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Tree species preferences for foraging site and ways in which the preferences affect the distribution, abundance and species composition of arboreal woodland avifauna

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... being a thesis presented in candidature for

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This is to certify that none of the material contained in this thesis has previously been submitted for a degree in this or any other university.

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ABSTRACT

The tree species preferences by six arboreal bird species and their role in structuring the bird communities in woodland were investigated in two sites in County Durham. Each bird species showed a preference or avoidance for most of the tree species in both study sites. The patterns of tree preference were different for each bird species, and were the basis for efficient partitioning of the foraging niches in woodland. Bird species showed significantly less overlap in tree species choice than in any of the other four niche dimensions examined, making it the most important dimension of the foraging niche. The tree species preferences of the bird species were reflected in the distribution of the birds within the woods. For each pair of bird species the degree of similarity in tree species choice and birds' distribution in the wood were identical. Bird species richness was predictable from tree species richness. There were significant positive correlations between all pairs of the following factors: bird species diversity, tree species diversity, bird species richness, tree species richness, bird density, and the percentage of broadleaved trees. Bird density was negatively correlated with the size of the wood (or compartment), apparently due to an edge effect. Seasonal and year to year changes in the tree preference by birds were explicable in terms of changes in the relative abundance of arthropod prey and other foods available in the trees.

CHAPTER 1

INTRODUCTION

The study of forest bird ecology has in recent years been largely involved in population dynamics, studies of the ecology of single bird species, and modelling in competition and optimal foraging. The development of the niche theory early this century led to studies that attempted to describe the habitat of each bird species. Most studies looked for differences in the feeding habits, since spatial and food related dimensions of the niche were considered important. This produced the concept of vertical zonation in woodland bird communities (e.g. Colquhoun, 1941 and Colquhoun & Morley, 1943). Around the same time Lack (1933) and later MacArthur & MacArthur (1961) studied the ways the bird community is affected by the vegetation, and took the vertical zonation of vegetation as a key factor that allows the coexistence of bird species within a forest system. MacArthur & MacArthur (1961) published their theory of the dependence of bird species diversity on foliage height diversity, which gained widespread support, and further evidence for it was produced by MacArthur et al. (1966), Karr & Roth (1971), and Moss (1978a). The concept of horizontal separation of the feeding niche is more recent. Hartley (1953) recognized the use of different parts of the tree as a possible means of niche separation, and Edington & Edington (1972) developed further the concept of partitioning of the feeding niche by choice of different feeding sites (e.g. trunk, branch, twig).

The current ecological thinking accepts a combination of vertical and horizontal zonation as the baseline for studies on foraging behaviour, and this is regarded as fact by conservationists in their arguments in favour of one woodland and against another. However, recent work does not support this approach fully (Orians, 1969; Wiens, 1974; Willson, 1974; Tomoff, 1974; Roth 1976; Erdelen, 1984).

Work by Hartley (1953) and Gibb (1954) showed that birds can divide up their habitat by choosing to feed in different tree species. However, neither of these researchers continued investigations of tree choices further, and later work on this topic was stifled by the categoric statement by MacArthur & MacArthur (1961) that "plant species diversity ..... has nothing to do with bird species diversity", because "natural selection would tend to eliminate a situation in which bird species diversity depended on tree species diversity", and their failure to show a relationship between bird and tree species diversities. However, MacArthur & MacArthur (1961) took selective foraging to involve all or nothing responses only, and ignored partial preferences. Neither did they appreciate the strong correlation that exists between foliage height diversity and tree species diversity, whereby the two measure more or less the same thing. The lack of residual in the regression analysis of MacArthur & MacArthur (1961), after the effect of foliage height diversity had been removed, is explainable by this correlation.

Work on selective use of trees - tree preference - was revived in America since the seventies (Sturman, 1968; Willson, 1970;

Austin & Smith, 1972; Holmes & Robinson, 1981; Franzreb, 1983b). The work showed that birds in temperate regions show distinct preferences for certain species of tree for foraging, thereby establishing niche separation between the different species of birds. However, the studies only established the existence of preferences with little attempt to find out why the preferences existed or what consequence they might have to the bird community. Tree preferences are still being ignored in work in Europe (but see Ulfstrand 1975), and many have been satisfied simply to distinguish between broadleaved and coniferous tree species (Moss 1978b; Newton 1986; NCC 1986).

The only evidence for this division is the faunal lists of insect species associated with each tree species (Southwood, 1961; Southwood et al, 1982), on which the native broadleaves come on top of the list with the highest numbers of species associated with them, whilst conifers and introduced species support only few insect species. The validity of interpreting these faunal lists by others as evidence for some tree species being better foraging sites for birds (e.g. Peterken, 1981) has been virtually unchallenged. The tree species with the largest diversity of insect species are attractive to the entomologist, but birds seem to show less interest in whether they feed on one or twenty species of caterpillar, as long as they are palatable. The availability of quantities of insects and other foods is of prime importance to the birds (Gibb & Betts 1963), not the prey species diversity.

When the biomass and abundance of insects on different species of trees is examined, it becomes clear that some of the introduced

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trees, including conifers, support high densities of insects, and some native tree species turn out to be low in the ranking (e.g. Bevan, 1987). This ought to be enough to raise a suspicion that the relationship between birds and trees may be more complicated than is generally thought, and that the individual tree species present, regardless of whether they are broadleaved or coniferous, may play an important role in structuring the bird community in the wood.

In the face of the current large scale commercial afforestation with coniferous trees, there is increasing interest in and concern about the value of plantation forests as animal and plant habitat. Large areas of the plantations are currently at the start of the second rotation, and there are also plans for more land be put under commercial forestry. 26,000 ha was planted in 1988 (Forestry Commission, 1989). A number of surveys have suggested that plantation forests are of low value for wildlife (e.g. Moss, 1978a, 1978b; Williamson, 1969). The small number of bird species has in most cases been attributed to the forests being a monoculture of non-native tree species and to the structural uniformity of the plantations, which, being even-aged and generally lacking a subcanopy and understorey, do not provide suitable habitat for shrub nesting species. Nor do they allow spatial separation of bird species in the canopy, and so the diversity and numbers of birds that can occupy these forests is reduced.

Forest plantations form an extensive habitat. The Forestry Commission currently owns 892,000 ha of plantations (House of Commons Report, 1987), which is less than half of the afforested area in Britain. Despite this, ecologists have paid little

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attention to plantations, and many conservations bodies do not recognize plantations as potential wildlife habitat. The Nature Conservancy Council and some other conservation organisatins, are currently pressing for changes in forestry plantations to make them more attractive to wildlife.

This study was initiated to establish tree species preferences for some common birds inhabiting British woodlands, including plantations, and to establish the importance of tree preferences in the structuring of the bird community in a wood. The study concentrated on the arboreal guild of birds, and therefore conclusions drawn from the study can only be applied to the bird species that are dependent on the canopy layer of the wood for their presence. The ground dwelling species can be assumed to be affected by different aspects of the woodland, and are left outside the scope of this investigation, as are species that only use the wood for roosting and/or nesting and feed outside the boundaries of the wood.

CHAPTER 2

METHODS

2.1 Study sites

    Two study sites were chosen; Hamsterley Forest and Great High
Wood in County Durham (Fig 2.1).

2.1.1 Hamsterley Forest

    Hamsterley Forest is a Forestry Commission plantation near
Barnard Castle in County Durham (54° 40' N 1° 54' W) (Fig 2.2). It
is a primarily coniferous forest, but there is a considerable
broadleaved element, particularly in the valleys and on the
streamsides. About 90% of the total area consists of conifers with
sitka spruce (<u>Picea sitchensis</u>) being the most dominant tree
species over a large part of the forest. The range of altitudes
within the forest is 150-430m above sea level. The parts of the
forest at high altitude (more than 250m above the sea level) are
almost exclusively coniferous. These areas are of the typical
'blanket forest' type containing large areas of even-aged, one or
two species stands of trees. It was all planted within a period of
three years in the early 1950's, and consists predominantly of
sitka spruce and Scots pine. These stands are impenetrable in the
unbrushed, unthinned pole-stage of growth. The low lying, eastern
parts of the forest have more variety in age structure and species

Fig 2.1: Map of Great Britain to show the
location of Great High Wood and
Hamsterley Forest.

Great High Wood
Hamsterley Forest
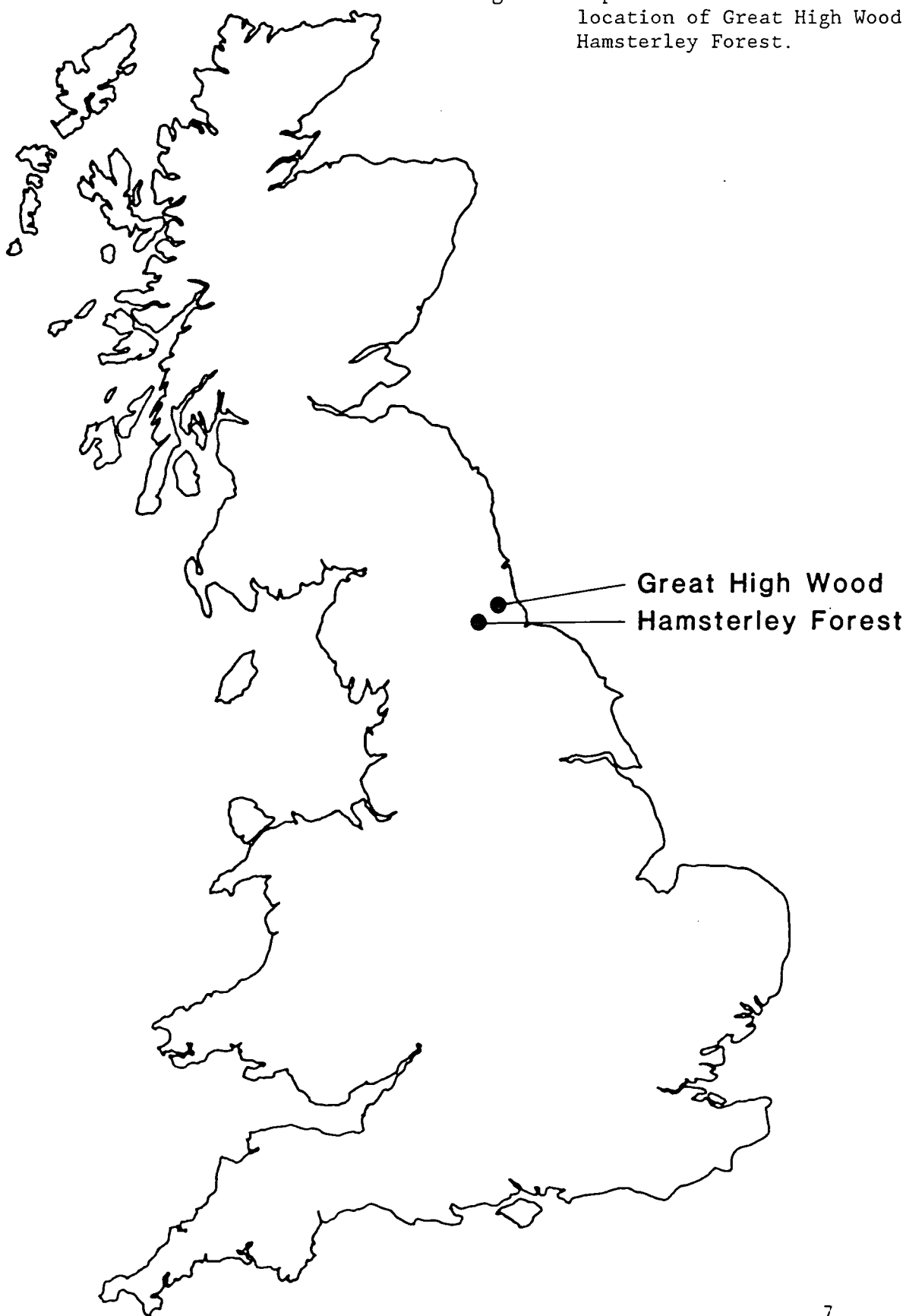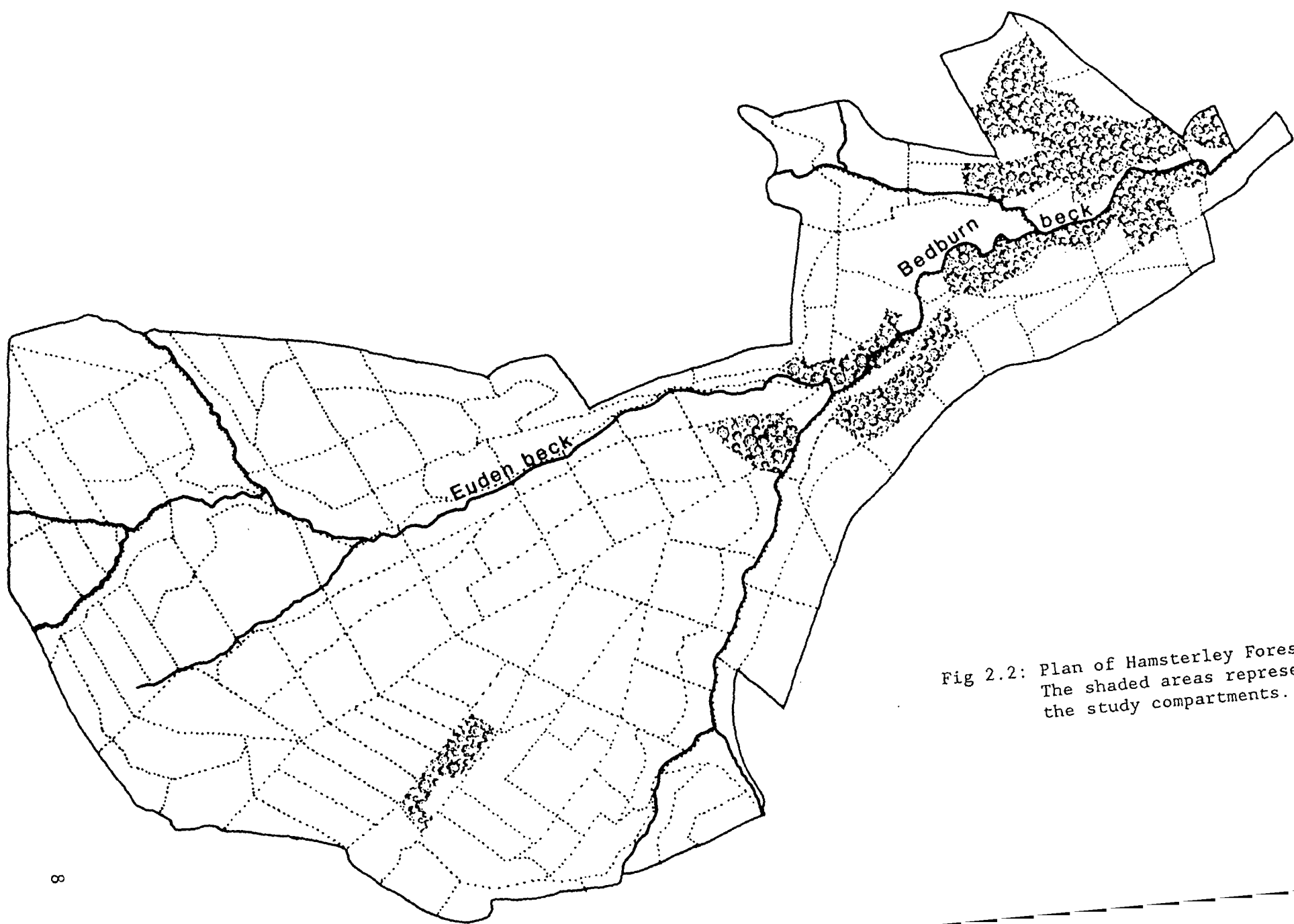
Fig 2.2: Plan of Hamsterley Forest. The shaded areas represent the study compartments.

Bedburn beck

Euden beck

composition. This part is the original core of the forest, where planting was spread over many years since the early part of this century. Some of the plantations in this part of the forest were planted on a site of mature oakwood, while most of Hamsterley Forest is afforested moorland.

The forest is divided into blocks of trees referred to as compartments. Each compartment contains a uniform stand of even-aged trees, and hence there is little structural diversity within the compartments. None of the compartments contains a shrub layer. Generally only one or two tree species were planted together in any one compartment, but some compartments contain as many as 4-6 crop species. In addition, small groups and belts of broadleaved trees have been planted as a conservation measure, and there has also been considerable natural regeneration of broadleaved trees in some localities. These additional trees result in up to 14 tree species to be found in a single compartment.

The total forest area of Hamsterley Forest is ca. 2000 ha, of which the study area covered 150 ha. A total of 31 compartments were chosen for the study, the majority adjacent or in close proximity to each other, and situated in the older part of the forest. The study compartments were chosen to represent a wide selection of tree species of similar age. Each study compartment was planted in the 1930's or early 1940's, with the exception of one compartment of beech, which was planted in the late part of the last century. The selection of a single age class reduced the variability in tree sizes and thereby the possible biases of unequal canopy sizes. The canopy size is known to differ from one

tree species to another in natural conditions. However, in Hamsterley Forest trees of each species were planted at the same density, effectively forcing the canopy of each species to be of similar size. In addition to this, the trees in the study compartments were not old enough for natural thinning to have occurred and the accompanying expansion of tree crowns to have taken place. Because of the structure of Hamsterley Forest it was unnecessary to compensate for tree volumes, and the tree frequencies could be used directly in calculations of tree species preferences. The compartments provided a set of uniform study sites with tree species composition the main variability between them. The size of the study compartments varied between 1 and 16 ha (compartment sizes are given in Appendix 2). The tree frequencies of each compartment were available from the forest record, but because of the selective thinning of some compartments and the natural regeneration of broadleaves, it was necessary to sample most of the compartments in order to obtain more accurate data on tree composition. The distance measures (reviewed by Cottam & Curtis, 1956), so widely and successfully used in sampling of trees, were not appropriate for Hamsterley Forest (since they require trees to be randomly distributed) and a transect method was used. The width of the transects was 4m, and they were placed at right angles to any obvious pattern in the distribution of tree species, thereby running either lengthways or across the compartment. The number of transects varied with the size of the compartment, and their total area covered ca. 10% of the area. The

Table 2.1

Overall tree species composition in the study
compartments in Hamsterley Forest

Common name	Scientific name	Abbreviation	Frequency
Oak	*Quercus robur*	Oa	23%
European larch	*Larix decidua*	EL	18%
Scots pine	*Pinus sylvestris*	SP	17%
Japanese larch	*Larix caempferi*	JL	7%
Birch	*Betula pendula*	Bi	7%
Beech	*Fagus sylvatica*	Be	6%
Norway spruce	*Picea abies*	NS	6%
Sitka spruce	*Picea sitchensis*	SS	5%
Alder	*Alnus glutinosa*	Al	4%
Western hemlock	*Tsuga heterophylla*	WH	3%
Ash	*Fraxinus excelsior*	As	2%
Sycamore	*Acer pseudoplatanus*	Sy	1%
Rowan	*Sorbus aucuparia*	Ro	1%

based on a sample of ca. 10,000 trees

tree species present in the study compartments and their relative
frequencies are listed in Table 2.1.

2.1.2 Great High Wood

Great High Wood is a seminatural broadleaved wood of 28 ha
(Fig 2.3). It is a former SSSI owned by the University of Durham
and is located on the outskirts of Durham city (1° 34'W 54° 46'N).
The arrangement of the mature trees shows that the wood was
originally planted, but natural regeneration has obscured the
original patterns to a large extent. Six species of trees are
common in Great High Wood, and another 10 species are present at
lower densities. Elder, hawthorn and other shrubs are also present.
All age groups of trees are represented from seedlings to mature
trees, forming a mixture of species and good structural diversity
over most of the wood. The only exceptions are three areas of
uniform larches, which were planted in the 1960's when the wood was
managed by the Forestry Commission. The same transect method was
used to establish the tree frequencies as in Hamsterley Forest. A
list of the tree species present in the wood and their relative
frequencies is presented in Table 2.2. Tree volumes differed more
between species in Great High Wood than in Hamsterley Forest. This
was considered a possible source of bias if tree frequencies were
used to calculate the tree preferences of the birds. However, when
the preferences based on tree frequencies were calculated, it was
found that in most cases the preferences went against the trend in
canopy sizes. Therefore using frequencies based on tree volumes

rather than numbers would only have accentuated the preference and avoidance patterns already established. A good example of this is the strong avoidance by all bird species of beech, which has a large canopy volume, and the strong preference for larch with small canopy volume. Clearly, compensating for volumes would not have changed the outcome. Therefore, the use of tree frequencies for calculating the tree preference index in Great High Wood was considered justified, and was used in order to standardize the techniques used in the two study sites.

2.2 The bird fauna in the woods

Seventeen species of passerines, which were largely arboreal and commonly observed, were recorded in both forests. The main part of the study concentrated on six species, which were resident throughout the year and observed in large enough numbers to allow statistical analysis to be performed on the data: blue tit *Parus caeruleus*, great tit *Parus major*, coal tit *Parus ater*, goldcrest *Regulus regulus*, chaffinch *Fringilla coelebs*, and treecreeper *Certhia familiaris*. These six species formed ca. 85% of the arboreal bird fauna in Hamsterley Forest and 91% in Great High Wood. Tables 2.3 and 2.4 list the relative abundance of all the arboreal passerine bird species in the two woods. The scientific names of the bird species are listed in Appendix 1.

road

WOOD

HIGH

stream

road

GREAT

beck
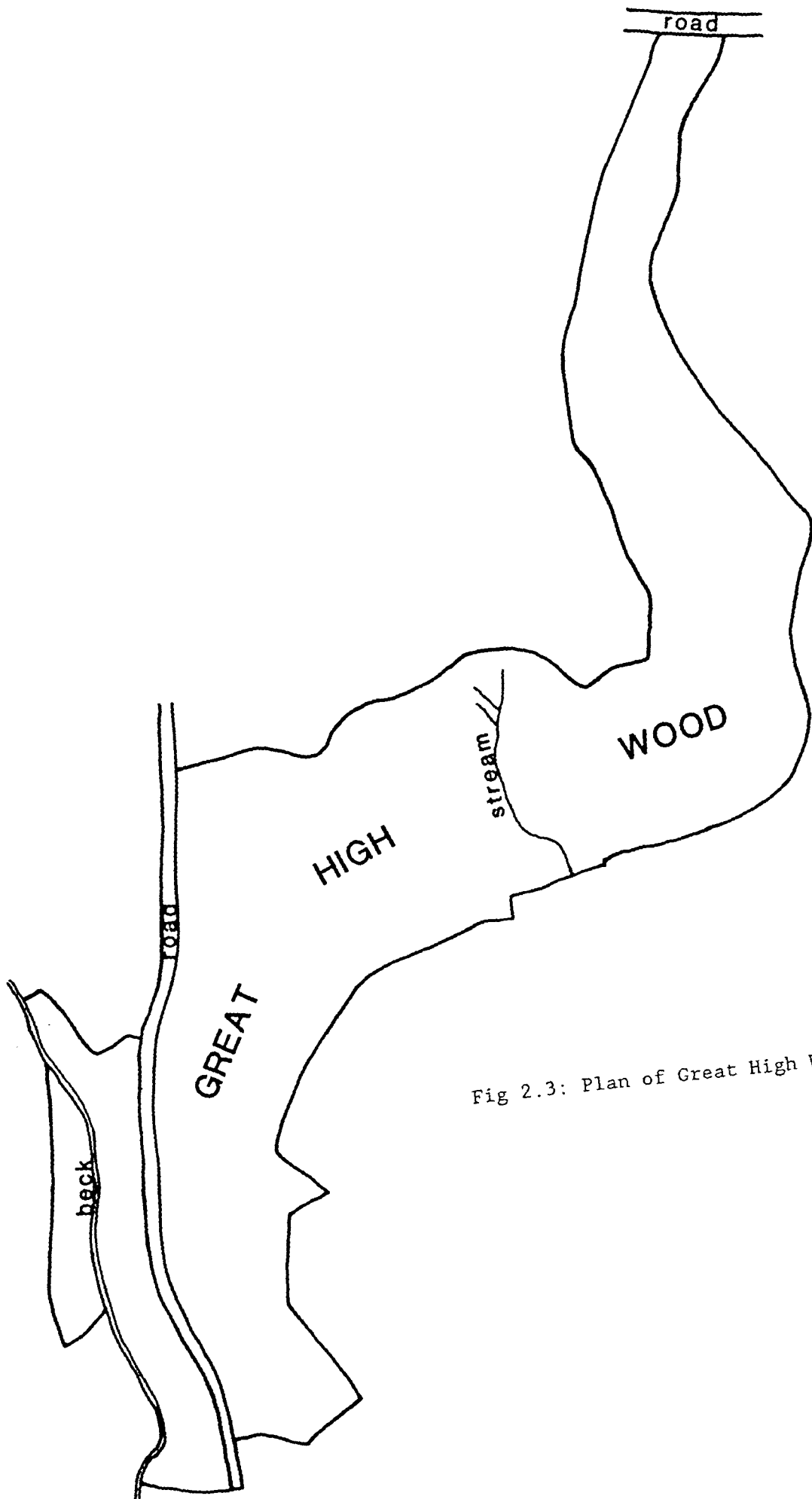
Fig 2.3: Plan of Great High Wood.

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Table 2.2

Tree species composition in Great High Wood

Common name	Scientific name	Abbreviation	Frequency
Oak	*Quercus robur*	Oa	26%
Beech	*Fagus sylvatica*	Be	24%
Sycamore	*Acer pseudoplatanus*	Sy	21%
Larches*	*Larix sp.*	Lx	10%
Birch	*Betula pendula*	Bi	7%
Holly	*Ilex aquifolium*	Ho	4%
Elm	*Ulmus procera*	Em	2%
Others (see below**)		Ot	6%

based on a sample of ca. 1300 trees

*   The larches consisted of 40% European larch and 60% of a hybrid between the European and Japanese larch with <1% of Japanese larch. Since birds responded to the European larch and the hybrid in the same manner, no distinction was made between them.

**   Other trees present were wild cherry (*Prunus avium*), alder (*Alnus glutinosa*), ash (*Fraxinus excelsior*), rowan (*Sorbus aucuparia*), Scots pine (*Pinus sylvestris*), sweet chestnut (*Castanea sativa*), horse chestnut (*Aesculus hippocastanum*), yew (*Taxus baccata*), each of which were present at frequencies of 1.5% or below.

2.3 Data collection

The field observations were made between March and October inclusive in 1984, 1985 and 1986. The visits to the study sites were evenly spread over the field season with 13-17 days of fieldwork during each calendar month. Fieldwork was carried out between 8am and 4pm. No observations were made at dusk or dawn because of the great fluctuations in bird counts at these times (Verner & Ritter, 1986). Weather conditions are known to affect the detectability of birds (Grubb, 1975, 1977; Robbins, 1981). Therefore, no fieldwork was carried out on rainy days, or on days when wind speed exceeded Beaufort 5 (12mph), which is the windspeed at which Robbins (1981) found a strong decline in numbers of birds detected in a census. Observations on foraging birds and estimates of bird density were made throughout the season, except for a three week period in June when the birds were feeding nestlings. During this period other work was carried out, which, however, is outside the scope of this thesis. The data collected consisted of i) density estimates of arboreal passerines, ii) spot observations of foraging birds, and iii) timed observations of foraging bouts.

Density estimates of passerines were obtained concurrently with other data collection. There are three commonly used and accepted methods of censusing woodland birds: territory mapping, and transect and point counts. Territory mapping was inappropriate for this study, since the field season extended beyond the birds' breeding season. Transect and point counts are both acceptable methods for census work throughout the year, and both methods are

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widely used. Transect counts require the observer to walk along a straight line through the wood and count each bird seen within a predetermined distance from the line. Point counts are effectively transect counts at zero speed: all birds within a predetermined distance of the observation point are counted for a period of time. Both the time and distance varies with the habitat and the bird species under study. Generally, transect counts are better suited to large uniform tracts of forest, while point counts perform better in more fragmented environments. Dawson & Bull (1975) reported that the two techniques were equally effective in detecting birds in woodland environment. Point counts are generally thought to be affected less by variations in the habitat (Dawson & Bull, 1975; Källander et al. 1977; Ramsey & Scott, 1979; Reynolds et al. 1980; Svensson 1980).

A point count technique was selected to establish the bird densities in this study for two main reasons. Firstly, the detectability of birds in different tree species is not constant. Secondly, the detectability of each bird species differs. The point count method allows each area to be searched for a longer period of time than transects, thereby allowing the less detectable bird species to be found. This reduces the bias of differential detectability between bird species as well as between areas with different tree species composition. Thirdly, transect counts require the observer to travel at a constant speed along the transect, while the time interval between successive point counts does not need to be constant. Since observations on foraging birds were made during the same visit as the density counts, this

requirement for transect counts could not be easily met. It was established during preliminary observations that all arboreal birds could be detected within 30m radius of the observer in each of the tree types in the study area. Therefore birds that were seen or heard within 30m radius of the point were counted. Each point count was limited to five minutes in order to minimize the effect of birds moving into or out of the area. It was estimated that the efficiency of these counts was about 80-90%. The densities of all 17 species of birds were calculated from these counts. The bird density would be expected to increase significantly after the nesting season. However, only a small, non-significant increase in the bird density was found, and this was confined to the two months immediately after fledging. Therefore, it appears that the post-breeding dispersal occurs quickly after fledging, and does not significantly alter the bird densities in the study areas. It was considered on these grounds that density measurements for the whole field season could be pooled together. The bird densities used in the analysis were the mean densities calculated from all censuses made during the study. The bird densities measured in this study are comparable with those found by Morse (1978), Moss (1978), and Williamson (1974a, 1974b, 1975). For instance, Williamson (1974a, 1974b,1975) reported densities of blue tits ranging 0.2-1.8/ha and coal tits 0.3-1.7/ha in Scotland, which are similar to the densities in Hamsterley Forest in corresponding wood types. The great tit, goldcrest and treecreeper densities were also comparable, but Scottish woods tended to support higher densities of chaffinches than my study sites.

Table 2.3

Percent frequencies of sightings of all arboreal bird species in
the study compartments in Hamsterley Forest

| Common name | Percentage | | | |
	1984	1985	1986	3 yrs
Blue tit	14.0	19.4	15.6	16.6
Great tit	6.5	8.0	4.0	6.2
Coal tit	33.2	27.3	38.3	32.7
Goldcrest	11.8	15.6	6.8	11.6
Chaffinch	23.2	13.4	18.2	17.9
Treecreeper	1.8	2.1	1.8	1.9
Long-tailed tit	0.4	1.4	0.8	0.9
Siskin	0.1	2.4	0.9	1.2
Crossbill	0.0	3.6	5.8	3.3
Phylloscopus sp.	5.6	4.4	5.0	4.9
Willow tit	0.3	0.2	0.3	0.2
Nuthatch	0.7	0.8	0.5	0.7
Spotted flycatcher	1.8	0.7	0.6	1.0
Pied flycatcher	0.2	0.7	1.3	0.7
Blackcap	0.7	0.1	0.3	0.3

based on a total of ca. 10,600 sightings

Table 2.4

Percent frequencies of sightings of all arboreal bird species in
Great High Wood

Common name	Frequency			
	1984	1985	1986	3 yrs
Blue tit	53.9	52.9	58.1	54.8
Great tit	20.4	22.7	18.1	20.6
Coal tit	5.3	5.3	8.0	6.1
Goldcrest	1.6	1.7	0.6	1.3
Chaffinch	6.6	6.1	5.9	6.2
Treecreeper	1.6	1.7	2.6	1.9
Long-tailed tit	0.7	2.3	0.8	1.3
Nuthatch	2.7	1.9	2.9	2.5
Phylloscopus sp.	6.1	2.7	1.9	3.6
Blackcap	1.0	0.5	0.8	0.8
Spotted flycatcher	0.0	0.0	0.3	0.1
Willow tit	0.2	0.2	0.0	0.1
Siskin	0.0	0.6	0.0	0.2
Goldfinch	0.0	1.4	0.0	0.6

based on a total of 8,000 sightings

The main analyses were based on spot observations of the birds that were encountered. When a bird was found in a tree, it was identified, and the following details recorded of its location and behaviour: i) the tree species the bird was seen in, ii) height of the bird above ground, iii) height of the tree, iv) position of the bird within the tree (i.e. trunk, inner and outer branches, and inner and outer twigs) and v) the activity of the bird at the time of the initial sighting. If the bird was feeding, the substrate from which food was obtained (e.g. bark, leaf, cone), the feeding posture (perched, hanging, hovering) and the method of obtaining the food (glean - picking the prey item from the surface, probe - manipulate the substrate in order to get at food concealed within the plant tissue, sally - a flight off a perch to capture airborne prey) was recorded. For each observation the time of the day, the compartment the bird was found in (Hamsterley Forest only) and temperature in the shade were recorded. These details, which were obtained as the bird was first seen, formed the standard spot observations on which the majority of the analyses are based. All variables were recorded for each observation, but in some cases it was not possible to determine the substrate from which the prey was taken.

The height of the foraging bird and the tree height were estimated by eye as each observation was made. The accuracy of these estimates was calibrated before the commencement of the fieldwork by comparing estimated tree heights with measurements of the trees using simple trigonometry, and these were repeated frequently during the field season to ensure consistency.

Only one feeding observation was recorded for each bird as long as it remained within the tree in which it was first seen. A second observation was recorded only if the bird moved to feed in another tree. This applies both to the spot observations and the timed feeding bouts.

