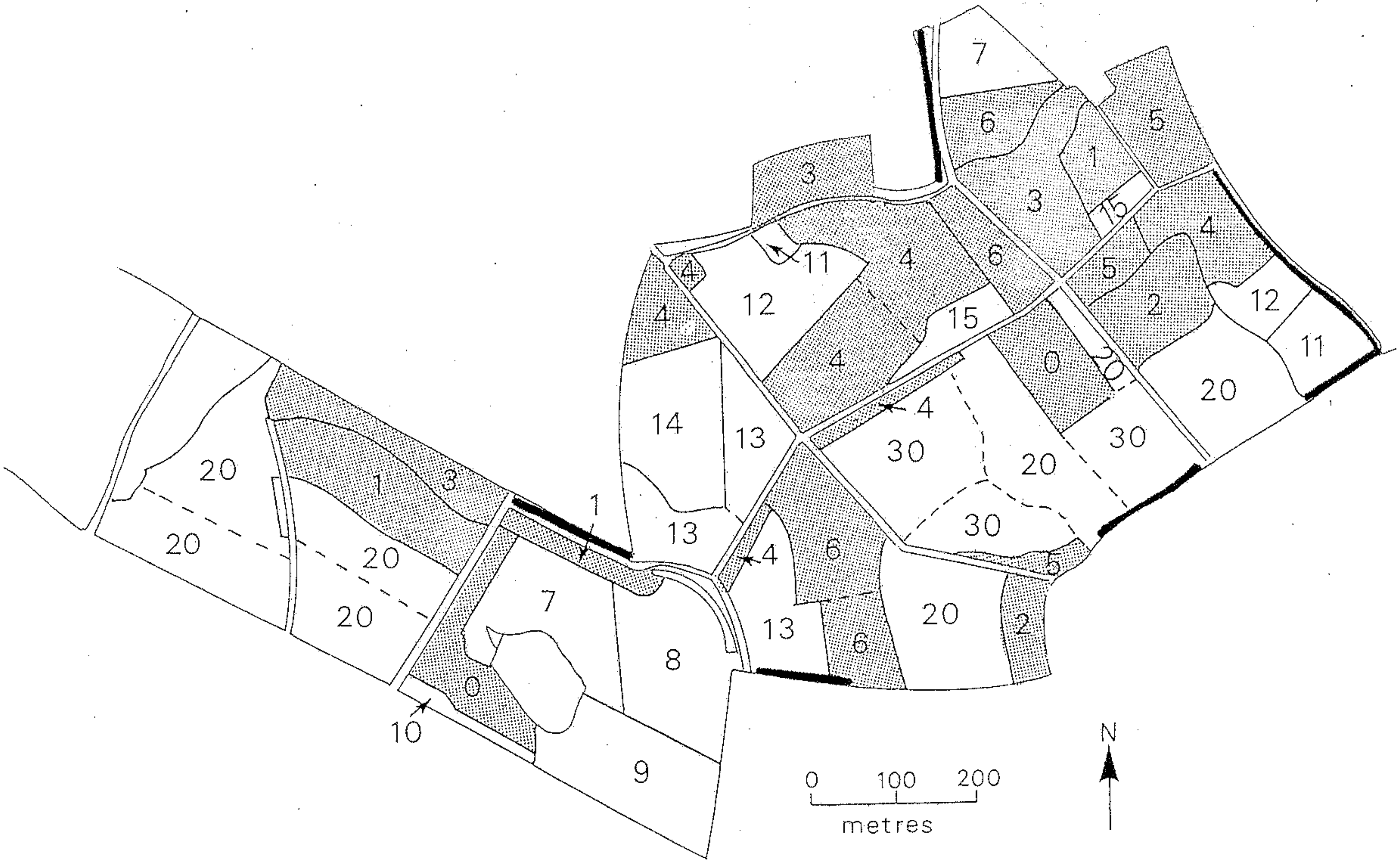


FIGURE 3. Bradfield Woods showing the distribution of coppice panels in 1987. Numbers indicate age of the coppice. Coppice of six and fewer summers growth is shaded. Heavy lines at the woodland edge indicate where coppicing had recently been carried out on the woodbank.

3. METHODS

3.1 Mapping the distribution of the birds

The aim of the bird counts was to produce an unbiased picture of the distribution of each species within the Woods. A territory mapping method was used (Marchant 1983, International Bird Census Committee 1969) in which the entire wood was visited on several occasions and the locations and activities of all birds were plotted on 1:2500 maps. All panel boundaries and other features necessary to allow plotting any detected bird to within some 10 - 15m accuracy were marked on the 1:2500 maps. Within several panels, and along certain edges, red plastic markers were placed at 50m intervals to assist accurate mapping. Each detected bird is termed a "registration". At the end of the fieldwork the registrations were transferred to species-specific maps and these were interpreted in terms of apparent territories based mainly on patterns of clustering in the registrations and records of simultaneously singing males. Although we subsequently use the term "territories", it should be realised that this technique of delimiting territory boundaries can give only a crude idea of the exact boundaries; fieldwork with individually marked birds and playback would be required to obtain greater accuracy.

The analyses concentrate on "songbirds" which we define as all passerines excluding Corvidae and starling (scientific names of birds are given in Table 2). Songbirds were the most appropriate group of birds to investigate because they generally hold relatively small territories which can be readily related to woodland management on the scale that is typical of most coppiced woods. Many non-songbird species, however, range over large areas (Fuller & Marchant 1985) making it very difficult to assess the effects of coppice management on their distributions. Although we attempted to estimate numbers of non-songbird species in Bradfield Woods it should be recognised that the accuracy of these estimates will generally be lower than those for songbirds. In the case of Pheasant, an estimate of numbers was made from the mean count of males during April. Woodpigeon, Woodcock and Jay were proved to breed in the Woods but territory mapping was entirely inapplicable to these species so no estimates are given.

Bird counts were made during three periods: 13 - 16 April (4 morning and 2 late evening visits), 18 - 22 May (4 morning, 1 early evening), 25 - 26 June (2 morning visits). Most morning visits started at about sunrise and were completed by about midday. The late evening visits were conducted mainly for Song Thrushes which sing particularly strongly at dusk (Tomialojc & Lontkowski 1989). The April visits were timed to coincide with a period when most resident species, such as tits and Nuthatches, were singing strongly. By mid May most of these birds were silent and extremely difficult to detect but visits at this time were essential to record summer visitors, especially Sylvia warblers and Nightingale which reach peak song activity during May. On each visit the entire study plot was covered by two observers (R.J.Fuller and A.C.B.Henderson) who worked simultaneously, one covering Felsham Hall Wood east of Broad Ride, the other covering Monks' Park Wood together with Bottom Fell and Strawberry Bank. The observers alternated between these two parts of the Woods on consecutive visits and a different route was used on each visit.

These two precautions were taken to avoid any systematic bias in the mapped distribution of registrations. On each visit the observers aimed to walk within 50m of every part of the Woods.

For the purposes of analysis it was necessary to allocate territories to individual panels. Obviously where a territory was entirely located within a single panel this created no problem. Where the registrations in a territory were located in two or more panels, the territory was divided between these panels on the basis of the proportions of its registrations recorded in each.

3.2 Vegetation structure and composition

Within each panel of 0.5ha or larger (n = 40), four 25m dimeter recording circles were positioned at random. All circles were at least 12.5m from the panel edge and at least 25m from the edge of other circles. Smaller panels (n = 10) were sampled with a single circle. An additional 5 circles were recorded in secondary woodland and one in Hewitt's Meadow. Within each circle a series of vegetation measurements was made (i - vi below), all by one observer (R.J.Fuller), between July and November 1987. Foliage density and cover estimates were assessed in July and August, well before leaf-fall. The great storm of October did not affect the measurements.

(i) Foliage density A 30 x 50cm chequerboard with 8 bright red and 7 white 10 x 10cm squares was used to estimate the density of foliage by measuring the distance at which the the board was judged to be half obscured by vegetation. This distance is termed the half extinction distance (HED). Two such sightings were made from the centre of each circle, one on a random compass bearing, the other at 180^{o} from this bearing. On each sighting HED was measured at 0.5m (the field layer) and 1.5m (the shrub layer) above ground. In some very old and open panels HED would have extended beyond the edge of the panel, therefore, any HED greater than 40m was ascribed a value of 45m. An index of foliage density was calculated for each panel for the field and shrub layers separately. The index was the reciprocal of the median of all HEDs (n=8 for panels at least 0.5ha) x 100. Hence, a panel with a very dense shrub layer where the median HED was 5m would have an index of 20, while a very open panel with few shrubs and an HED of, say 25m would have an index of 4. This method has been found to adequately characterise the woodland understorey profile in previous studies of bird-habitat relationships (Fuller & Whittington 1987, Fuller, Stuttard & Ray 1989).

(ii) Coppice stature The maximum heights of the underwood growing from the five stools closest to the circle centre were estimated to the nearest 0.5m using a graduated rod as a guide. The maximum stem diameters at breast height were also measured for these stools.

(iii) Coppice canopy cover A visual estimate of the percentage of the ground directly shaded by the underwood canopy, to the nearest 5%. Cover values were also estimated individually for alder, ash, birch and hazel.

(iv) Ground cover A visual estimate of of the ground cover of all herbs, grasses and bramble *Rubus fruticosus*, to the nearest 5%. Bramble, although prolific in many coppiced woods, was virtually absent from more than 75% of the recording circles.

(v) Tree and shrub species composition All stools and standards were counted within each circle, including those touching the boundary. All discernably discrete clusters of stems were counted as separate stools providing there was bare ground between the clusters. In the case of ash, however, old stools had sometimes fragmented into several pieces and the criterion was used that any such clusters of stems not separated by more than one metre were counted as a single stool. Standards were defined as any single stem or tree of 10cm or greater diameter at breast height. The cover of single-stem shrubs, such as blackthorn *Prunus spinosa*, was estimated in 10% cover classes.

(vi) Distribution of standards Paired stereoscopic aerial photographs, taken in October 1985, were used to locate all large standards (with estimated crown diameters of at least 10m) and these were plotted on maps and allocated to panels. Only in one panel had standards been felled since the photographs were taken so a direct count of large standards was made in that panel.

(vii) Edge effects Two types of habitat measurements were made to assess whether vegetation structure was different at the edges of panels (i.e. where two panels of different age abutted) to that at the centre of panels. First, the density of the shrub layer was measured as follows. All panel boundaries (n = 8) were identified where a 40m transect could be laid out either side of, perpendicular to the edge with the centre of the transect lying on the boundary between the panels. This transect had to be at least 30m from all other edges. The density of the shrub layer was assessed, using the method described above, at 5m intervals along the transect. At each sampling location two measurements were made either side of, and perpendicular to, the transect line. For analysis the mean of these two values was used. The second measurements were of ash and hazel stool heights which were measured to the nearest 0.5m. These were made close to the edges (<15m from the edge) and in the centre (>30m from the edge) of three panels 0, 2 and 4 years growth.

(viii) Effects of standards on coppice growth Two types of measurement were made. First, all oak standards (>40cm DBH) growing in coppice of 0,1,2 and 4 year old coppice were visited. Paired samples were used as follows. Percent coppice cover within 5m of the tree was estimated by eye and compared with coppice cover within a 5m radius of a nearby point, at the same distance from the panel edge, but not under another standard. Second, three areas with clusters of 5 to 9 oak standards were selected in panels of 0,2 and 4 years growth. For ash and hazel stools within 5m of the standard, heights were measured to the nearest 0.5m. The heights of an equivalent number of stools were then measured that were not under the canopy of a standard.

3.3 Choice of habitat variables and data analysis

Detrended correspondence analysis (DCA) was used to identify broad patterns in bird assemblages (Gauch 1982). Multiple regression analysis was used to define relationships of particular species and of bird community attributes with vegetation. Choice of variables for such analyses always presents a problem. Models created by regression techniques, particularly where many independent variables are used, are notoriously unstable so it was desirable to keep the number of habitat variables to a minimum whilst retaining as much descriptive capability as possible within them. We sought to achieve this in several ways without judging subjectively which variables might be important to birds. A primary condition was that the final variables should contain as little multicollinearity as possible; this was achieved using the tests in Freund & Little (1986). Variables were retained which could be comprehended and manipulated by woodland managers. A balance was also sought between variables which measured woodland structure and ones which measured plant species composition. This approach produced a set of 10 habitat variables (Table 1).

In each analysis the SAS RSQUARE procedure (Freund & Little 1986) was used to examine all possible combinations of variables to determine those models which fitted the data best using up to 4 habitat variables. The SAS STEPWISE procedure was then applied to these variables to determine the optimum model defined as that explaining the highest amount of variance in the bird variable and where all the habitat variables both entered and remained significant ($P<0.05$) with the addition of further variables. All bird densities were log+1 transformed. Visual inspection of bivariate plots showed that transformation of variables, to produce linearity, was necessary only for SHRUB (logarithmic) and for HEIGHT (quadratic) for analyses of the full data set of 40 panels.

4. RESULTS

4.1 Total numbers of species and territories

Forty three species were considered to be breeding in Bradfield Woods in 1987, of which 29 were songbirds. The numbers of territories estimated for the entire study area are given in Table 2. A total of 516 territories was recorded, 451 (87%) of which were songbirds. These totals are equivalent to overall densities of 832 and 727 territories/km^2 respectively. The most abundant species was Willow Warbler, which contributed 14% of the songbird territories, followed by Robin (11%), Blue Tit (9%), Garden Warbler (8%) and Blackbird (7%). Migrant species (Nightingale, warblers and Spotted Flycatcher) contributed 36% of the songbird territories. These blanket statistics conceal enormous spatial variation in bird density and bird community composition within the Woods.