In 1984 and 1985, the duration of feeding bouts in different tree species was recorded together with the number of attempts to capture prey (hereafter referred to as an attack on a prey item) within that time. A feeding bout is defined as a period of continuous foraging during which the bird does not engage in any other activity than search for food and feed. Each feeding bout was timed with a stopwatch from the moment a bird commenced foraging in a new tree until an activity other than foraging was observed, or the bird flew to another tree. Only complete bouts were measured. Because of the distance between the observer and the birds, it was not feasible to establish a rate of success for the foraging birds.

In 1985 and 1986 the density of insects in the common tree species was sampled in order to study the possibility of a connection between the tree preferences and the prey availability in the trees. One sample was taken from six trees of each species on every sampling date. These trees were located in the study compartments, and the same compartments were used for insect sampling each time. The samples were collected from approximately 4m above ground. A terminal branch was selected, enclosed in a muslin bag, which was closed up with a drawstring, and then cut from the tree. The arthropods were killed with ethyl acetate before the bag was opened and the animals extracted by hand. The insects

were identified to family and the other arthropods to class. The animals were counted and their length was measured.

Due to the extent of the study area in Hamsterley Forest it was not possible to visit every compartment at each visit to the forest. This resulted in an uneven number of visits to the compartments. To compensate for this discrepancy, the frequencies of tree species in each compartment were weighted with the time I spent in the compartment for calculations of tree preference. For instance, if twice as much time was spent in compartment A than in compartment B, the tree frequency used in the calculations would be based on trees in compartment A counted twice plus trees in compartment B counted once. The tree frequencies in table 2.1 are weighted in this way and hence, strictly speaking, are frequencies at which each tree species was encountered rather than straightforward tree proportions in the study site as a whole. In most cases the difference between the actual tree frequencies and the weighted encounter frequencies is only small.

2.4 Analysis of data

Most data were put into computer files and SPSS (Statistical Package for the Social Sciences; Hull & Nie, 1981) was used for statistical analyses.

Student's t, paired t-test and chi-square were used in hypothesis testing. Probability level of $p < 0.05$ was used throughout to reject the null-hypothesis. The result was noted as non-significant (n.s.) if $p > 0.05$. The degrees of freedom are

presented with each X^2 value. For most t-tests the degrees of freedom were high, with $t \geq 1.96$ indicating significance. For reasons of clarity, the degrees of freedom are shown for t-tests only if they were less than 30. Mean +/- one standard error are presented where appropriate. Only significant values of X^2 and t-test are shown in the text.

The tree preferences shown by the birds were calculated as tree preference index (TPI):

$$TPI = \frac{obs - exp}{exp}$$

where obs = the observed number of birds seen feeding in

the tree species

exp = the number of birds expected to feed in that

tree species calculated from the percent

frequency of the tree species

Index values close to zero indicate random use of the tree species, whereas values significantly above zero indicate preference and significantly below zero avoidance of that tree species. The minimum value for the index is -1. Chi-square was used to determine significance.

A number of indices and other measures exist for calculation of the extent of similarity or difference in the habitat utilization by two species of animals, generally referred to as niche overlap. They range from simple coefficients used to describe the co-occurrence of two species (eg. Sorensen's coefficient of similarity) and indices that rely on probability distributions (eg.

Morisita's index of similarity) through to overlap indices based on information theory. Horn (1966), Schoener (1968), Hurlbert (1978) and Lawlor (1980) have published reviews and evaluations of the various overlap indices, and therefore detailed discussion is not included here. Some of the overlap indices measure probability of interspecific encounter and are generally derived from Lotka-Volterra equations, a.o. Morisita's index of overlap. Horn (1966) proposed an overlap index based on Shannon & Wiener information theory. Despite the wide use of these indices they are thought by many (e.g. Hurlbert, 1973) to be inappropriate as indices of overlap.

Another frequently used index is

$$C_{xy} = 1 - 1/2 \left(\sum |p_{xi} - p_{yi}| \right) = \sum \min(p_{xi}, p_{yi})$$

where p_{xi} is the fraction of individuals of species X and p_{yi} the fraction of individuals of species Y in each habitat variable examined. This was suggested by Goodall (1973) to be the most appropriate measure of 'species distributional similarity'.

In the current study, an overlap index was required that would compare the frequency distributions of two or more bird species over a series of categories into which each niche dimension is divided. It was also required that significance tests could be performed on the data in order to establish whether the overlap between two bird species is low enough to facilitate niche partitioning. These criteria were satisfied by the index recommended by Goodall (1973). Furthermore, since Goodall's index

measures the frequency distribution of birds between the categories of each niche dimension, the resource state abundance, which was discussed by Hurlbert (1978), does not cause problems when interpreting the results. Southwood (1966) used the same index as Goodall (1973) with the exception that instead of proportions he used percentages of individuals found in each category of the habitat variable, and called the index percentage similarity, %S. All calculations of niche overlap in this study used Southwood's percentage similarity. The following hypothetical situation illustrates the calculation of the niche overlap. If species A and B use the same five habitat categories, the overlap between the two species in this niche dimension would be:

category   a   b   c   d   e

A   26%   14%   10%   1%   49%

B   12%   30%   8%   22%   28%

%S= 12+14+8+1+28=63%

This measure of similarity/overlap between two bird species indicates how similar their choices are with respect to each habitat variable considered. The percentage similarity will be referred to as the niche overlap, and it was calculated for five niche dimensions (tree choice, choice of position within a tree, height of the foraging station above ground, height of the foraging tree, substrate) and for combinations of these. The lower the overlap in relation to any of the niche dimensions, the more that dimension contributes towards niche partitioning.

A source of arbitrariness that affects all indices of overlap is the choice of categories used in the calculation of the index.

Depending on the number and boundaries of these categories, overlap between the same two distributions could range from zero to very near one. Therefore, care needs to be taken in particular in dividing continuous distributions. (See Schoener,1968, for a discussion on choice of categories within a niche parameter.) In the current study, only some of the niche dimensions were affected by this bias. The height intervals of both bird and tree heights were chosen after careful preliminary analysis. Initially, overlap was calculated for 1m intervals, and recalculated with increasingly larger intervals. At shorter intervals there was little change in the calculated overlap value, but as height intervals were increased to 5m and beyond, the overlap between pairs of bird species increased significantly suggesting that intervals that the birds reacted to were being grouped together. Therefore, the height categories chosen represent the optimum divisions: further grouping would lead to loss of information, but a larger number of categories would not increase the accuracy of the results. The foraging heights of the birds and the heights of the trees were divided into four groups: 0-4m, 4-8m, 8-12m, >12m. Tree species, substrates, and positions within a tree are naturally discrete units. As such they are obvious choices for niche categories, and therefore pose no similar problems to those encountered with height intervals. The number of categories in these niche dimensions is determined by the habitat, not by the observer, and therefore the maximum segregation obtainable by bird species depends on the diversity of the niche in any one dimension. This results in a greater chance of niche partitioning in some habitats than others,

and the extent to which the birds take advantage of the differing numbers of habitat categories available is investigated.

Bird species diversity and tree species diversity were calculated for individual compartments in Hamsterley Forest and for the two forests as a whole using Shannon and Weaver diversity index (H):

$$H = -\sum_{i=1}^{S} \frac{n_i}{N} \ln \frac{n_i}{N}$$

where H = index of diversity

n = number of birds in a tree species

N = total number of birds of that species

S = number of tree species

ln = natural logarithm

All calculations and significance values are based on figures rounded to two decimal places.

Additional methods are presented where appropriate in the following chapters.

CHAPTER 3

PATTERNS OF TREE USE IN GREAT HIGH WOOD '

3.1 Tree species preferences

The initial assumption to be tested was that birds do not differentiate between tree species, but are equally likely to feed in any tree they encounter independent of its species.

Table 3.1 shows the percent frequencies at which the six bird species were feeding in each of the tree species present in Great High Wood. Blue and great tits and treecreepers foraged mainly on oak, and also used sycamore, larch and birch extensively. However, the extent to which each bird species used these tree species was different. Foraging by the chaffinch was split almost equally between oak, sycamore and larch, with only few birds feeding in the other tree species. Coal tits and goldcrests fed primarily in larch, but coal tits used oak more extensively ^{o}than goldcrests, while goldcrests were found more frequently than coal tits in sycamore and holly. Holly was also used by blue and great tits. Elm and the uncommon species of tree (see Table 2.2 for species) were only used to a minor extent by all the bird species. Beech was virtually ignored by all the bird species, despite it making up 24% of all trees in the wood.

The tree preference indices (Table 3.2) indicate that each bird species preferred some tree species and tended to avoid others. Oak was preferred by blue and great tits and treecreepers,

Table 3.1

Percentage of feeding observations in each tree species for six
species of birds in Great High Wood, March - October, 1984-86

Tree species	Blue tit	Great tit	Coal tit	Gold-crest	Chaf-finch	Tree-creeper
Oak	41.0	32.7	19.4	11.4	32.1	56.3
Beech	2.8	1.8	2.3	0.0	2.1	4.7
Sycamore	19.8	21.6	8.1	12.7	33.7	10.2
Larch	12.9	13.4	56.9	55.7	22.8	16.9
Birch	10.5	14.3	6.4	6.3	4.1	8.3
Holly	5.1	9.8	4.0	11.4	0.5	1.2
Elm	2.5	1.8	1.7	0.0	3.6	0.0
Others	5.4	4.6	1.2	2.5	1.0	2.4
Sample size	3003	768	346	79	193	254

Table 3.2

Tree preference index of six bird species in Great High Wood,
March - October 1984-86

Tree species	Blue tit	Great tit	Coal tit	Gold-crest	Chaf-finch	Tree-creeper
Oak	0.58*	0.26*	-0.25*	-0.56*	0.24	1.17*
Beech	-0.88*	-0.93*	-0.90*	-1.00*	-0.91*	-0.80*
Sycamore	-0.05	0.04	-0.61*	-0.39	0.61*	-0.51*
Larch	0.28*	0.33*	4.64*	4.52*	1.26*	0.68*
Birch	0.55*	1.11*	-0.06	-0.06	-0.39	0.22
Holly	0.21*	1.31*	-0.04	1.69*	-0.88*	-0.72*
Elm	0.39*	0.03	-0.02	-1.00	1.05	-1.00*
Others	-0.12	-0.25	-0.81*	-0.58	-0.83*	-0.61*
Sample size	3003	768	346	79	193	254

* = significant preference or avoidance (chi-square)

while coal tits and goldcrests tended to avoid the tree. Beech was strongly avoided by all the birds, while they tended to be neutral to sycamore, with only chaffinches showing a preference for it. Larch was universally preferred, with the strongest affinity shown by coal tits and goldcrests. This strong preference for larch caused the apparent avoidance of oak by both these species, and the avoidance of sycamore by coal tits, since both oak and sycamore were used to a considerable degree (Table 3.1) by both bird species. Birch was preferred by blue and great tits (Table 3.2), and elm only by blue tits. The use of holly was strongly divided to a preference by blue and great tits and goldcrests, and avoidance by chaffinces and treecreepers. The uncommon tree species were avoided by all birds, this avoidance being significant for three of the bird species. It is possible that these trees were sufficiently rare not to be profitable for the birds to search them out, but that the birds fed habitually in other species of trees. This is likely to be the case for at least some of the tree species, e.g. alder was used very little in Great High Wood, but in Hamsterley Forest, where it is considerably more abundant, it was preferred by some of the bird species (see Table 4.3).

The data presented above shows that tree species were not used in proportion to their frequency by the bird species, and therefore the null hypothesis is rejected.

Each bird species used the tree species to a different extent (Table 3.1). These differences in tree use were investigated by comparing pairs of bird species in each tree species (Table 3.3). A significant difference in the extent a tree species is used by two

Table 3.3

Comparison of pairs of bird species to indicate differences in the extent to
which tree species were used by each bird species in Great High Wood, March
- October, 1984-86. Figures are differences in the percentage between two
bird species, and are indicated for the bird species that used the tree more
frequently. Stars indicate significant differences (chi-square).

Bird species	Oak	Beech	Sycam.	Larch	Birch	Holly	Elm	Other
Blue tit:								
Great tit	8.3*	1.0	-	-	-	-	0.7	0.8
Coal tit	21.6*	0.5	11.7*	-	4.1*	1.1	0.8	4.2*
Goldcrest	29.6*	2.8	7.1	-	4.2	-	2.5	2.9
Chaffinch	8.9*	0.7	-	-	6.4*	4.6*	-	4.4*
Treecreeper	-	-	9.6*	-	2.2	3.9*	2.5*	3.0
Great tit:								
Blue tit	-	-	1.8	1.5	3.8*	4.7*	-	-
Coal tit	13.3*	-	13.5*	-	7.9*	5.8*	0.1	3.4*
Goldcrest	21.3*	1.8	8.9	-	8.0	-	1.8	2.1
Chaffinch	0.6	-	-	-	10.2*	9.3	-	3.6*
Treecreeper	-	-	11.4*	-	6.0*	8.6*	1.8	2.2
Coal tit:								
Blue tit	-	-	-	44.0*	-	-	-	-
Great tit	-	0.5	-	43.5*	-	-	-	-
Goldcrest	8.0	2.3	-	1.2	0.1	-	1.7	-
Chaffinch	-	0.2	-	34.1*	2.3	3.5*	-	0.2
Treecreeper	-	-	-	40.0*	-	2.8	1.7	1.2
Goldcrest:								
Blue tit	-	-	-	42.8*	-	6.3*	-	-
Great tit	-	-	-	42.3*	-	1.6	-	-
Coal tit	-	-	4.6	-	-	6.4*	-	1.3
Chaffinch	-	-	-	32.9*	2.2	10.9*	-	1.5
Treecreeper	-	-	2.5	38.8*	-	10.2	-	0.5
Chaffinch:								
Blue tit	-	-	13.7*	9.9*	-	-	1.1	-
Great tit	-	0.3	12.1*	9.4*	-	-	1.8	-
Coal tit	12.7*	-	25.6*	-	-	-	1.9	-
Goldcrest	20.7*	2.1	21.0*	-	-	-	3.6	-
Treecreeper	-	-	23.5*	5.9	-	-	3.6*	-
Treecreeper:								
Blue tit	15.3*	1.9	-	-	-	-	-	-
Great tit	23.6*	2.9*	-	3.5	-	-	-	-
Coal tit	36.9*	2.4	2.1	-	1.9	-	-	1.2
Goldcrest	44.9*	4.7	-	-	2.0	-	-	-
Chaffinch	24.2*	2.6	-	-	4.2	0.7	-	1.4

bird species indicates the potential of niche partitioning with respect to that tree species. This difference in the use of tree species by pairs of bird species is hereafter called relative tree preference. The blue tit preferred oak more than the other bird species, excepting the treecreeper, and differences in the relative preference were also found in sycamore, birch and holly. The treecreeper had the strongest relative preference for oak, which was the only tree species in which it foraged relatively more extensively than other bird species. The great tit preferred birch and holly relatively more than the other bird species, with somewhat lower affinity to oak and sycamore. The coal tit and goldcrest preferred larch relatively more than any other bird species, and the goldcrest also showed a strong relative preference for holly. The chaffinch preferred sycamore relatively more than any other bird species, but it also preferred oak more than the coal tit and the goldcrest, and larch more than the blue and great tits, making it intermediate between these two groups of bird species in its tree species choice.

There were few significant differences in the use of beech, elm and the uncommon tree species (see Table 2.2) between bird species (Table 3.3), whereas most bird species differed significantly in their use of oak, sycamore, larch, birch and holly. Therefore, it was these tree species that afforded a chance of niche separation between the bird species.

The bulk of the observations for each of the bird species were obtained in three or four species of tree. For blue and great tits the three most extensively used tree species accounted for about

70% of all feeding observations, while for the other bird species this figure was 80-90% (Table 3.1), which reflects the time spent foraging in and the proportion of food obtained from these trees. The relative importance of these tree species differed for each bird species (Table 3.4).

It appears that with the different distribution of birds among the tree species, different tree species that are preferred, and differences. in the strength of preference for most tree species, the tree species is a way of niche partitioning between the species in the guild of arboreal passerine birds. Therefore, tree species preferences should be taken into consideration in studies into avian community structure, competition and foraging behaviour.

3.2   Seasonal differences in tree use

Tree preferences cannot be expected to remain rigid throughout the year, since the food availability on the tree species does not remain constant (Gibb & Betts, 1963). The monthly tree use of the blue tit in 1984 (Fig 3.1) and 1985 (Fig 3.2) was investigated. Considerable seasonal changes and differences between the two years in the extent of the use of each tree species is evident from these figures. In 1984 oak was used considerably more in the first half of the year, while the use of oak in 1985 remained high throughout. A common feature in both years is the peak use of oak in May and June. In 1984 larches were used considerably in the early spring and in the autumn from August onwards, but this did not occur in 1985, when the use of larch remained low throughout the year. This

Table 3.4

Rank order of the four tree species that were used most extensively
by six bird species in Great High Wood, March - October, 1984-86

Blue tit	Great tit	Coal tit	Goldcrest	Chaffinch	Treecreeper
oak	oak	larch	larch	sycamore	oak
sycamore	sycamore	oak	sycamore	oak	larch
larch	birch	sycamore	holly	larch	sycamore
birch	larch	birch	oak	birch	birch
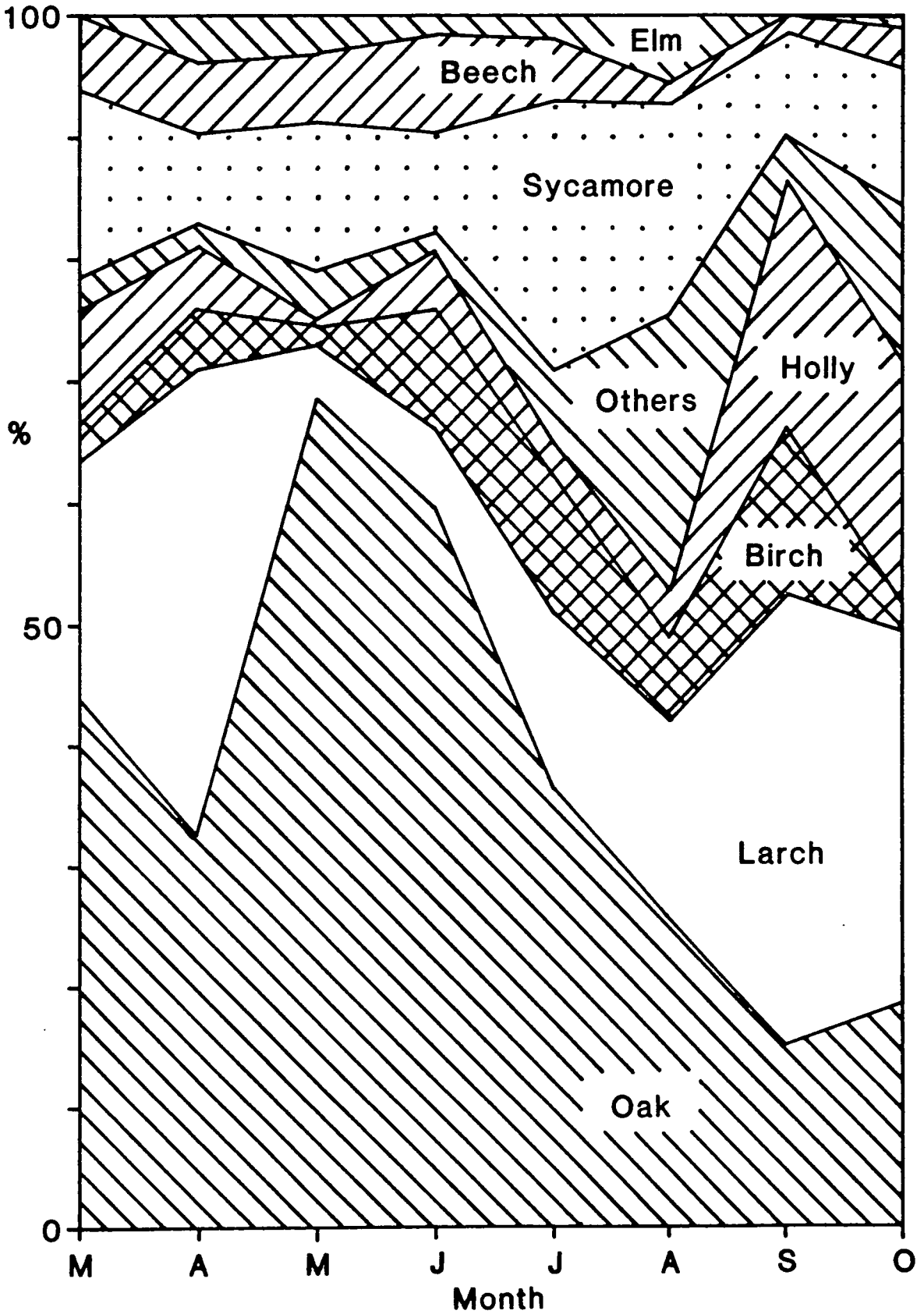
Fig 3.1: Use of tree species by the blue tit in each month
         between March and October in 1984 in Great High
         Wood.   29
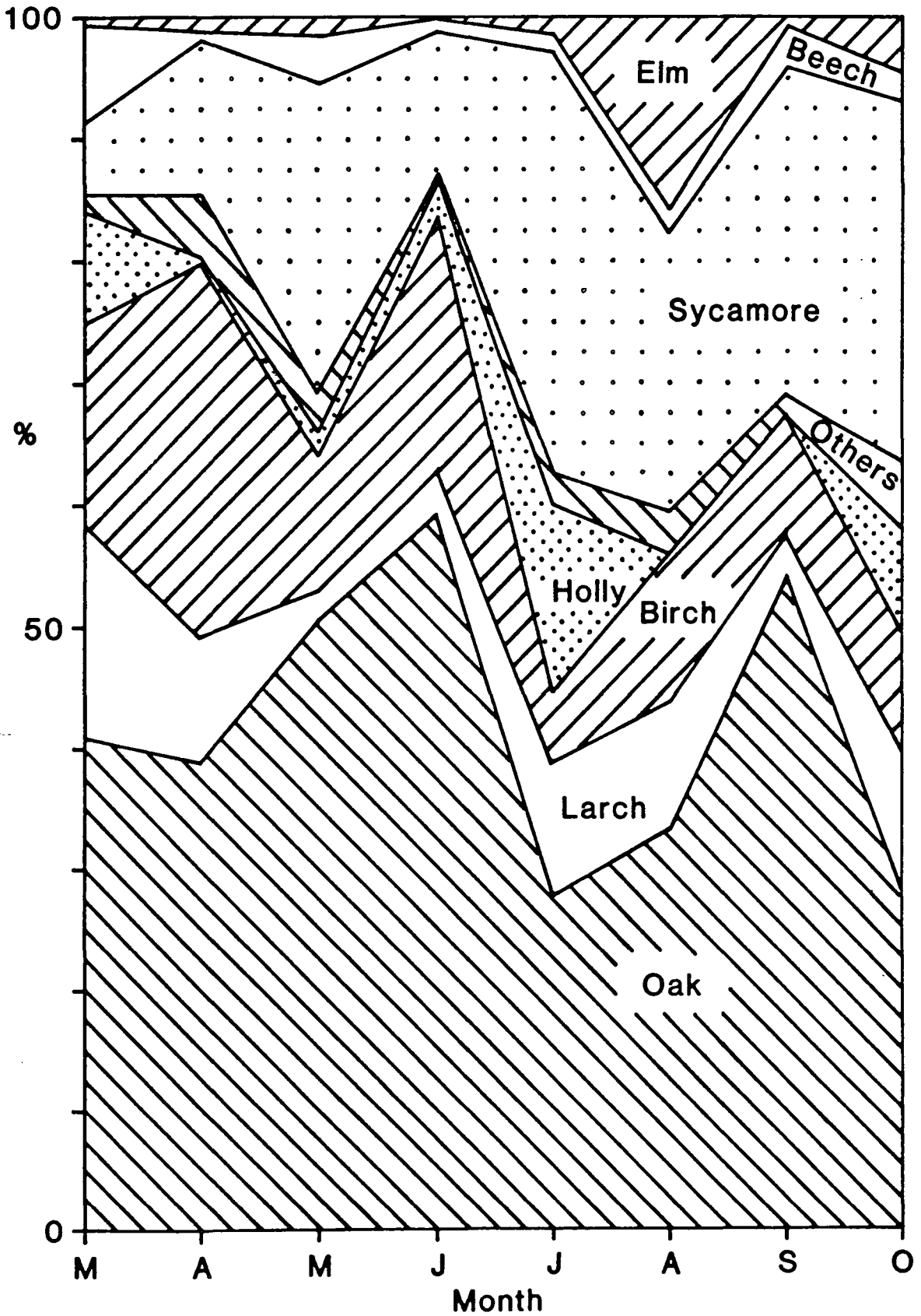
Fig 3.2: Use of tree species by the blue tit in each month
         between March and October in 1985 in Great High
         Wood.   30

appears to be compensated by an increase in the use of birch in the spring and by maintaining a prominent use of oak in the autumn. Sycamore was used extensively throughout both years with a peak in late spring in May, and in the late summer. Elm and the uncommon tree species were used at low level for most of the year with peak use in August. This was due to the availability of fruit or flowers in some of these tree species at this time of the year. Monthly changes in tree species use was evident for all other five bird species.

The main changes in the tree species use occurred from June to July, and therefore the year was divided into two seasons at this point. This division yielded the maximum difference between the seasons and it also coincided with the end of the nesting season and the start of the flocking season. The period of March - June will be referred to as the early season and that of July - October the late season. The frequencies of feeding observations in each tree species in the two seasons are presented in Table 3.5 and the corresponding preference indices in Table 3.6.

The blue tit and the chaffinch used oak more extensively in the early than in the late season, while none of the other bird species changed the extent of their use of oak (Table 3.7). There was a tendency to use larch more in the late season by all bird species except the goldcrest, but this difference was significant only for the great tit and the chaffinch. There was practically no seasonal change in the use of beech. All bird species used holly more extensively in the late season, but this change was significant only for the blue and great tits. Similarly, only the

Table 3.5

Percentage of feeding observations in each tree species for six
bird species in two seasons (March - June and July - October)
in Great High Wood, 1984-86

Tree species	Blue tit	Great tit	Coal tit	Gold- crest	Chaf- finch	Tree- creeper
March-June:						
Oak	47.5	36.2	19.2	11.5	41.7	58.9
Beech	3.5	0.0	5.5	0.0	1.7	5.6
Sycamore	14.7	32.6	8.2	3.8	38.3	5.6
Larch	11.8	8.2	52.1	73.1	10.0	14.5
Birch	14.1	13.6	9.6	3.8	5.0	12.1
Holly	3.4	3.6	1.4	0.0	0.0	0.8
Elm	1.7	1.8	4.1	7.7	2.5	0.0
Others	3.3	3.9	0.0	0.0	0.8	2.4
Sample size	1506	279	73	26	120	124
July-October:						
Oak	34.4	30.7	19.4	11.3	16.4	53.8
Beech	2.1	2.9	1.5	0.0	2.7	3.8
Sycamore	24.9	15.3	8.1	17.0	26.0	14.6
Larch	14.1	16.4	58.2	47.2	43.8	19.2
Birch	6.8	14.7	5.5	7.5	2.7	4.6
Holly	6.9	13.3	4.8	17.0	1.4	1.5
Elm	3.3	1.8	1.1	0.0	5.5	0.0
Others	7.5	4.9	1.5	0.0	1.4	2.3
Sample size	1497	489	273	53	73	130

Table 3.6

Seasonal tree preference index of six species of birds in
Great High Wood, 1984-86

Tree species	Blue tit	Great tit	Coal tit	Gold- crest	Chaf- finch	Tree- creeper
March-June:						
Oak	0.83*	0.39*	-0.26	-0.56	0.61*	1.27*
Beech	-0.85*	-1.00*	-0.77*	-1.00*	-0.93*	-0.77*
Sycamore	-0.29*	0.56*	-0.61*	-0.82	0.84*	-0.73*
Larch	0.17*	-0.18	4.16*	6.24*	-0.01	0.44
Birch	1.09*	1.01*	0.41	-0.43	-0.26	0.78*
Holly	-0.20	-0.15	-0.62	-1.00	-1.00*	-0.81
Elm	-0.06	0.01	1.32	-1.00	0.41	-1.00*
Others	-0.46*	-0.35	-1.00*	0.26	-0.86*	-0.60
Sample size	1506	279	73	26	120	124
July-October:						
Oak	0.33*	0.18*	-0.25*	-0.56*	-0.37	1.07*
Beech	-0.91*	-0.88*	-0.94*	-1.00*	-0.89*	-0.84*
Sycamore	0.19*	-0.26*	-0.61*	-0.19	0.25	-0.30
Larch	0.40*	0.62*	4.77*	3.67*	3.34*	0.91*
Birch	0.01	1.17*	-0.19	0.11	-0.60	-0.32
Holly	0.62*	2.14*	0.12	3.01*	-0.68	-0.64
Elm	0.85*	0.04	-0.38	-1.00	2.09*	-1.00*
Others	0.23*	-0.19	-0.76*	-1.00*	-0.77	-0.62
Sample size	1497	489	273	53	73	130

* = significant preference or avoidance (chi-square)

Table 3.7

Changes in the frequency at which each tree species was used from
the early to the late season in Great High Wood, 1984-86

Tree species	Blue tit	Great tit	Coal tit	Gold-crest	Chaf-finch	Tree-creeper
Oak	0.72*	0.85	1.01	0.98	0.39*	0.91
Beech	0.60*	inf *	0.27	1.00	1.59	0.68
Sycamore	1.69*	0.47*	0.99	4.47	0.68	2.61*
Larch	1.19	2.00*	1.12	0.65	4.38*	1.32
Birch	0.48*	1.08	0.57	1.97	0.54	0.38
Holly	2.03*	3.69*	3.42	inf	inf	1.88
Elm	1.94*	1.00	0.27	0.00	2.20	1.00
Others	2.27*	1.26	inf	1.00	1.75	0.96

notes: figures are <u>percentage in late season</u>
                     percentage in early season

     * = significant difference between the two seasons (t-test)

blue tit increased its use of elm and the uncommon tree species from the early to the late season.

Great tits and chaffinches used sycamore more extensively in the early season, coal tits remained unchanged, and the other three bird species used sycamore more in the late season (Table 3.7). Sycamore leaves are large with long petioles. This makes the extraction of prey from the leaves difficult for the birds, particularly for the heavy species like the great tit, which are unable to balance on the petioles. Therefore, great tits and chaffinches used sycamore more in the early part of the year before the sycamore leaves were fully expanded. Blue tits and goldcrests were light enough to hang from the leaves and petioles, and by that means reached a food source that was largely out of reach of the larger and heavier species later in the summer. This was reflected in the increase in the use of sycamore in the late season by blue tits and goldcrests. The increased use of sycamore by the treecreeper later in the summer reflected the availability of adult aphids on the trunks of the trees as they were blown off leaves.

Great tits and goldcrests were feeding on birch more in the late season, while the other species used the tree more extensively in the early season. However, only blue tits changed significantly.

The number of tree species that were preferred or avoided (Table 3.6), was greater in the late season for the tits and the goldcrest, while the chaffinch showed stronger discrimination of tree species in the early season.

Bird species were shown to prefer different tree species in section 3.1, and it was suggested that this provided a means of

niche partitioning between the bird species. However, only the overall tree preferences were considered. Since temporal differences in tree use between the bird species were found, the possibility of further niche partitioning through the differences in the seasonal tree use between blue and great tits was investigated (Table 3.8). Blue tits used oak more than great tits throughout the year, but the extent to which the tree species was used by the two species of birds became more similar as the year advanced. There was no overall difference between the two bird species in their use of sycamore, and both species used it extensively. However, the seasonal difference was marked. In both years great tits used sycamore significantly more in the early season and blue tits in the late season. The seasonal tree preference indices (Table 3.6) indicate that both these birds preferred the tree only in one season, resulting in the overall neutrality of the birds to sycamore in Table 3.2.

Seasonal differences between blue and great tits were found also on birch (Table 3.8), on which blue tits foraged more frequently in the early, and great tits in the late season, but this difference was significant only in the late season. The use of larch was similar to that of oak, with blue tit influence stronger in the early season. There were no consistent seasonal differences in the use of the remaining tree species, which therefore are not thought to have temporal effect on the bird species.

There were more significant differences in the tree use by blue and great tits in the second half of the year than in the first (Table 3.8). This is likely to be due to a greater diversity

Table 3.8

Differences in the seasonal tree use of blue and great tits
in Great High Wood in 1985 and 1986

Tree species	1985		1986	
	March-June	July-Oct	March-June	July-Oct
Oak	1.17	0.91	7.10*	1.37*
Beech	inf.	3.57	inf.	0.32
Sycamore	0.55*	1.75*	0.29*	1.94*
Larch	1.73	1.13	0.79	0.59*
Birch	1.05	0.47*	2.73	0.28*
Holly	1.10	0.77	0.48	0.48*
Elm	0.56	5.29	inf.	1.52
Others	1.21	0.56	0.37	1.13
N Blue tit	732	401	302	602
N Great tit	168	148	32	161

notes: figures are %blue tit/%great tit

   * = significant difference between the two bird species (chi-square)

of good food sources available to the birds in the late summer and autumn than in the spring. The birds have to converge onto the fewer profitable feeding sites in the spring, which is followed in the early summer by a convergence onto the tree species which provide the best caterpillar crops for the nestlings. Only later in the summer will the birds have a chance to partition the available food sources more thoroughly.

3.3 Foraging height

The trees were divided into four vertical zones to investigate the height distribution of the foraging birds: 0-4m, 4-8m, 8-12m, 12-20m. These zones are the best fit to highlight the vertical distribution pattern of the birds in this study.

The 4-8m zone was used by far most extensively (Fig 3.3), while very few birds were seen feeding above 12 metres. The differences in the height distribution of blue and coal tits and chaffinches seem practically negligible. Great tits and treecreepers used somewhat lower levels of the canopy, while goldcrests were evenly distributed in the zones between 0 and 12 metres. The even distribution of goldcrests is probably due to the extensive use of larches, whose canopy is more uniformly spread over the height range than any of the other tree species. The chaffinch was the only bird species to use the 12-20m zone to a considerable degree, with 9% of the birds in that zone. There were no significant differences between bird species in their distribution between the height zones (t-test).
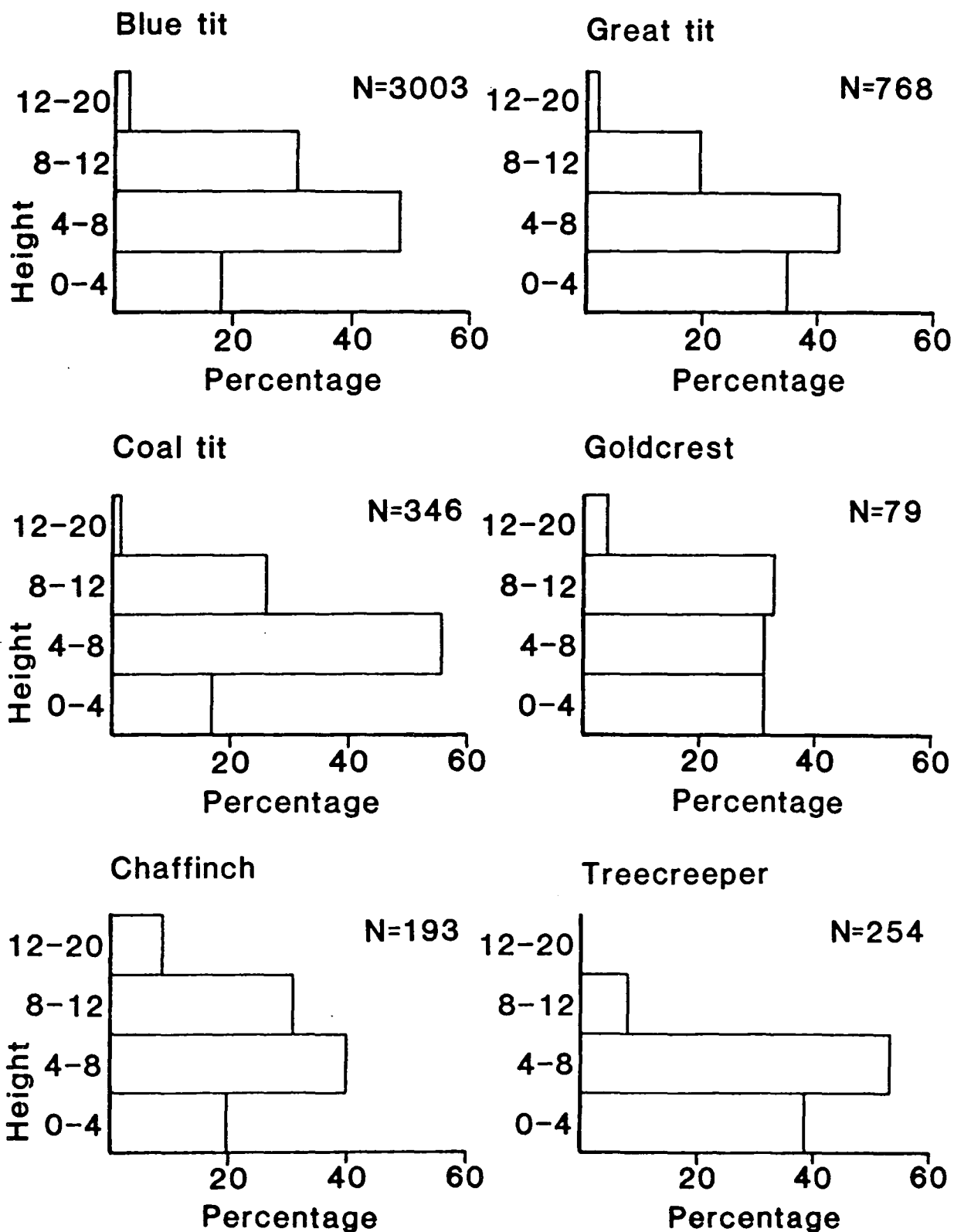
Fig 3.3: Percentage frequency of feeding observations of
         six bird species at four height intervals in trees
         in Great High Wood, March - October, 1984-86.   39

Out of a total of 4643 observations on foraging birds, 48% were found in the height zone 4-8m. The second most extensively used was the 8-12m zone (27% of observations), with 22% of the observations at 0-4m. Only 3% of the birds fed at heights over 12m.

3.4 Position within the canopy whilst feeding

Birds concentrated their foraging on the branches throughout the canopy and on the twigs on the outer parts of the canopy (Table 3.9). The trunk was used very little, except by the treecreepers, which spent most of their feeding time on the trunk of the trees, only occasionally venturing onto the proximal part of the main branches. Because of this major difference in the choice of feeding station by the treecreepers, the rest of this section deals only with the other five species of birds, which foraged primarily in the canopy.

Dead branches were used little for foraging, despite them forming a voluminous feeding niche, particularly in the larches. The coal tit and goldcrest, due to their affinity for larches, foraged on dead branches more often than the other species. However, only the coal tit differed significantly from the other bird species in its use of the dead branches ($X^2 = 7.94$, 1 d.f.).

The main branches of trees were the primary perching sites whilst feeding for all five bird species (Table 3.9). The goldcrest foraged on the branches more often in the inner than outer canopy (t=2.79), and the chaffinch was more commonly found on branches in the outer than inner canopy (t=3.76). The blue and great tits used

Table 3.9

Percentage of each bird species feeding in each location
within the trees in Great High Wood, March - October 1984-86

Location	Blue tit	Great tit	Coal tit	Gold- crest	Chaf- finch	Tree- creeper
Inner tree:						
branch (dead)	0.8	1.6	1.7	1.3	1.0	0.0
branch (live)	28.7	34.6	37.0	54.4	28.5	9.8
twig (live)	5.9	4.8	4.3	5.1	3.1	0.0
Outer tree:						
branch (dead)	0.5	0.3	1.7	1.3	0.5	0.0
branch (live)	30.9	36.9	30.6	32.9	46.6	2.8
twig (dead)	0.1	0.0	0.0	0.0	0.0	0.0
twig (live)	31.2	19.5	20.8	3.8	18.1	0.0
Trunk	1.9	2.3	3.8	1.3	2.1	87.4
Sample size	3003	768	346	79	193	254

the branches in the inner and outer canopy to the same degree. The use of the twigs in the inner parts of the trees was very similar for all the five species. The blue tit used the twigs in the outer part of the tree more than the other bird species (BT-GT t=7.00, BT-CT t=4.43, BT-GC t=11.84, BT-CF t=4.50), while the goldcrest avoided the twigs (only 3.8% of the observations), concentrating on the branches. Great tit, coal tit and chaffinch did not differ from each other in their use of twigs.

The bird species differed in the extent to which they used the different thicknesses of branches (Fig 3.4). The blue tit used twigs more than the other species (BT-GT t=7.15, BT-CT t=4.80, BT-GC t=8.51, BT-CF t=5.17) and had the lowest use of branches, while the goldcrest used branches most extensively (GC-BT t=8.51, GC-GT t=4.36, GC-CT t=4.12, GC-CF t=2.85) and twigs least. The great tit, coal tit and chaffinch did not differ significantly from each other in the extent to which they used branches and twigs as a foraging substrate.

The goldcrest was the only bird species that spent more time foraging in the inner than outer parts of trees (t=2.93; Fig 3.5), whereas the other four bird species were observed up to twice as often in the outer parts of trees (BT:t=22.08, GT:t=6.74, CT:t=2.68, CF:t=6.90). Of these four species, the blue tit and the chaffinch had almost identical distribution, and they were found significantly more often in the outer parts of trees (t=3.04 between blue tit and great tit) than the great tit and the coal tit, which did not differ significantly from each other.
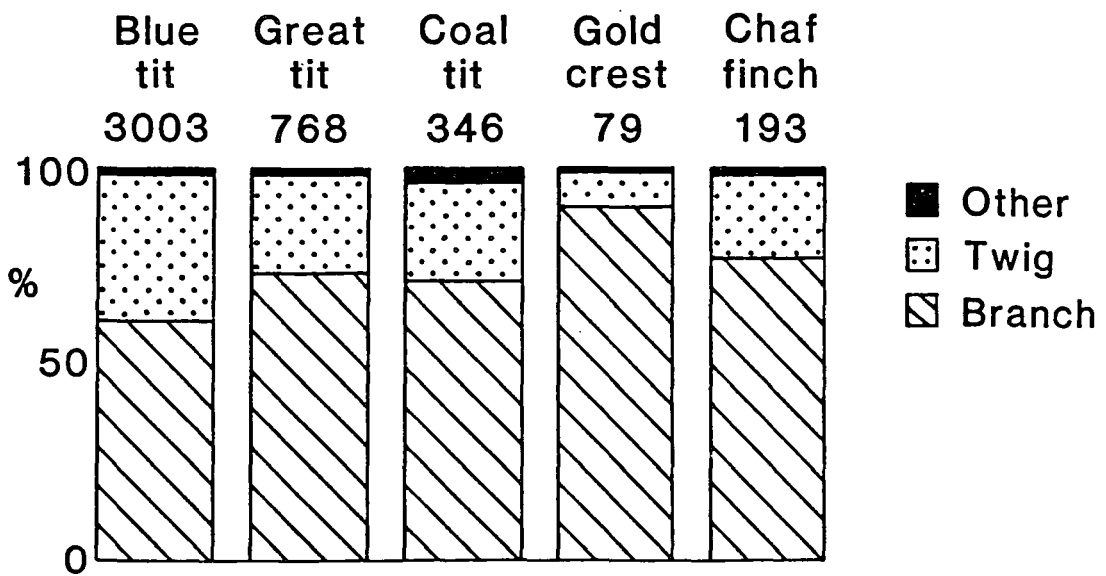
Fig 3.4: Percent frequency of the use of branches and twigs
as perches by foraging birds in Great High Wood,
1984-86. Sample sizes are shown at the top of each
column.
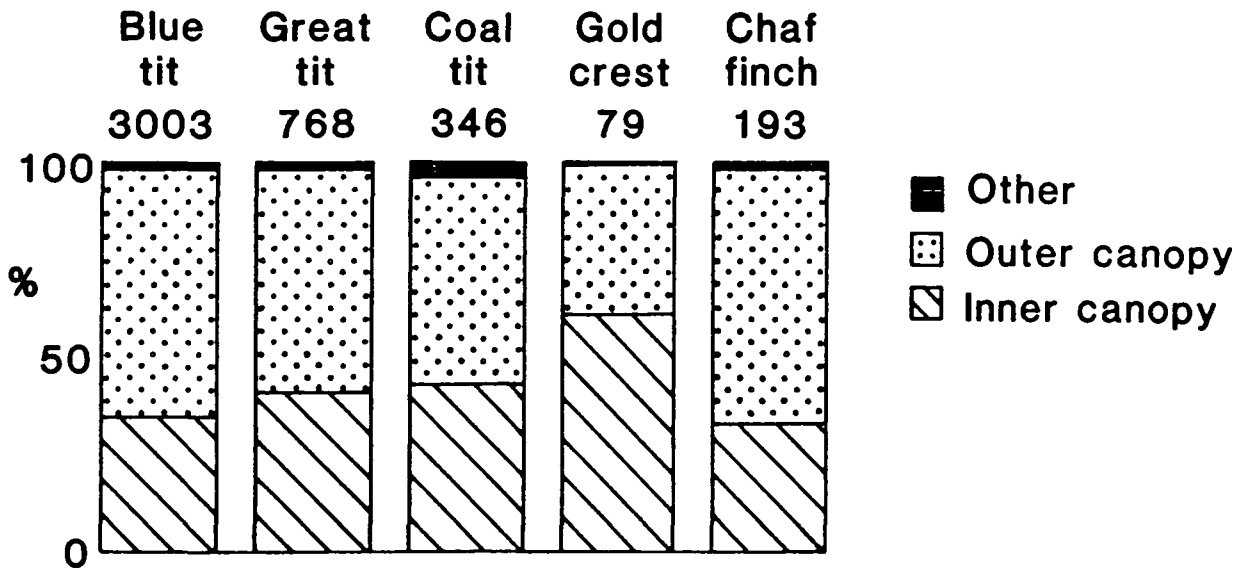
Fig 3.5: Percent frequency of the use of inner and outer
parts of the canopy by foraging birds in Great
High Wood, 1984-86. Sample sizes are shown at the
top of each column.

The results show that the position of the foraging bird within a tree has the potential to offer a means of niche separation between bird species, as described by Edington & Edington (1972).

3.5 The substrates from where food was obtained

The bark and the foliage were the primary sources of food for all the bird species, with other substrates used little (Table 3.10). Treecreepers obtained their food exclusively from the bark. Goldcrests obtained food from the bark of trees twice as often as from the foliage ($X^2 = 6.15$ ld.f), and it was the only species that used bark more extensively than leaves. Whether goldcrests preferred foraging on bark and therefore fed in the central parts of the trees on the main branches (Fig 3.5 section 3.4.), or whether the position within the tree affected the substrate choice, cannot be established from the data.

The remaining bird species foraged among the foliage for 40-60% of the time (Table 3.10). During the spring blue tits foraged extensively among the buds of oak, sycamore, and larch. Chaffinches concentrated on sycamore buds, while the buds on oak and larch were used by great tits. Coal tits and goldcrests did not forage among the buds. All species obtained food from the leaves. Blue tits, great tits and chaffinches searched for food among the flowers on birch, oak and sycamore. In most cases they captured insects from the flowers, but the flower itself was fed on frequently, particularly birch catkins. This feeding on nectar and pollen from catkins has been previously documented by Kay (1985),

Table 3.10

Percentage frequency of each substrate as a source of food
for each bird species in Great High Wood, March - October, 1984-86

Substrate	Blue tit	Great tit	Coal tit	Gold-crest	Chaf-finch	Tree-creeper
Bark	28.3	27.9	33.5	61.8	42.5	100.0
Leaf	45.2	57.7	49.1	36.4	41.0	0.0
Bud	19.2	9.5	3.8	0.0	11.9	0.0
Flower	5.0	3.2	0.0	0.0	3.0	0.0
Cone	1.4	0.0	12.9	1.8	0.0	0.0
Seed	0.1	0.0	0.8	0.0	0.8	0.0
Nut	0.1	0.5	0.0	0.0	0.0	0.0
Fruit	0.3	0.2	0.0	0.0	0.0	0.0
Air	0.1	0.0	0.0	0.0	0.0	0.0
Misc.	0.2	0.9	0.0	0.0	0.8	0.0
Sample size	2158	430	263	55	134	243

who reported on blue tits feeding on plant material from willow catkins. Only coal tits foraged on cones (13% of feeding observations), where they extracted seeds. Few observations were obtained on foraging on substrates other than those mentioned above (e.g. fruit, lichen, moss).

Differences in the substrate from where the food was obtained was slight between the bird species. Some difference was afforded by the use of buds early in the spring since some of the species foraged more extensively on the buds than others. Therefore, the possibility of a greater difference in substrate use at budburst was investigated. The year was divided into March - May and June - October for this purpose.

Blue and great tits foraged more extensively on buds (Table 3.11) than the other three bird species (BT-CT t=3.43, BT-GC t=269.0, BT-CF t=2.01, GT-CT t=2.46, GT-GC t=8.43), while coal tits foraged most extensively on the leaves (CT-BT t=3.23, CT-GT t=2.89, CT-GC t=2.16, CT-CF t=2.22). There was no difference in the extent to which blue and great tits foraged on leaves and buds. The differences in the extent of the use of buds appeared to come about by the choice of tree species, which leafed out at different times, and therefore their foliage was classified as buds for a different period of time. Since the extent of foraging on buds was linked to the tree choice in this way, they appeared to represent the same feeding niche, and can therefore be combined in the analysis of the origin of prey.

The use of all foliage during budburst was similar and non-significant for most bird species (Table 3.11). Only the

Table 3.11

Percentage of observations when birds foraged on bark
and foliage during the budburst and the rest of the study period
in Great High Wood, 1984-86

March - May: Substrate	Blue tit	Great tit	Coal tit	Gold-crest	Chaf-finch
Bark	26.2	23.7	25.5	83.3	40.7
Leaf	20.9	20.6	44.7	16.7	24.1
Bud	42.5	42.3	21.3	0.0	29.6
Leaf + bud	63.4	62.9	66.0	16.7	53.7
June - October: Substrate	Blue tit	Great tit	Coal tit	Gold-crest	Chaf-finch
Bark	30.1	29.1	35.2	55.8	43.8
Leaf + bud	65.4	68.5	50.0	41.9	52.5

goldcrest differed significantly because of its more extensive use of bark (GC-BT t=4.29, GC-GT t=3.90, GC-CT t=3.85, GC-CF t=2.91). In the summer and autumn the blue and great tits differed significantly from the other three bird species in their use of the foliage (BT-CT t=4.20, BT-GC t=3.07, BT-CF t=2.24, GT-CT t=4.35, GT-GC t=3.35, GT-CF t=2.61). The coal tit was the only bird species that changed the extent of its use of foliage during the year (decreased use,t=2.08). The blue tit increased (t=2.01) and the goldcrest decreased (t=2.09) its use of bark. It can be concluded that the bird species did not differ in their choice of feeding sites more in the spring than during the rest of the year. Therefore, there was no seasonality in the birds' use of different substrates, and the major difference between the bird species appeared to be the relative importance of bark and leaves as a source of food.

3.6   How the food was obtained

Gleaning (picking prey up from the surface of plant material) was the commonest method of prey capture. Only blue tits were observed probing into the bark of trees and tearing the bark in order to get at prey. This occurred primarily on oak.

A total of 77% of all birds were perching on a branch or a twig when foraging, with only 23% hanging from the perch. Only blue tits, great tits and coal tits were observed hanging - 25%, 8% and 23% respectively. No bird was observed hovering or making aerial sallies to obtain prey.

3.7 Duration of the feeding bouts by the blue tit

The time blue tits spent feeding in each tree species is investigated in detail in this section. The data on the other bird species was inadequate for this analysis. Table 3.12 shows the number of observations of feeding bouts, duration of the bouts, feeding rates and details of the attacks on prey. There were considerable differences in the mean duration of a feeding bout in different tree species, and similar differences existed in the mean number of attacks on prey during a feeding bout. For instance, on average only ten attacks on potential prey were recorded from birds foraging on beech, while the figure was twice that on birch. However, the feeding rate was similar in each tree species. The lowest rate was in beech of 22.9 attacks per minute, and the highest in birch of 31.0 attacks per minute.

Figure 3.6 shows the relationship between the mean duration of a feeding bout (X) and the mean number of attacks on prey during a feeding bout (Y). The relationship is linear and highly significant ($Y = 0.65X - 6.23$, $r = 0.95$, 6 d.f. $p<0.001$). This shows that blue tits spent a longer time foraging in some tree species than in others, and that larger numbers of prey items were located during the longer foraging bouts. The intercept in the graph is not significantly different from zero.

The above leads to the assumption that birds would feed selectively in the tree species where they can feed for longer without interruptions. The selective feeding is expressed as tree preference index (section 3.1), and when the preference index

Table 3.12

Duration of feeding bouts and numbers of attacks on prey by blue tit
in each tree species in Great High Wood, March - October, 1984-85

Tree species	Number of bouts	Number of attacks	Attacks/ bout	Time (sec)	Time/ bout	Feeding rate	TPI
Oak	183	3390	18.52	7291	39.84	27.9	0.60
Beech	20	209	10.45	548	27.40	22.9	-0.86
Sycamore	54	834	15.44	1742	32.28	28.7	-0.17
Larch	89	1504	16.90	3123	35.09	28.9	0.38
Birch	35	714	20.40	1382	39.49	31.0	0.66
Holly	11	146	13.27	312	28.36	28.1	0.28
Elm	8	113	14.13	262	32.75	25.9	0.21
Others	26	417	16.04	869	33.42	28.8	-0.18

notes: the feeding rate is displayed as attacks per minute
         TPI = tree preference index
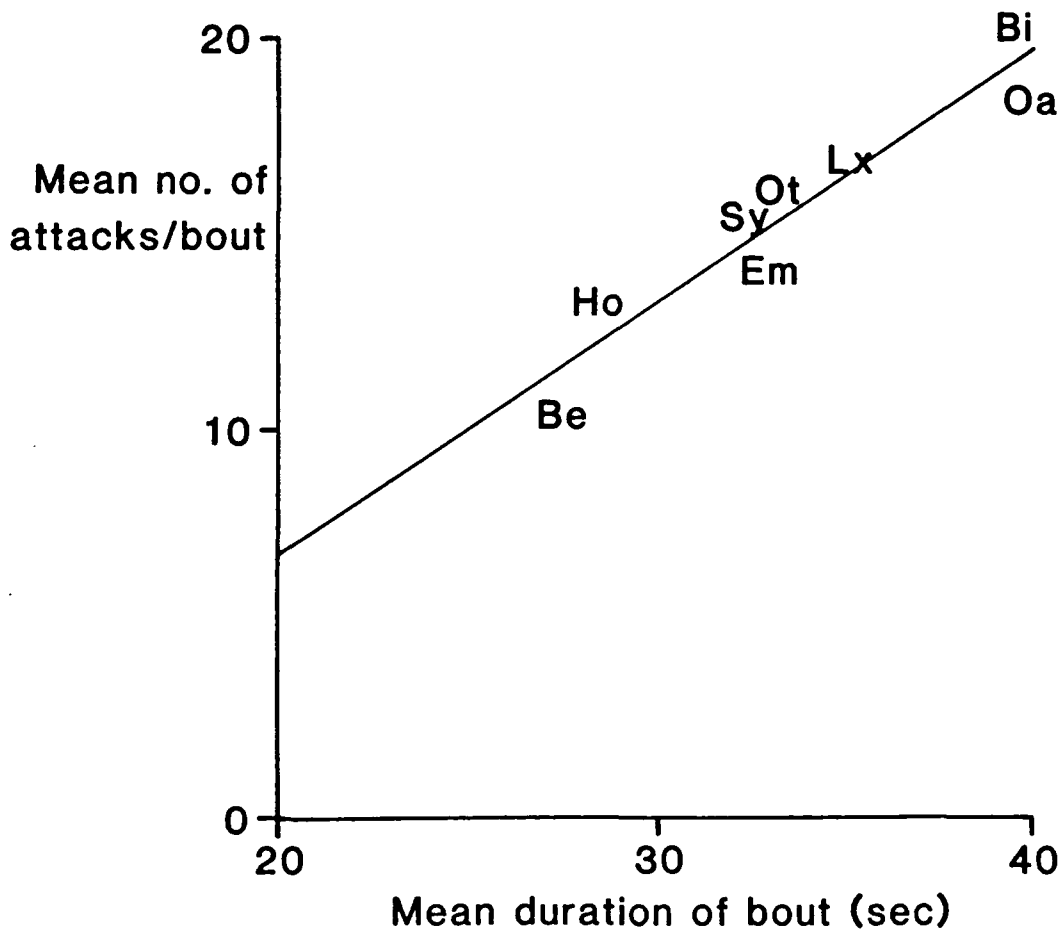
Fig 3.6: The relationship between mean number of attacks on prey and mean duration of a feeding bout in different tree species for the blue tit in Great High Wood, 1984-85. $Y = 0.65(+/-0.09)X - 6.23$, $r = +0.95$, 6 d.f. (See Table 2.2 for abbreviations of tree species.)

calculated for data of 1984 and 1985 (Y) is plotted against the mean duration of the feeding bout (X) in each tree species (Figure 3.7), a highly significant linear regression line is obtained (Y = 0.08X - 2.72, r=0.76, 6 d.f. p<0.001). This shows that the blue tits foraged for longer in the tree species they preferred.

Because of the correlation between the tree preference index (TPI) and the duration of the feeding bout, it is possible that the observed preferences were the result of birds remaining longer in some tree species than in others, rather than visiting them more frequently. If this was the case, the scale of difference in the tree preference index and the duration of feeding bout should be equal. Clearly, this is not the case (Table 3.12). For example, the preference index for oak by the blue tit was 0.6, and for beech -0.86, while the bout durations were 39.84 sec and 27.40 sec respectively. The bout duration for oak was about 50% more than for beech, while the preference for beech would have had to increase by 1800% to reach that shown for oak. Clearly, the time birds spent in the two tree species did not account for the differences in the tree preferences. The same conclusion is arrived at when comparing most of the pairs of tree species. Only in a small number of cases the duration of the foraging bout accounts wholly for the differences in TPI.

The effect of the duration of visit on tree preference index can also be examined by correcting the index for the differences in the duration of visits to the tree species examined. This produces the same conclusion; the duration of visits is of only minor importance and the frequency of visits to the tree species is the

main factor involved. Details of the calculations are given below. As a larger proportion of the birds feed in a particular tree species, the tree preference index increases and does so in an arithmetic manner. However, the amount of increase in the TPI varies between tree species. Because of this linearity, it is possible to calculate the effect of the duration of a foraging bout on the preference index of each tree species. If a bird feeding in tree B spends the same time during each foraging bout as in tree A, the effect of the difference in bout duration on the tree preference index for tree B would be as follows:

$$\text{changed TPI(tree B)} + 1 = 1 + \text{TPI(tree B)} * \frac{\text{bout duration in tree A}}{\text{bout duration in tree B}}$$

The addition of one to the value removes the negative values, and needs to be subtracted from the final result. Using figures for oak (tree A) and beech (tree B) from Table 3.12 as examples, the preference for beech would change to:

$$\text{changed TPI(beech)} = 0.14 * \frac{39.84}{27.40} = 0.20 - 1 = -0.80$$

if the birds foraged in beech for as long as they did in oak. The modification of the preference for beech increased the index by 0.06. This represents only 4% of the original difference of 1.46 between the preference indices for the two tree species. Therefore it is evident that the differences in the preference for the two

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tree species are real and caused by the birds discriminating against one tree species and in favour of the other.

Following this procedure, it is possible to modify the tree preference index to correct for the effect of different feeding bout durations. Fig. 3.8 illustrates the effect of bout duration on the tree preference of blue tit for each tree species. The actual index is indicated with a solid circle, and the regression lines represent the way this index would change with average feeding bouts of different duration. Increasing the duration of the foraging bout increases the TPI for each of the tree species. The regression lines of the modified TPIs do not cross, and therefore, the rank order of tree species by the preference index at any one bout duration within the observed range of 27-40sec remains the same. This rank order is the same as the rank order of trees by TPI without correcting for bout duration, except that holly changed from fourth to the most preferred species. The differences between the tree species persist (Fig 3.8). This shows that despite a part of the tree preferences of the blue tit being explainable in terms of differences in duration of feeding bouts in the tree species, it is not the main reason for the existence of tree preferences. It can be concluded from this that birds actively search out their preferred trees like oak and birch, and avoid e.g. beech.

cause of the existence of tree preferences. It is therefore clear that there is a behavioural response to the individual tree species, the birds actively searching out the preferred trees like oak and birch, and avoiding e.g. beech.
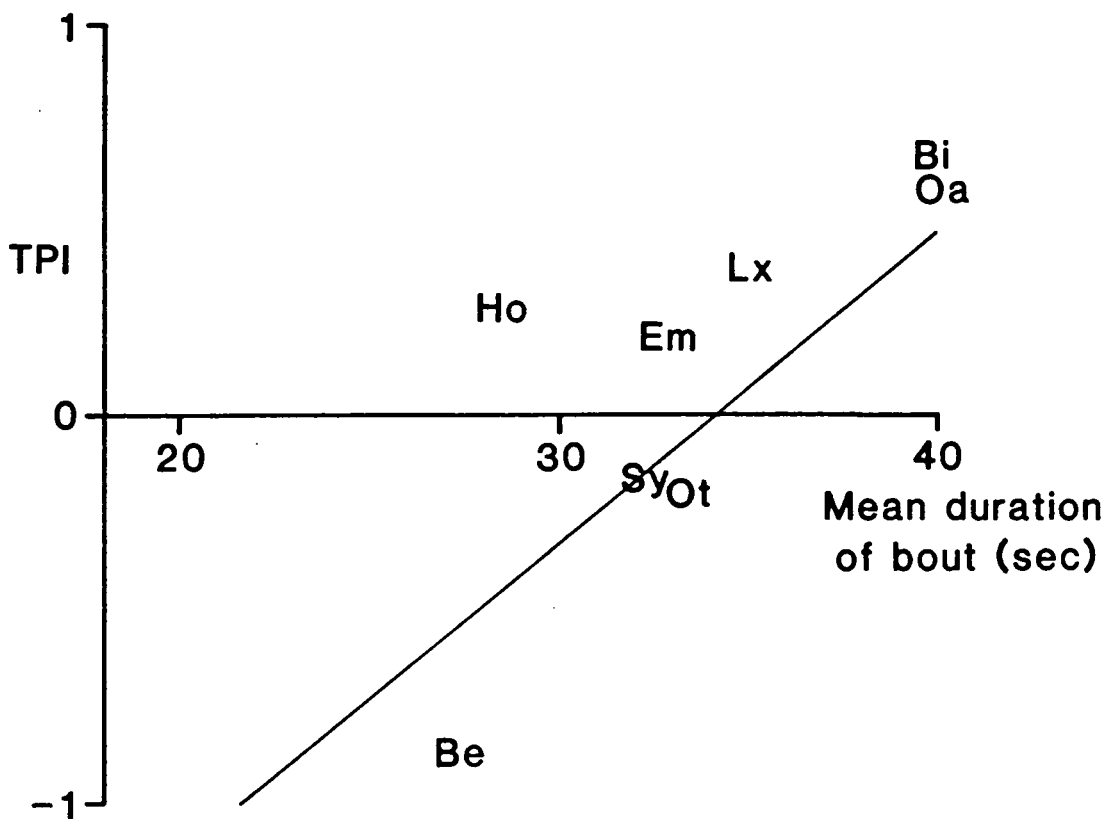
Fig 3.7: The relationship between the blue tit tree
preference (TPI) and the duration of feeding bouts
in each tree species in Great High Wood, 1984-85.
Y = 0.08(+/-0.03)X - 2.72, r = +0.76, 6 d.f. (See
Table 2.2 for abbreviations of tree species.)
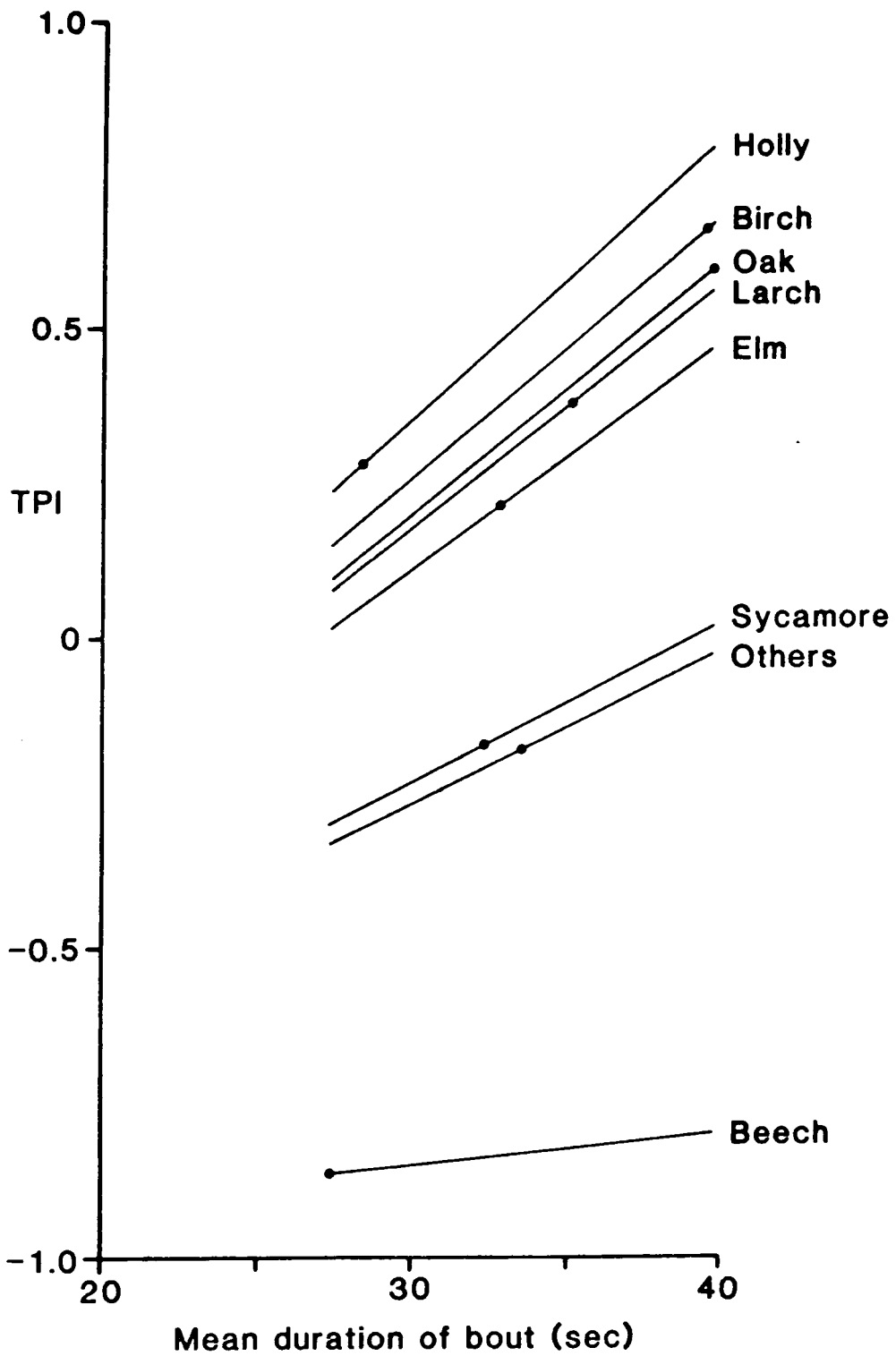
Fig 3.8: The relationship between blue tit tree preference
(TPI) and mean duration of feeding bout for each
tree species, together with modified tree
preferences assuming bouts of different duration
(see text) in Great High Wood, 1984-86.
(● = original TPIs, _____ = regression for
modified TPIs)

3.8 Differences in tree use between years

Figure 3.9 lists the percentage of feeding observations in each tree species separately for the three years of the study. The results on goldcrest are not complete for this section, because the high mortality during the winter of 1985-1986 almost exterminated the goldcrest population in Great High Wood. This is reflected in that only seven birds were observed feeding during 1986, and therefore data on goldcrest in 1986 were omitted.