There were 43 nestboxes in Bradfield Woods in 1987. Of the 28 boxes used all were occupied by Blue Tits with exception of a single Great Tit, Starling, Wren and Nuthatch. The abundance of Blue Tits in the Woods may therefore have been artificially

TABLE 1. Variables used to define attributes of individual coppice panels within Bradfield Woods in 1987. See text for description of methods for measuring vegetation and sample sizes

SHRUB	Density of shrub layer foliage (index)
HEIGHT	Mean coppice height (m)
COCOV	Mean overall coppice canopy cover (%)
STAND1	Density of standard trees >10m crown diameter
STAND2	Mean number of standards >25cm dbh
STOOLS	Mean number of coppice stools (all species)
ALDER	% of stools contributed by alder
ASH	% of stools contributed by ash
BIRCH	% of stools contributed by birch
TRSP	Mean number of tree and shrub species

Means refer to mean numbers or estimates per 25m diameter recording circle. dbh = diameter at breast height. In the models summarised in Tables 3 and 4, HEIGHT was applied as a quadratic transformation and SHRUB as a logarithmic transformation.

TABLE 2. Estimated numbers of territories of breeding birds in Bradfield Woods in 1987

Mallard *Anas platyrynchos*	4
Sparrowhawk *Accipiter nisus*	1
Kestrel *Falco tinnunculus*	1
Red-legged Partridge *Alectoris rufa*	P
Pheasant *Phasianus colchicus*	25
Moorhen *Gallinula chloropus*	4
Turtle Dove *Streptopelia turtur*	17
Cuckoo *Cuculus canorus*	2
Tawny Owl *Strix aluco*	2-3
Kingfisher *Alcedo atthis*	P
Green Woodpecker *Picus viridis*	1
Great Spotted Woodpecker *Dendrocopos major*	4-5
Lesser Spotted Woodpecker *Dendrocopos minor*	1
Swallow Hirundo rustica	P
Wren *Troglodytes troglodytes*	20
Dunnock *Prunella modularis*	24
Robin *Erithacus rubecula*	51
Nightingale *Luscinia megarhynchos*	17
Blackbird *Turdus merula*	32
Song Thrush *Turdus philomelos*	12
Redwing *Turdus iliacus*	P
Mistle Thrush *Turdus viscivorus*	P
Reed Warbler *Acrocephalus scirpaceus*	P
Lesser Whitethroat *Sylvia curruca*	1
Whitethroat *Sylvia communis*	4
Garden Warbler *Sylvia borin*	36
Blackcap *Sylvia atricapilla*	25
Chiffchaff *Phylloscopus collybita*	14
Willow Warbler *Phylloscopus trochilus*	64
Spotted Flycatcher *Muscicapa striata*	1
Long-tailed Tit *Aegithalos caudatus*	6
Marsh Tit *Parus palustris*	15
Willow Tit *Parus montanus*	8
Coal Tit *Parus ater*	2
Blue Tit *Parus caeruleus*	41
Great Tit *Parus major*	26
Nuthatch *Sitta europea*	4-5
Treecreeper *Certhia familiaris*	4
Magpie *Pica pica*	1
Jackdaw *Corvus monedula*	1
Carrion Crow *Corvus corone*	1
Starling *Sturnus vulgaris*	P
House Sparrow *Passer domesticus*	1
Chaffinch *Fringilla coelebs*	19
Greenfinch *Carduelis chloris*	15
Goldfinch *Carduelis carduelis*	P
Linnet *Carduelis cannabina*	P
Redpoll *Carduelis flammea*	P
Bullfinch *Pyrrhula pyrrhula*	8
Yellowhammer *Emberiza citrinella*	1

P = species which were recorded but not thought to be holding territory. Woodpigeon *Columba palumbus*, Woodcock *Scolopax rusticola* and Jay *Garrulus glandarius* bred in the Woods in 1987 but their numbers were not estimated. Nomenclature follows Voous (1973, 1977).

inflated and their distribution could have been affected by the location of boxes.

4.2 Patterns in the bird assemblages of Bradfield Woods

An initial exploration of the bird assemblages associated with the 40 largest panels in Bradfield Woods was made using DCA without downweighting for rare species. Ordination of the panels on the first three DCA axes produced marked clustering into age classes (Fig.4). Plots of axis 1 against axis 2 separated coppice panels of 3 to 9 years from all other panels, but when axis 1 was plotted against axis 3, three groups of panels could be identified. From the DCA analysis, therefore, three broad assemblages of birds could be discerned relating to three age classes of coppice: 0-2 years, 3-9 years and more than 9 years. Clearly age of the coppice was a major determinant of variation in bird assemblages within Bradfield Woods.

4.3 Vegetation structure in relation to coppice age

Major changes in vegetation structure that were associated with the growth and development of the coppice in Bradfield Woods are illustrated in Fig.5. Despite the fact that the samples for different year-classes were composed of panels which inevitably varied in factors such as soil type and tree species composition, very clear age-related changes in coppice structure were evident. Coppice height and stem diameter increased almost linearly up to 20 years. Coppice canopy cover rapidly closed following cutting and was virtually fully closed by the sixth year. Ground cover was greatest during years 1 to 3 when the canopy was open. Foliage in the shrub and field layers thickened quickly following cutting to reach a maximum in year 4. Thereafter, this foliage became progressively more poorly developed and from 9 years remained stable but very sparse. This pattern of shrub and field layer structure was undoubtedly a response to the shade level beneath the closing coppice canopy.

4.4 Bird distribution in relation to coppice age

The density of each species was calculated for each year-class of coppice by dividing the total number of territories in panels of that year-class by the total hectares of coppice in that year-class. The densities of the most abundant songbirds are shown for different ages of coppice in Fig.6. The species have been arranged so that those apparently preferring young coppice appear at the top and those making greater use of old coppice at the bottom. Whitethroat was very closely tied to the young open growth. The other five common migrant species - Garden Warbler, Willow Warbler, Nightingale, Chiffchaff and Blackcap - were also very strongly associated with the younger coppice, although each peaked 2 or 3 years later than Whitethroat, at about the time of canopy closure. Several resident species also reached maximum density in growth of 5 to 7 years with Dunnock in particular favouring young coppice. No species attained highest densities in old coppice. Panels older than 20 years were dominated by Robin, Great Tit and Blue Tit. Of the non-songbirds only Turtle Dove showed a clear trend with age of the coppice. Like the migrant songbirds, the

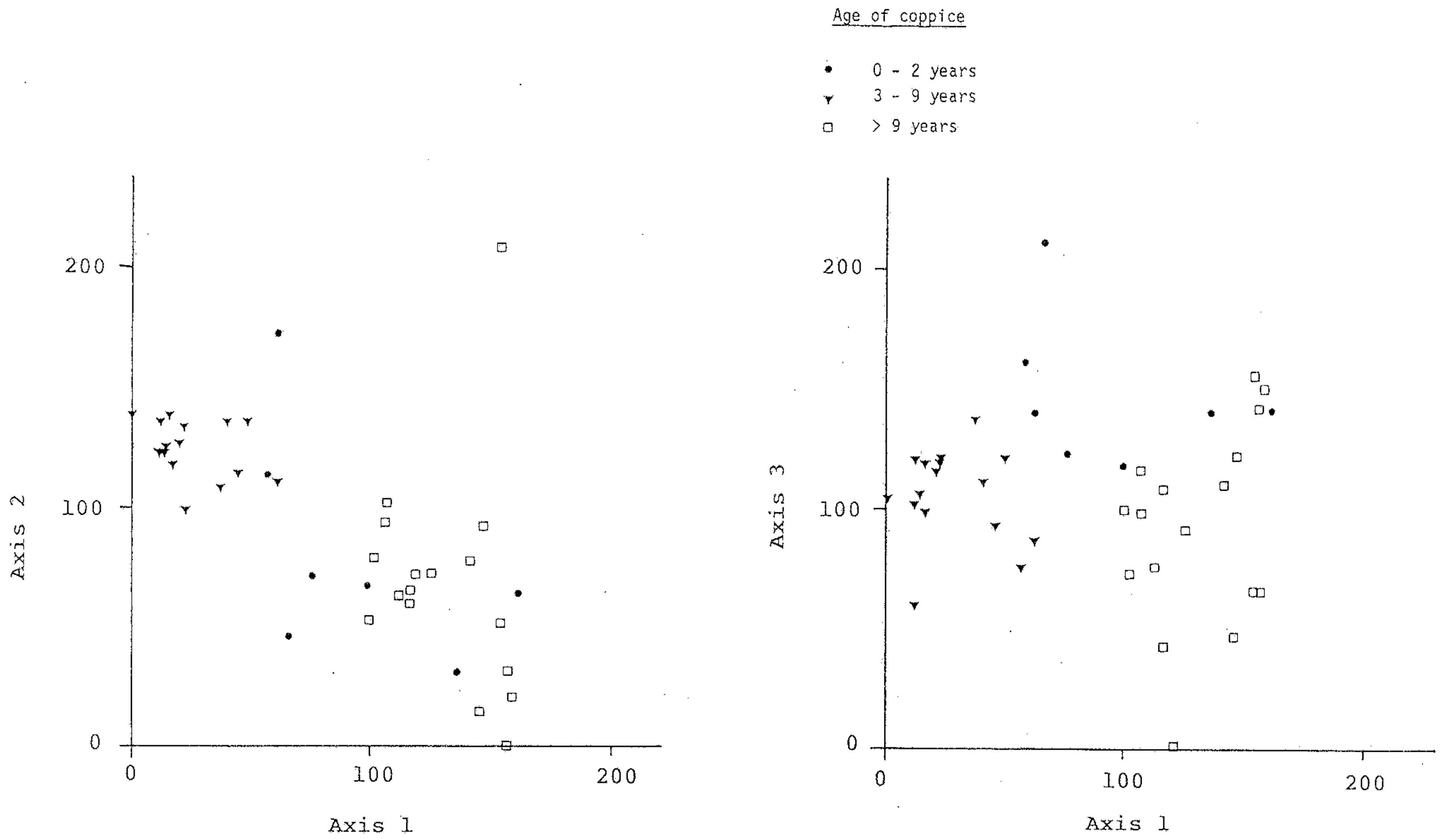


FIGURE 4. DCA ordination of 40 coppice panels in terms of their bird assemblages.

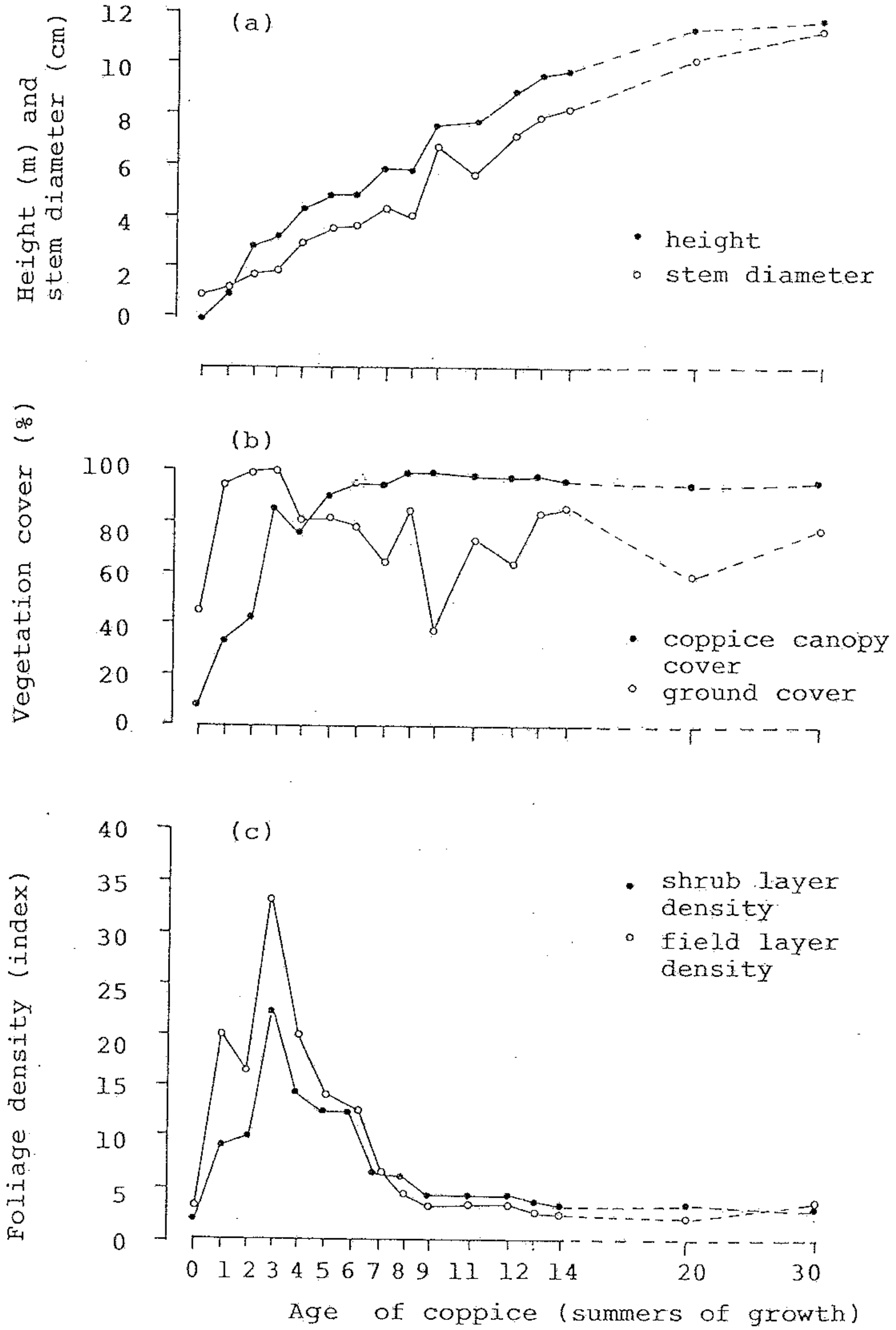


FIGURE 5. Vegetation structure in relation to age of the coppice: (a) coppice height and stem diameter (b) coppice cover and ground cover (c) density of the shrub and field layers. The values plotted are means of all measurements made in each year-class.