The extent to which most tree species were used remained similar from one year to the next (Fig 3.9). However, some large changes did occur. Goldcrests increased their use of oak by four-fold from 1984 to 1985, while chaffinches used oak less each year of the study, changing from 43% in 1984 to only 10% in 1986. This decline was counterbalanced by an increase in the use of sycamore in 1985 and of larch in 1986.

Despite some of these large changes it can be concluded that some tree species were used extensively each year, while others were consistently avoided. Oak was used by all bird species, even by coal tits and goldcrests (Fig 3.9), which are classically regarded as birds of conifers. Larch, too, was used extensively in each year as a feeding site by all six bird species. The use of larch was lower by all bird species in 1985, but in most cases it still remained as one of the most extensively used tree species in the wood. In contrast with oak and larch, beech was used infrequently in each year. Slightly more blue tits, great tits and chaffinches were found in beech in 1984, which was the only year
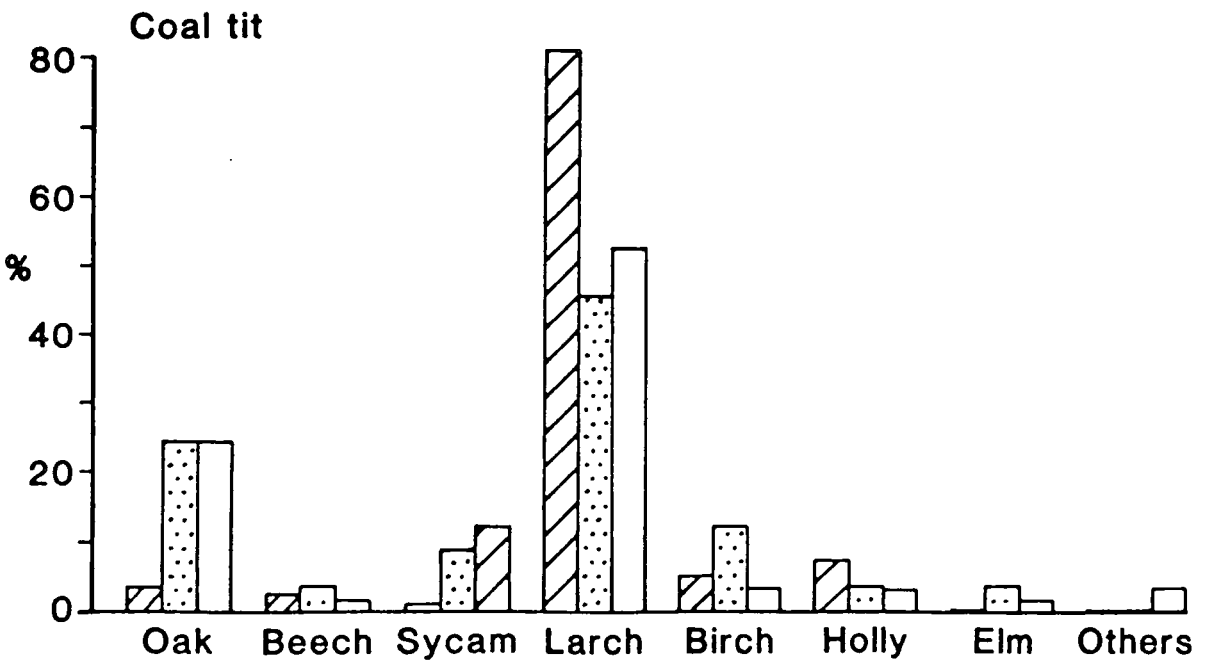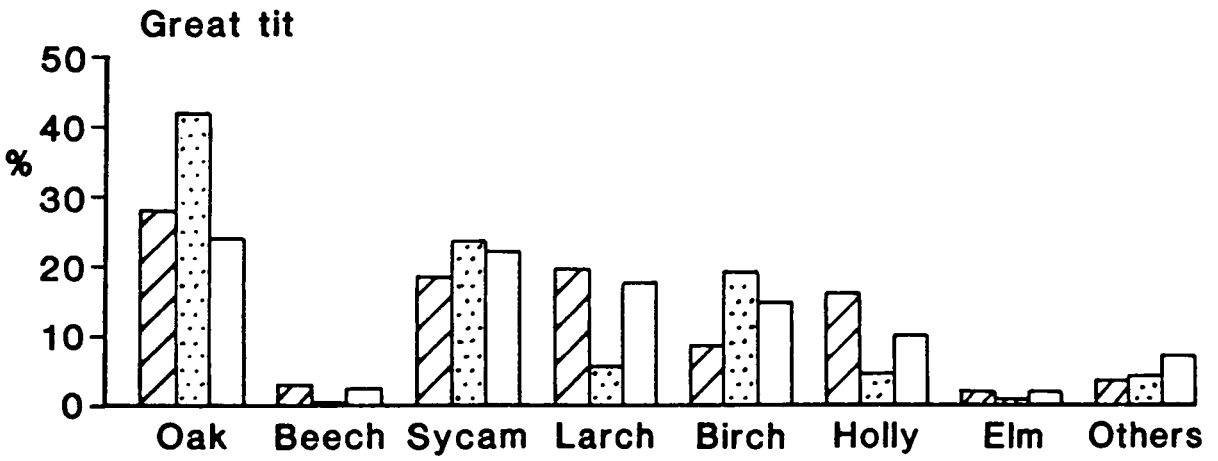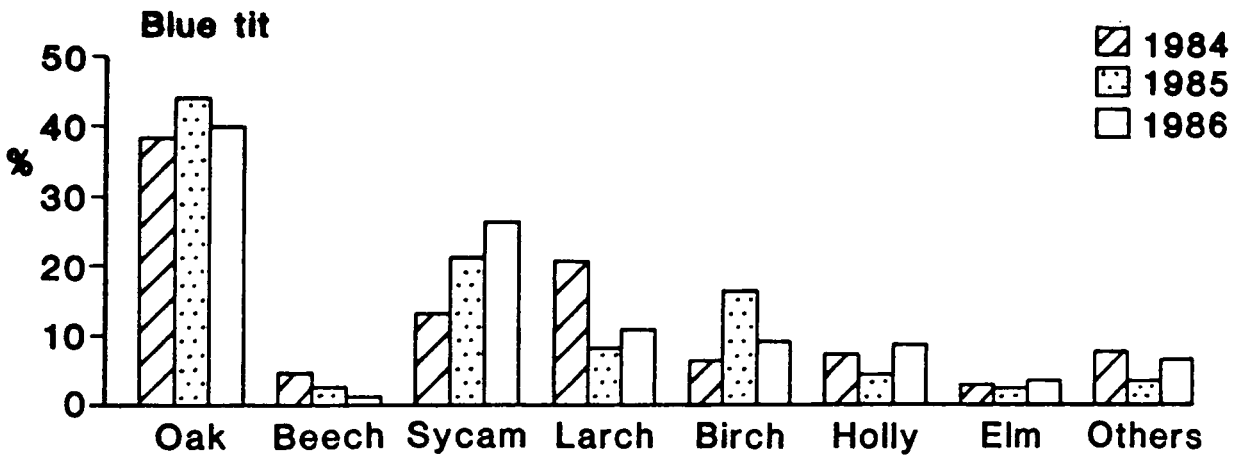
Fig 3.9: Percentage use of tree species by each bird
species in Great High Wood in 1984, 1985 and 1986.
Sample sizes as per Table 3.13.
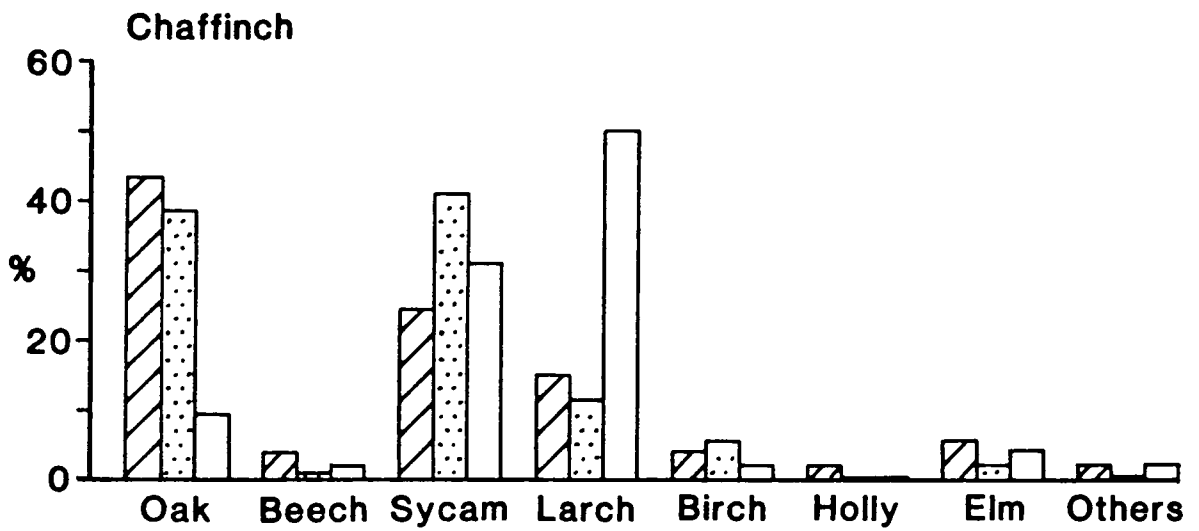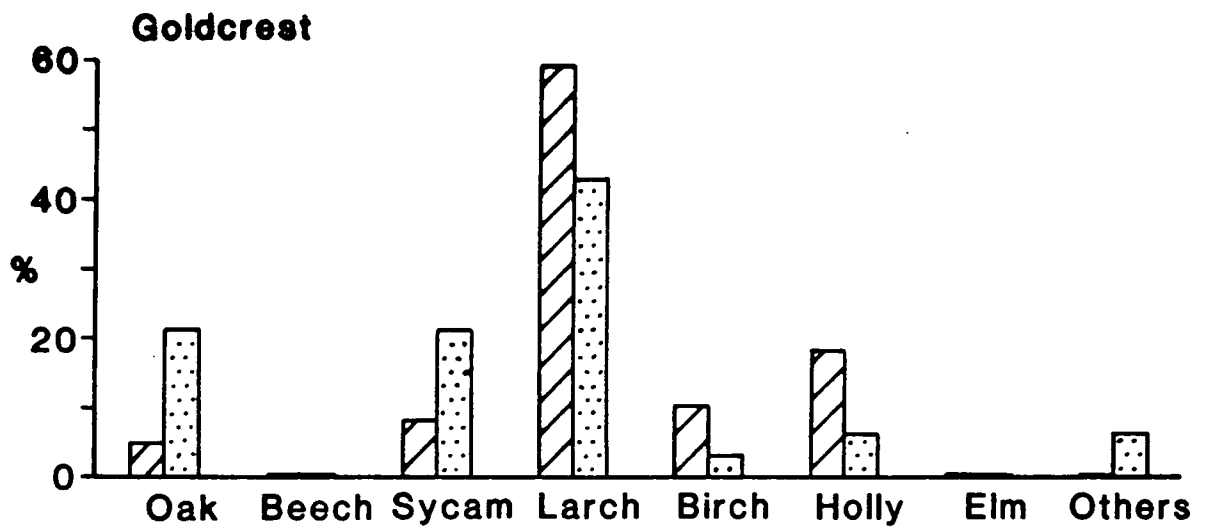
Fig 3.9: contd...

with a good beechmast crop, than in the other years. However, this difference was only significant for blue tits (chi-square in '84-'85 6.79 and '84-'86 16.42, 2 d.f.). The magnitude of the fluctuations in the use of beech were similar for all six bird species, but the changes in the use of beech were not correlated with the availability of beechmasts for the coal tit, goldcrest and treecreeper. Even at best only less than 5% of any one bird species were seen on beech, and since beech made up 24% of the trees in the wood, this still represented strong avoidance. Similar avoidance of beech was found by Hartley (1953) in Wytham Wood, Oxfordshire.

The use of sycamore increased throughout the three years for blue tits and coal tits, and increased and levelled off for great tits, chaffinches and treecreepers. This is likely to be the result of the food availability in different tree species, and is investigated in greater detail in Chapter 7.

In each year between one and four tree species were preferred by each bird species, and the same number were avoided (Table 3.13). A lack of discrimination was evident only for few tree species. In most cases a tree species that was preferred in one year, was also preferred in other years. However, the relative importance of each tree species for the birds varied from one year to another. This was probably caused by the relative abundance of arthropod prey and availability of fruit and nuts on each tree species, which cannot be assumed constant, and by the population level of arboreal birds in the wood, which can cause displacement of bird species due to competitive pressure. See Alerstam et al.

Table 3.13

Tree preference index of six species of birds in each year in
Great High Wood, March - October

Tree species	Blue tit	Great tit	Coal tit	Gold-crest	Chaf-finch	Tree-creeper
1984:						
Oak	0.48*	0.09	-0.86*	-0.80*	0.67*	1.09*
Beech	-0.81*	-0.87*	-0.90*	-1.00*	-0.84*	-0.80*
Sycamore	-0.37*	-0.11	-0.94*	-0.63*	0.18	-0.65*
Larch	1.05*	0.95*	7.02*	4.84*	0.50	0.59
Birch	-0.13	0.25	-0.30	0.51	-0.44	0.64
Holly	0.74*	2.83*	0.69	3.24*	0.56	-0.71
Elm	0.34	0.31	-1.00	-1.00	2.19*	-1.00
Others	0.23	-0.43	-1.00*	-1.00	-0.67	-0.19
Sample size	966	259	84	39	53	81
1985:						
Oak	0.70*	0.61*	-0.06	-0.18	0.49*	1.30*
Beech	-0.90*	-0.99*	-0.86*	-1.00*	-0.95*	-0.89*
Sycamore	0.00	0.14	-0.60*	0.02	0.96*	-0.44*
Larch	-0.20*	-0.44*	3.50*	3.20*	0.13	0.16
Birch	1.33*	1.80*	0.74*	-0.55	-0.16	0.92*
Holly	-0.10	0.05	-0.21	0.43	-1.00	-1.00
Elm	0.10	-0.29	0.90	-1.00	0.28	-1.00
Others	-0.52*	-0.38	-1.00*	0.00	-1.00*	-0.79
Sample size	1133	316	119	33	88	77
1986:						
Oak	0.54*	-0.08	-0.06		-0.63*	1.13*
Beech	-0.95*	-0.89*	-0.94*		-0.92*	-0.74*
Sycamore	0.22*	0.07	-0.43*		0.47	-0.45*
Larch	0.05	0.75*	4.20*		3.95*	1.17*
Birch	0.29*	1.14*	-0.59		-0.72*	-0.69
Holly	0.04	1.32*	-0.34		-1.00	-0.51
Elm	0.81*	0.17	-0.20		1.17	-1.00
Others	0.02	0.19	-0.54		-0.68	-0.83*
Sample size	904	193	143		52	96

* = significant preference or avoidance (chi-square)

(1974) for an example of bird species composition affecting the tree choices of individual bird species.

A preference hierarchy of tree species in each year of the study was constructed for the three species of tits (Table 3.14). In each year oak was near the top of the hierarchy for the blue tit, and larch for the coal tit. Beech was avoided most strongly each year, and hence it was consistently at or near the bottom of the hierarchy for each bird species. Some other tree species changed considerably in their status from one year to the next. For example, the blue and great tits preferred larch in 1984 and 1986, but avoided it in 1985, in which year birch and sycamore gained in importance as a foraging site. Similarly, there were changes in the importance of holly for both these bird species, and of elm for the blue tit. There were fewer changes in the relative tree preferences of the coal tit, and most of them were due to the changes in the strength of preference for larch, on which over half of the birds were feeding in each year.

3.9 Discussion

Birds have been shown to prefer some tree species and reject others. These preferences were different for each bird species, with blue and great tits having the most similar preferences of the six species studied. Birds concentrated foraging onto certain heights within a tree, and used some of the available feeding stations more extensively than others. There was little difference

Table 3.14

Preference hierarchy of tree species for blue tit, great tit and coal tit
in Great High Wood, March - October, 1984-86

	Blue tit			Great tit			Coal tit		
	1984	1985	1986	1984	1985	1986	1984	1985	1986
Prefer	larch holly oak	birch oak	elm oak birch sycam	holly larch	birch oak	holly birch larch	larch	larch elm	larch
Neutral	elm other birch	elm sycam holly	larch holly other	elm birch oak sycam other	sycam holly elm other	other elm sycam oak	holly birch oak	birch oak holly	oak elm holly sycam other birch
Avoid	sycam beech	larch other beech	beech	beech	larch beech	beech	beech sycam elm other	sycam beech other	beech

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in the substrate choice between bird species. Tree preferences were not rigid, but changed from one year to the next and between seasons. These changes took place within limits, and therefore a tree species that was preferred one year was likely to be preferred also on subsequent years.

Bird species differed most from each other in their choice of tree species. The partitioning of the niche by tree species appears to act in any one point in time, and therefore tree preferences calculated for a period of a year or longer underestimate the differences between bird species, since temporal changes in tree preference become obscured.

CHAPTER 4

TREE PREFERENCE AND ITS INFLUENCE ON BIRD DISTRIBUTION IN HAMSTERLEY FOREST

4.1 Tree preferences shown by birds in Hamsterley Forest

The birds had a choice of 13 tree species in the study compartments in Hamsterley Forest. Each tree species was used by most or all of the bird species (Table 4.1), but the extent to which the trees were used was different for each species of bird. The great tit concentrated its foraging primarily on the broadleaves with oak and birch used most extensively, while the goldcrest had the most coniferous choice of tree species.

Birds of each species spent the majority of their foraging time on three or four of the tree species available. This accounted for 78-83% of the feeding effort for each bird species, and is comparable with Great High Wood. Treecreepers were an exception being more evenly distributed between the tree species. The extensively used tree species, which provided the majority of food for the birds, differed both in the identity of the trees and in the relative importance of those tree species for each bird species (Table 4.2). The only exception was the blue and great tits which obtained the bulk of their food from the same tree species, but even for these bird species the relative importance of the tree species differed. In addition, each bird species was seen feeding

Table 4.1

Percentage of feeding observations in each tree species for six species
of birds in Hamsterley Forest. March - October 1984-86

Tree species	Blue tit	Great tit	Coal tit	Gold-crest	Chaf-finch	Tree-creeper
Oak	38.6	42.5	8.2	4.7	13.4	17.0
European larch	19.7	13.3	30.3	23.8	38.0	21.9
Scots pine	5.8	5.3	31.7	30.0	14.0	18.4
Japanese larch	2.1	0.6	7.9	2.1	16.4	7.5
Birch	15.8	16.7	6.2	3.7	3.1	11.1
Beech	1.2	3.6	0.3	0.3	0.7	1.7
Norway spruce	0.5	0.6	4.1	9.3	3.7	2.8
Sitka spruce	0.2	1.1	5.6	17.4	2.5	2.8
Alder	5.7	7.5	1.7	2.2	3.5	9.4
Western hemlock	0.7	0.0	1.1	3.6	0.3	1.4
Ash	2.6	0.6	0.6	0.0	1.2	2.6
Sycamore	7.1	4.2	1.7	2.5	2.6	2.6
Rowan	0.7	4.2	0.6	0.5	0.5	0.7
Sample size	1210	360	2296	774	1023	424

Table 4.2

Rank order of the four tree species that were used most
extensively by six bird species in Hamsterly Forest,
March - October, 1984-86

Blue tit	Great tit	Coal tit	Gold- crest	Chaf- finch	Tree- creeper
oak	oak	s. pine	s. pine	e. larch	e. larch
e.larch	birch	e. larch	e. larch	j. larch	s. pine
birch	e. larch	oak	s. spruce	s. pine	oak
sycamore	alder	j. larch	n. spruce	oak	birch

more often than expected in at least one other species of tree which was present at a low frequency, and as such was not an important foraging site. Many of these secondary tree species, notably sycamore, are of major importance in woodlands where they are more abundant.

Out of a total of 78 combinations of bird and tree species, 64 showed significant preference (25) or avoidance (39) (Table 4.3). This indicates that the bird species discriminated between most tree species, and were rarely neutral to them. Strong preferences for certain tree species existed (e.g. sycamore), while others were avoided (e.g. beech), by each of the bird species. Apart from sycamore and beech, the response to a particular tree species varied from one bird species to another, different complements of trees being preferred by the different bird species. These differences were substantial, and are therefore a possible means of separating the feeding niches of the bird species in Hamsterley Forest, as well as in Great High Wood.

Most tree species were preferred by up to three out of the six bird species (Table 4.3). Oak was preferred by blue and great tits, and avoided by the other species. European larch was preferred most by coal tits, goldcrests and chaffinches, whereas only chaffinches preferred Japanese larch. Coal tits and goldcrests preferred Scots pine, while blue and great tits tended to avoid the tree. Birds on birch and alder were sharply divided into two groups: the trees were preferred by blue tits, great tits and treecreepers, and avoided by the other three species. The remaining tree species attracted few birds. Goldcrests showed a preference for sitka and

Table 4.3

Tree preference index of six bird species in Hamsterley Forest.
March - October 1984-86

Tree species	Blue tit	Great tit	Coal tit	Gold-crest	Chaf-finch	Tree-creeper
Oak	0.68*	0.85*	-0.64*	-0.80*	-0.42*	-0.26*
European larch	0.10	-0.25*	0.70*	0.34*	1.14*	0.23*
Scots pine	-0.66*	-0.69*	0.86*	0.76*	-0.18*	0.08
Japanese larch	-0.70*	-0.92*	0.14	-0.70*	1.35*	0.08
Birch	1.23*	1.36*	-0.13	-0.47*	-0.56*	0.57*
Beech	-0.79*	-0.38	-0.94*	-0.95*	-0.88*	-0.71*
Norway spruce	-0.92*	-0.91*	-0.32*	0.56*	-0.38*	-0.53*
Sitka spruce	-0.95*	-0.76*	0.20*	2.70*	-0.46*	-0.40
Alder	0.32*	0.74*	-0.60*	-0.49*	-0.18	1.19*
Western hemlock	-0.97*	-1.00*	-0.64*	0.18	-0.90*	-0.54*
Ash	0.22	-0.73*	-0.71*	-1.00*	-0.44*	0.24
Sycamore	6.32*	3.29*	0.75*	1.53*	1.72*	1.67*
Rowan	-0.45	2.43*	-0.53*	-0.57	-0.60*	-0.42
Sample size	1210	360	2296	774	1023	424

* = significant preference or avoidance (chi-square)

Norway spruce, whilst coal tits preferred only the former, the other species avoiding these trees. Rowan was preferred only by great tits, and birds were either neutral to ash or avoided it. Beech and western hemlock were avoided by all six bird species in the wood.

To establish the relationships of the bird species in each species of tree, the frequency of use of each tree species was compared for pairs of bird species (Table 4.4) as was described in section 3.1. The blue tit and great tit had stronger relative preferences for oak, birch and alder than any other bird species. Blue tit had also a stronger relative preference for ash than those shown by any other bird species. Significantly stronger relative preference for sycamore was only shown by the blue tit and for rowan by the great tit. The significantly higher use of beech by the great tit than the other bird species merely reflects that it did not reject the tree species as strongly as the other birds, and does not convey existence of any affinity for beech. The relative preferences shown by the blue and great tits indicate that their strongest affinity was for certain broadleaved trees, despite the extensive use of some conifers, notably European larch. In contrast, the goldcrest showed significantly stronger preferences than other bird species for coniferous trees, with a particular affinity for the spruces. The coal tit's relative preferences were widespread over most of the tree species, with the strongest affinity for the larches and Scots pine. The chaffinch preferred both species of larch more strongly than any other bird species. The treecreeper cannot be said to have a particular affinity for

Table 4.4.

Comparison of pairs of birds to indicate differences in the extent to which tree species were used by each bird species in Hamsterley Forest, March - October, 1984-1986. Figures are differences in the percentage between two bird species, and are indicated for the bird species that used the tree more frequently. Stars indicate significant difference (chi-square). See Table 2.1 for abbreviations of tree species.

Bird species	Oa	EL	SP	JL	Bi	Be	NS	SS	Al	WH	As	Sy	Ro
Blue tit:													
Great tit	-	6.4*	0.5	1.5	-	-	-	-	-	0.7	2.0*	2.9	-
Coal tit	30.4*	-	-	-	9.6*	0.9*	-	-	4.0*	-	2.0*	5.4*	0.1
Goldcrest	33.9*	-	-	-	13.1*	0.9*	-	-	3.5*	-	2.6*	4.6*	0.2
Chaffinch	25.2*	-	-	-	13.7*	0.5	-	-	2.2*	0.4	1.4*	4.5*	0.2
Treecreeper	21.6*	-	-	-	4.7*	-	-	-	-	-	-	4.5*	-
Great tit:													
Blue tit	3.9	-	-	-	0.9	2.4*	0.1	0.9	1.8	-	-	-	3.5*
Coal tit	34.3*	-	-	-	10.5*	3.3*	-	-	5.8*	-	-	2.5*	3.6*
Goldcrest	37.8	-	-	-	13.0*	3.3*	-	-	5.3*	-	0.6	1.7	3.7*
Chaffinch	29.1*	-	-	-	13.6*	2.9*	-	-	4.0*	-	-	1.6	3.7*
Treecreeper	25.5*	-	-	-	5.6*	1.9	-	-	-	-	-	1.6	3.5*
Coal tit:													
Blue tit	-	10.6*	25.9*	5.8*	-	-	3.6*	5.4*	-	0.4*	-	-	-
Great tit	-	17.0*	26.4*	7.3*	-	-	3.5*	4.5*	-	1.1	-	-	-
Goldcrest	3.5*	6.5*	1.7	5.8*	2.5*	-	-	-	-	-	0.6	-	0.1
Chaffinch	-	-	17.7*	-	3.1*	-	0.9	3.1*	-	0.8*	-	-	0.1
Treecreeper	-	8.4*	13.3*	0.4	-	-	1.3	2.8*	-	-	-	-	-
Goldcrest:													
Blue tit	-	4.1*	24.2*	-	-	-	8.8*	17.2*	-	2.9*	-	-	-
Great tit	-	10.5*	24.7*	1.5	-	-	8.7*	16.3*	-	3.6*	-	-	-
Coal tit	-	-	-	-	-	-	5.2*	11.8*	0.5	2.5*	-	0.8	-
Chaffinch	-	-	16.0*	-	0.6	-	5.6*	14.9*	-	3.3*	-	-	-
Treecreeper	-	1.9	11.6*	-	-	-	6.5*	14.6*	-	2.2*	-	-	-

Table 4.4 contd.

Chaffinch:

	1	2	3	4	5	6	7	8	9	10	11	12	13
Blue tit	-	18.3*	8.2*	14.3*	-	-	3.2*	2.3*	-	-	-	-	-
Great tit	-	24.7*	8.7*	15.8*	-	-	3.1*	1.4	-	0.3	0.6	-	-
Coal tit	5.2*	7.7*	-	8.5*	-	0.4	-	-	1.8*	-	0.6	0.9	-
Goldcrest	8.7*	14.2*	-	14.3*	-	0.4	-	-	1.3	-	1.2*	0.1	-
Treecreeper	-	16.1*	-	8.9*	-	-	0.9	-	-	-	-	-	-

Treecreeper:

	1	2	3	4	5	6	7	8	9	10	11	12	13
Blue tit	-	2.2	12.6*	5.4*	-	0.5	2.3*	2.6*	3.7*	0.7*	-	-	-
Great tit	-	8.6*	13.1*	6.9*	-	-	2.2	1.7	1.9	1.4	2.0	-	-
Coal tit	8.8*	-	-	-	4.9*	1.4*	-	-	1.3*	0.3	2.0*	0.9	0.1
Goldcrest	12.3*	-	-	5.4*	7.4*	1.4*	-	-	7.2*	-	2.6*	0.1	0.2
Chaffinch	3.6	-	4.4*	-	8.0*	1.0	-	0.3	5.9*	1.1*	1.4	-	0.2

any of the tree species, since its relative preferences were scattered throughout the range of the tree species available. The tree species choice by the blue and great tits was the most broadleaved, whilst the coal tit and goldcrest chose coniferous trees most frequently. The chaffinch and treecreeper appear to be intermediate to these two groupings. This comparison shows that despite foraging in the same tree species, the relative use of the trees by each bird species was significantly different from other bird species to allow niche partitioning by tree species choice.

Hamsterley Forest had five tree species in common with Great High Wood: oak, beech, sycamore, larch and birch. Of these, beech was avoided by all birds to a similar extent in both woods (Table 4.5). Oak and sycamore were commoner in Great High Wood, and larch in Hamsterley Forest. The bird species tended to show more extreme reaction, i.e. stronger preference or avoidance, to each of these tree species in the wood where it was present at lower frequency. In 17/18 combinations of bird and tree species (94%: $X^2=14.22$, 1 d.f. p<0.001) the discrimination of oak, sycamore and larch was stronger when the tree species was rarer. Only the treecreeper in oak deviated from this pattern. Birch was present at similar frequency in both woods and therefore was not included in the above calculation. This shows that as long as a tree species is used by a bird species, the preference or avoidance for it is stronger when the tree species is less abundant.

Table 4.5

Tree preference indices for tree species that were present both in
Hamsterley Forest and in Great High Wood, March - October,
1984-86

Tree species	Wood	Blue tit	Great tit	Coal tit	Gold-crest	Chaf-finch	Tree-creeper
Oak	GHW	0.58*	0.26*	-0.25*	-0.56*	0.24	1.17*
	HF	0.68*	0.85*	-0.64*	-0.80*	-0.42*	-0.26*
Beech	GHW	-0.88*	-0.93*	-0.90*	-1.00*	-0.91*	-0.80*
	HF	-0.79*	-0.38	-0.94*	-0.95*	-0.88*	-0.71*
Sycamore	GHW	-0.05	0.04	-0.61*	-0.39	0.61*	-0.51*
	HF	6.32*	3.29*	0.75*	1.53*	1.72*	1.67*
Larch	GHW	0.28*	0.33*	4.64*	4.52*	1.26*	0.68*
	HF	0.10	-0.25*	0.70*	0.34*	1.14*	0.23*
Birch	GHW	0.55*	1.11*	0.06	-0.06	-0.39	0.22
	HF	1.23*	1.36*	-0.13	-0.47*	-0.56*	0.57*

notes: * = significant preference or avoidance (chi-square)
      GHW = Great High Wood, HF = Hamsterley Forest

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4.2 Seasonal changes in tree use

The tree species use by the blue tit (Fig 4.1) changed considerably from one month to the next. Oak was used only a little in the spring, but its use was extensive from May onwards with a peak in June. Birch and alder were used mainly during the spring months, and sycamore, Scots pine and European larch in the late summer and autumn. The monthly tree use by the coal tit (Fig 4.2) differed from that by the blue tit, mainly because of the prominent use of conifers. However, the pattern of tree use was similar for the two species. The coal tit, too, used birch and alder mainly in the spring, oak mostly in June, and sycamore and the conifers somewhat more frequently in the late summer and autumn. Despite the different levels of use of the tree species by the two bird species, the timing of the most extensive use of the tree species coincided. This was probably in response to periods of high prey availability on the tree species. Gibb & Betts (1963) showed similar changes in tree use from broadleaves to conifers by titmice in Breckland pine and surrounding broadleaves, and showed that this change was due to changes in insect biomass - broadleaved trees were more profitable foraging sites early in the year, and conifers later in the year, with insects beginning to be abundant on conifers from June or July onwards.

The frequency of the use of tree species in the early and late season are presented in Table 4.6. Some of the tree species were used consistently throughout the year, while others were used only in one season. Blue tits used oak more in the late season (Table
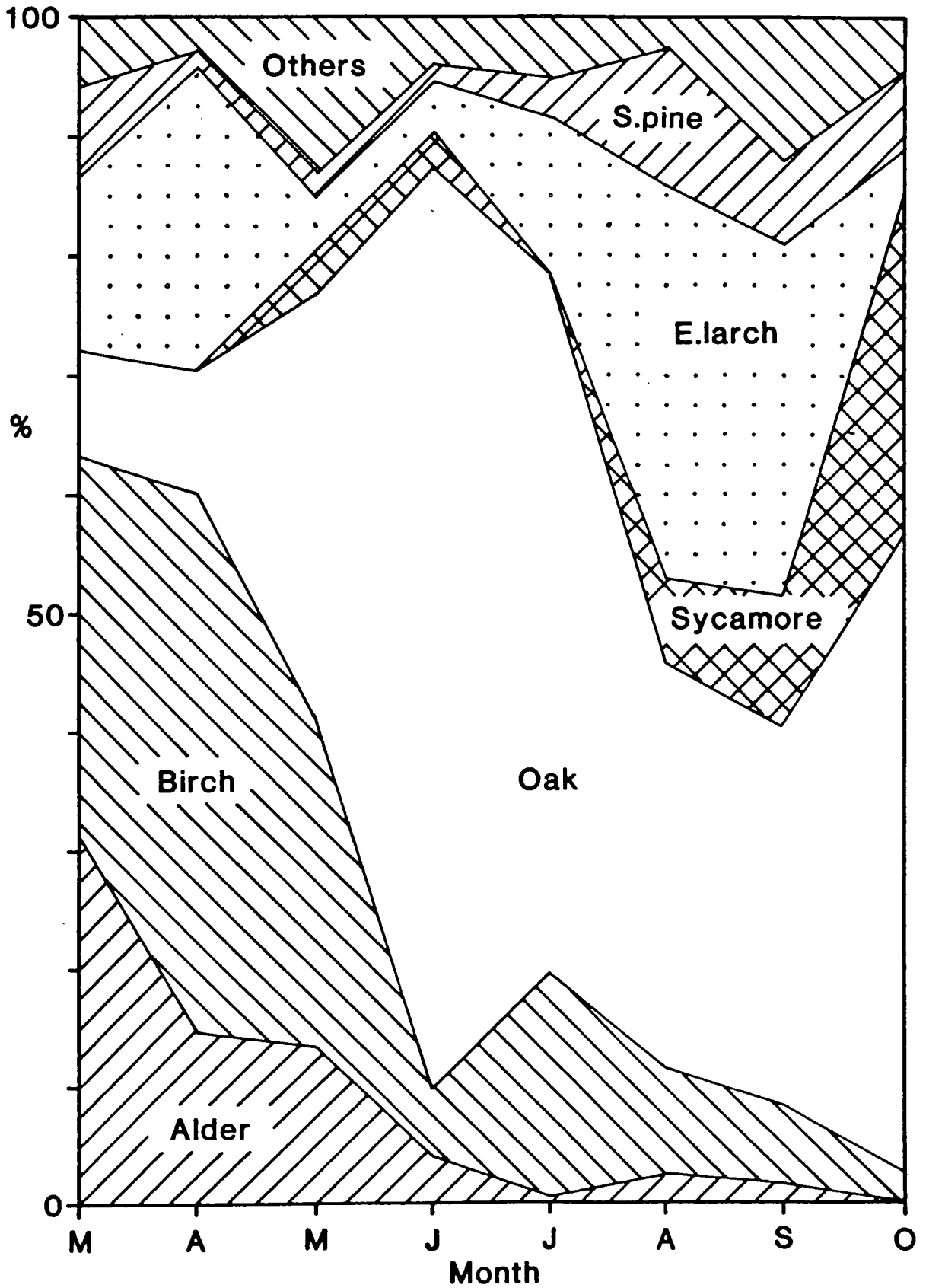
Fig 4.1: Use of tree species by the blue tit in each month
between March and October in Hamsterley Forest,
1984-86.
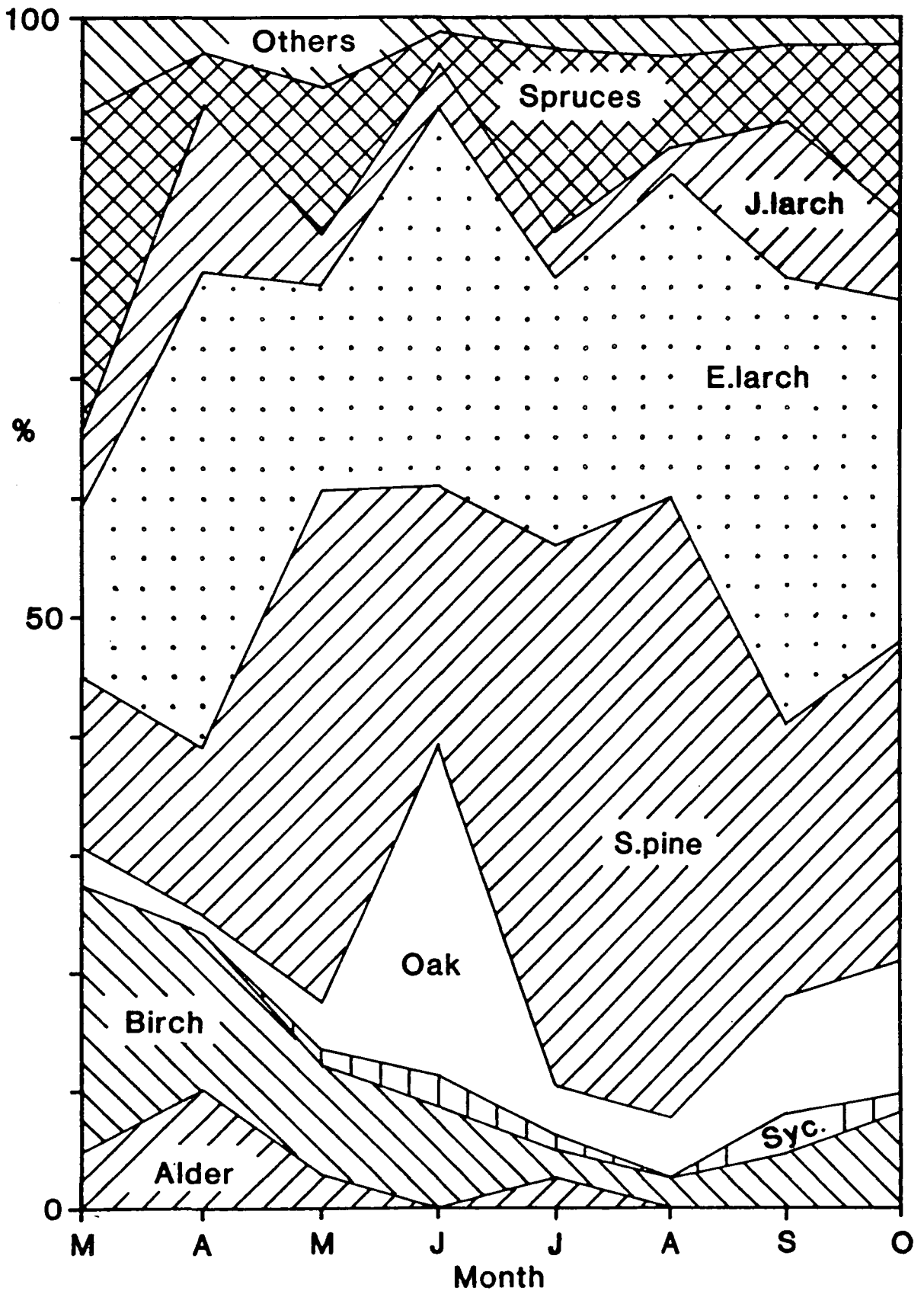
Fig 4.2: Use of tree species by the coal tit in each month
         between March and October in Hamsterley Forest,
         1984-86.

Table 4.6

Percentage of feeding observations in each tree species for six bird
species in two seasons (March - June and July - October)
in Hamsterley Forest, 1984-86

Tree species	Blue tit	Great tit	Coal tit	Gold-crest	Chaf-finch	Tree-creeper
March-June:						
Oak	32.6	45.0	8.9	9.2	18.4	21.1
European larch	11.5	11.6	28.6	28.4	31.3	13.4
Scots pine	2.3	6.2	24.8	19.9	9.5	8.6
Japanese larch	1.3	0.8	7.5	1.9	14.7	1.0
Birch	28.7	10.1	11.9	5.0	3.4	18.7
Beech	0.5	0.0	0.7	0.4	1.4	2.9
Norway spruce	0.3	0.0	4.2	8.8	4.6	3.3
Sitka spruce	0.0	2.3	4.5	18.8	3.2	3.8
Alder	15.1	10.1	4.9	4.6	3.2	19.1
Western hemlock	0.0	0.0	1.4	2.7	0.0	1.4
Ash	4.7	1.6	1.0	0.0	3.2	3.3
Sycamore	1.8	10.1	1.0	0.0	6.6	3.3
Rowan	1.0	2.3	0.5	0.4	0.6	0.0
Sample size	383	129	573	261	348	209
July-October:						
Oak	41.4	41.1	8.0	2.3	10.8	13.0
European larch	23.5	14.3	30.8	21.4	41.5	30.2
Scots pine	7.4	4.8	34.0	35.1	16.3	27.9
Japanese larch	2.4	0.4	8.1	2.1	17.3	14.0
Birch	9.8	20.3	4.3	3.1	3.0	3.7
Beech	1.6	5.6	0.2	0.2	0.3	0.5
Norway spruce	0.6	0.9	4.0	9.6	3.3	2.3
Sitka spruce	0.4	0.4	6.0	16.8	2.2	1.9
Alder	1.3	6.1	0.6	1.0	3.7	0.0
Western hemlock	0.1	0.0	1.0	4.1	0.4	1.4
Ash	1.6	0.0	0.5	0.0	0.1	1.9
Sycamore	9.6	0.9	1.9	3.7	0.6	1.9
Rowan	0.5	5.2	0.6	0.6	0.4	1.4
Sample size	827	231	1723	513	675	215

4.7), while goldcrests, chaffinches and treecreepers used the tree significantly more in the early season. Great and coal tits showed no seasonality in the use of oak. European larch was used by all birds except by goldcrests more in the late season. Scots pine, too, was used more frequently later in the year. Only treecreepers showed seasonal differences in the use of Japanese larch, and no seasonality was apparent for either species of spruce, western hemlock or rowan. Beech was used little throughout the year, except by great tits which responded to the presence of beechmasts and increased their use of beech in the late season. Alder and ash were used more in the early season. Birch was used more extensively in the early season by all except great tits. Great tits, chaffinches and treecreepers used sycamore more in the early season, while the other three species did so in the late season. Blue tits changed their foraging patterns most during the year, and great tits and coal tits changed least. An overall shift from broadleaved to more coniferous choice of tree species in the course of the year is apparent.

Birds showed a preference or avoidance for most of the tree species in both seasons (Table 4.8), but there was a tendency towards more significant discrimination of tree species in the late season by many bird species (larger number of significant preferences and avoidances). The seasonal differences in the tree choice were similar to those observed in Great High Wood.

Table 4.7

Changes in the frequency at which each tree species was used
from the early to the late season in Hamsterley Forest,
1984-86

Tree species	Blue tit	Great tit	Coal tit	Gold- crest	Chaf- finch	Tree- creeper
Oak	1.27*	0.91	0.90	0.25*	0.59*	0.62*
European larch	2.04*	1.23	1.08	0.75*	1.33*	2.25*
Scots pine	3.22*	0.77	1.37*	1.76*	1.72*	3.24*
Japanese larch	1.85	0.50	1.08	1.11	1.18	14.00*
Birch	0.34*	2.01*	0.36*	0.62	0.88	0.20*
Beech	3.20	inf *	0.29	0.50	0.21	0.17
Norway spruce	2.00	inf	0.95	1.09	0.72	0.70
Sitka spruce	inf	0.17	1.33	0.89	0.69	0.50
Alder	0.09*	0.60	0.12*	0.22*	1.16	0.00*
Western hemlock	inf	-	0.71	1.52	inf	1.00
Ash	0.34*	0.00	0.50	-	0.03*	0.58
Sycamore	5.33*	0.09*	1.90	inf *	0.09*	0.58
Rowan	0.50	2.26	1.20	1.50	0.67	inf

notes: figures are   <u>percentage in late season</u>
                         percentage in early season

    * = significant difference between the two seasons (t-test)

Table 4.8

Seasonal tree preference index of six species of birds in
Hamsterley Forest, 1984-86

Tree species	Blue tit	Great tit	Coal tit	Gold- crest	Chaf- finch	Tree- creeper
March-June:						
Oak	0.30*	0.79*	-0.65*	-0.63*	-0.27*	-0.16
European larch	-0.32*	-0.31	0.70*	0.69*	0.86*	-0.20
Scots pine	-0.85*	-0.59*	0.62*	0.31*	-0.38*	-0.44*
Japanese larch	-0.79*	-0.87*	0.22	-0.69*	1.38*	-0.84*
Birch	2.67*	0.29	0.52*	-0.36	-0.56*	1.39*
Beech	-0.90*	-1.00*	-0.87*	-0.93*	-0.73*	-0.46
Norway spruce	-0.95*	-1.00*	-0.26	0.57*	-0.18	-0.40
Sitka spruce	-1.00*	-0.47	0.03	3.25*	-0.28	-0.13
Alder	1.66*	0.77*	-0.14	-0.19	-0.44*	2.36*
Western hemlock	-1.00*	-1.00	-0.49*	-0.02	-1.00*	-1.00*
Ash	0.68*	-0.44	-0.62*	-1.00*	0.13	0.20
Sycamore	0.77	8.77*	0.02	-1.00	5.41*	2.25*
Rowan	-0.09	1.02	-0.54	-0.67	-0.50	-1.00
Sample size	383	129	573	261	348	209
July-October:						
Oak	1.07*	1.05*	-0.60*	-0.88*	-0.46*	-0.35*
European larch	0.31*	-0.20	0.73*	0.20*	1.32*	0.69*
Scots pine	-0.59*	-0.73*	0.91*	0.97*	-0.09	0.57*
Japanese larch	-0.67*	-0.94*	0.10	-0.71*	1.36*	0.90*
Birch	0.60*	2.32*	-0.30*	-0.49*	-0.52*	-0.39
Beech	-0.85*	-0.46*	-0.98*	-0.98*	-0.97*	-0.95*
Norway spruce	-0.90*	-0.86*	-0.33*	0.59*	-0.46*	-0.61*
Sitka spruce	-0.92*	-0.91*	0.26*	2.53*	-0.53*	-0.61*
Alder	-0.55*	1.05*	-0.78*	-0.67*	0.25	-1.00*
Western hemlock	-0.96*	-1.00*	-0.69*	0.28	-0.86*	-0.56
Ash	0.10	-1.00	-0.67*	-1.00*	-0.90*	0.31
Sycamore	9.89*	-0.01	1.18*	3.22*	-0.32	1.12
Rowan	-0.60	3.29*	-0.52*	-0.52	-0.63	0.15
Sample size	827	231	1723	513	675	215

* = significant preference or avoidance (chi-square)

4.3 Foraging height

The foraging heights of birds were divided into the same height zones as in Great High Wood (section 3.3.). The height zone most commonly used by all three species of titmice was 4-8m (Fig 4.3), whereas treecreepers were most often seen at 0-4m. Goldcrests and chaffinches were feeding most often at heights of 8-12m, with the 4-8m zone being used by almost as many birds. The difference in the use of these two height zones, despite being small, was significant for both species (GC:t=3.40, CF:t=3.15). The 4-8m zone was used most frequently by the foraging birds as a whole (46% of all observations) with 38% of the birds seen in the zone of 8-12m, 13% at 0-4m, and only 3% above 12 metres. The height distribution of the five bird species did not differ significantly from each other, which suggests that they did not partition their feeding niche by vertical stratification.

The mean foraging height for all species combined was 7.73m in Hamsterley Forest and 7.16m in Great High Wood. This difference was not significant. There was no difference in the height distribution of any bird species in the two woods.

4.4 Position within the canopy whilst feeding

The most frequently used feeding positions were the branches throughout the canopy, and the twigs in the outer canopy (Table 4.9), which together accounted for over 80% of the observations of all tits, goldcrests and chaffinches.
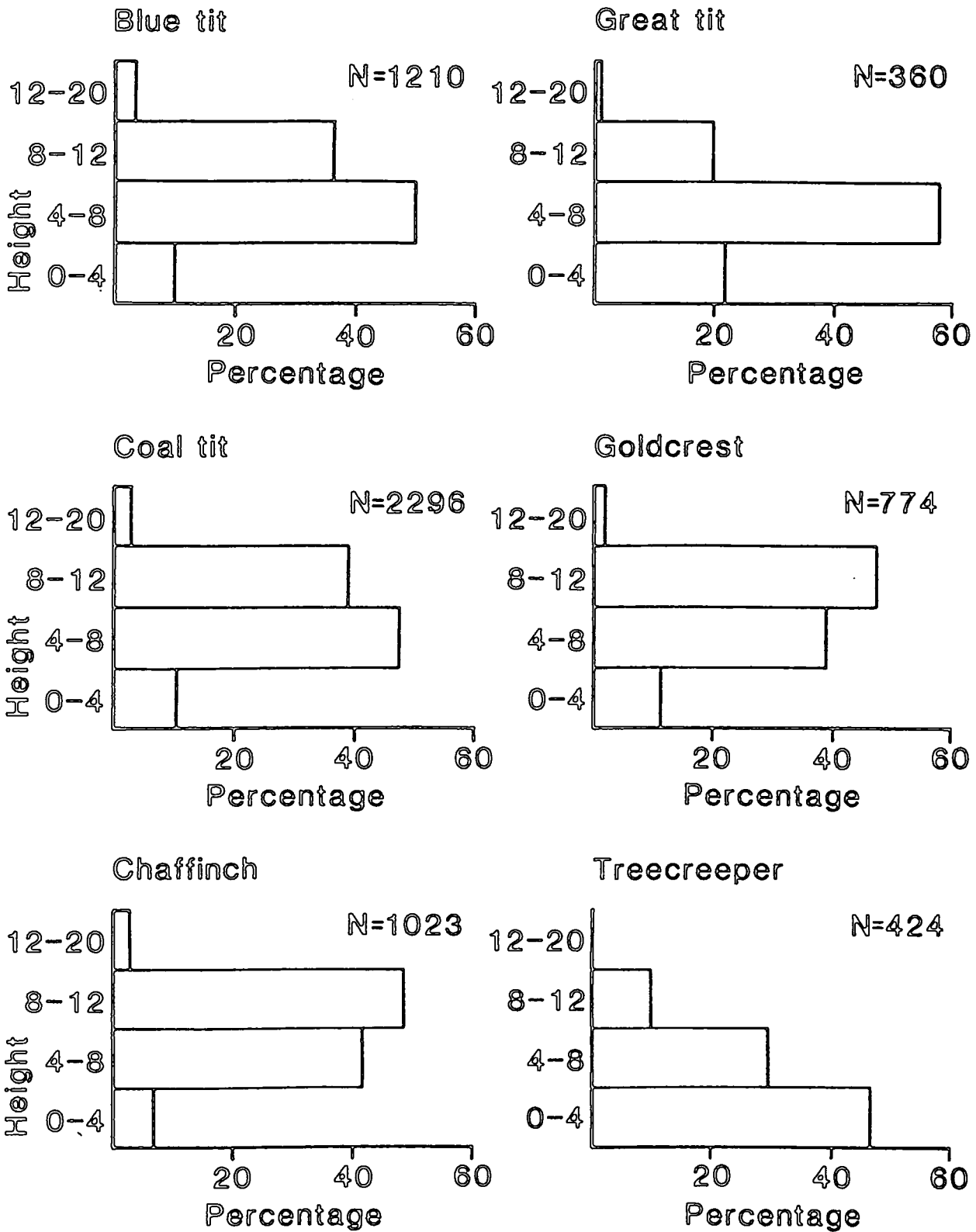
Fig 4.3: Percentage frequency of feeding observations of
six bird species at four height intervals in trees
in Hamsterley Forest, March - October, 1984-86.

Table 4.9

Percentage of each bird species feeding in each location within
the trees in Hamsterley Forest, March - October 1984-86

Location	Blue tit	Great tit	Coal tit	Gold-crest	Chaf-finch	Tree-creeper
Inner tree:						
branch (dead)	3.0	3.6	10.7	8.0	5.8	0.2
branch (live)	21.7	34.4	24.7	38.5	33.9	6.6
twig (dead)	0.2	0.0	0.0	0.0	0.0	0.0
twig (live)	6.8	7.8	3.8	4.1	0.9	0.2
Outer tree:						
branch (dead)	1.7	0.8	2.5	2.6	1.2	0.0
branch (live)	25.0	37.2	27.4	34.4	52.0	0.7
twig (dead)	0.5	0.0	0.0	0.0	0.0	0.0
twig (live)	40.3	15.6	26.0	11.2	6.3	0.0
Trunk	0.8	0.6	4.9	1.2	0.0	92.2
Sample size	1210	360	2296	774	1023	424

Dead branches formed an important feeding location for the coal tit and goldcrest. These two species used dead branches significantly more often than the other bird species (X^2 = 106.0, 1 d.f. p<0.001). The majority of foraging on dead branches took place in the larches, spruces and Scots pine, and it was significantly more extensive than in Great High Wood by all bird species (BT t=5.89, GT t=2.20, CT t=8.11, GC t=3.85, CF t=4.98).

Treecreepers foraged almost exclusively on the trunks of the trees, which few other birds did, and therefore occupied a foraging niche which overlapped little with that of the other bird species.

All bird species except the blue tit foraged more extensively on branches than on twigs (GT t=16.65, CT t=25.59, GC t=36.47, CF t=74.83) (Fig 4.4). The blue tit did not differ in the use of branches and twigs. The chaffinch used branches most and the blue tit least (t=25.03 between the bird species). The difference in the extent of use of branches was significant for each pair of bird species (BT-CT t=8.41, CT-GT t=4.43, GT-GC t=2.81, GC-CF t=6.00).

The goldcrest was the only species to use the inner canopy more frequently than the outer canopy (Fig 4.5), but this difference was not significant in Hamsterley forest (t=0.87). All other bird species used the outer canopy significantly more often than the inner canopy (BT t=18.85, GT t=2.09, CT t=11.48, CF t=8.66). The blue tit foraged in the outer canopy more than the other bird species (BT-GT t=4.71, BT-CT t=6.81, BT-GC t=8.60 BT-CF t=3.96), while the great tit, coal tit and chaffinch did not differ from each other in their use of the outer and inner parts of trees.

Blue
tit
1210

Great
tit
360

Coal
tit
2296

Gold
crest
774

Chaf
finch
1023

100

%

50

0

■ Other
▣ Twig
◩ Branch
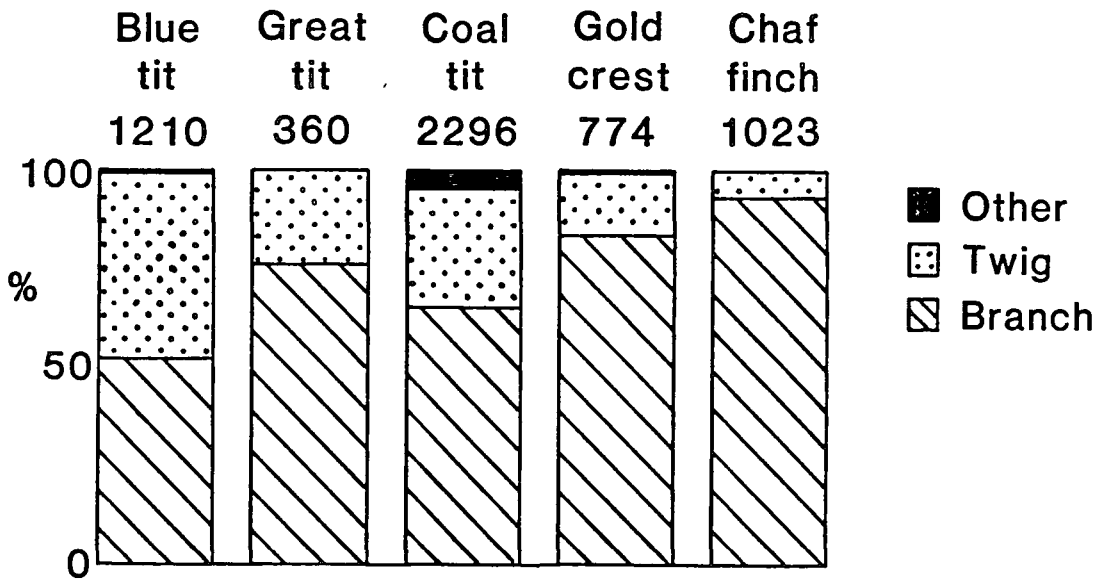
Fig 4.4: Percent frequency of the use of branches and twigs as perches by foraging birds in Hamsterley Forest, 1984-86. Sample sizes are shown at the top of each column.
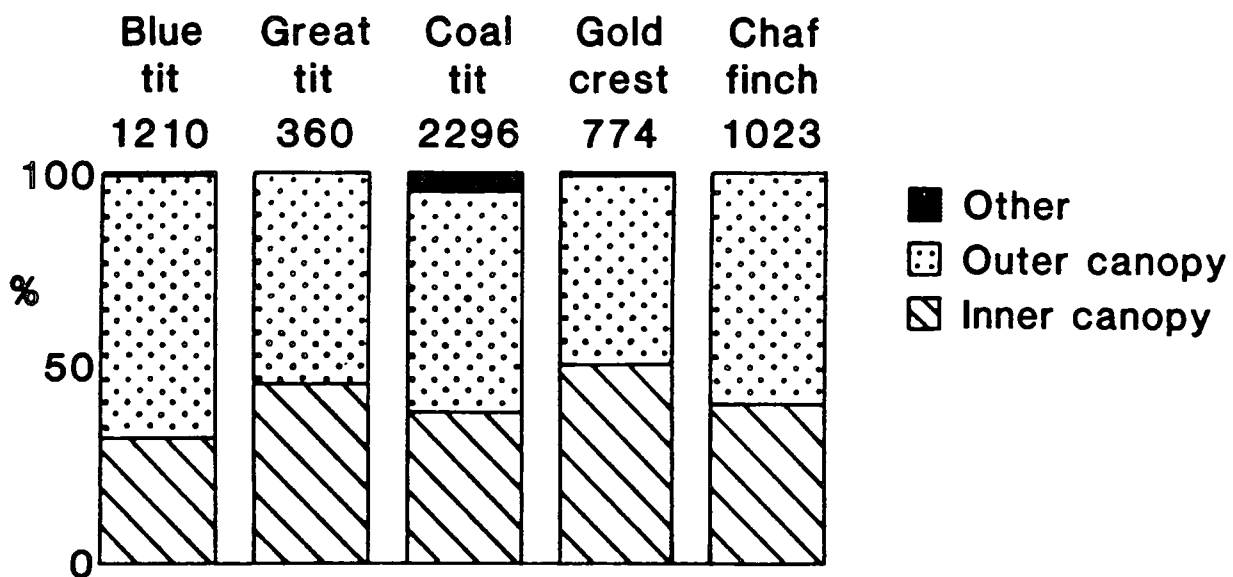
Fig 4.5: Percent frequency of the use of inner and outer
parts of the canopy by foraging birds in
Hamsterley Forest, 1984-86. Sample sizes are shown
at the top of each column.

The use of different positions within a tree was the same in Hamsterley Forest and in Great High Wood, indicating insensitivity to differences in the structure of the wood.

4.5   The substrates from where the food was obtained

The bark and the foliage were the commonest sources of food (Table 4.10). The goldcrest was the only species to forage on bark more often than on the leaves (t=4.44), all other species were seen foraging significantly more often among the foliage (46-67% of the time). All species except the great tit searched for food among the buds in the spring. The great tit was present in the wood in low numbers until May, by which time the availability of leaves in the broadleaved tree species resulted in the lack of foraging on buds. A comparison of the use of leaves and buds is presented in Table 4.11. The differences in the use of buds and leaves by the bird species reflected the proportion of coniferous tree species used as foraging site. Therefore the leaf and bud can be considered effectively the same foraging substrate. No seasonal differences in foliage use could be detected, and the major differences between the bird species appeared to be the relative importance of bark and leaves as a source of food.

All species, but particularly the coal tit, were seen feeding on cones (Table 4.10), and the great tit fed on nuts (including beechmast). However, apart from the differences in the use of the bark and foliage, only the foraging among the flowers by the blue tit and on cones by the coal tit were extensive enough for the

Table 4.10

Percentage frequency of each substrate as a source of food for
each bird species in Hamsterley Forest, March - October
1984-86

Substrate	Blue tit	Great tit	Coal tit	Gold-crest	Chaf-finch	Tree-creeper
Bark	23.8	24.8	37.7	54.3	32.4	97.0
Leaf	56.2	66.8	46.4	41.0	58.9	0.5
Bud	9.2	0.0	3.3	6.0	3.9	0.0
Flower	7.4	0.4	2.5	0.4	0.8	0.0
Cone	2.2	2.0	8.6	0.2	3.3	0.0
Seed	0.1	0.0	0.0	0.0	0.0	0.0
Nut	0.3	4.8	0.2	0.0	0.0	0.0
Lichen	0.3	0.8	1.3	0.0	0.6	0.0
Misc.	0.6	0.4	0.2	0.0	0.0	0.3
Sample size	979	250	1754	549	643	401

Table 4.11

Percentage of observations when birds foraged on bark and
foliage during the budburst and the rest of the study
period in Hamsterley Forest, 1984-86

March - May: Substrate	Blue tit	Great tit	Coal tit	Gold- crest	Chaf- finch
Bark	14.9	48.5	28.0	50.3	41.3
Leaf	14.6	39.4	25.0	26.5	32.8
Bud	37.2	0.0	18.0	21.3	13.2
Leaf + bud	52.1	39.4	43.0	47.8	46.0

June - October: Substrate	Blue tit	Great tit	Coal tit	Gold- crest	Chaf- finch
Bark	26.7	21.2	39.7	53.3	28.6
Leaf + bud	69.7	71.0	50.8	46.7	70.0

substrates to be considered important in partitioning of the foraging niche.

4.6 How the food was obtained

Gleaning was the predominant form of prey capture. Only one blue tit and two coal tits were observed probing into cracks in the bark and tearing the plant material. All bird species except the chaffinch were seen hanging from a branch or a twig to obtain prey, but it was commonly used only by blue and coal tits. 6% of blue tits and 3% of coal tits were observed hanging. Only chaffinches were observed to capture flying prey.

4.7 Duration of feeding bouts

Periods of uninterrupted foraging, during which the bird did not engage into any other activity than search for food and feed, were timed for all bird species studied in 1984 and 1985 to obtain information on feeding rates and times spent foraging in different species of tree before moving to another feeding location. Adequate data were obtained for the blue and coal tits, goldcrest and chaffinch (Tables 4.12-4.15). Each bird species attacked prey at different rates (mean attack rate: BT-27.1/min, CT-27.4/min, GC-24.2/min, CF-11.4/min), but the rate of attack by any one bird species on potential prey was similar in all tree species. However, the mean number of attacks in a feeding bout (Y) and the mean duration of a bout (X) differed from one tree species to another.

Table 4.12

Duration of feeding bouts and numbers of attacks on prey by blue
tit in each tree species in Hamsterley Forest,
March - October, 1984-85

Tree species	Number of bouts	Number of attacks	Attacks/ bout	Time (sec)	Time/ bout	Feeding rate	TPI
Oak	52	941	18.10	1990	38.27	28.4	0.69
E. larch	32	534	16.69	1125	35.16	28.5	0.25
S. pine	12	148	12.33	354	29.50	25.1	-0.71
Birch	30	544	18.30	1242	41.40	26.3	1.12
Alder	23	413	17.96	917	39.87	27.0	0.49

notes: the feeding rate is displayed as attacks per minute
          TPI = tree preference index

Table 4.13

Duration of feeding bouts and numbers of attacks on prey by coal tit
in each tree species in Hamsterley Forest, March - October
1984-85

Tree species	Number of bouts	Number of attacks	Attacks/ bout	Time (sec)	Time/ bout	Feeding rate	TPI
Oak	14	107	7.64	218	15.57	29.4	-0.64
E. larch	64	859	13.42	1894	29.59	27.2	0.60
S. pine	54	650	12.04	1726	31.96	22.6	0.95
J. larch	13	137	10.54	272	20.92	30.2	-0.23
Birch	20	228	11.40	482	24.10	28.3	0.02
N. spruce	8	76	9.50	163	20.38	28.0	-0.26
S. spruce	11	108	9.82	249	22.64	26.0	0.50

notes: the feeding rate is displayed as attacks per minute
          TPI = tree preference index

Table 4.14

Duration of feeding bouts and numbers of attacks on prey by goldcrest
in each tree species in Hamsterley Forest, March - October,
1984-85

Tree species	Number of bouts	Number of attacks	Attacks/ bout	Time (sec)	Time/ bout	Feeding rate	TPI
E. larch	24	263	10.96	655	27.29	24.1	0.42
S. pine	34	349	10.26	920	27.06	22.8	0.61
Birch	3	21	7.00	64	21.33	19.7	-0.50
N. spruce	10	109	10.90	257	25.70	25.4	0.57
S. spruce	27	392	14.52	777	28.78	30.3	2.84
Alder	2	11	5.50	24	12.00	27.5	-0.46
W. hemlock	5	35	7.00	106	21.20	19.8	0.33

notes: the feeding rate is displayed as attacks per minute
          TPI = tree preference index

Table 4.15

Duration of feeding bouts and numbers of attacks on prey by chaffinch
in each tree species in Hamsterley Forest, March - October
1984-85

Tree species	Number of bouts	Number of attacks	Attacks/ bout	Time (sec)	Time/ bout	Feeding rate	TPI
Oak	18	117	6.50	534	29.67	13.1	-0.27
E. larch	54	414	7.67	1868	34.59	13.3	0.86
S. pine	13	62	4.77	373	28.69	10.0	-0.10
J. larch	19	157	8.26	766	40.32	12.3	1.21
S. spruce	6	23	3.83	168	28.00	8.2	-0.27

notes: the feeding rate is displayed as attacks per minute
          TPI = tree preference index

The relationship between these two variables is shown for the blue tit in Fig 4.6 and for the coal tit in Fig 4.7. The regression for each is linear and significant (blue tit:y = 0.51x - 2.10, r = +0.96, 3 d.f. p<0.01; coal tit:y = 0.30x + 3.44, r = +0.91, 5 d.f. p<0.01). Similar regression was obtained for the goldcrest (y = 0.47x - 1.53, r = +0.87, 5 d.f. p=0.01) and for the chaffinch (y = 0.32x - 4.08, r = +0.88, 3 d.f. p<0.05).