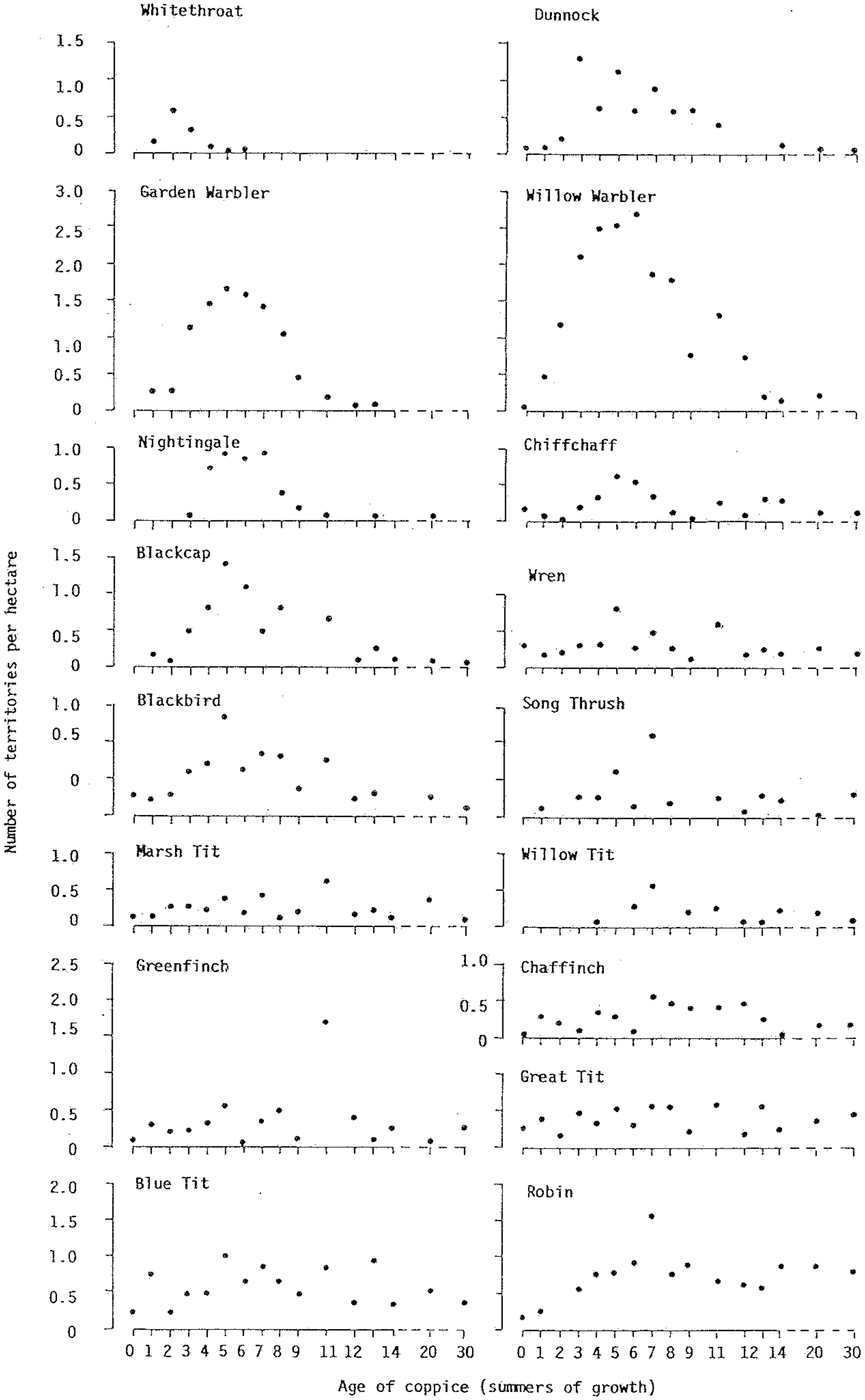


Figure 6. Densities of songbird species in relation to age of the coppice. The three most abundant species in each year-class have been selected.

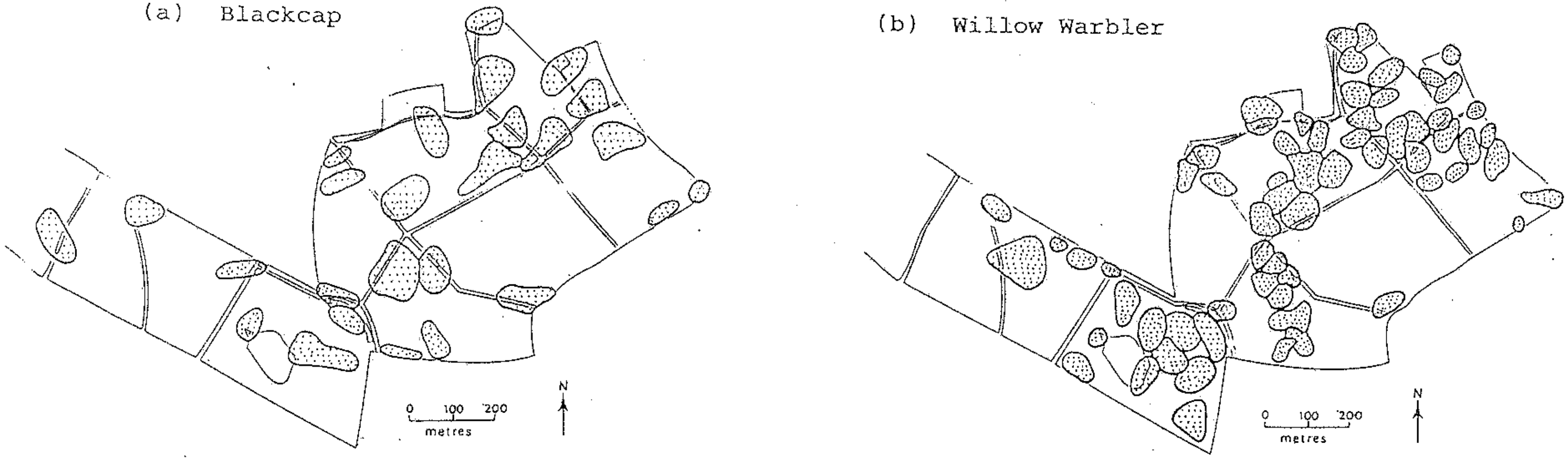
dove was strongly associated with young coppice, reaching peak density in 5 year growth.

As an example, the patterns of territory distribution within the Woods are illustrated for four species in Fig.7. Comparison with Fig.3, which shows the distribution of young coppice panels, will help to emphasise the importance of coppice age in determining the distribution of certain species. Of the species illustrated, Willow Warbler and Blackcap were strongly tied to areas of young coppice whereas Marsh Tit and Robin were more evenly distributed through the Woods.

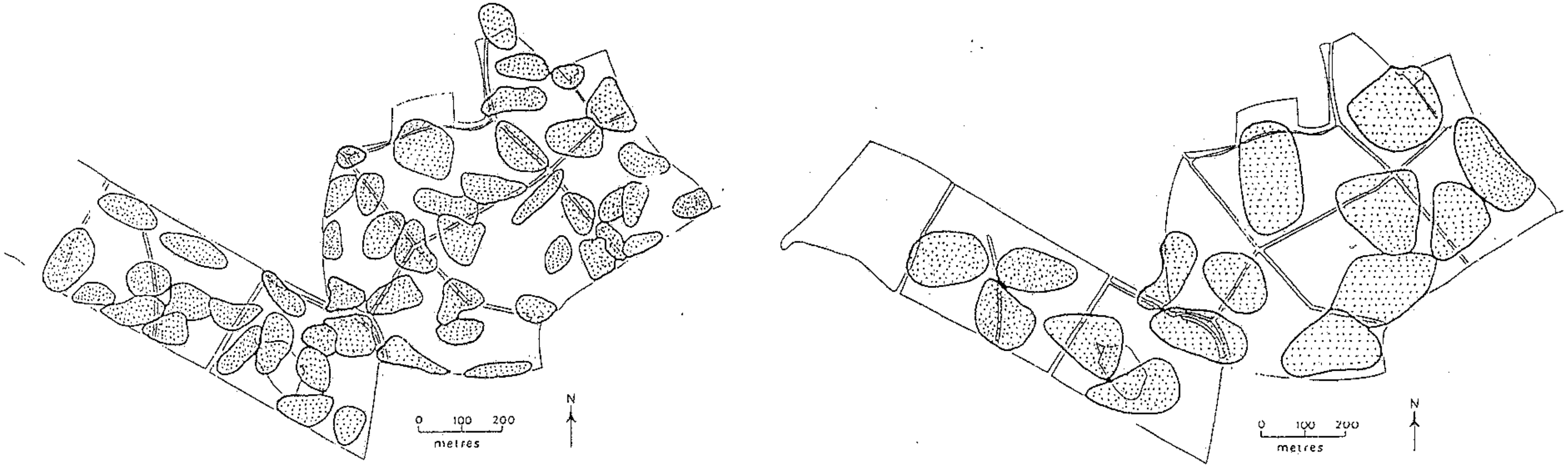
4.5 Trends in songbird communities with coppice age

The total density of songbirds was relatively low in very young and in old coppice; maximum density was in 5 year growth (Fig.8a). Purely for statistical reasons, a relationship is to be expected between numbers of individuals and of species (Connor & McCoy 1979, James & Rathbun 1981). It was not surprising, therefore, that the numbers of species followed a similar pattern to that shown by density, with a peak between years 3 and 7 (Fig.8b). The relatively large number of species recorded in 20 year coppice was probably a result of the relatively large area of that year class (Fig.2). The technique of rarefaction was used to explore the possibility that the observed trends in species number might be a consequence of such sampling effects. Rarefaction is a method of estimating the expected numbers of species in a random sample of individuals drawn from a community (James & Rathbun 1981, James & Wamer 1982). The technique was used to standardise the numbers of species according to both the areas of the samples and the numbers of individuals within them. Expected numbers of species were estimated for sample areas of 2ha (Fig.8c) and for samples of 10 individuals (Fig.8d). Some year classes were omitted from the analyses because they gave insufficient samples. Correcting for sample area confirmed that species numbers were highest in coppice of 3 - 8 years (Fig.8c). This effect, however, was due to the very high densities of birds supported by this stage of coppice growth, because when the numbers of individuals within the samples were standardised, species number showed barely any variation with coppice age (Fig.8d). Dominance - a simple measure of diversity - indicated that the oldest coppice carried the least diverse bird communities in Bradfield (Fig.8e). Dominance was stable, or perhaps slightly decreased, up to about 11 years, thereafter it rose as the songbird communities became increasingly dominated by Robin, Blue Tit and Great Tit. In growth of 8 to 12 years these three species contributed 20% to 32% of the songbird territories but in the four oldest year-classes they contributed 47% to 60%.

Songbird community composition changed markedly with coppice age. This is illustrated with respect to the main families of songbirds in Figs.9 and 10. Warblers strongly selected coppice of 3 to 8 years; thrushes also were most abundant at the canopy-closure period; tits and finches showed no clear trends except that finches avoided the oldest coppice. Densities of hole and crevice nesters were virtually identical to those for tits. In terms of percentage composition (Fig.10) warblers were the dominant group between 2 and 8 years but as the coppice aged it became increasingly dominated by tits and thrushes.


(a) Blackcap

(b) Willow Warbler


(c) Robin

(d) Marsh Tit

FIGURE 7. Distribution of territories in 1987 of Blackcap, Willow Warbler, Robin and Marsh Tit.

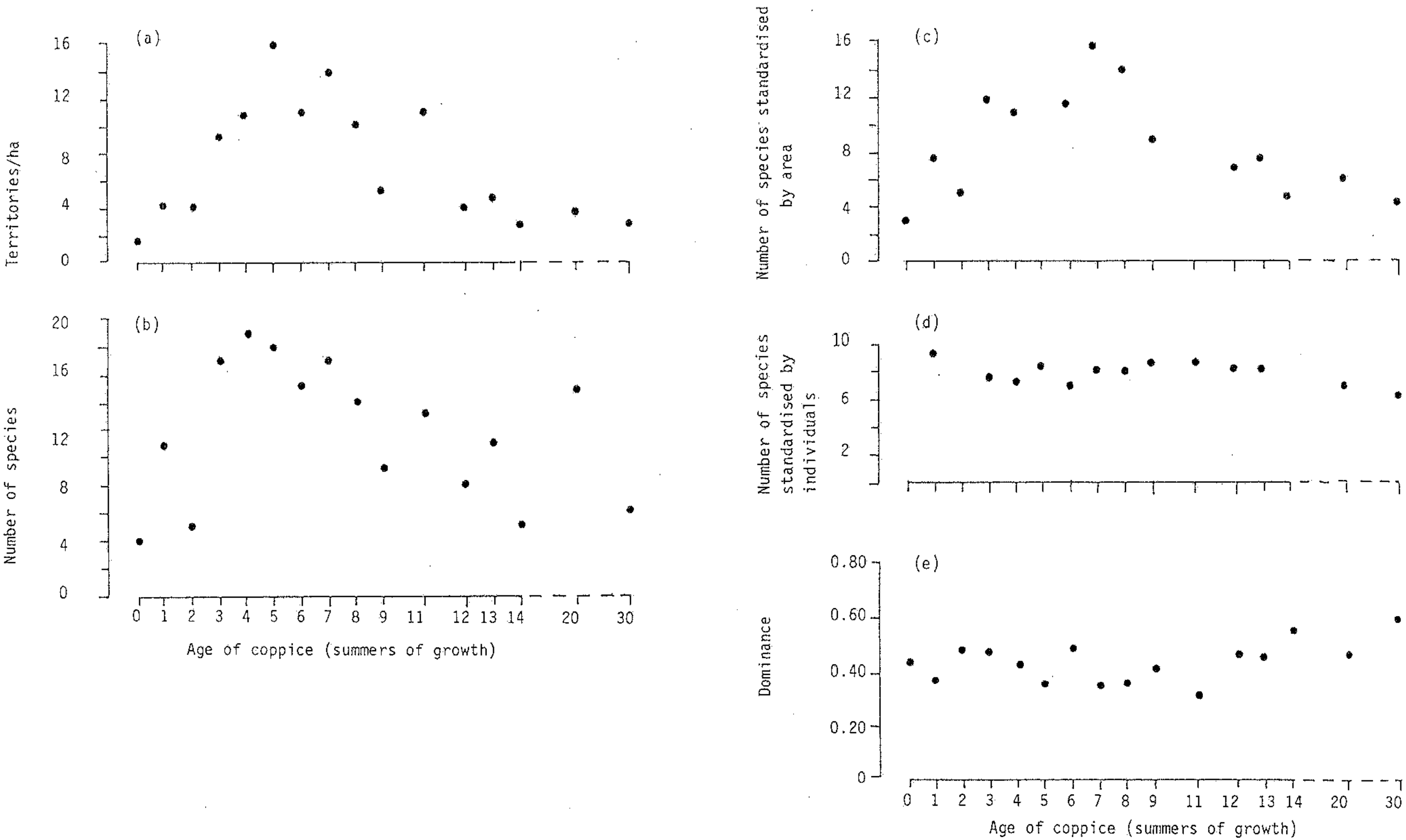


Figure 8. Songbird community parameters in relation to age of coppice: (a) total density, (b) number of species (those with at least 0.5 territory), (c) number of breeding species expected in 2 ha, (d) number of species expected in a sample of 10 individuals, (e) dominance - the proportion of the total territories contributed by the three most abundant species.