When the tree preference index calculated for 1984-85 (Y) was plotted against the mean duration of feeding bout (X) in each tree species, a linear and significant relationship was obtained for three of the four bird species. The regression for the blue tit was y = 0.14x - 4.77, r = +0.96, 3 d.f. p<0.01, (Fig. 4.8), and for the coal tit y = 0.09x - 2.07, r = +0.93, 5 d.f. p<0.01, (Fig. 4.9). The regression for the chaffinch was y = 0.13x - 3.90, r = +0.96, 3 d.f. p<0.01, and for the goldcrest y = 0.13x - 2.49, r = +0.68, 5 d.f. which was just non-significant, probably because of the small number of observations obtained for the species. The slope of the regression line for each bird species did not differ significantly, suggesting that the relationship between tree preference index and the duration of a feeding bout was the same for all birds independent of their respective feeding rates.

Data on blue tit from the two study sites shows that foraging was not affected by the tree species composition or the structure of the wood. The feeding rate and the duration of the feeding bouts of blue tit were almost identical in the two woods for each tree species present in both. Similarly, the mean feeding rate and the
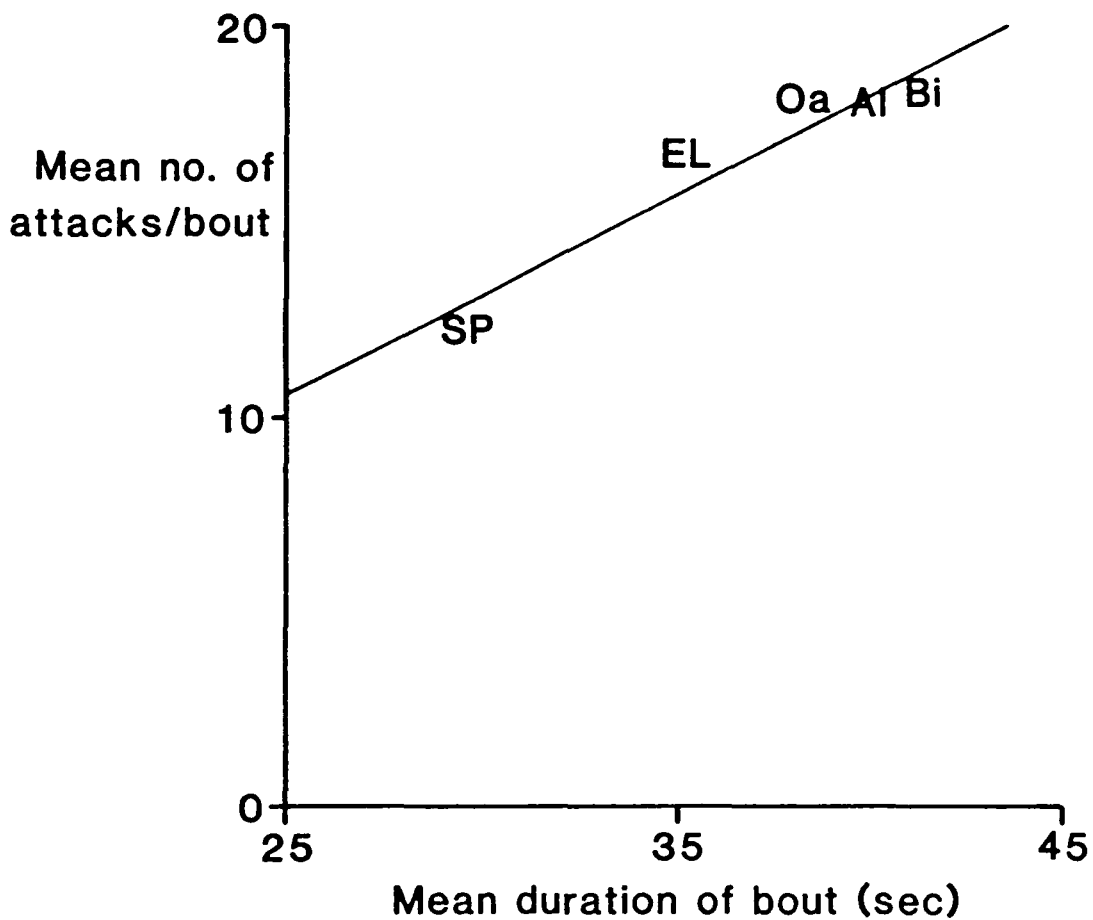
Fig 4.6: The relationship between mean number of attacks on
prey and mean duration of a feeding bout in
different tree species for the blue tit in
Hamsterley Forest, 1984-85.
Y = 0.51(+/-0.09)X - 2.10, r = +0.96, 3 d.f. (See
Table 2.1 for abbreviations of tree species.)
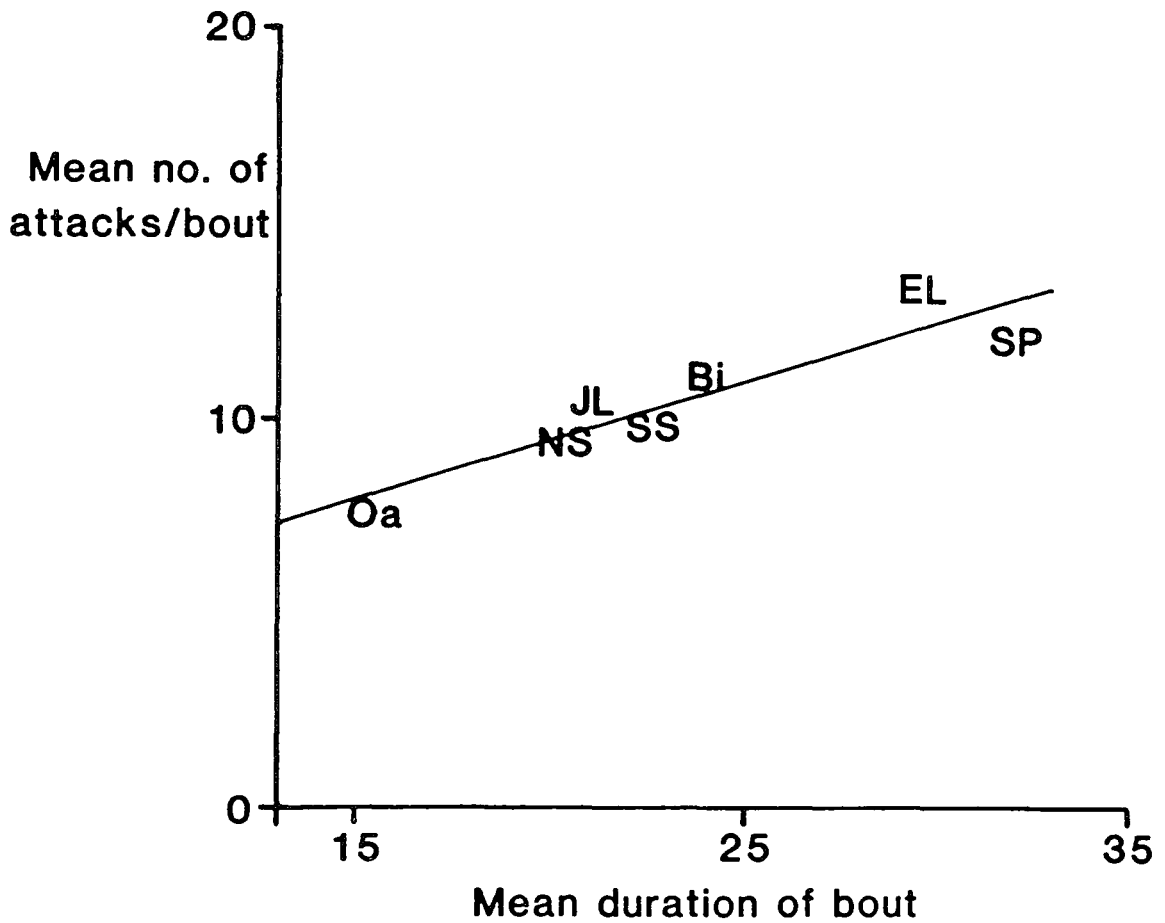
Fig 4.7: The relationship between mean number of attacks on
prey and mean duration of a feeding bout in
different tree species for the coal tit in
Hamsterley Forest, 1984-85.
Y = 0.30(+/-0.06)X + 3.44, r = +0.91, 5 d.f. (See
Table 2.1 for abbreviations of tree species.)

1

Bi

Oa

Al

TPI

EL

0

25   35   45

Mean duration
of bout (sec)

SP

−1
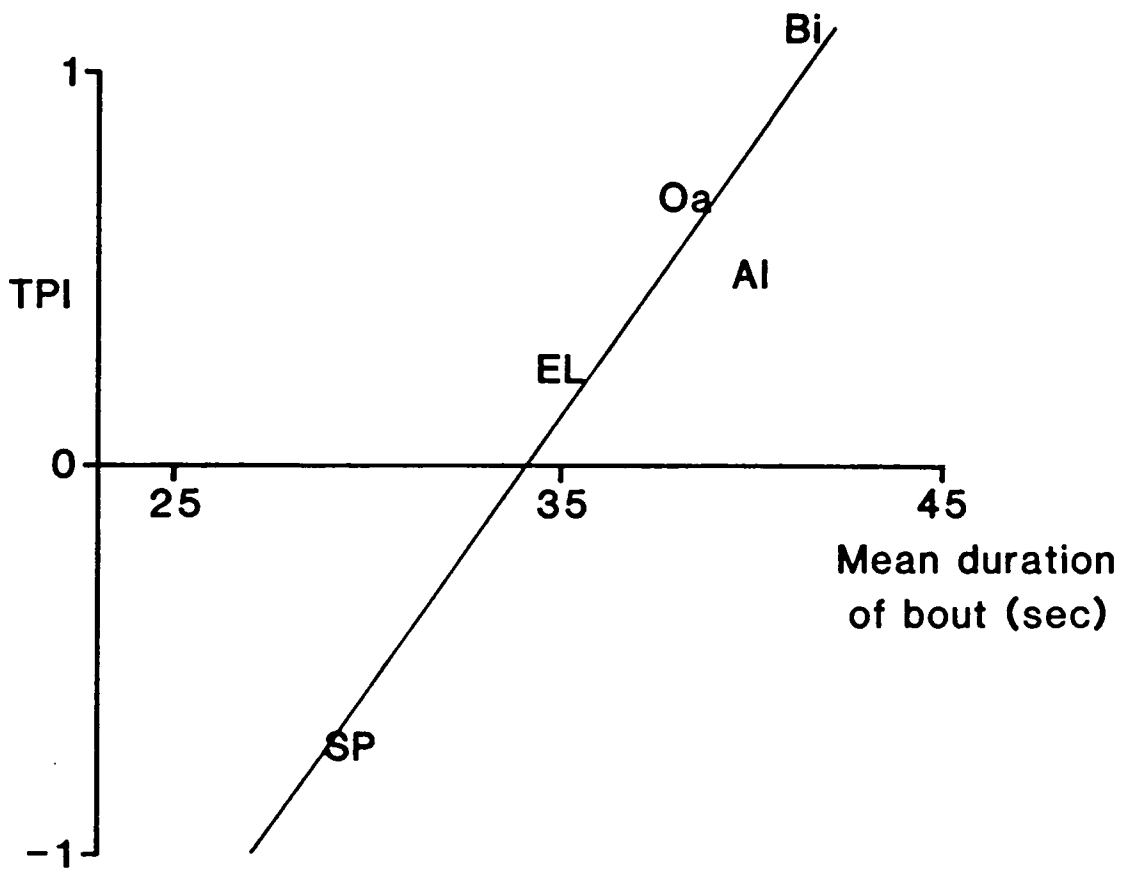
Fig 4.8: The relationship between the blue tit tree
preference (TPI) and the duration of feeding bouts
in each tree species in Hamsterley Forest,
1984-85. $Y = 0.14(+/-0.02)X - 4.77$, $r = +0.96$,
3 d.f. (See Table 2.1 for abbreviations of tree
species.)
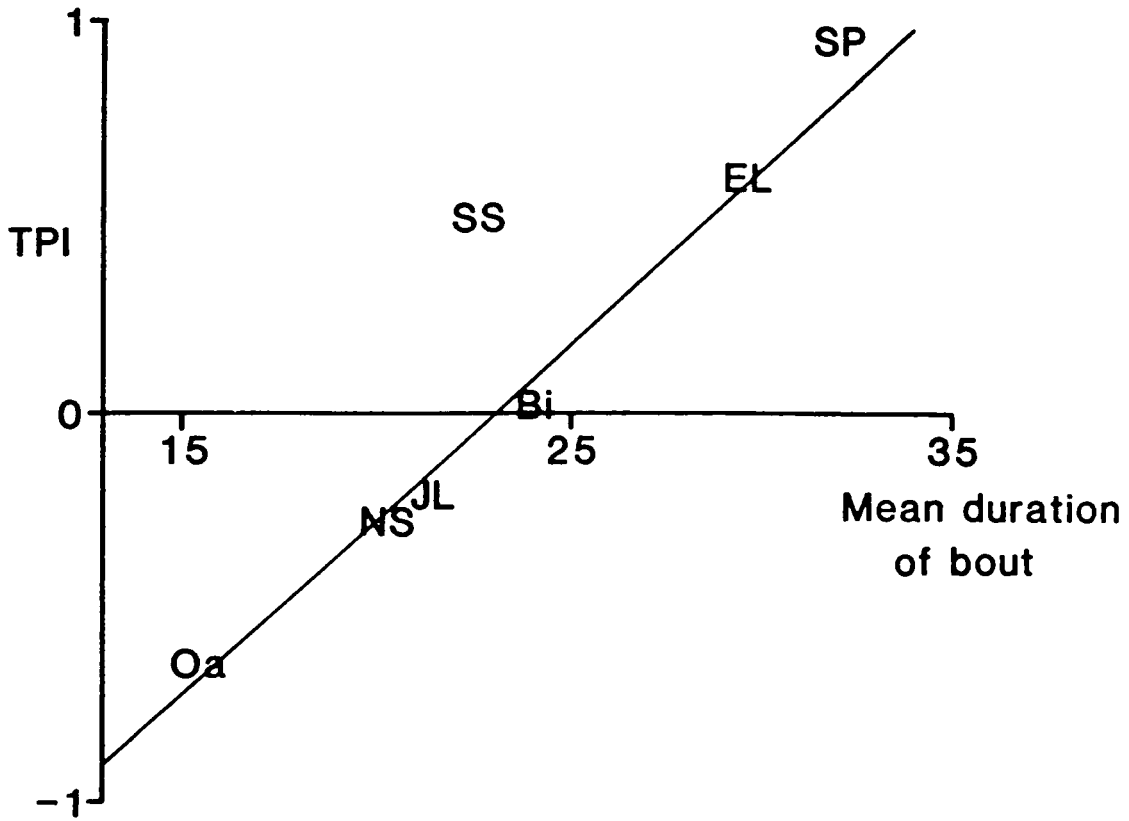
Fig 4.9: The relationship between the coal tit tree
preference (TPI) and the duration of feeding bouts
in each tree species in Hamsterley Forest,
1984-85. $Y = 0.09(+/-0.02)X - 2.07$, $r = +0.93$,
5 d.f. (See Table 2.1 for abbreviations of tree
species.)

mean duration of a feeding bout for all tree species combined did not differ.

Conversion of tree preference indices as described in section 3.7 revealed that the differences in the tree preferences were only partially accounted for by the differences in the duration of feeding bouts (Figs. 4.10 & 4.11; Table 4.16), leaving 30-80% of the difference caused by the birds choosing to feed in some tree species more frequently than in others. Therefore, the birds actively searched out the preferred tree species, and were able to recognise and avoid the trees they did not wish to feed in.

Observational evidence for the active selection of tree species was obtained from both woods. In Great High Wood a large proportion of the beeches were grouped together with few other trees among them. Few birds were seen in these beech stands. On numerous occasions a flock was observed moving through the wood, and as it reached the edge of the beech, the birds changed direction and continued along the edge of the stand, only visiting trees of other species. In some occasions a flock entered a beech stand, but the birds used other tree species as 'stepping stones' as they moved through. Very rarely were the beeches actually used. In Hamsterley Forest the presence of beech at high density reduced the bird density in the compartment, and beech was not used. An extreme example of this was a stand of pure beech, which was rarely visited by the birds, while the neighbouring compartments of Scots pine, sitka and Norway spruce were used regularly.
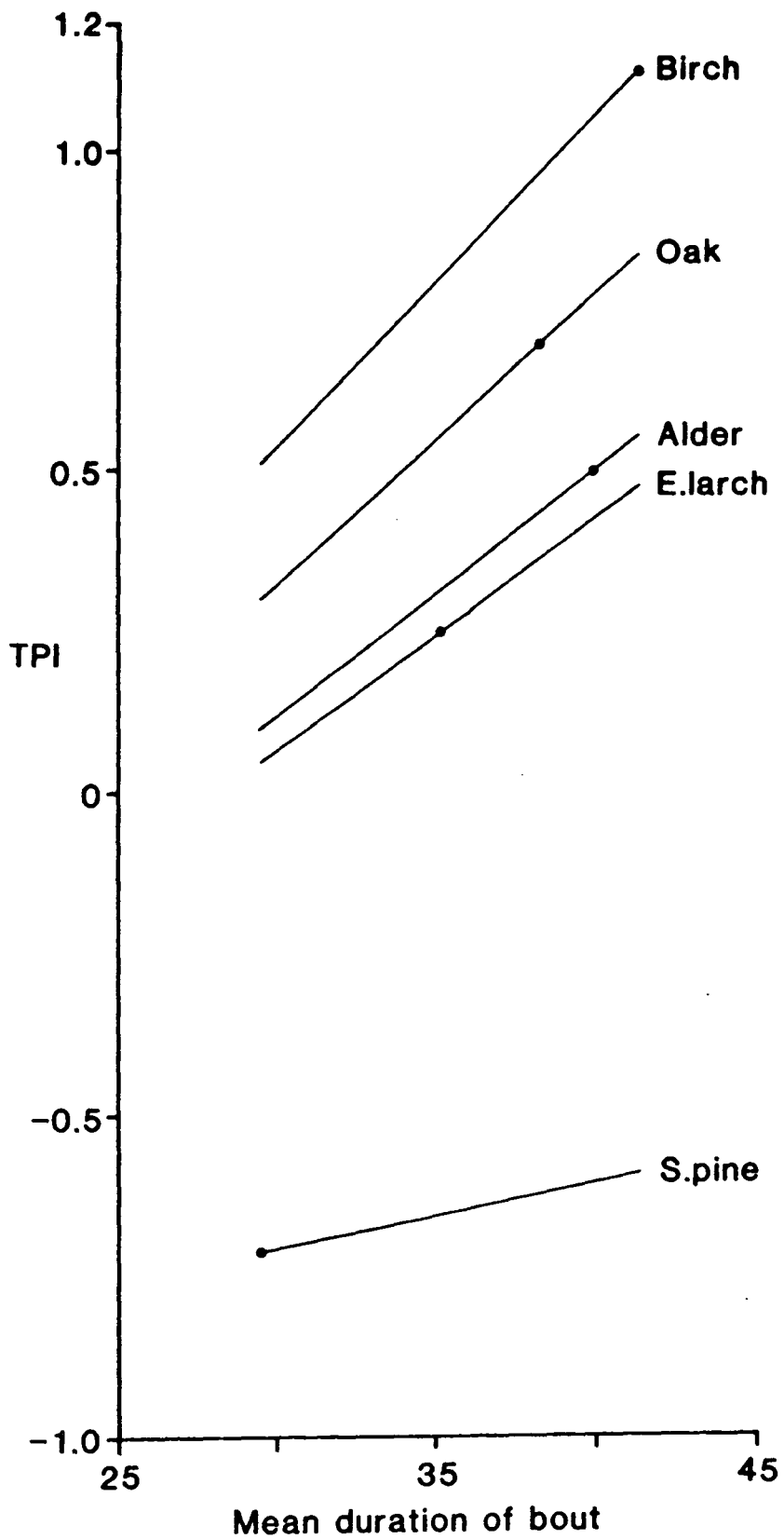
Fig 4.10: The relationship between blue tit tree preference
(TPI) and mean duration of feeding bout for each
tree species, together with modified tree
preferences assuming bouts of different duration
(see text) in Hamsterley Forest, 1984-86.
(● = original TPIs, _____ = regression for
modified TPIs)

101
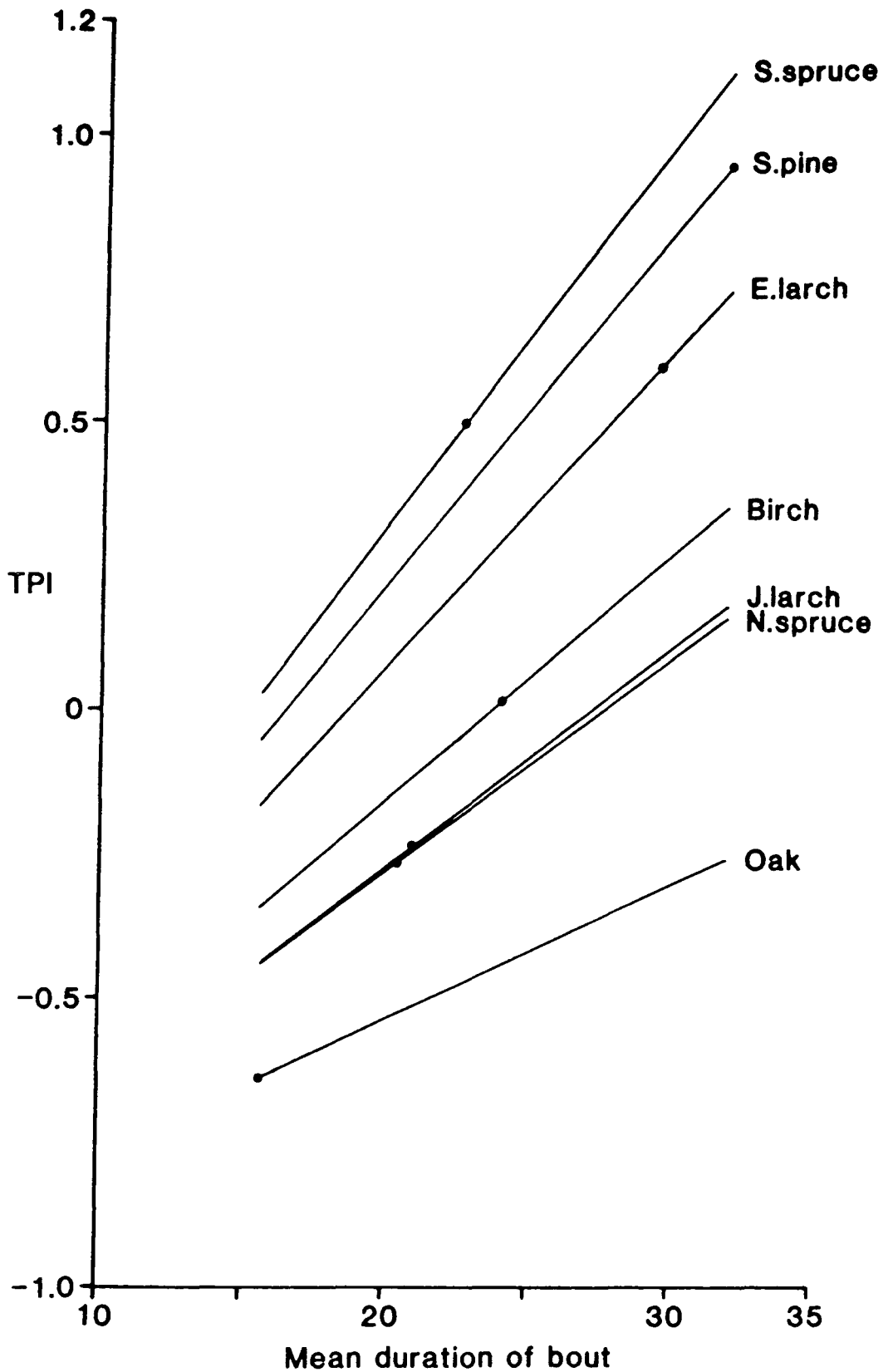
Fig 4.11: The relationship between coal tit tree preference
(TPI) and mean duration of feeding bout for each
tree species, together with modified tree
preferences assuming bouts of different duration
(see text) in Hamsterley Forest, 1984-86.
(● = original TPIs, _____ = regression for
modified TPIs)

Table 4.16

Tree preference indices (TPI) calculated from the different durations
of foraging bout for blue tit, coal tit, goldcrest and
chaffinch (Tables 4.12-4.15) in Hamsterley Forest,
March - October, 1984-85

Blue tit

	Oa	EL	SP	Bi	Al
Tree considered					
Observed TPI	.69	.25	-.71	1.12	.49
TPI adapted from					
Oak (Oa)	-	.36	.38	.96	.43
E. larch (EL)	.55	-	.35	.80	.31
S. pine (SP)	.30	.05	-	.51	.10
Birch (Bi)	.83	.47	.41	-	.55
Alder (Al)	.76	.42	.39	1.04	-

Coal tit

	Oa	EL	SP	JL	Bi	NS	SS
Tree considered							
Observed TPI	-.64	.60	.95	-.23	.02	-.26	.50
TPI adapted from							
Oak (Oa)	-	-.16	-.05	-.43	-.34	-.43	.03
E. larch (EL)	-.32	-	.81	.09	.25	.07	.96
S. pine (SP)	-.26	.73	-	.18	.35	.16	1.12
J. larch (JL)	-.52	.13	.28	-	-.11	-.24	.39
Birch (Bi)	-.44	.30	.47	-.11	-	-.12	.60
N. spruce (NS)	-.53	.10	.24	-.25	-.14	-	.35
S. spruce (SS)	-.48	.22	.38	-.17	-.04	-.18	-

Goldcrest

	EL	SP	Bi	NS	SS	Al	WH
Tree considered							
Observed TPI	.42	.61	-.50	.57	2.84	-.54	.33
TPI adapted from							
E. larch (EL)	-	.62	-.36	.67	2.64	.23	.72
S. pine (SP)	.41	-	-.37	.65	2.61	.22	.70
Birch (Bi)	.12	.27	-	.30	1.85	-.04	.34
N. spruce (NS)	.34	.53	-.40	-	2.43	.16	.61
S. spruce (SS)	.50	.71	-.33	.76	-	.30	.81
Alder (Al)	-.38	-.29	-.72	-.27	.60	-	-.25
W. hemlock (WH)	.10	.26	-.50	.30	1.83	-.05	-

Chaffinch

	Oa	EL	SP	JL	SS
Tree considered					
Observed TPI	-.27	.86	-.10	.21	-.27
TPI adapted from					
Oak (Oa)	-	.60	-.07	.63	-.23
E. larch (EL)	-.15	-	.09	.90	-.10
S. pine (SP)	-.29	.54	-	.57	-.25
J. larch (JL)	-.01	1.17	.26	-	.05
S. spruce (SS)	-.31	.51	-.12	.53	-

4.8 Year to year differences in tree use

The frequency at which each bird species foraged in most species of trees varied only little from one year to another (Table 4.17), and it did not affect the importance of that tree species for the birds. However, a few of the changes were prominent.

Blue and great tits changed their preference (Table 4.18) for alder into avoidance during the three year period of the study, which also happened to blue tits in European larch. Coal tits and treecreepers increased their use of Japanese larch over the three years from avoidance to preference. Coal tits' preference for sitka spruce and treecreepers' preference for birch changed into avoidance in 1986. Great tits showed preference for beech in 1984, which was the only year with a good crop of beechmasts. Apart from this, beech was universally avoided.

A common feature of all the bird species was the increase in the use of sycamore from 1984 to 1985 (Table 4.18). While most species increased their use of sycamore further in 1986, the use of sycamore by chaffinches dropped in Hamsterley Forest in 1986 and the use of larch increased. In 1986 sawfly larvae were common on larch, and chaffinches fed on them in preference to most other foods available (65% of chaffinches foraged in larches in 1986, Table 4.17). Interestingly, only chaffinches responded to the presence of the sawfly larvae. The changes in the use of tree species from one year to another were similar in the two woods, and therefore were likely to be caused by the same factors.

Table 4.17

Percentages of feeding observations of six bird species in each tree
species in Hamsterley Forest in each year, March - October

Tree species	Blue tit	Great tit	Coal tit	Gold-crest	Chaf-finch	Tree-creeper
1984:						
Oak	41.5	28.7	5.7	2.5	16.1	17.5
European larch	19.0	17.2	22.2	20.6	36.7	16.5
Scots pine	6.5	6.6	44.2	27.1	12.2	9.7
Japanese larch	0.7	0.8	4.0	2.9	18.1	2.9
Birch	11.8	18.9	5.4	2.2	3.3	17.5
Beech	1.0	10.7	1.2	0.4	0.8	1.9
Norway spruce	0.3	0.0	4.4	10.8	1.8	0.0
Sitka spruce	0.0	0.0	6.7	27.4	4.6	3.9
Alder	14.7	12.3	2.3	1.1	2.8	23.3
Western hemlock	0.3	0.0	2.3	4.0	0.0	1.9
Ash	0.3	1.6	0.2	0.0	2.3	1.0
Sycamore	2.9	0.8	0.3	0.4	0.8	1.9
Rowan	1.0	2.5	1.1	0.7	0.5	1.9
Sample size	306	122	652	277	392	103
1985:						
Oak	35.4	47.5	9.9	7.4	16.5	16.4
European larch	22.6	9.9	31.9	27.1	23.2	19.2
Scots pine	4.1	5.5	23.8	27.7	20.5	17.4
Japanese larch	2.9	0.6	6.9	1.1	12.1	6.1
Birch	17.4	14.9	9.2	4.8	4.0	13.1
Beech	0.7	0.0	0.0	0.3	1.3	1.9
Norway spruce	0.8	0.0	4.9	9.3	4.9	5.2
Sitka spruce	0.5	2.2	7.3	11.2	1.3	3.8
Alder	3.4	6.1	2.7	3.7	6.7	7.0
Western hemlock	0.0	0.0	0.8	3.5	0.0	1.4
Ash	3.4	0.0	0.9	0.0	0.9	4.2
Sycamore	8.5	6.6	1.4	3.5	8.0	4.2
Rowan	0.3	6.6	0.3	0.5	0.4	0.0
Sample size	615	181	769	376	224	213
1986:						
Oak	42.2	56.1	8.7	0.8	9.1	17.6
European larch	14.2	15.8	34.9	20.7	47.4	32.4
Scots pine	8.7	1.8	29.4	43.8	12.0	28.7
Japanese larch	1.7	0.0	11.8	3.3	17.2	14.8
Birch	16.6	17.5	4.1	4.1	2.5	0.9
Beech	2.8	0.0	0.0	0.0	0.2	0.9
Norway spruce	0.0	3.5	3.0	5.8	4.9	0.9
Sitka spruce	0.0	0.0	3.3	14.0	1.2	0.0
Alder	1.0	1.8	0.3	0.0	2.5	0.9
Western hemlock	0.0	0.0	0.5	3.3	0.7	0.9
Ash	3.1	0.0	0.7	0.0	0.2	0.9
Sycamore	8.7	3.5	3.0	4.1	1.5	0.0
Rowan	1.0	0.0	0.5	0.0	0.5	0.9
Sample size	289	57	875	121	407	108

Table 4.18

Tree preference index of six species of birds in each year
in Hamsterley Forest, March - October

Tree species	Blue tit	Great tit	Coal tit	Gold-crest	Chaf-finch	Tree-creeper
1984:						
Oak	1.39*	0.65*	-0.67*	-0.85*	-0.07	0.01
European larch	0.11	0.01	0.31	0.21	1.16*	-0.03
Scots pine	-0.61*	-0.61*	1.66*	0.63*	-0.26*	-0.42
Japanese larch	-0.94*	-0.93*	-0.64*	-0.74*	0.62*	-0.74*
Birch	0.62*	1.60*	-0.26	-0.70*	-0.54*	1.41*
Beech	-0.84*	0.76*	-0.80*	-0.94*	-0.87*	-0.68
Norway spruce	-0.96*	-1.00*	-0.40*	0.46*	-0.76*	-1.00*
Sitka spruce	-1.00*	-1.00*	0.38*	4.61*	-0.06	-0.21
Alder	1.92*	1.44*	-0.54*	-0.78*	-0.44*	3.63*
Western hemlock	-0.89*	-1.00*	-0.24	0.31	-1.00*	-0.36
Ash	-0.85*	-0.27	-0.93*	-1.00*	0.02	-0.57
Sycamore	2.88*	0.08	-0.59	-0.52	0.01	1.56
Rowan	-0.09	1.29	0.00	-0.33	-0.52	0.81
Sample size	306	122	652	277	392	103
1985:						
Oak	0.29*	0.73*	-0.64*	-0.73*	-0.40*	-0.40*
European larch	0.31*	-0.42*	0.85*	0.57*	0.35*	0.12
Scots pine	-0.77*	-0.68*	0.37*	0.59*	0.18	0.00
Japanese larch	0.01	-0.81	1.38*	-0.63*	3.16*	1.11*
Birch	1.35*	1.01*	0.24	-0.35	0.46	0.77*
Beech	-0.89*	-1.00*	-1.00*	-0.95*	-0.77*	-0.68*
Norway spruce	-0.84*	-1.00*	-0.05	0.80*	-0.05	0.00
Sitka spruce	-0.89*	-0.51	0.62*	1.49*	-0.70*	-0.16
Alder	-0.25	0.33	-0.40*	-0.18	0.47	0.55
Western hemlock	-1.00*	-1.00*	-0.68	0.40	-1.00*	-0.43
Ash	0.40	-1.00*	-0.63*	-1.00*	-0.63	0.73
Sycamore	6.30*	4.73*	0.24	1.99*	5.94*	2.65*
Rowan	-0.75*	3.97*	-0.80*	-0.60	-0.66	-1.00
Sample size	615	181	769	376	224	213
1986:						
Oak	0.70*	1.56*	-0.65*	-0.97*	-0.63*	-0.29
European larch	-0.28*	-0.20	0.77*	0.05	1.41*	0.65*
Scots pine	-0.50*	-0.90*	0.70*	1.54*	-0.30	0.66*
Japanese larch	-0.73*	-1.00	0.85*	-0.48	1.70*	1.33*
Birch	1.61*	1.75*	-0.35*	-0.35	-0.61*	-0.85*
Beech	-0.47	-1.00	-1.00*	-1.00*	-0.95*	-0.82*
Norway spruce	-1.00*	-0.29	-0.40*	0.17	-0.01	-0.81
Sitka spruce	-1.00*	-1.00	-0.30*	1.96*	-0.74*	-1.00*
Alder	-0.65	-0.41	-0.89*	-1.00	-0.17	-0.69
Western hemlock	-1.00*	-1.00	-0.88*	-0.14	-0.81*	-0.76
Ash	1.14*	-1.00	-0.53	-1.00	-0.83*	-0.36
Sycamore	7.41*	2.41	1.89*	3.02*	0.43	-1.00
Rowan	-0.18	-1.00	-0.64*	-1.00	-0.61	-0.27
Sample size	289	57	875	121	407	108

A preference hierarchy of tree species was constructed for blue and coal tits (Table 4.19) for each year separately. Less than a quarter of the tree species were preferred by the birds, and about half of the tree species were avoided to a greater or lesser degree. The same tree species tended to be preferred each year. The preferred tree species differed for the two species of birds.

4.9   Ways in which bird density and diversity are affected by the tree composition

Birds in each compartment were censused (see Methods) every time a compartment was visited. The coal tit was the most common species (one third of the birds, see Table 2.3). The chaffinch, blue tit and goldcrest were also common (10-20% of total), the great tit was present at frequency of 6%, but no other bird species exceeded 4% of the total numbers. Year to year changes in the relative   frequencies   of   bird   species   were   small   and non-significant.

Densities of birds per hectare were obtained by dividing the number of birds censused by the number of visits to the study site and by the size of the area. The overall bird densities in the study area of Hamsterley Forest were as follows: blue tit 0.45/ha, great tit 0.17/ha, coal tit 0.88/ha, goldcrest 0.31/ha, chaffinch 0.50/ha and treecreeper 0.05/ha. The remaining bird species were pooled with a combined density of 0.36/ha. This brings the total density of arboreal passerines to 2.72 birds per hectare, which was considerably lower than the density of 4.18 birds per hectare in

Table 4.19

Preference hierarchy of tree species for blue tit and coal tit
in Hamsterley Forest, March - October, 1984-86

| | Blue tit | | | Coal tit | | |
	1984	1985	1986	1984	1985	1986
Prefer	sycam. alder oak birch	sycam. birch e.larch oak	sycam. birch ash oak	s. pine s.spruce e.larch	j.larch e.larch s.spruce s.pine	sycam. j.larch e.larch s.pine
Neutral	e.larch rowan	ash j.larch alder	rowan beech alder	rowan birch w.heml sycam.	birch sycam. n.spruce w.heml	ash
Avoid	s.pine beech ash w.heml j.larch n.spruce s.spruce	rowan s.pine n.spruce s.spruce beech w.heml	e.larch s.pine j.larch n.spruce s.spruce w.heml	n.spruce alder j.larch oak beech ash	alder ash oak rowan beech	s.spruce birch n.spruce rowan oak w.heml alder beech

Great High Wood. The term bird density will be used to refer to the density of all arboreal passerines, unless otherwise qualified.

The fluctuations in the bird density between the compartments ranged from 0.5 to 10.5 birds per hectare (Table 4.20), with a mean of 3.55. These differences were found to be correlated with the compartment size. When the bird density was plotted against the compartment size it was found to be declining significantly as the compartment size increased (Fig 4.12). This effect was strongest in the small compartments and the relationship was log-linear. The relationship between bird density (Y) and compartment size (X) yielded a linear negative correlation after the log-transformation of the compartment size (Y = -5.25X + 6.60, r = -0.65, 29 d.f.), Fig 4.13. Bird density decreased rapidly as compartment size increased. All compartments that were 3 hectares or smaller supported bird densities in excess of the overall bird density of 2.72 birds/hectare, while only a third of the larger compartments supported higher than average bird densities.

Because of the exceptionally strong effect of the compartment size on bird density in the smaller compartments, the possibility that this was caused by edge effect was investigated. The curve superimposed onto Figure 4.12 represents the length of edge per unit area of wood at each compartment size from one to sixteen hectares, assuming that the compartments are circular in shape. This curve follows the data on bird density well, and the steepness of the curve for compartments of up to five hectares shows that there is a sharp decrease in the amount of edge per unit area of wood up to this size, but that the change in the amount of edge is

Table 4.20

Density (birds per hectare) of each bird species in compartments
in Hamsterley Forest, March - October, 1984-86

Compartment	Blue tit	Great tit	Coal tit	Gold-crest	Chaf-finch	Tree-creeper	Others	Total birds
0000	3.31	1.28	0.79	0.69	2.03	0.00	1.53	9.63
0011	0.00	0.01	0.43	0.37	0.33	0.02	0.15	1.30
0012	0.60	0.10	2.23	1.78	0.76	0.06	0.76	6.29
0014	0.55	0.08	2.69	0.97	0.60	0.17	0.46	5.52
0031	0.95	0.15	1.39	0.80	0.69	0.00	0.41	4.40
0041	0.15	0.00	1.86	0.65	1.52	0.03	0.14	4.35
0054	0.14	0.00	1.05	0.12	0.97	0.00	0.05	2.33
0101	0.46	0.16	1.41	0.10	0.30	0.12	1.17	3.72
0103	0.26	0.10	1.51	0.40	0.93	0.05	0.05	3.40
0111	1.28	0.96	1.06	0.13	1.54	0.10	0.55	5.62
0112	0.70	0.14	0.44	0.24	0.23	0.11	0.19	2.04
0113	0.66	0.03	0.99	0.20	0.63	0.07	0.30	2.88
1514	0.00	0.09	1.00	1.08	0.43	0.03	0.00	2.62
0403	0.13	0.12	0.14	0.03	0.05	0.00	0.05	0.50
0690	0.08	0.04	0.86	0.59	0.31	0.08	0.03	1.99
0712	0.03	0.00	0.33	0.17	1.87	0.00	0.00	2.39
1416	0.12	0.04	0.74	0.28	0.38	0.02	0.12	1.69
1435	2.44	1.20	0.91	0.59	1.15	0.39	2.79	9.47
1442	0.55	0.26	1.32	0.03	0.93	0.13	0.39	3.60
1445	1.56	1.06	1.56	0.64	1.88	0.34	3.51	10.56
1552	0.65	0.28	0.10	0.14	0.23	0.08	0.60	2.98
1562	0.01	0.00	0.80	0.73	0.16	0.01	0.03	1.73
1601	0.00	0.02	0.44	0.24	0.29	0.02	0.11	1.12
1602	0.00	0.00	0.65	0.34	0.06	0.02	0.01	1.09
1620	0.34	0.17	0.26	0.07	0.12	0.00	0.09	1.06
1630	1.12	0.32	0.72	0.14	0.51	0.08	0.63	3.52
1640	1.85	0.75	0.20	0.08	0.56	0.02	0.83	4.30
2163	0.00	0.00	0.41	0.06	0.52	0.04	0.00	1.03
2171	0.32	0.10	1.38	0.24	1.36	0.10	0.41	3.92
2181	0.52	0.15	0.67	0.18	0.45	0.06	0.58	2.61
4051	0.05	0.04	1.63	0.32	0.24	0.02	0.11	2.41
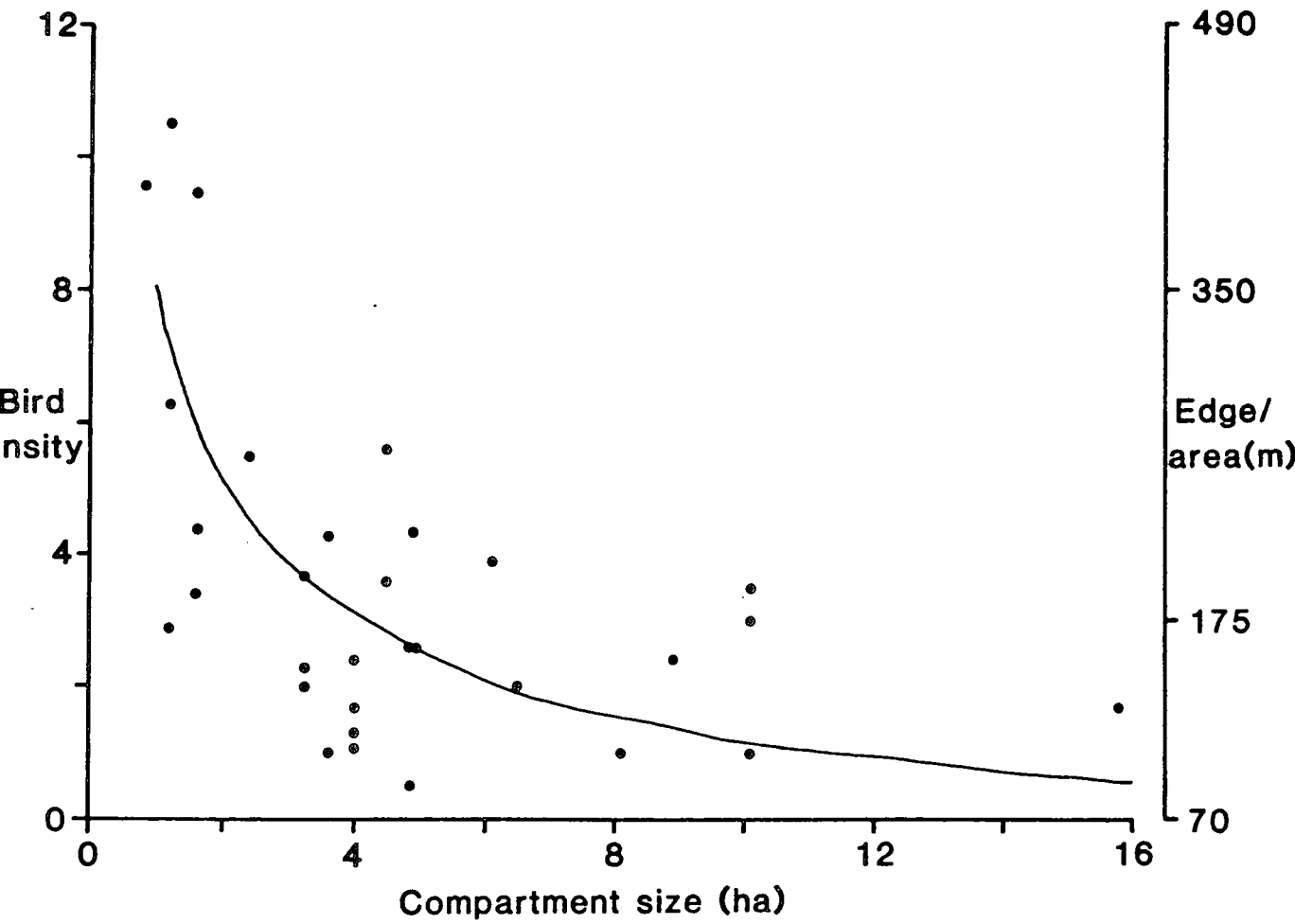
Fig 4.12: The relationship between the density of all bird
species and the compartment size in Hamsterley
Forest, 1984-86. The curve represents a
theoretical edge/unit area assuming circular
compartments.
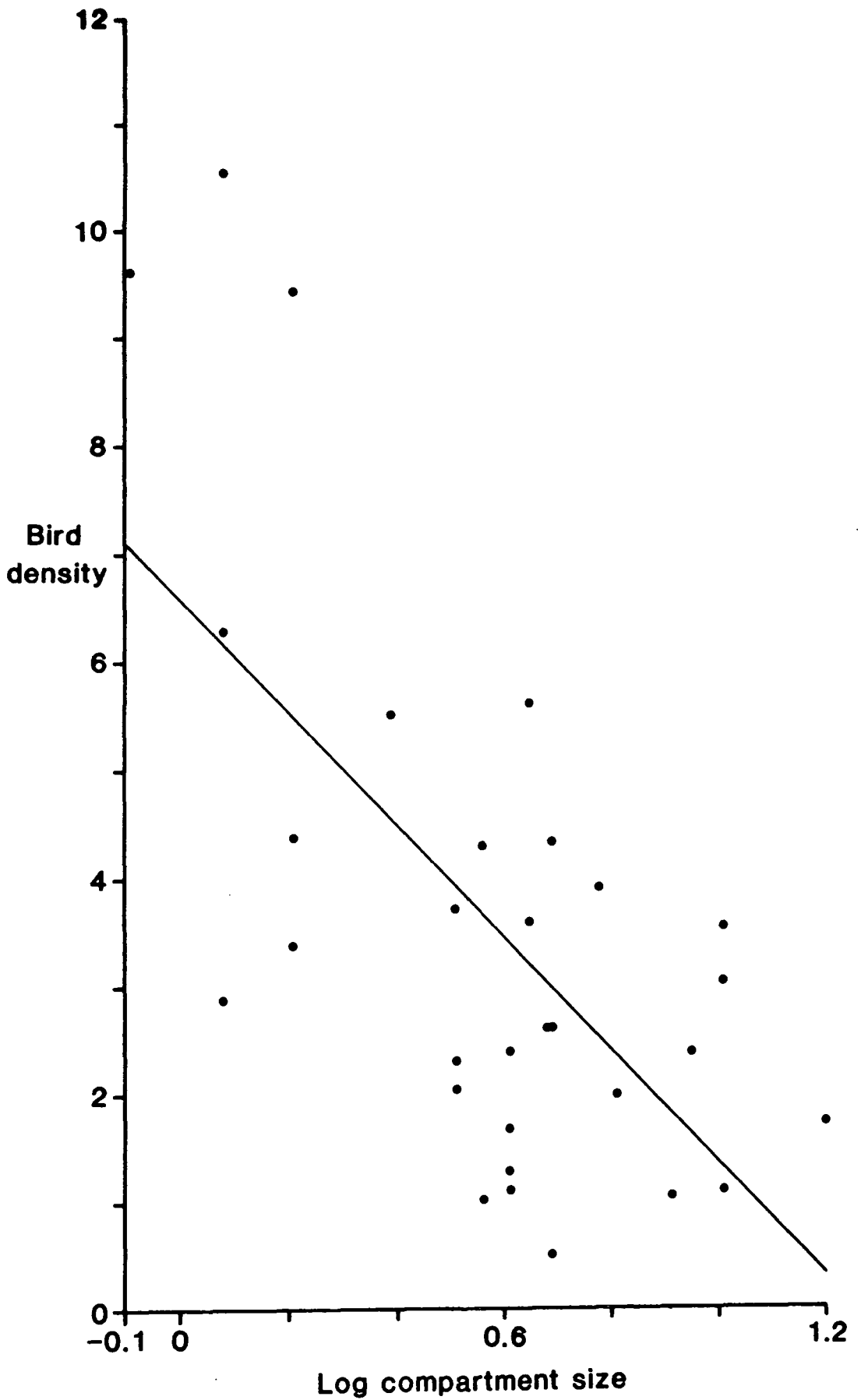
Fig 4.13: The relationship between the total bird density
and the logarithm of compartment size.
$Y = -5.25(+/-1.14)X + 6.60$, $r = -0.65$, 29 d.f.

nominal as the compartment size increases beyond five hectares. A good correlation was found between the bird density and the amount of edge per unit area (Fig 4.14), with a correlation coefficient of +0.70. This shows that the amount of edge available for the birds is a major determinant of bird density. In reality many of the compartments were not circular, which is the primary cause of the scatter in Fig 4.14. However, the assumption of circular compartments is an adequate approximation.

The blue tit and the chaffinch densities (Y) were negatively correlated with the compartment size (X) (blue tit: $Y = -0.08X + 1.01$, $r = -0.36$, 29 d.f. $p < 0.05$; chaffinch: $Y = -0.07X + 1.05$, $r = -0.42$, 29 d.f. $p < 0.05$). The densities of the other common bird species were not area related. The compartment size was not correlated with any other parameter measured.

As the number of tree species in a compartment increased (Fig.4.15), there was a significant increase in the density of birds ($r = +0.60$, 29 d.f. $p < 0.001$). Thus the more diverse compartments supported, on average, higher densities of birds than compartments with only one or two tree species. On average the addition of two tree species increased the bird density by one bird per hectare, which corresponds to a 28% increase of the mean density in compartments of 3.55 birds per hectare. The bird density in Great High Wood of 4.18 birds per hectare in an area with 8 tree species, when fitted into Figure 4.15 of bird density against numbers of tree species in Hamsterley Forest, lies close to the regression line. This suggests that the relationship between bird density and tree species richness in the two study sites is
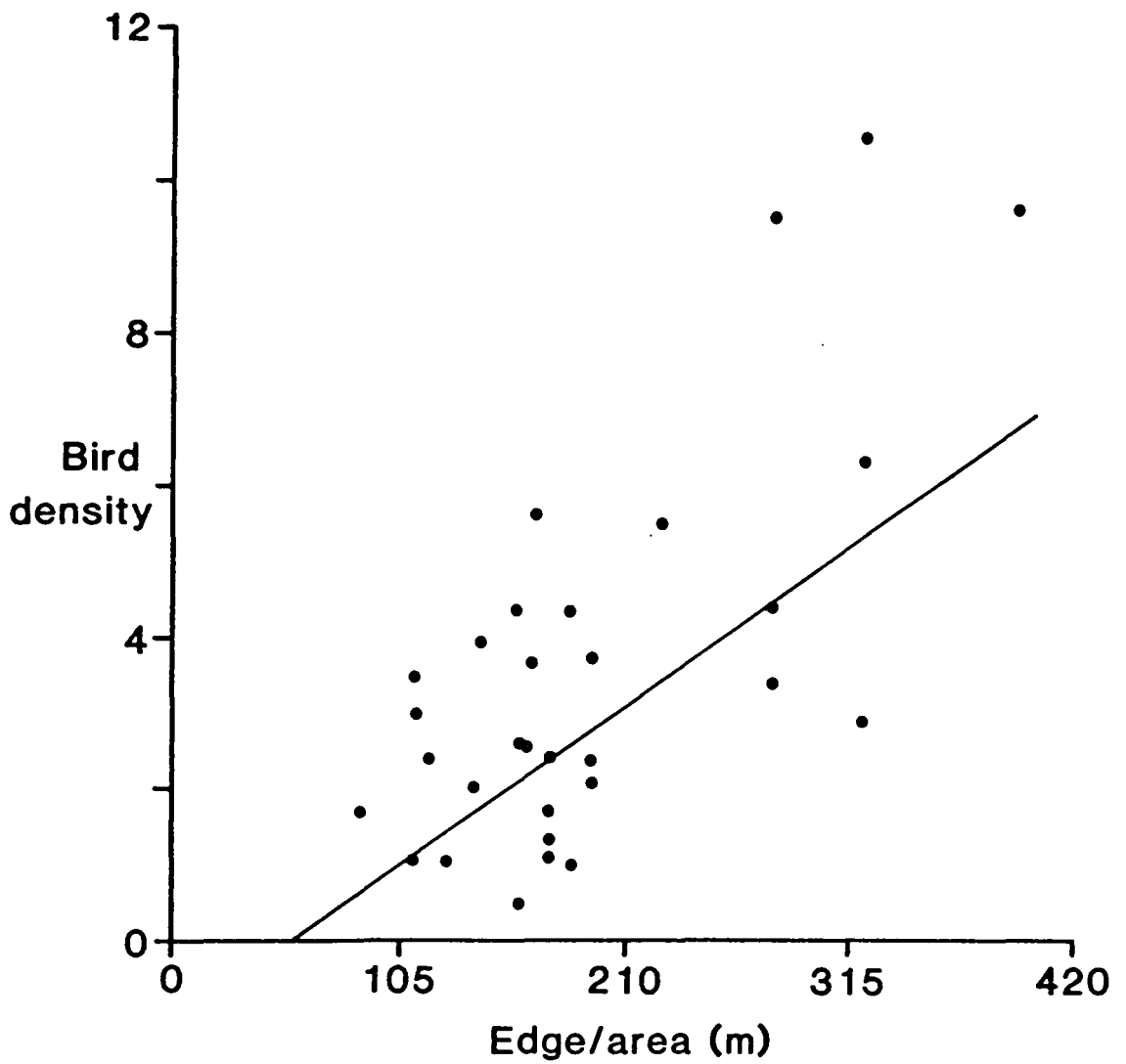
Fig 4.14: The relationship between the density of all bird
species and the amount of edge/unit area in
compartments in Hamsterley Forest, 1984-86.
$Y = 0.02(+/-0.005)X - 1.12$, $r = +0.70$, 29 d.f.

Fig 4.15: The relationship between the density of all bird
species and tree species richness in compartments
in Hamsterley Forest, 1984-86.
$Y = 0.47(+/-0.12)X + 1.13$, $r = + 0.60$, 29 d.f.
The bird density in Great High Wood is shown ($\bigcirc$)
but was not used in the calculation of the
regression.

similar, and that the relationship found within Hamsterley Forest can be extrapolated to other woodlands. It appears that the difference in the overall bird density in the two woods is due to the large local variations in bird density in Hamsterley Forest caused by the variations in tree species richness.

The bird density was influenced by the tree species richness and the compartment size in a dissimilar way. Therefore, the effect of the two was investigated in a three-way regression (Fig 4.16). The correlation between bird density and the other two variables was equal and opposite ($r = +0.66$ between bird density and tree species and $r = -0.65$ between bird density and compartment size, 29 d.f.). A three-way regression between the variables yielded a correlation coefficient of $+0.77$ (28 d.f., N=31). The combination that maximizes the bird density appears to be small compartments with a large number of tree species. Intermediate densities are found in small compartments with lower tree species richness, and the lowest densities are in large, species poor compartments.

The broadleaved content of the compartments varied from 0 to 100%. This was not correlated with the compartment size ($r = -0.07$ 29 d.f.). Out of the bird species the blue tit ($Y = 0.01X + 0.11$, $r = +0.65$, 29 d.f. $p<0.001$) and the great tit ($Y = 0.01 X + 0.03$, $r = +0.61$, 29 d.f. $p<0.001$) densities were correlated with the amount of broadleaved trees. There was no relationship between the other bird species and the broadleaved content of the compartments, but despite this the overall bird density was related to the amount of broadleaves ($Y = 0.03 + 2.61$, $r = +0.38$ 29 d.f. $p<0.05$), albeit weakly. The abundance of broadleaved trees (X) affected the bird
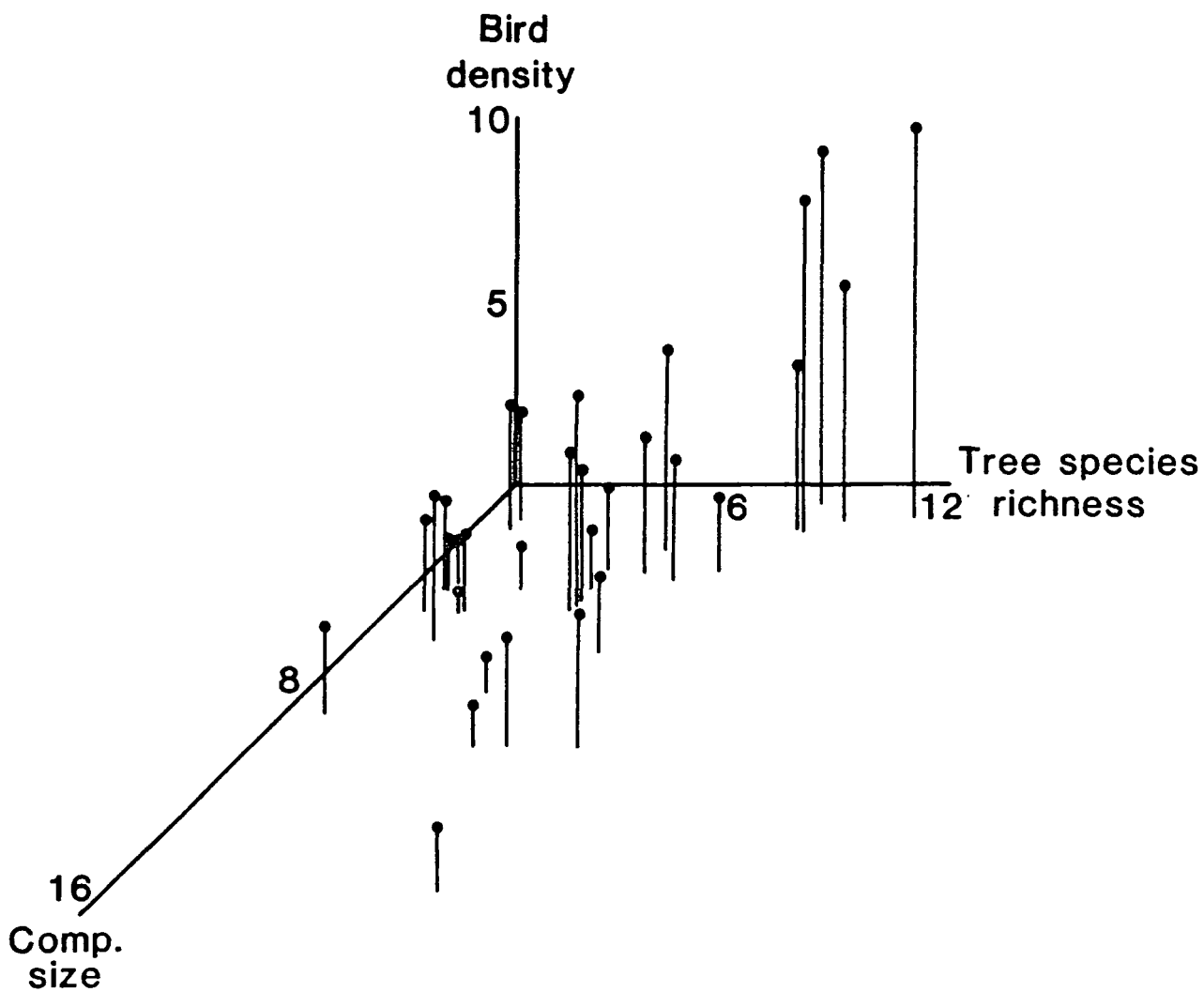
Fig 4.16: A three-dimensional representation of the
relationship between the total bird density, tree
species richness and compartment size in
Hamsterley Forest, 1984-86. r = + 0.77, 28 d.f.
p < 0.001.

species diversity (Y) (Y = 0.01X + 1.34, r = +0.64, 29 d.f. p<0.001) and the bird species richness (Y) (Y = 0.04X + 7.65, r = +0.49. 29 d.f. p<0.01) in the compartments, resulting in more species rich and more diverse bird fauna in compartments with higher percentage of broadleaves.