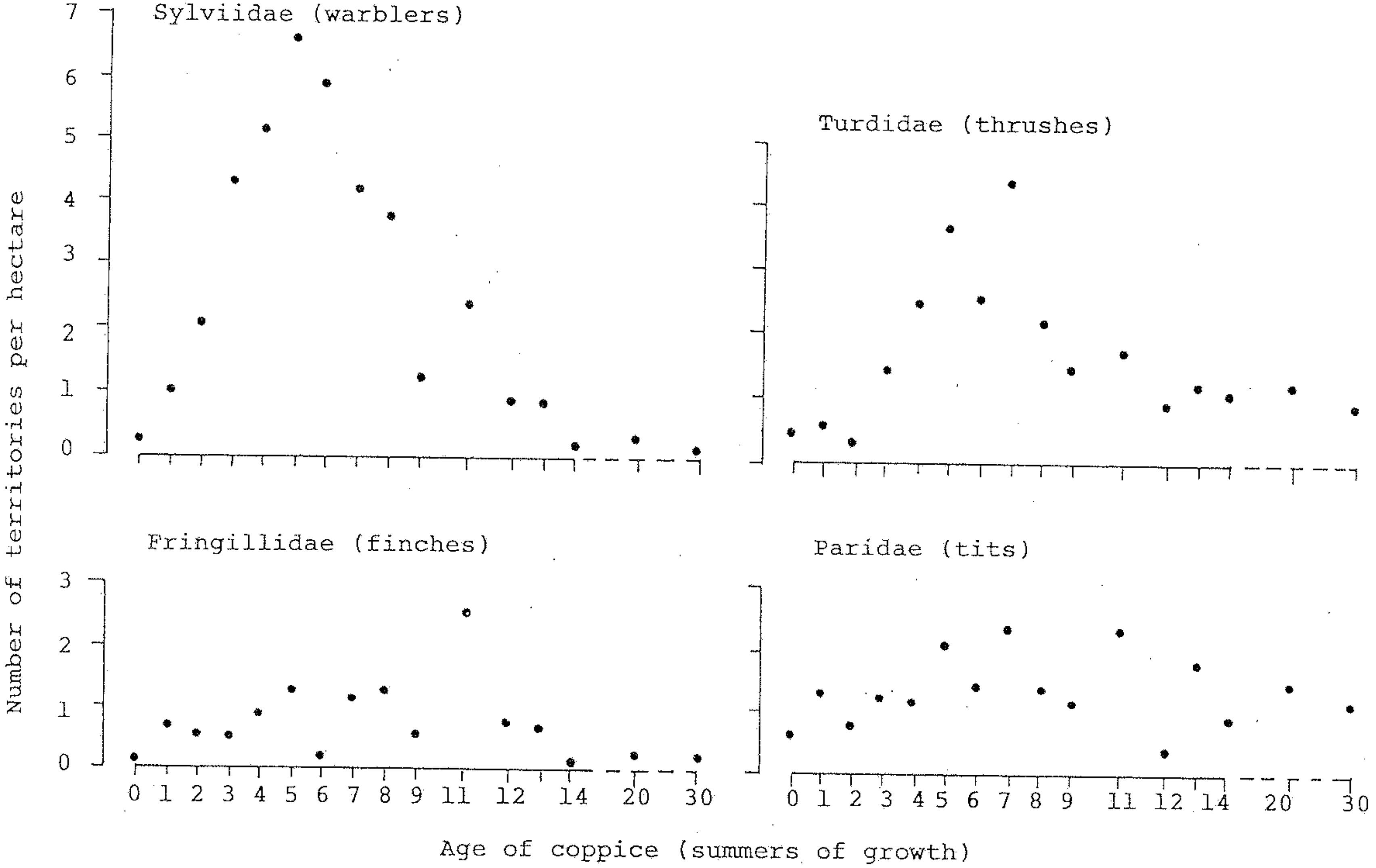


FIGURE 9. Distribution of four families of songbirds in relation to age of the coppice.

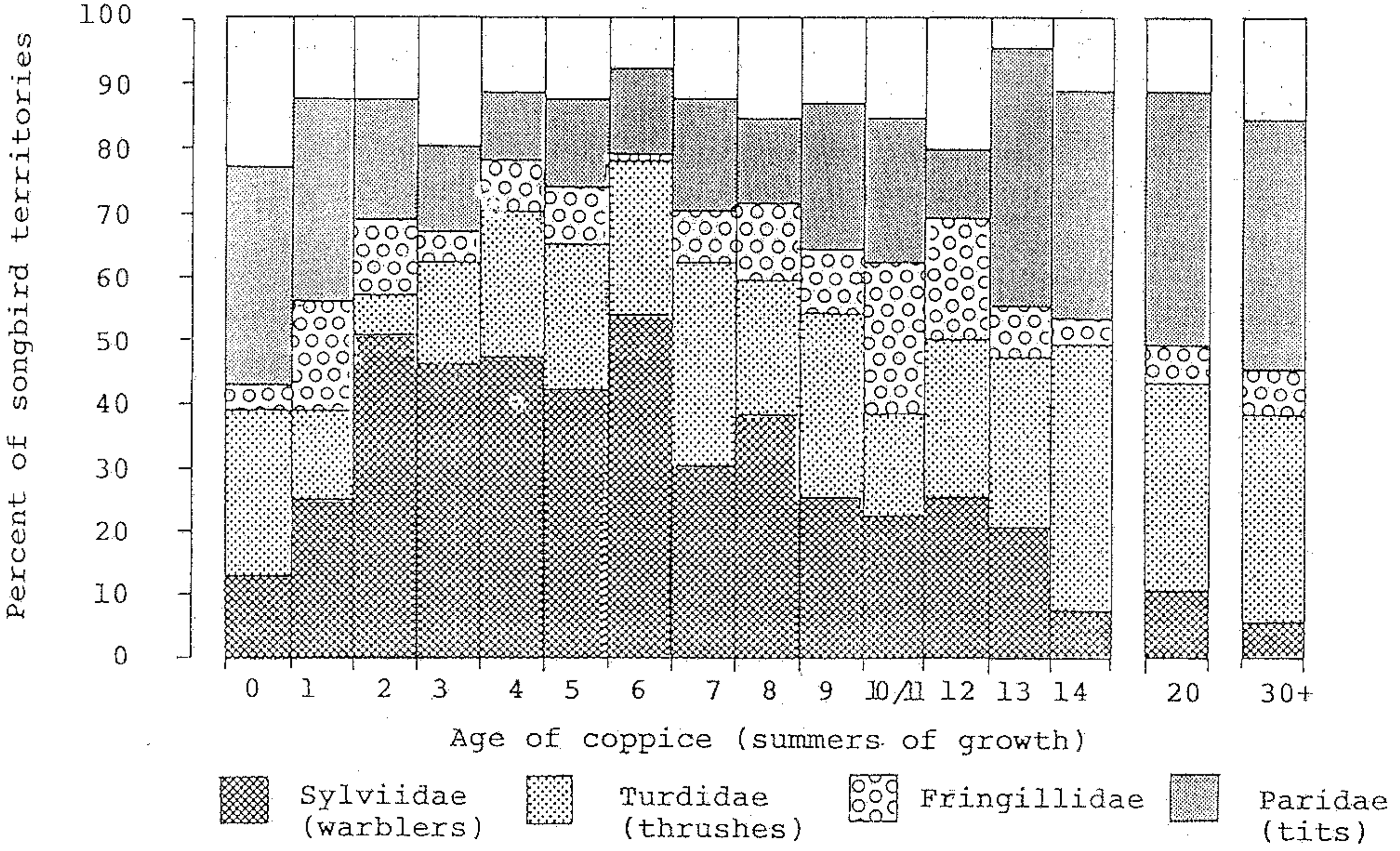


FIGURE 10 Percentage composition of the songbird community in relation to the age of the coppice.

The most striking change in community composition was that for migrant songbirds which were almost entirely associated with young coppice (Fig.11a). Resident species also tended to be least numerous in very young or very old coppice (Fig.11b). Between years 2 and 5 migrants and residents were approximately equally abundant but thereafter resident species became increasingly dominant (Fig.11c). The migrants included two species, Blackcap and Chiffchaff, which winter mainly around the Mediterranean; the remaining species migrate south of the Sahara. Exclusion of Blackcap and Chiffchaff made no difference to the patterns in Fig.11.

Relationships between year-classes in terms of the similarity of their songbird species composition were explored TWINSPAN. Several runs were made using different input parameters and a similar classification was obtained in each case. Two consistent features emerged. First, the middle-aged growth (years 3 - 8) was clearly distinguished from the other years. This was a result of the high concentration of migrant species in these year-classes. Second, the bird communities in very young coppice (less than 3 years) were always more similar to those found in old coppice than to those in middle-aged growth. Years 1 and 2 were always grouped close together, presumably a reflection of the greater abundance of Whitethroat than in any other years. An example of a TWINSPAN classification is given in Fig.12 in which 7 end-groups were identified using three levels of division. High densities of Garden Warblers were the best indicator for discriminating between the two main groups of years in Fig.12.

4.6 Bird distribution in relation to vegetation

The strong influence of age of the coppice on the bird communities probably acts largely through the striking changes in vegetation structure that occur as the coppice grows (Fig.5). Relationships between bird distribution and vegetation were explored directly for those 40 coppice panels of at least 0.5ha.

First, an attempt was made to interpret what gradients of vegetation, if any, the DCA axes represented (Fig.4). This was done through regression analyses in which the scores attained by panels on each of the four DCA axes were used as dependent variables (Table 3). Axis 1 represented a gradient of decreasing density of shrub layer foliage because SHRUB accounted for 66% of the variance. The combination of low height but high canopy closure suggests that axis 2 represents the middle stages of growth, probably the period of 4 to 8 years growth. Therefore, both axes 1 and 2 measure gradients in vegetation structure associated with the growth and development of the coppice. Axis 3 on the other hand appears to represent a gradient in the density of stools. Axis 4 is difficult to interpret because, like axis 1, it was most closely related to the density of the shrub layer although in this case the relationship was rather weak. Relationships between particular species and vegetation are examined below.

Regression analysis was used to relate the densities of eight species to vegetation characteristics (Table 4). Most of the variables selected, including the first two in each case, were measures of vegetation structure. Abundance of five of the species was modelled most closely by a combination of height

TABLE 3. Interpretations of gradients in bird assemblages (DCA axes) in terms of vegetation. Variables are listed in the order they were entered in multiple regression models (see text), together with the sign of the relationship and the cumulative % variance explained. The variables are defined in Table 1

AXIS 1	- SHRUB (66%)	+ HEIGHT (70%)	- COCOV (79%)
AXIS 2	- HEIGHT (25%)	+ COCOV (47%)	- STOOLS (53%)
	- ALDER (58%)		
AXIS 3	- STOOLS (33%)	- COCOV (45%)	+ TRSP (55%)
AXIS 4	- SHRUB (21%)	+ STOOLS (35%)	

TABLE 4. Regression models accounting for variation in density of selected bird species and groups of songbirds in coppice panels. Variables are listed in the order they were entered in the models, together with the sign of the relationship and the cumulative % variance explained. The variables are defined in Table 1. Number of species (1) is the total number of species; (2) is the number of territory holding species defined as those with a density of at least 0.5 territories per hectare.

Dependent variable	Independent variable(s)
Wren	+ STAND1 (11%)
Dunnock	- HEIGHT (33%) + COCOV (53%) - ALDER (59%) - ASH (66%)
Robin	+ COCOV (30%) + STOOLS (38%)
Nightingale	- HEIGHT (15%) + COCOV (44%)
Blackbird	- HEIGHT (18%) + COCOV (38%) - STOOLS (47%)
Garden Warbler	- HEIGHT (34%) + COCOV (60%) - STOOLS (65%)
Blackcap	- HEIGHT (16%) + COCOV (53%) - STOOLS (59%)
Willow warbler	+ SHRUB (67%) + COCOV (71%) - HEIGHT (83%) + BIRCH (85%)
Hole-nesters	+ STAND1 (14%)
Hole-nesters (-BT)	no variables significant
All migrants	+ SHRUB (64%) + COCOV (67%) - HEIGHT (81%) - STOOLS (85%)
All songbirds	+ STAND1 (31%) + SHRUB (40%) + COCOV (48%)
All songbirds(-BT)	+ SHRUB (46%) + COCOV (54%) - HEIGHT (65%)
No.of species (1)	- HEIGHT (19%) + COCOV (49%)
No.of species (2)	- HEIGHT (19%) + COCOV (53%)

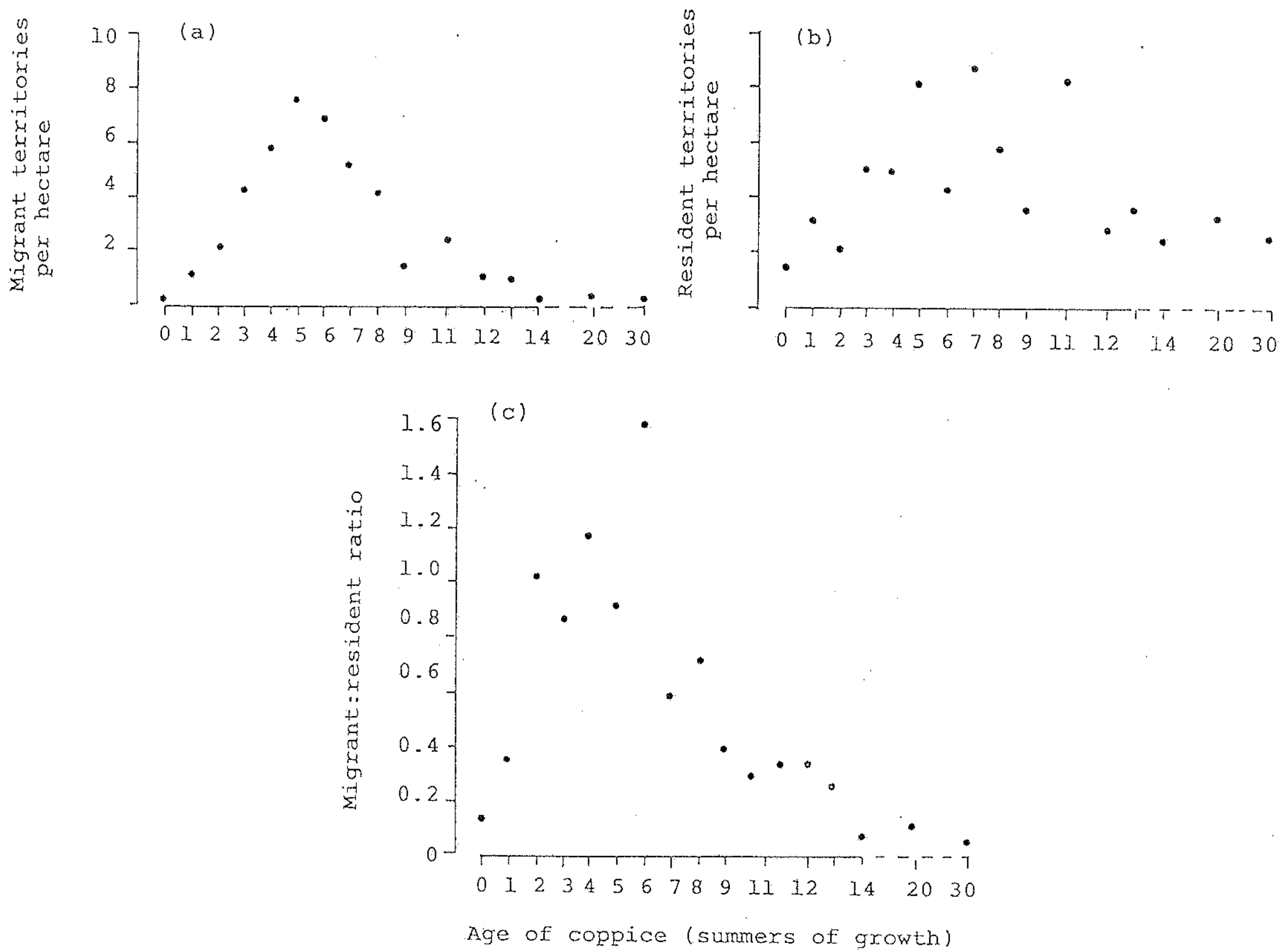


FIGURE 11. Songbird community composition in terms of migrant and resident species shown as: (a) densities of migrants (b) densities of residents (c) the ratio of migrant to resident territories. Migrants are defined as all warblers and Nightingale.

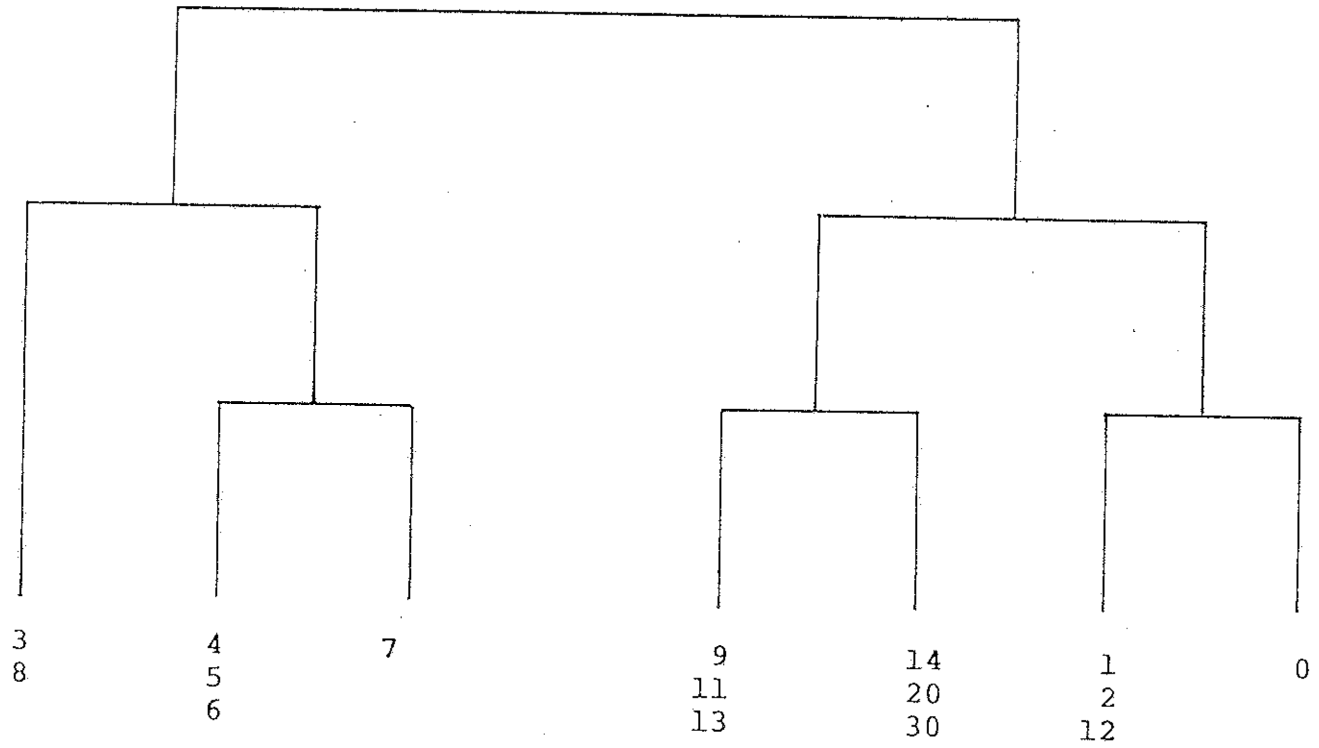


FIGURE 12. A classification of the bird communities in different coppice year-classes by TWINSPAN

(negative) and canopy cover (positive), indicating a close association with the middle stages of growth when the coppice canopy was still relatively low but nearly closed. This stage of coppice growth approximately coincided with the period when the shrub layer reached peak density. Indeed, had a stepwise approach been used, without any attempt to find optimum models, SHRUB would have featured as the first variable in several other models, including each of those where HEIGHT and COCOV entered first. In the case of Dunnock and Garden Warbler, SHRUB explained more than 50% of the variance. Shrub density featured very strongly in the optimum models for Willow Warbler, all migrants and total density (excluding Blue Tit). Relationships between four species and density of the shrub layer are shown in Fig.13. The density of large standard trees entered as the first variable in the models for the density of hole-nesting species and for all songbirds. This may have been an artefact arising from the placement of nest boxes on large standards because the relationship was not significant when Blue Tits was excluded from the analysis.

Height featured strongly in the regression models but it was not linearly related to most bird densities, necessitating a quadratic transformation. Several species were confined to very narrow bands of vegetation height (Fig.14). This was particularly striking for Nightingale which was virtually absent from coppice less than 3m and taller than 7m.

The models outlined in Table 4 apply to the whole coppice cycle across which there is enormous variation in the structure of the vegetation. At this scale it is not surprising, therefore, that structural variables, such as canopy height, canopy cover and density of the shrub layer, should account for so much of the variation in bird distribution. If it were possible to control these gross "successional" changes in vegetation structure, one might find that bird distribution was related to rather different factors. This possibility was explored by examining relationships between birds and vegetation within particular stages of the coppice cycle. Two stages were selected: 3 - 8 years and 10 - 30 years of growth. Panels within these groups were identified by DCA as being relatively homogeneous in terms of bird community composition (Fig.4). The sample sizes of panels of at least 0.5ha were small for both groups (n = 15, 17 respectively) so the predictive power of the analyses will be poor. Nonetheless, the analyses can be used to indicate some likely relationships and to draw comparisons with those based on the entire coppice cycle. The same 10 vegetation variables were retained as used in analysis of the entire coppice cycle.

Tables 5 and 6 give the results of regression analysis for the young and old growth respectively. The most striking result was that variables measuring plant species composition featured relatively strongly in comparison with the analysis for the full coppice cycle. Measures of plant species composition contributed 8% of the significant variables in Table 4 compared with 45% in Tables 4 and 5 combined. In particular, birch entered first in four models, acting with a negative effect in each. Height entered first in four models and shrub layer density in two.

TABLE 5. Regression models accounting for variation in density of selected bird species and groups of songbirds in coppice panels of 3 to 8 years of age (n = 15). See Table 4 for a full list of dependent variables; only those for which significant models were constructed are shown here.

Dependent variable	Independent variable(s)		
Dunnock	- ALDER (48%)	- COCOV (71%)	- ASH (82%)
Robin	+ HEIGHT (47%)		
Nightingale	- SHRUB (29%)		
Blackbird	- BIRCH (37%)		
Hole-nesters	+ HEIGHT (40%)		
Hole-nesters (-BT)	+ STOOLS (28%)		
All songbirds	- BIRCH (28%)	+ HEIGHT (53%)	
All songbirds (-BT)	- BIRCH (29%)	+ HEIGHT (53%)	- STOOLS (67%)
No.of species (2)	- SHRUB (27%)	- BIRCH (53%)	

TABLE 6. Regression models accounting for variation in density of selected bird species and groups of songbirds in coppice panels of 10 to 30 years of age (n = 17). See Table 4 for a full list of dependent variables; only those for which significant models were constructed are shown here.

Dependent variable	Independent variable(s)
Robin	+ STOOLS (25%)
All migrants	- BIRCH (38%) - STOOLS (57%) + STAND1 (70%) - ALDER (86%)
No.of species (1)	- HEIGHT (33%) - TRSP (54%) + ASH (72%)
No.of species (2)	- HEIGHT (28%)

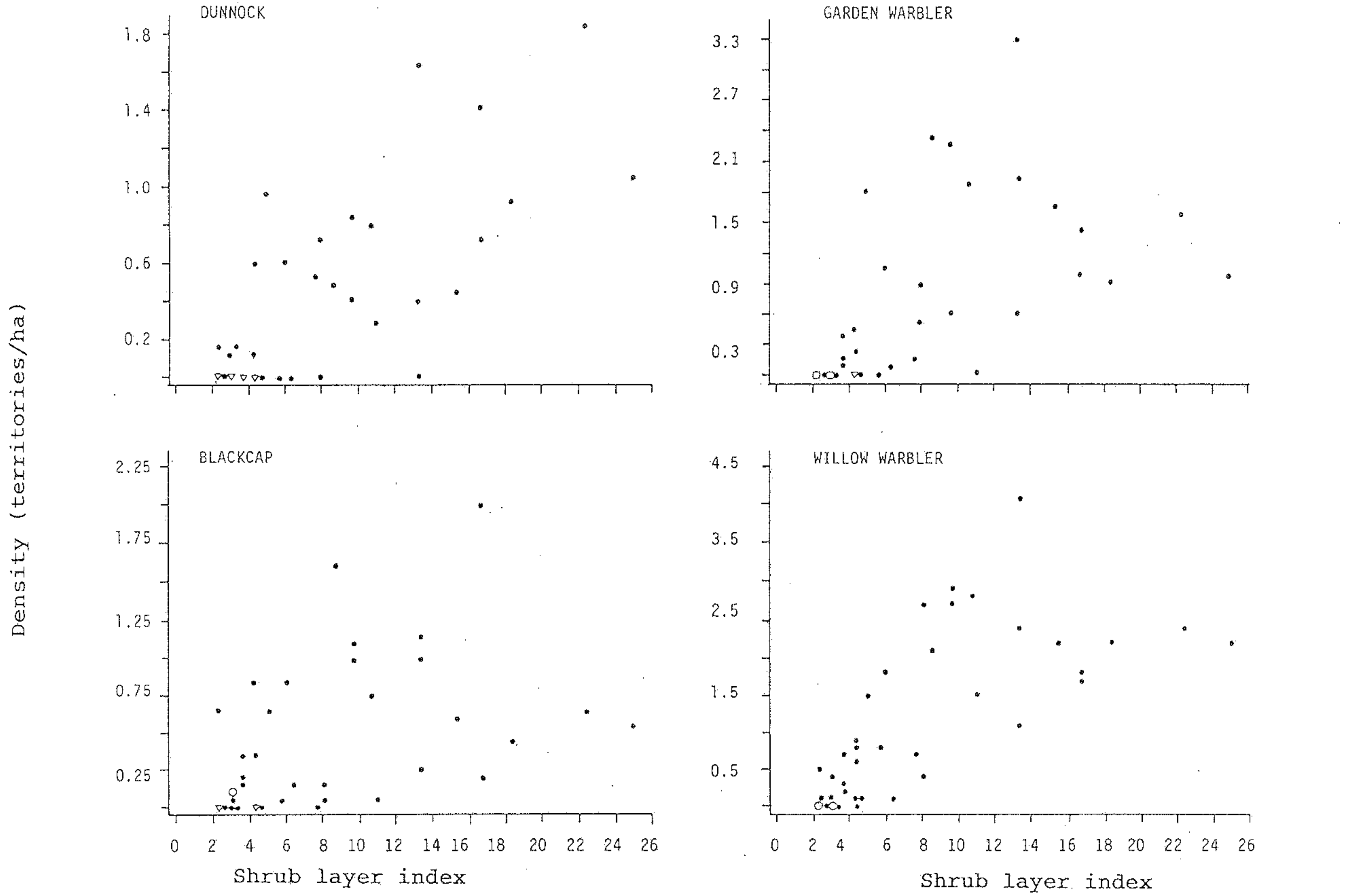


FIGURE 13 Densities of four bird species in relation to the foliage density in the shrub layer. Each point represents a single panel with the exception that open circles indicate 2 panels, open triangles 3 and open squares 4.

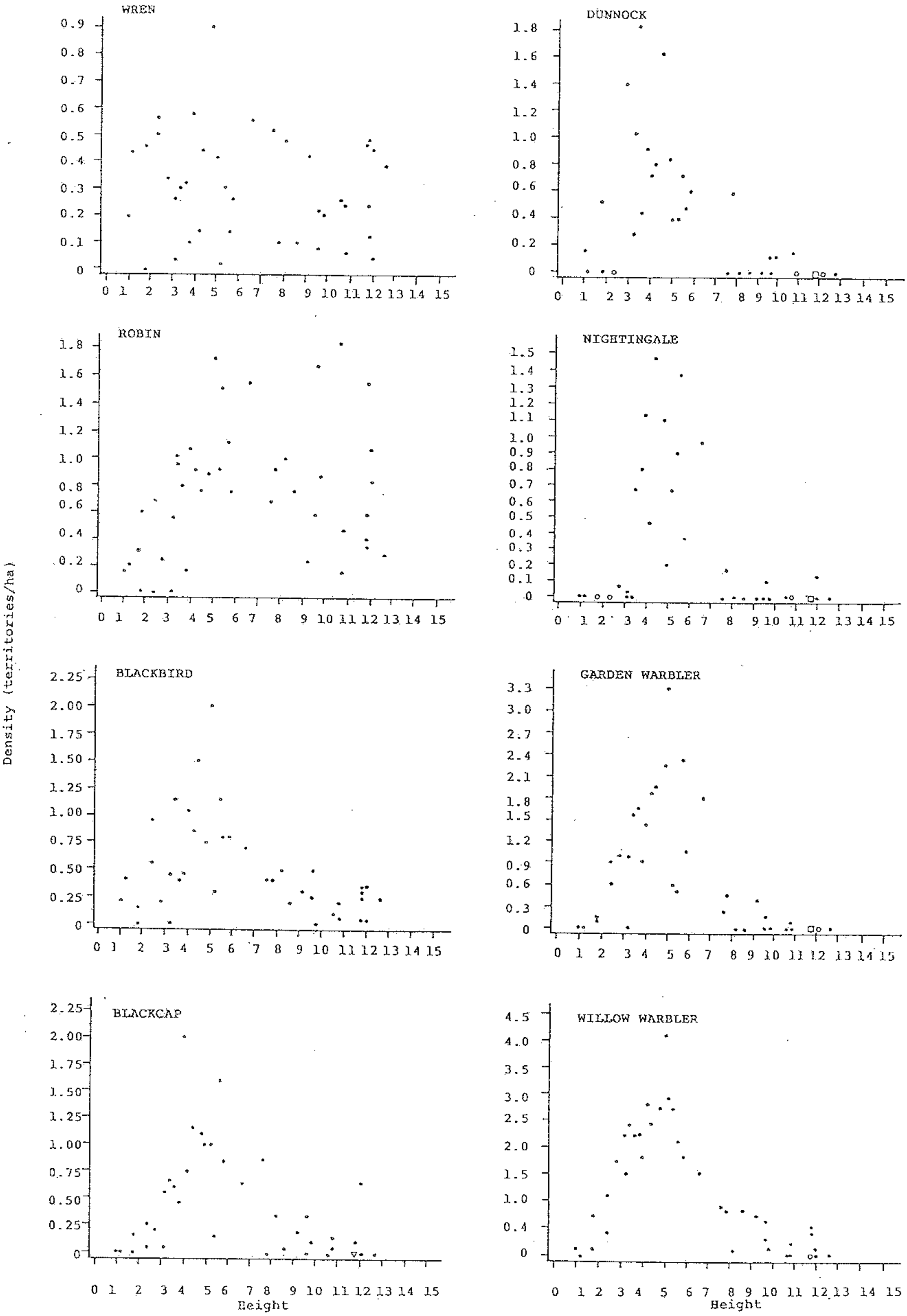


FIGURE 14 Densities of eight bird species in relation to coppice height. Each point represents a single panel with the exceptions that open circles indicate 2 panels, open triangles 3 and open squares 4.

4.7 Size and shape of panels

Coppice woodlands vary greatly in the size and shape of their panels. Do such factors affect the colonisation of panels by birds? This was investigated in two ways. Firstly, by exploring effects of panel size and shape on bird densities. Secondly, by a more indirect approach which involved assessing the extent to which edge effects existed within panels in their vegetation structure.

All panels of 3 to 8 years of age were used in the first analysis. Panels of this age were chosen for they were reasonably homogeneous with respect to their bird assemblages (Fig.4). A total of 21 panels were available ranging in size from 0.1 to 2.0 ha. An index of shape was calculated by dividing the perimeter of the panel (m) by the area (square m.). Analysis aimed to assess whether the size and shape of panels was associated with the density of selected species. The species considered were the nine listed in Table 4. Presence-absence data were not considered suitable for this analysis (Haila 1988). Wrens were found to be significantly more abundant in small panels (Spearman $r = -0.48$, $P<0.05$) but no other species were associated with panel area and none with panel shape. Plots of area and shape against species densities were also examined to check for non-linear relationships but none were evident.

There was evidence that vegetation structure was affected by the proximity of a panel edge in a rather complex manner. Shrub layer profiles across panel edges are shown in Fig.15. Profiles (a) to (d) are for panels where young coppice abuts old coppice; profiles (e) to (h) are where two young panels abut. In this context "young" coppice is six years or less. Two year growth abutting old coppice showed marked suppression of the shrub layer at the edge of the panel (profile b). There were, however, no strong edge effects in 4 to 6 year coppice at the edge of old panels (profiles 4 and 6). Nor was there evidence of any edge suppression of coppice growth where two young panels abutted. For several of the profiles, edge effects were apparent within the older of the two panels, but unlike most of the younger panels, the sign of the correlation coefficient was negative. That is to say, the shrub layer was denser at the edge of a panel where it adjoined younger growth. This phenomenon was particularly marked within old coppice and six year coppice. No significant differences were found between the height of stools at the edges and centres of panels.

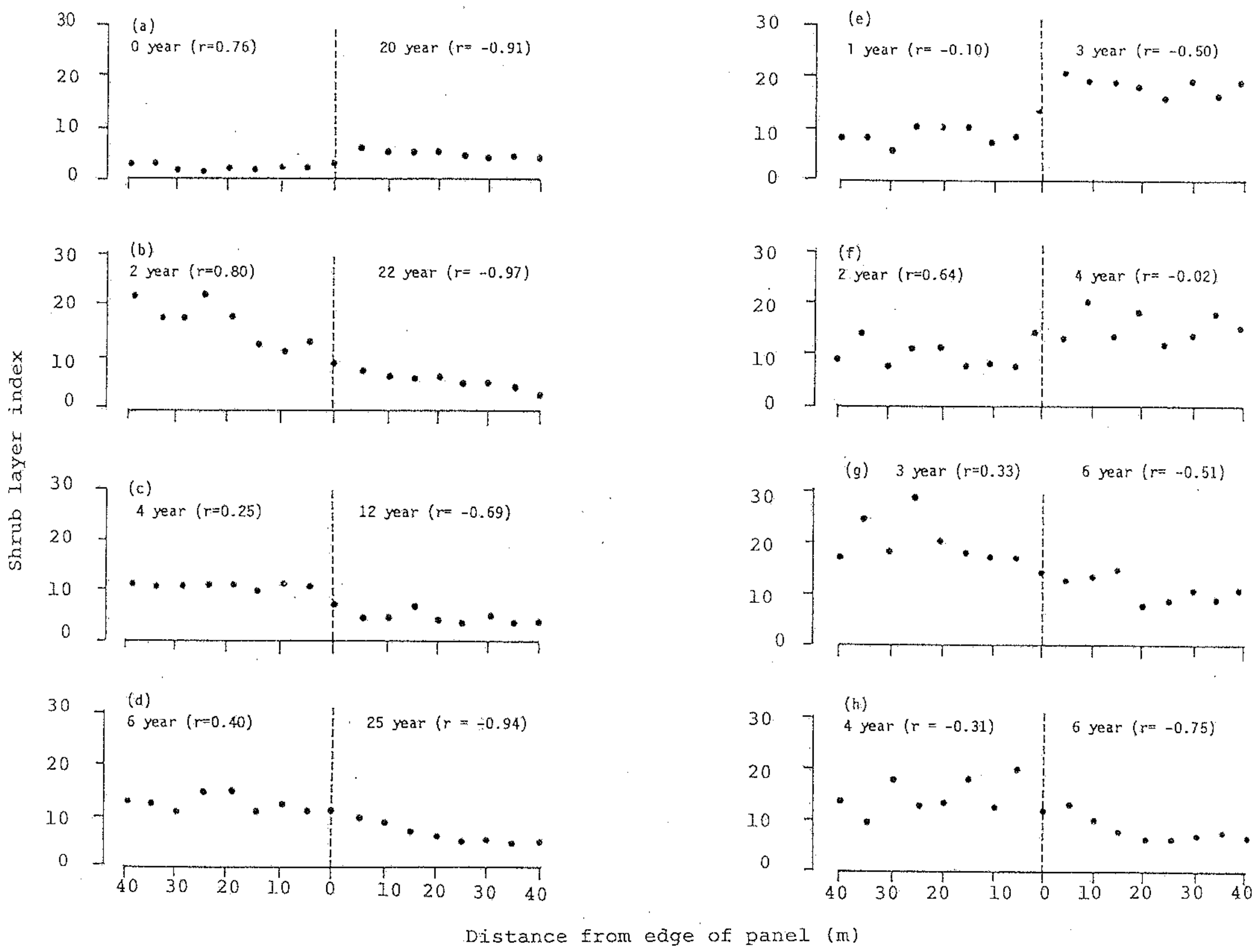


FIGURE 15 Shrub layer indices (see methods) in relation to distance from edge of panels. The panel edge is marked with a vertical broken line. For each panel, the age of the coppice growth is shown, together with the Spearman rank correlation coefficient indicating the strength of association between the shrub layer and distance from the edge.

5. DISCUSSION

5.1 How typical are the results from a single year?

This is important not merely for purposes of comparison with other studies but because species may alter their patterns of habitat selection at different population densities. In particular, there are theoretical reasons to expect that birds may occupy sub-optimal habitats, and perhaps a wider range of habitats, in years when numbers are high (O'Connor & Fuller 1985). The BTO's Common Birds Census (CBC) was used to assess to what extent the 1987 population levels of breeding birds in Bradfield Woods were typical of the levels that might be expected in an average year. The woodland population trends revealed by the CBC were examined for all the 15 most abundant species listed in Table 2, excluding Nightingale and Marsh Tit for which no woodland CBC indices are available (Marchant et al 1990).

The previous winter had not been sufficiently severe to cause exceptional overwinter mortality of resident species. The populations of residents were not, therefore, depressed markedly below recent average levels. The majority of species showed population levels in 1987 that were not discernably different to those over the last decade. Exceptions were as follows. Dunnock was at it lowest recorded level in woodland, having recently undergone a gradual decline. There was, however, no significant difference between the 1986 and 1987 population levels (Marchant & Whittington 1988). Garden warbler populations in woodland have been rising since the mid 1970s and 1987 was the highest index value yet recorded and was significantly greater than that for 1986. High Garden Warbler populations were maintained in 1988 (Marchant & Whittington 1989). Conversely, woodland Greenfinches have been declining since the mid 1970s but their level was not significantly lower in 1987 than 1986. Although population levels of a few species in 1987 were appreciably lower or higher than those attained in recent years, this was always a consequence of a population trend rather than of any unexpected sudden population change occurring in 1987. We conclude, therefore, that the results obtained in 1987 were likely to be broadly typical of those that would have been obtained in any recent year. It is possible, however, that Garden Warbler populations may have increased somewhat over the last decade (the CBC index increased by 87% during this time) and that it may now be occupying a slightly different range of coppice year classes as a result.

5.2 Comparisons with other coppiced woodlands

Although coppicing is widely practised as a nature conservation technique there have been surprisingly few studies of bird populations in other coppiced woodlands. Quantitative information on territory densities in relation to age of coppice are available from two other woods:

(i) Longbeech Wood, Kent (Fuller & Moreton 1987): sweet chestnut Castanea sativa coppice with very few standards.

(ii) Brasenose Wood, Oxford (Fuller & Steel 1990): mixed coppice with a high density of standards.

Information on habitat selection of birds in relation to coppice age, based on distribution of registrations rather than of territories, is also available from Ham Street Woods National Nature Reserve, Kent (Fuller, Stuttard & Ray 1989). This wood is mixed coppice with a high density of standard trees and, at the time of the ornithological survey (1969-73), had a similar ratio of young to old coppice as Bradfield in 1987.

From an ornithological viewpoint, the most interesting and distinctive feature of coppice woodlands is their populations of breeding summer visitors, which can benefit from the young growth created by coppicing. The basis for this pattern of habitat selection is discussed by Helle & Fuller (1988). In each of these woods warblers and other migrant species selected coppice at around the canopy-closure period. The strength of this response varied considerably, however, with Bradfield supporting by far the highest densities of summer visitors (Fig.16). Densities of warblers in Ham Street Woods were also high: the overall densities of warblers at Ham Street and Bradfield, were both approximately 2 pairs per hectare. Clearly, Bradfield Woods are amongst the best coppice habitats for migrant birds in terms of breeding densities.

In Bradfield the old coppice was strongly avoided by many species. This result is consistent with findings in the other coppice woodlands listed above and elsewhere Fuller (1988). Coppice of more than nine years held very different bird assemblages to younger coppice, largely because it was avoided by warblers and Nightingales. The overall density of songbirds was lowest in coppice older than eleven years. No species were confined to this old coppice, although it was possible that some, such as Marsh and Willow Tits, could only find suitable nest sites there but ranged widely in young coppice. Blackbird and Wren were scarcer in the old coppice of Bradfield than elsewhere (Fuller & Steel 1990, Fuller, Stuttard & Ray 1989). Further, the overall density of songbirds declined far more steeply after canopy closure at Bradfield than in other woods. It is possible that tree species composition may be responsible for these differences in songbird populations. Much of the older coppice in Bradfield contains a large amount of birch which was not so abundant in the other woods. This probably reflects the relatively acidic nature of the underlying soils and raises the possibility that much of the older coppice in Bradfield is on soils of relatively low productivity (Rackham 1980). A positive association between soil productivity and bird numbers in woodlands has been demonstrated by Newton, Wyllie & Mearns (1986).

5.3 Patterns of habitat selection

Three distinct phases were recognised by Fuller & Moreton (1987) in the development of breeding bird communities in commercial sweet chestnut coppice. These were "establishment" (years 0-4 when the canopy was still very open, "canopy-closure" (years 4-10) and "maturation" (year 11 and older). Establishment was characterised by high densities of Tree Pipits Anthus pratensis, Whitethroats, Linnets and Yellowhammers; canopy-closure by Willow Warblers and maturation by Robins and tits. The Bradfield bird community can be classified in exactly the same groups (Fig.4), although the most striking division was that between the birds associated with years 3-8 and those with all other years (Fig.12). The timing of the three phases shows detailed differences between

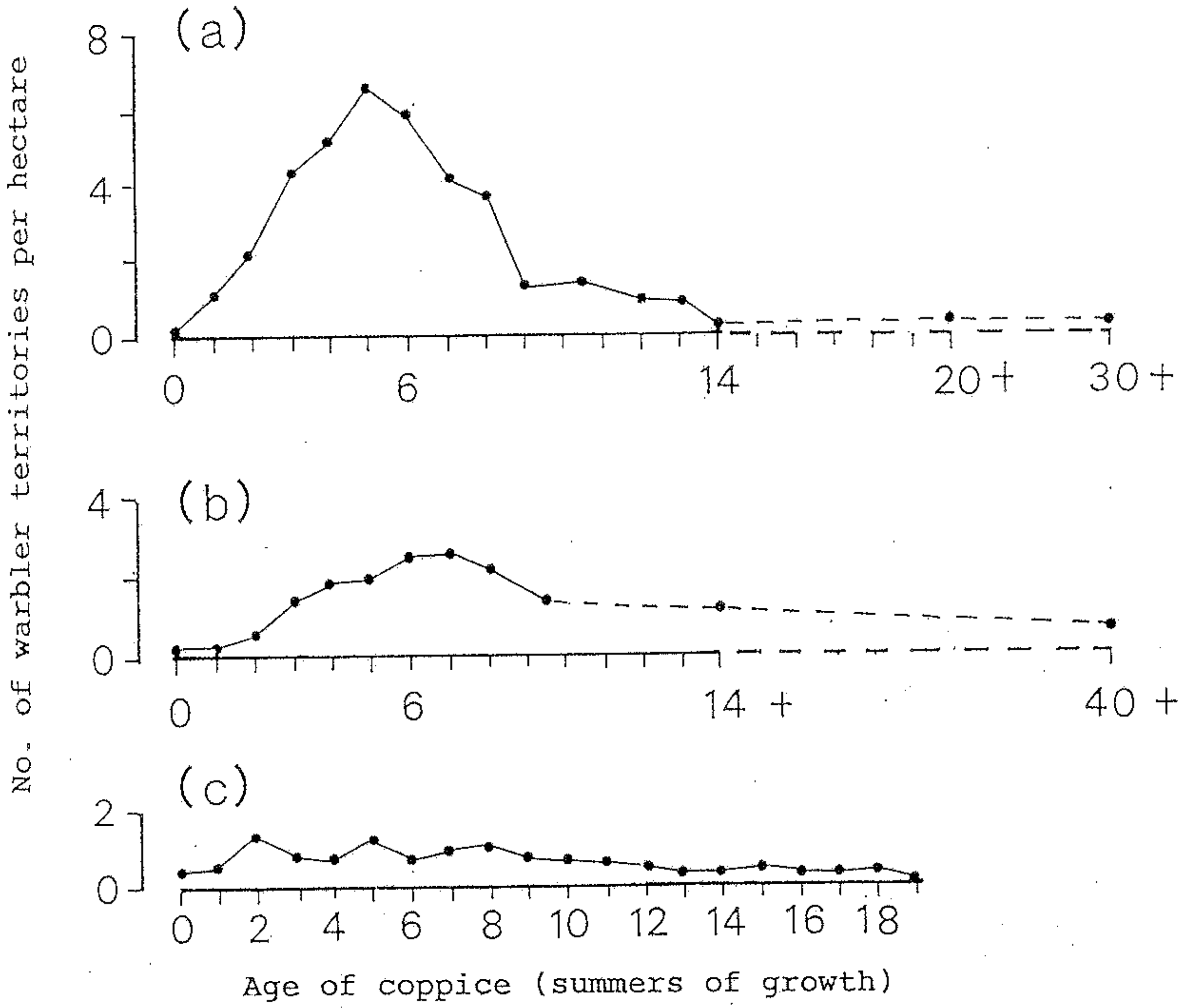


FIGURE 16. Densities of warblers in relation to age of coppice in three actively coppiced woods: (a) Bradfield Woods, (b) Brasenose Wood and (c) Longbeech Wood. The woods are described in the text.

the commercial sweet chestnut and the traditional mixed coppice. Nonetheless, it appears that, despite considerable differences in both plant and bird species composition, the three-phase model of development in coppice bird communities has general applicability. This suggests the birds are responding to certain attributes that all coppice systems have in common. This study provides evidence that relevant factors are changes in the openness of the habitat and in the associated development and subsequent disappearance of field and shrub layers. At the scale of the entire coppice cycle, gradients in overall bird community composition and structure were determined by changes in the physical architecture of the coppice vegetation. The evidence came from three sources. First, the main gradients in composition of bird assemblages were explained by trends in vegetation structure (Table 3). Second, there was very close matching between many of the temporal trends in bird densities and community measures (Figs. 6 and 8) and those in vegetation structure (Fig.5). Third, all of the models relating birds to vegetation were dominated by measures of vegetation structure (Table 4). Without manipulating the vegetation experimentally, it is not possible to say exactly which components of the complex of structural changes are significant to different species. Nonetheless, it is worth noting that the density of the shrub layer emerged as the factor explaining the main variation in bird assemblages (axis 1 in Table 3) and it was also the single variable that explained most variation in density of six of the eight species examined.

Close examination of Figs.5 and 6 shows that several species reached peak density _just_ after the shrub layer reached peak density. This idea was further supported by the fact that optimum models of bird density selected the combination of low height and high canopy cover rather than density of the shrub layer. In terms of habitat selection, these results have several possible interpretations. One is that birds such as Blackcap and Nightingale select a habitat in which the canopy is virtually closed but where the shrub layer is still dense, although starting to thin out. This is supported by the finding that densities of Nightingales in young coppice were lower in panels with a relatively dense shrub layer (Table 5). Another possibility is that the birds respond to the density of foliage at a height above 1.5m, which was the maximum height at which it was measured in the present study. Whatever the exact mechanism determining the distribution of warblers and Nightingales within Bradfield Woods, the density of the shrub layer is an important factor in determining habitat suitability for these birds because woods with sparse coppice regrowth have relatively poor densities of warblers (Fuller & Steel 1990, Fuller in press).

Rather different relationships between bird distribution and vegetation were evident when young and old coppice were examined separately. Plant species variables featured far more frequently in these relationships (Tables 5 and 6). This does suggest that when one compares plots of similar habitat structure, more subtle responses of birds to vegetation are likely to be detected. Since MacArthur & MacArthur (1961) demonstrated a strong link between bird species diversity and foliage height diversity, many attempts have been made to model bird distribution and community patterns in terms of simple measures of habitat structure, often ignoring the potential role of plant species composition. This approach is grossly simplistic (James & Wamer 1982, Rotenberry 1985). It is worth noting here that the substantial differences in the densities and species composition of birds in sweet chestnut and mixed coppice (Fuller, Stuttard & Ray 1989) are probably at least partly a consequence of botanical differences. Insect numbers in sweet chestnut coppice are appreciably lower than those in other native coppiced shrubs (Hill, Roberts & Stork 1989).

It is known that studies conducted at different spatial scales can detect different patterns of avian habitat occupancy and that they can lead to different conclusions about which factors influence bird diversity (Wiens 1981, Wiens & Rotenberry 1981). Scale considerations are also relevant with respect to habitat structure and choice of study sites needs to be matched to the precise objectives of the research. The coarsest scale at which birds respond to vegetation is at the level of forest succession, or other situations where different growth stages are present. At this scale, birds clearly distribute themselves according to specific forms of vegetation determined by height, foliage density etc. Individual stages of woodland development represent a much finer scale within which habitat selection is likely to be determined by a different set of cues, some structural, some based on plant species composition. This idea needs testing in different study areas where a range of habitat structure and tree species composition are available.

The present study tells us little about exactly why it is that different bird species and community parameters respond to different components of the habitat. For example, was the negative influence of birch on several bird variables an indirect one acting through soil fertility and invertebrate abundance (see above)? Also, it is difficult to know whether apparent selection of avoidance of particular tree species is itself a response to the structure of the tree itself or a response to its associated invertebrate fauna. Such questions require an experimental approach.

5.4 Coppice management and bird populations

Coppice systems vary in several respects including rotation length, density of standards, panel size and panel layout. The results of this study are relevant to understanding how each of these components of the system can affect the nature of bird communities. First, however, what are the distinctive features of coppice bird communities that distinguish them from those associated with other management systems? The answer to this question will help to indicate the ornithological objectives of coppice management. As shown above, certain types of mixed coppice, of which Bradfield Woods is a fine example, support remarkably high densities of breeding warblers and Nightingales. Comparable densities of summer visitors are found only in some types of scrub and occasionally in young plantations. High forest systems, on the other hand, can support far higher populations of hole-nesting birds than coppice. Nuthatches, most tits and woodpeckers generally are more abundant in woods with higher numbers of large trees. Coppice and high forest systems support very different communities of breeding birds, both of which are intrinsically interesting and valuable in conservation terms. Woodland management strategies should, ideally, aim to create a balance of both types of habitats, although not necessarily within the same wood.

Compared with other systems of woodland management, coppice is exceptional in providing a relatively large area of young growth with a dense shrub layer. In most high forest systems, the proportion of land covered by young growth is far smaller than in coppice, and often does not develop the same dense vegetation structure. Large, actively-coppiced, mixed broad-leaved woodlands are scarce. It is highly desirable, therefore, that such woods continue to be treated in a way that enhances, or at least maintains, their value as habitats for wildlife associated with young growth. The influence of rotation length, density of standards and panel size on this objective is discussed below. It should be borne in mind that any recommendations concerning future management relate only to breeding birds and that they will not necessarily benefit other wildlife (see Fuller & Warren (1989a,b) for effects of coppice management on other wildlife).

(i) Rotation length Long coppice rotations clearly would not benefit populations of breeding migrants and probably would not enhance the overall abundance and diversity of songbirds in Bradfield. The effect of rotation length on the density of warblers is modelled in Fig.17. With the entire wood under a very short rotation of 12 years or less, the predicted warbler population exceeds 200 pairs. Such short rotations are, however, an unrealistic proposition for the entire wood. Rotations of 20 to 25 years would still create habitats for some 120 to 140 pairs of warblers but with rotations exceeding 30 years the likely population would be less than 100 pairs. By operating a split coppice rotation with a short (say 12 years) rotation alongside a longer rotation, the warbler population could be increased substantially for any given cycle length (Fig.17). The present objective of maintaining such a split rotation in Bradfield Woods is clearly a good strategy for warblers. From an ornithological point of view it is desirable to devote as large a proportion of the wood as possible to the short rotation and to keep the long rotation as short as possible.

(ii) Density of standards The density of large standard trees in Bradfield Woods is currently low compared with that in some other coppiced woods e.g. Brasenose Wood and Ham Street Woods. This probably leads to lower numbers of Nuthatches, tits, and woodpeckers in Bradfield than might have occurred had the density of standards been higher. There was some evidence that those panels with relatively more standard trees held higher numbers of hole-nesting birds, although this could have been a reflection of the distribution of nest boxes. It is also possible that Chaffinches, which feed mainly in the canopy, also benefit from larger numbers of standards in coppiced woodlands (Fuller, Stuttard & Ray 1989). These observations do not, however, constitute a good argument for increasing the numbers of standards in Bradfield Woods because doing so may have a negative effect on numbers of warblers and other summer visitors. The height and cover of the coppice was considerably suppressed under large standards (Table 7). It seems probable, therefore, that increasing the density of standards would reduce the vigour of the coppice and this could, in turn, lead to reduction in habitat

TABLE 7. Coppice growth in relation to presence of standard trees. Values are means; samples sizes were equal for both categories.

	Close to standard	Away from standard	P (Wilcoxon test)
Hazel stool height (1 year, n=58)	2.2m	2.3m	0.09
Hazel stool height (2 year, n=27)	2.0m	2.2m	0.29
Hazel stool height (4 year, n=30)	2.4m	2.8m	0.03
Ash stool height (2 year, n=18)	3.2m	4.1m	<0.01
Coppice cover (0-4 years, n=30)	36%	53%	<0.01

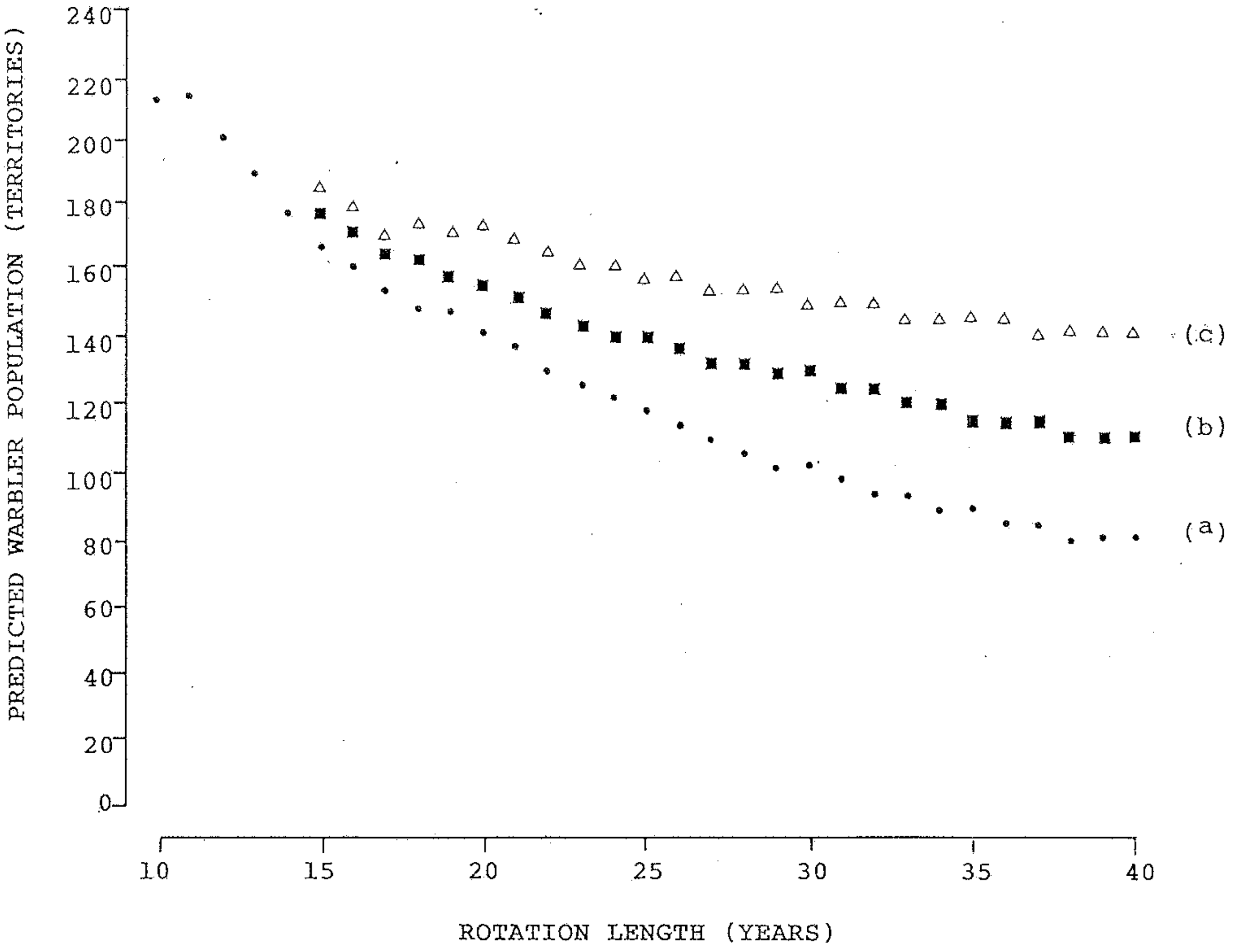


FIGURE 17. Predicted breeding populations of warblers in Bradfield Woods under three types of coppice rotation: (a) a single rotation in which the whole wood is cut on a 10-40 year cycle; (b) a split rotation with 25% of the wood cut on a 12 year cycle; (c) a split rotation with 50% on a 12 year cycle.

quality for migrants. Results from Ham Street Woods (Fuller, Stuttard & Ray 1989) indicated that summer visitors were less abundant in young coppice with high densities of standards. Relationships between standards and bird populations are unlikely to be simple. Although the vigour of the coppice may be lower close to standards, bramble and low shrubs may persist for longer in such places because there seems to be a period of the coppice cycle when the light penetrating the canopy of the standards is greater than that coming through the closing coppice canopy. Possibly, a small or moderate density of standard trees may benefit migrants, either by prolonging a well developed field and shrub layer, or by favouring bramble which creates a dense field layer.

(iii) Panel size and layout There was little evidence of any optimal areas or shapes of panels within Bradfield on the basis of species densities. Wren showed a preference for small panels for which there is no obvious explanation. The data set used for this analysis was not ideal because the panels inevitably varied in age (although this was controlled to some extent) and in location with respect to the age of adjacent panels.

Edge effects appear to be quite widespread amongst forest and woodland bird communities (Fuller 1988, Fuller & Whittington 1987, Hansson 1983, Helle 1985, Tiainen et al 1985). Several mechanisms could account for such edge effects, including spatial variations in insect abundance, plant species composition and habitat structure. Fuller & Whittington (1987) found that the relatively high density of the shrub layer at woodland edges could account for the preferences shown for edges by many species. In Bradfield Woods there was evidence of edge effects in vegetation structure within panels. It is possible that such effects could affect the quality of individual panels for some bird species by reducing - or even by increasing - the area over which there is a dense shrub layer. Where young coppice adjoined very old coppice, the shrub layer was suppressed in approximately the outer 20m (Fig.5). This may have been a consequence of shading or of browsing by deer. Large panels suffer far less from such edge effects than do small panels (Fig.18). Even with a slight edge effect, confined to just the outer 5m, reduction in the shrub layer would seem to be quite pronounced in panels of less than 0.3ha. To ensure the most prolific shrub layer, it is advisable that panels should be no less than 0.3ha and preferably more than 0.5ha. These recommendations apply particularly to panels being cut entirely within old coppice. Panels of this size are also desirable in that the territories of most small woodland passerines are rarely less than 0.3ha.

Edge effects on coppice regrowth were apparently less marked where one young panel was positioned next to another young panel rather than next to an old panel (Figs.15 b and f). This suggests an advantage in cutting in a systematic sequence so that panels of consecutive year classes are close to one another, or even adjacent, rather than widely spaced. A further advantage of such a coppice layout would be that the shading out of the shrub layer might be slightly delayed at those edges abutting younger coppice (Figs.15 g and h). Where a coppice rotation is being started afresh within abandoned coppice, it is clearly undesirable to scatter the young coppice panels amongst the old growth: the aim

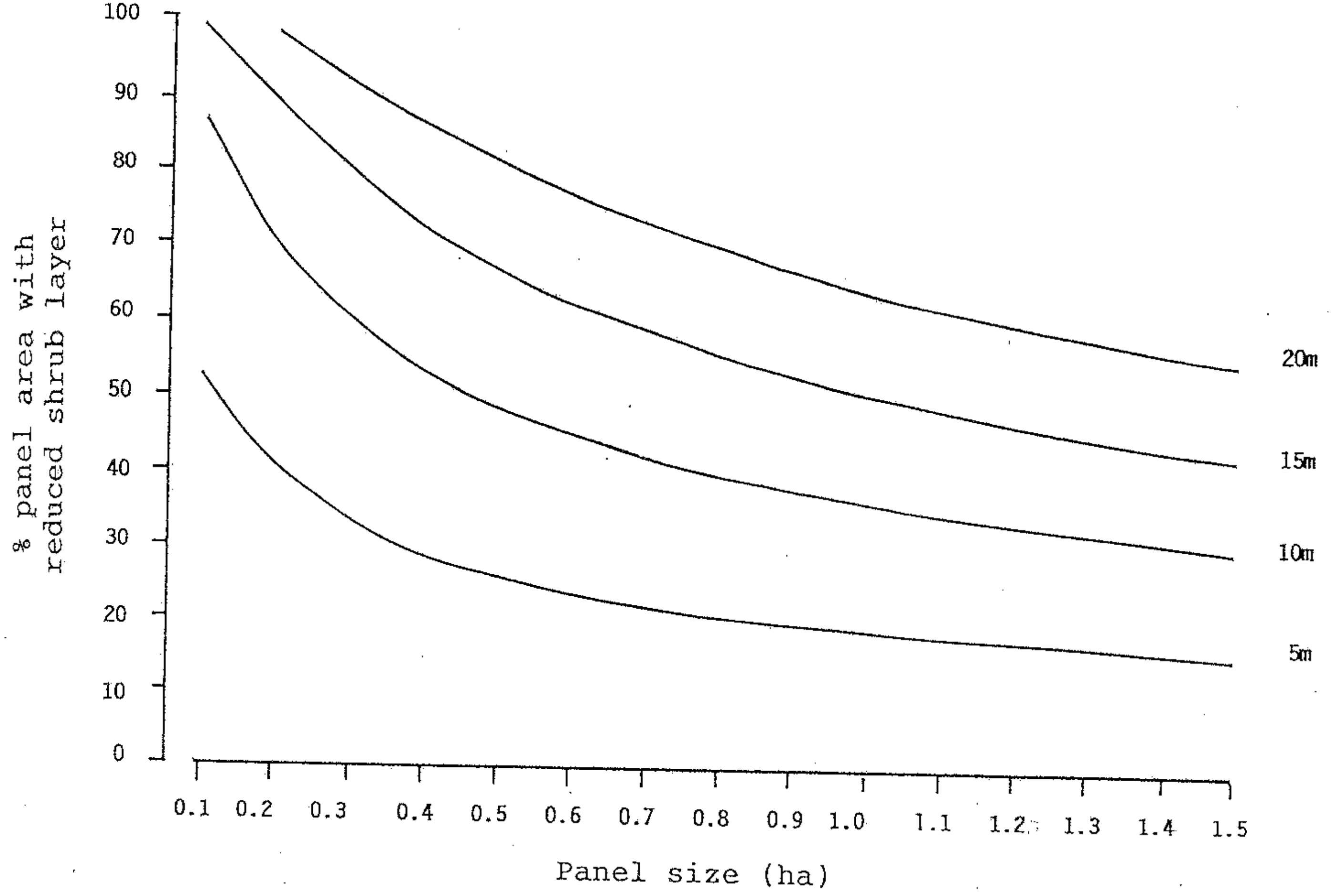


FIGURE 18 Predicted reduction in shrub layer (% area affected) where edge effects extend 5-20m from the panel boundary.

should be to locate the young growth in particular parts of the wood with consecutive year-classes adjacent to one another.

5.5 Suggestions for future research

The results in this paper are based on counts of birds. These have revealed interesting patterns of habitat selection which can form the basis of recommendations for optimising management. Counts reveal rather little, however, about the ways that birds actually utilise the coppice. For example, do feeding birds make particular use of certain age classes, tree species or edges between panels? Studies of marked individuals are needed to provide this detailed level of information which would be of both practical value and of academic interest.

There is a series of interesting questions to answer about the migrant birds. Exactly why migrant birds select coppice of 3 to 8 years is not known for certain (Helle & Fuller 1988). Research to assess whether the availablity of invertebrates altered during the coppice cycle would be extremely interesting in this context. A spin-off from such work is that it would provide more information on the conservation requirements of invertebrates within coppice cycles (Fuller & Warren 1990, in press). Nothing is known about the breeding distribution of individual migrants between years. Do individuals return to the same panels year after year, or do they shift their breeding sites as the vegetation within panels changes? There was some evidence of a time-lag in the response of some warblers, for example Willow Warbler, to the reduction in the shrub layer. Although the shrub layer had been greatly reduced by year 11, there was still a moderate density of birds in that year class (Fig.6), possibly as a result of site fidelity by individual birds. Does the age of individuals affect choice of habitat with respect to coppice age?

It would be valuable to test the predictions made in this report concerning habitat selection and rotation length. This could be done by repeating the census of Bradfield Woods in, say, 8 to 10 years time when most of the panel boundaries will have changed, and a large part of the present old coppice will have been cut. Densities of birds could be predicted in advance for each panel and then compared with the results of fieldwork.

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