The tree species richness was found to be a good predictor of bird species richness (Fig 4.17: Y = 0.65X + 5.82, r = +0.66, 29 d.f. p<0.001), with two species of birds added for every three additional tree species. Ulfstrand (1975) found a similar correlation between the variables in winter in Swedish woods. A plot of bird density against numbers of bird species (Fig.4.18) gives a significant correlation (r = +0.59, 29 d.f. p<0.001) with a slope of 0.47. This indicates a relationship between bird density and bird species richness of 0.47:1, which approximates to an increase of two bird species resulting in an increase in density of one bird per hectare. Therefore, the increase in the density was caused largely by the addition of new species rather than by increase in density of bird species found in compartments with fewer tree species. This resulted in an increase in the density of the rarer bird species, and in an increase in the bird species diversity (Fig. 4.19) with a higher tree species richness. There was also a dependence of the bird species richness (Y) on the tree species diversity (X) (Y = 1.90X + 7.55, r = +0.40, 29 d.f. p<0.05), and the bird and tree species diversities were correlated with each other (Y = 0.26X + 1.36, r = +0.46, 29 d.f. p<0.01). The values for species richness, diversity indices, compartment sizes and bird densities in each compartment are given in Appendix 2.
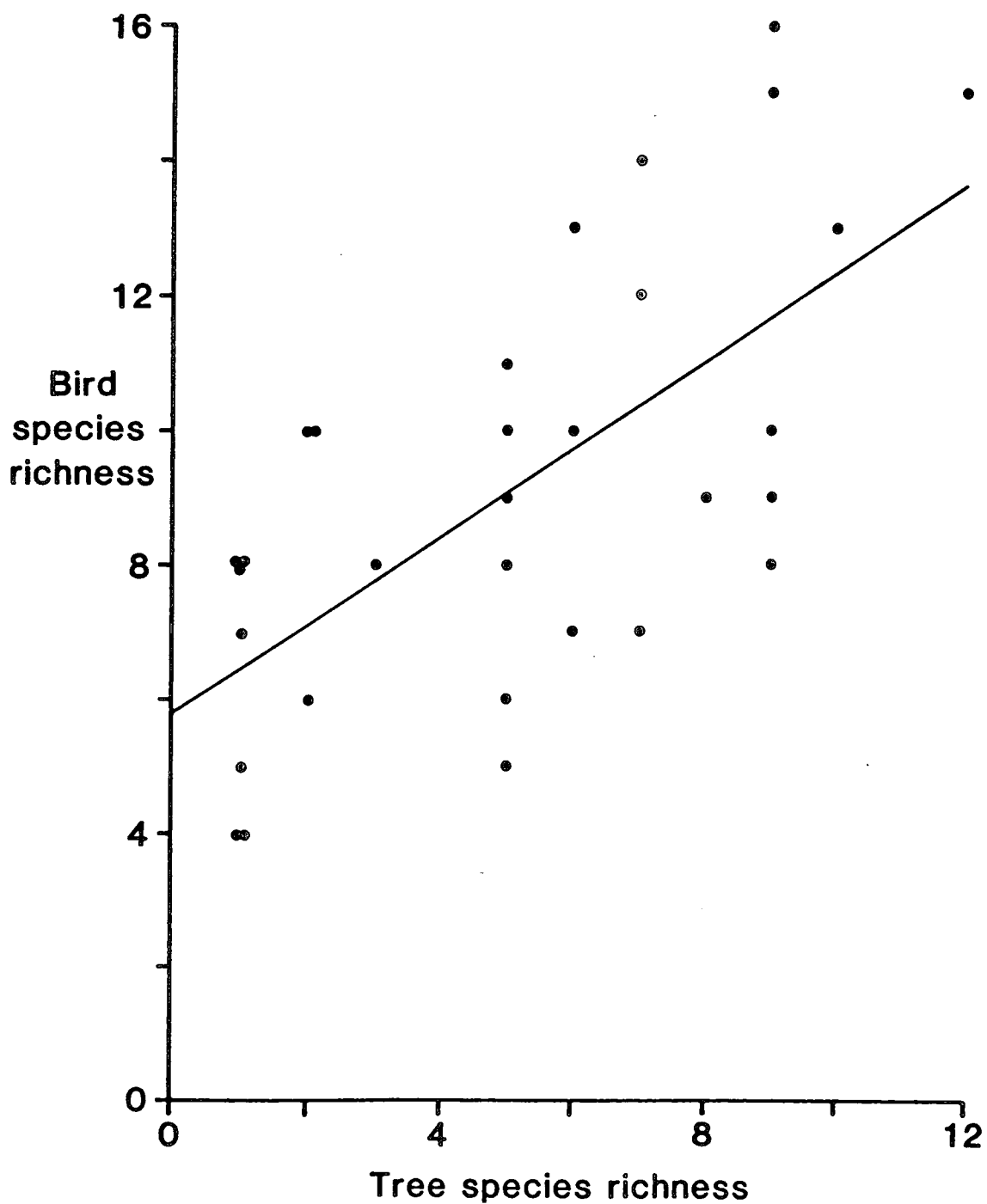
Fig 4.17: The relationship between bird species richness
and tree species richness in compartments in
Hamsterley Forest, 1984-86.
Y = 0.65(+/-0.14)X + 5.82, r = +0.66, 29 d.f.
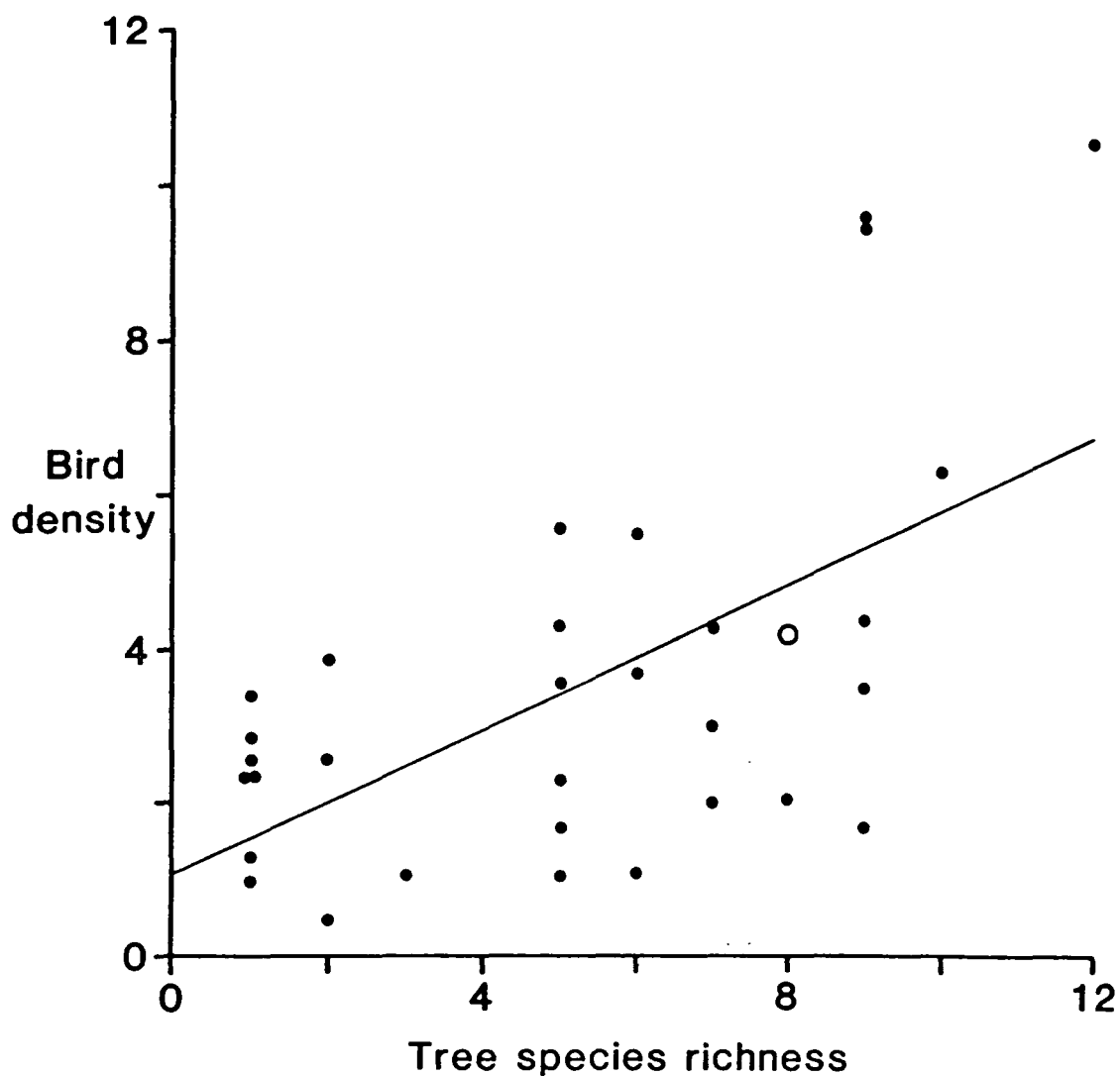Each point represents data for one compartment
over the three year period.
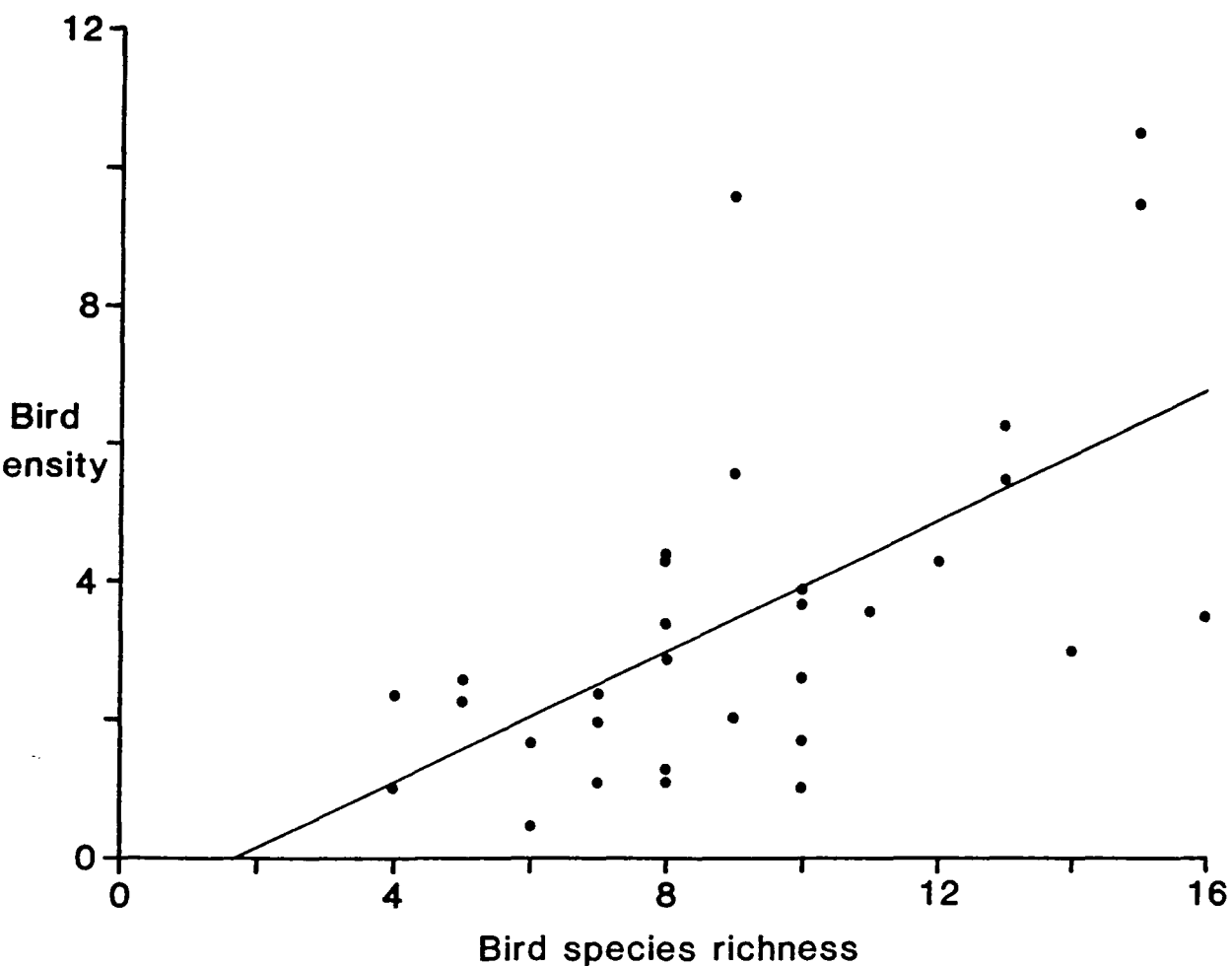
Fig 4.18: The relationship between the bird density and
bird species richness in compartments in
Hamsterley Forest, 1984-86.
Y = 0.47(+/-0.12)X - 0.76, r = +0.59, 29 d.f.
Each point represents data for one compartment
over the three year period.
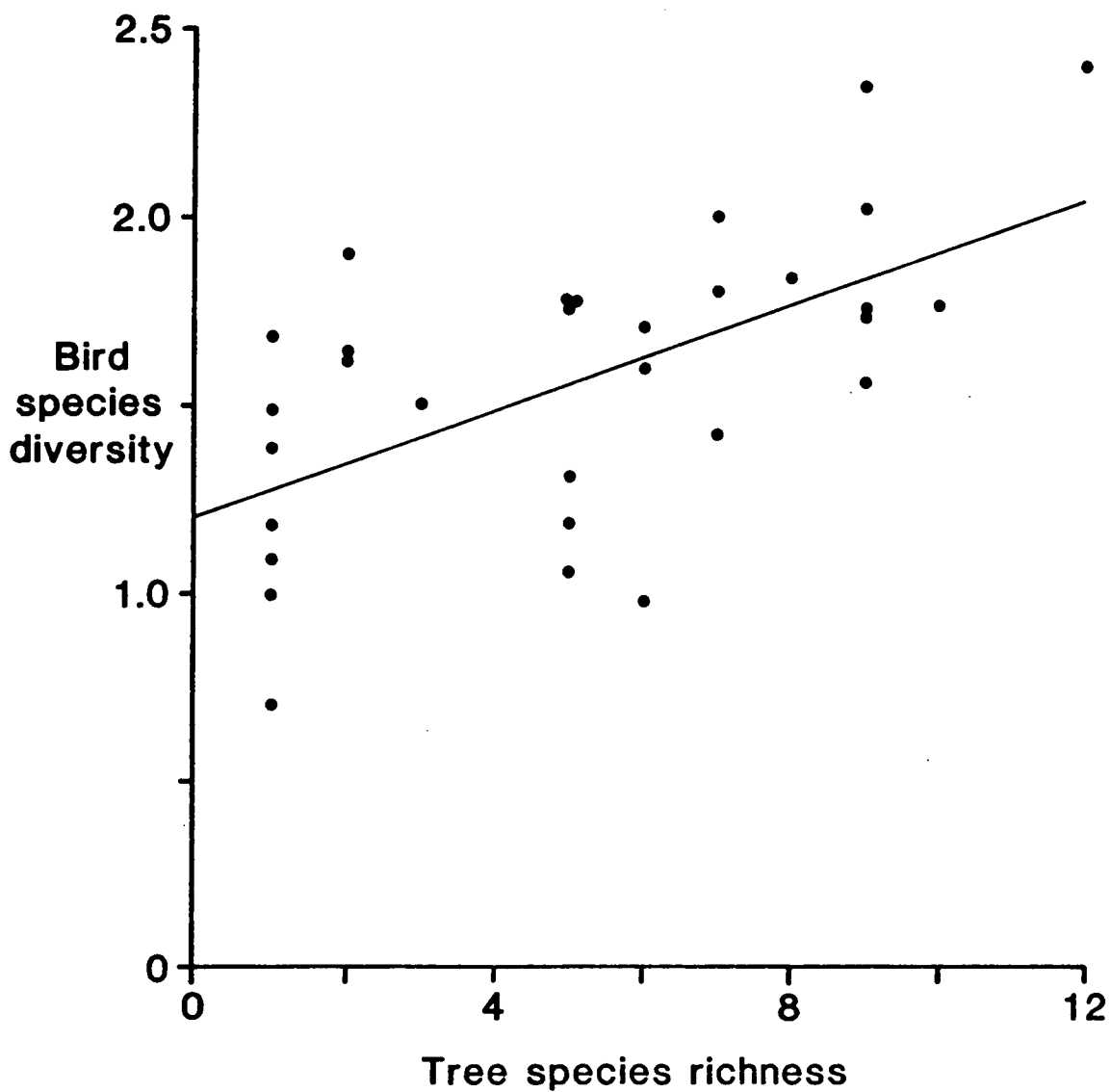
Fig 4.19: The relationship between bird species diversity
and tree species richness in compartments in
Hamsterley Forest, 1984-86.
Y = 0.07(+/-0.02)X + 1.21, r = + 0.60, 29 d.f.
Each point represents data for one compartment
over the three year period.

This increase in bird density and numbers of bird species present appeared to be due to the more diverse compartments offering a greater variety of feeding sites, hence allowing a larger number of bird species to coexist. The addition of tree species beyond four or five in the study compartments always involved tree species that were present at low densities (below 5%), showing that the effect of enhancing the desirability of an area of woodland comes about by the mere presence of extra tree species; they do not necessarily have to be abundant.

4.10 Discussion

Similar tree species preferences were established for bird species in Hamsterley Forest as in Great High Wood. Each bird species was found to have different tree preferences and different complement of tree species were used for foraging. However, there was little difference between the bird species in the foraging height, position within a tree and substrate use. Therefore it can be concluded that bird species differed from each other and between the sites primarily by the tree species choice.

The compartmental structure of Hamsterley Forest allowed the investigation into the effects of the composition of the wood on the arboreal birds (the relationships between the variables are summarised in Table 4.21). Bird density, diversity, and species richness were found to be determined by the tree species diversity and richness of the wood. Moreover, all measures of bird and tree diversity and species richness were significantly correlated with

Table 4.21

Summary of the significant correlations between bird densities,
measures of diversity and species richness in Hamsterley
Forest, March - October, 1984-86

	Bird density	Species bird	diversity tree	Species bird	richness tree	%broad- leaves	Comp. area
Density of:							
blue tit	yes	yes	yes	yes	yes	yes	yes
great tit	yes	yes	yes	yes	yes	yes	no
coal tit	yes	no	no	no	no	no	no
goldcrest	yes	no	no	no	no	no	no
chaffinch	yes	no	no	no	no	no	yes
treecreeper	yes	yes	no	yes	yes	no	no
all birds	-	yes	yes	yes	yes	no	yes
Species diversity:							
birds	yes	-	yes	yes	yes	yes	no
trees	yes	yes	-	yes	yes	yes	no
Species richness:							
birds	yes	yes	yes	-	yes	yes	no
trees	yes	yes	yes	yes	-	yes	no
% broadleaves	yes	yes	yes	yes	yes	-	no
Comp. area	yes	no	no	no	no	no	-

notes: all significant correlations are positive, except those involving
          the compartment size, which are all negative
          bird density = overall density per hectare
          area = compartment size in hectares

each other. Therefore it can be hypothesized that a change in one of these measures can cause a change in all of the others. While the compartment size had a negative effect on the bird density, it did not affect any of the other factors. Despite the percentage content of broadleaved trees being correlated with the species diversity and richness of both birds and trees, it only affected the density of blue and great tits, showing no correlation with the other common bird species. This shows that in Hamsterley Forest only the blue tits and the great tits were influenced by the broadleaf - conifer gradient, which would have been expected to affect also the coal tit and the goldcrest.

While structural diversity can improve a woodland as bird habitat by providing suitable habitat for the bird species that are dependent on the shrub layer, the plant species richness and diversity are paramount in improving the habitat for birds within a guild, as has been shown here for the arboreal guild of passerines.

CHAPTER 5

DIMENSIONS OF THE FORAGING NICHE

5.1 Niche breadth

The niche breadth in the tree choice was calculated using the Shannon-Weaver formula (see Methods). The niche breadth for each bird species was similar (Table 5.1) and there were no significant differences between the bird species (Mann-Whitney U-test) in either wood. The niche breadth was lower in Great High Wood than in Hamsterley Forest for each of the bird species. None of the bird species differed significantly in the two woods, but since the niche breadth was consistently lower in Great High Wood, the overall difference was significant (sign test: X^2=6.00, 1 d.f. p<0.05). This shows that there was a tendency for the birds to feed in a wider range of tree species in Hamsterley Forest. However, Hamsterley Forest contained more tree species than Great High Wood, and this difference in niche breadth may have been the result of the larger number of tree species available. The birds did not spread the bulk of their foraging over a wider range of tree species (cf. Tables 3.1 & 4.1), but the wider niche breadth in Hamsterley Forest was due to the inclusion of a larger number of tree species as minor foraging sites. Therefore it can be concluded that the niche breadth of a songbird species remains similar independent of the woodland it inhabits, and any differences in the

Table 5.1

Niche breadth of six bird species in Hamsterley Forest and in
Great High Wood, March - October, 1984-86

	Blue tit	Great tit	Coal tit	Gold-crest	Chaf-finch	Tree-creeper
Hamsterley Forest	1.83	1.81	1.86	1.91	1.87	2.16
Great High Wood	1.69	1.76	1.36	1.35	1.47	1.35

niche breadth are due to the number of tree species within the woodland.

Despite the similarity in the niche breadth of the bird species, the range of tree species used was different for each of the bird species in both woods.

5.2 Niche overlap

The examination of the overlap between bird species in five dimensions of the feeding niche showed that the tree species was the main single factor separating the bird species in Hamsterley Forest (Table 5.2) with the lowest percentage overlap between pairs of bird species. The only exception was the treecreeper, which, with its habit of feeding primarily on the trunks of trees, showed least overlap with the other bird species in the choice of feeding position within a tree. Because the treecreeper is not a canopy forager, it was left out of the consideration in this section, including all mean overlap figures, except where specifically mentioned.

The mean overlap between pairs of bird species (Table 5.2) in their use of tree species was 57%, which is in contrast to and significantly lower than the 76% overlap of feeding position ($t=2.92$) and 85% overlap of the height of the feeding station above ground ($t=4.29$). Combining the tree species and position within a tree produced a lower niche overlap than tree species alone, but the reduction in the overlap was not significant. The blue tit and great tit were the only pair of bird species where the position

Table 5.2

Percentage niche overlap between pairs of bird species in five
dimensions of the foraging niche and combinations of them in
Hamsterley Forest, March - October, 1984-86

Bird species	Tree spp.	Posi- tion	Subs- trate	Bird height	Tree height	Pos.+ height	Tree + pos.	Tree+pos. + height
Blue tit:								
great tit	89	74	83	80	86	65	63	52
coal tit	48	82	79	99	83	77	45	43
goldcrest	42	68	71	88	78	67	35	31
chaffinch	53	58	87	88	81	56	37	40
Great tit:								
blue tit	89	74	83	80	86	65	63	52
coal tit	40	77	75	78	69	63	37	34
goldcrest	35	89	66	71	65	66	33	28
chaffinch	45	83	87	69	67	63	43	38
Coal tit:								
blue tit	48	82	79	99	83	77	45	43
great tit	40	77	75	78	69	63	37	34
goldcrest	79	79	83	91	93	77	69	63
chaffinch	75	66	87	91	98	66	58	55
Goldcrest:								
blue tit	42	68	71	88	78	67	35	31
great tit	35	89	66	71	65	66	33	28
coal tit	79	79	83	91	93	77	69	63
chaffinch	60	83	78	96	93	80	54	50
Chaffinch:								
blue tit	53	58	87	88	81	56	37	40
great tit	45	83	87	69	67	63	43	38
coal tit	75	66	87	91	98	66	58	55
goldcrest	60	83	78	96	93	80	54	50
Treecreeper:								
blue tit	69	9	25	63	92	9	8	8
great tit	62	8	26	75	78	8	8	8
coal tit	74	13	40	64	90	13	12	11
goldcrest	63	9	42	60	84	9	7	7
chaffinch	74	8	34	59	88	14	14	8
mean+/-se excl.TC	57±5.8	76±3.0	80±2.2	85±3.2	81±3.6	68±2.4	47±4.1	43±3.6
mean+.-se treecreeper	68±2.5	9±0.9	33±3.4	64±2.9	86±2.5	11±1.2	10±1.4	8±0.8

TC = treecreeper

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made a large contribution to the reduction in the overlap. There was little change in the overlap for any other pair of bird species. The addition of the height of the bird above ground reduced the overlap only slightly, and this difference was not significant from the overlap in tree species use. However, the combination of tree species, position and height gave a lower mean overlap between pairs of bird species than position ($t=6.94$) or bird height ($t=8.67$) or these two variables combined ($t=5.68$). This shows that the tree species is an important factor in niche partitioning between bird species, and affords greater separation than any of the other niche dimensions investigated. The choice of substrate from where food was obtained and the height of the trees used for foraging overlapped, on average, significantly less than the height of the foraging bird, but when they were combined with the above three niche dimensions, the contribution to the reduction of the overlap value was marginal, and therefore they were not considered to be important means of niche partitioning for the five bird species studied.

The niche overlap in Great High Wood follows the pattern in Hamsterley Forest (Table 5.3). The tree species choice (mean overlap of 66%) partitioned the feeding niche of the bird species significantly more than any of the other four niche dimensions that were measured. The exceptions were the blue tit and great tit, which overlapped to a similar extent (84-89%) in all the niche dimensions, and the coal tit and goldcrest, which converged to forage predominantly in larches, making the height and substrate components more important than the tree species in niche

Table 5.3

Percentage niche overlap between pairs of bird species in five
dimensions of the foraging niche and combinations of them in
Great High Wood, March - October, 1984-86

Bird species	Tree spp.	Posi- tion	Subs- trate	Bird height	Tree height	Pos.+ height	Tree + pos.	Tree+pos. + height
Blue tit:								
great tit	89	87	87	84	90	79	80	71
coal tit	56	88	79	93	96	85	53	49
goldcrest	51	71	66	84	89	62	45	33
chaffinch	75	84	85	92	79	78	65	57
Great tit:								
blue tit	89	87	87	84	90	79	80	71
coal tit	56	93	81	81	87	78	52	48
goldcrest	56	79	64	85	90	71	51	43
chaffinch	76	90	82	82	74	77	70	62
Coal tit:								
blue tit	56	88	79	93	96	85	53	49
great tit	56	93	81	81	87	78	52	48
goldcrest	87	80	72	76	85	66	65	53
chaffinch	60	84	79	84	81	79	56	46
Goldcrest:								
blue tit	51	71	66	84	89	62	45	33
great tit	56	79	64	85	90	71	51	43
coal tit	87	80	72	76	85	66	65	53
chaffinch	53	71	79	87	71	67	51	44
Chaffinch:								
blue tit	75	84	85	92	79	78	65	57
great tit	76	90	82	82	74	77	70	62
coal tit	60	84	79	84	81	79	56	46
goldcrest	53	71	79	87	71	67	51	44
Treecreeper:								
blue tit	79	15	28	74	77	15	14	14
great tit	70	15	28	86	73	15	15	14
coal tit	56	16	34	78	80	16	16	15
goldcrest	48	14	62	71	72	14	8	7
chaffinch	67	15	43	68	90	15	15	14
mean+/-se excl.TC	66±4.6	83±2.4	77±2.4	85±1.5	84±2.5	74±2.3	59±3.4	51±3.4
mean+.-se treecreeper	64±5.4	15±0.4	39±6.3	76±3.2	78±3.3	15±0.4	14±1.4	13±1.5

TC = treecreeper

partitioning. As in Hamsterley Forest, the combined overlap of the position and height was greater than the overlap in tree species use. This difference was significant for all pairs of bird species except the blue tit and great tit pair and the coal tit and goldcrest pair. The overlap of the combination of the tree species and the position within a tree was lower than the overlap for tree species alone. Combining these with the height of the bird above ground level reduced the overlap further, and it was significantly lower than the overlap in tree species use. This shows that the spatial dimensions of the foraging niche were more important in Great High Wood than in Hamsterley Forest. However, the tree species choice remained the niche dimension that best separated the bird species.

Year to year changes in the overlap of tree species use were relatively small (Table 5.4). For most pairs of bird species the overlap was greatest in 1985 in both woods, but the difference in the mean overlap was not significant. Differences in the seasonal overlap were of similar magnitude to the yearly differences (Table 5.5). The blue tit and great tit overlapped equally in each season, as did the coal tit and goldcrest. Great tit tree choice in Hamsterley Forest was more similar to that of the other bird species in the early season, and in Great High Wood in the late season. The reason for this in Great High Wood appeared to be the diversification of tree species choice by the goldcrest and coal tit (Tables 3.6 & 3.7) whereby these species became more similar to the great tit in their tree choice. In Hamsterley Forest most bird species changed their tree species choice to include more

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Table 5.4

Percentage niche overlap of tree species use between pairs of bird
species in each year in Hamsterley Forest and in Great High
Wood, March - October, 1984-86

Bird species	Hamsterley Forest			Great High Wood		
	1984	1985	1986	1984	1985	1986
Blue tit:						
great tit	80	76	79	83	93	79
coal tit	43	55	42	40	61	58
goldcrest	34	49	34	47	60	11
chaffinch	51	65	40	80	76	54
Great tit:						
blue tit	80	76	79	83	93	79
coal tit	41	42	37	39	55	65
goldcrest	32	38	30	57	59	18
chaffinch	51	51	36	75	75	57
Coal tit:						
blue tit	43	55	42	40	61	58
great tit	41	42	37	39	55	65
goldcrest	71	82	68	76	78	52
chaffinch	58	76	77	28	53	78
Goldcrest:						
blue tit	34	49	34	47	60	11
great tit	32	38	30	57	59	18
coal tit	71	82	68	76	78	52
chaffinch	49	70	48	34	54	50
Chaffinch:						
blue tit	51	65	40	80	76	54
great tit	51	51	36	75	75	57
coal tit	58	76	77	28	53	78
goldcrest	49	70	48	34	54	50
Treecreeper:						
blue tit	72	69	47	79	81	69
great tit	77	58	38	68	74	61
coal tit	51	76	85	29	59	65
goldcrest	42	68	56	40	49	22
chaffinch	58	82	73	77	69	48
mean+/-se excl.TC	51±4.9	60±4.9	49±5.9	56±6.7	67±4.2	52±7.1
mean+.-se treecreeper	60±6.4	71±4.1	60±8.6	58±10.0	66±5.6	53±8.4

TC = treecreeper

Table 5.5

Seasonal percentage niche overlap of tree species use between pairs
of bird species in Hamsterley Forest and Great High Wood
March - October, 1984-86

| Bird species | Hamsterley | | Great High | |
	early	late	early	late
Blue tit:				
great tit	72	76	81	89
coal tit	44	50	55	56
goldcrest	35	43	34	55
chaffinch	47	51	76	80
Great tit:				
blue tit	72	76	81	89
coal tit	47	35	48	56
goldcrest	40	29	31	58
chaffinch	55	40	85	74
Coal tit:				
blue tit	44	50	55	56
great tit	47	35	48	56
goldcrest	80	77	71	85
chaffinch	72	74	47	68
Goldcrest:				
blue tit	35	43	34	55
great tit	40	29	31	58
coal tit	80	77	71	85
chaffinch	64	53	30	63
Chaffinch:				
blue tit	47	51	76	80
great tit	55	40	85	74
coal tit	72	74	47	68
goldcrest	64	53	30	63
Treecreeper:				
blue tit	76	56	84	77
great tit	67	40	65	74
coal tit	60	86	55	55
goldcrest	51	65	36	50
chaffinch	62	80	65	72
mean+/-se excl.TC	56$\pm$4.9	53$\pm$5.5	56$\pm$6.7	69$\pm$4.1
mean+.-se treecreeper	63$\pm$4.1	66$\pm$8.3	61$\pm$7.8	65$\pm$5.5

coniferous trees later in the year (Table 4.7). The great tit did
not change, and hence the overlap in the tree use between great tit
and the other bird species reduced.

The mean overlap between pairs of bird species in the five
niche dimensions (Table 5.6) was greater in Great High Wood for all
except the substrate and bird height above the ground, which did
not differ in the two woods. The overlap between pairs of bird
species in the tree species choice, foraging height and tree height
tended to be higher in the early season in Hamsterley Forest and in
the late season in Great High Wood. The overlap in the position and
substrate between bird species tended to be greater in the late
season in both woods. However, the seasonal differences were not
significant in either wood.

5.3   Niche overlap and bird community structure

The consistent differences in the overlap of tree use in the
two woods raised the question of a relationship between niche
overlap and tree species richness in a wood. To investigate this
the niche overlap of tree use was calculated for each compartment
in Hamsterley Forest, including only bird species with at least 10
feeding observations in that compartment. The treecreeper was
included in this analysis, since comparison with spatial measures
was not involved, and the mean overlap in tree choice including the
treecreeper did not differ from the mean overlap excluding the
treecreeper. A plot (Fig 5.1) of the mean percent similarity of
tree use between bird species in each compartment against the tree

Table 5.6

Mean percentage niche overlap between pairs of bird species for five
dimensions of the foraging niche in Hamsterley Forest and
Great High Wood, March - October, 1984-86

Bird species	Hamsterley			Great High		
	early	late	annual	early	late	annual
Tree sp.	56	53	57	56	69	66
Position	71	75	76	81	82	83
Substrate	69	81	80	70	80	77
Bird height	87	81	85	82	83	85
Tree height	84	79	81	81	83	84

These means are based on niche overlap of blue tit, great tit, coal tit,
goldcrest, and chaffinch. Treecreeper was excluded since it is not a canopy
foraging species.

Fig 5.1: The relationship between the mean overlap in tree
species use between pairs of bird species and the
tree species richness in compartments in
Hamsterley Forest, 1984-86.
$Y = -3.80(+/-0.57)X + 88.36$, $r = -0.78$, 29 d.f.
The overall values for Hamsterley Forest and Great
High Wood are shown in the graph for comparison,
but were not used in the calculation of the
regression.

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species richness yields a negative linear relationship (Y = -3.80X + 88.36, r = -0.78, 29 d.f. p<0.001). This shows that the overlap in the tree species choice between pairs of bird species was lower in compartments with greater tree species richness. The overlap reduced by ca.20% with each five additional tree species. This relationship suggests that woodlands with greater tree species richness allow considerably greater niche partitioning than species poor woods, and shows that as more tree species become available, birds take advantage of them and reduce their overlap with coexisting species. Interestingly, niche overlap in Great High Wood of 66%, with eight tree species, and the overall niche overlap of 57% in Hamsterley Forest with 11 tree species with frequency >1.5%, both fall within the points of individual compartments in Fig. 5.1.

The overlap in the tree species choice was also correlated with the number of bird species (Fig 5.2) in each compartment (Y = -2.26X + 89.54, r = -0.46, 29 d.f. p<0.01), with lower overlap in tree species choice in areas with higher numbers of bird species present. Because of the positive relationship between numbers of bird and tree species (Fig 4.17), it is evident that in areas with higher tree species richness more bird species are able to coexist with no increase in the overlap of their respective feeding niches.

The other three niche dimensions that were studied showed no correlation with tree species richness and bird species richness. This shows that the overlap in position, substrate and bird height varied within a narrow range independent of the tree species richness of the compartment, and independent of the number of bird

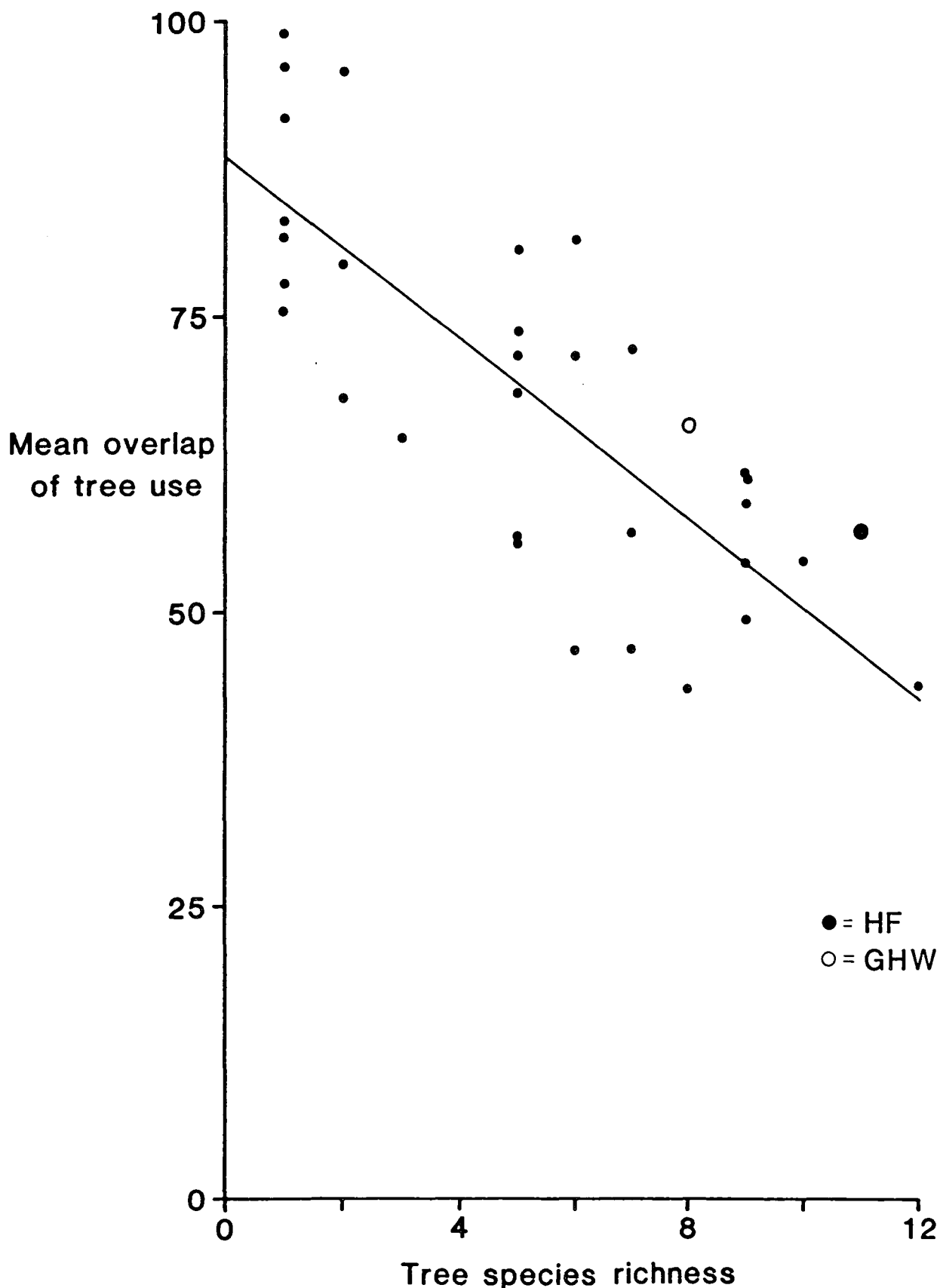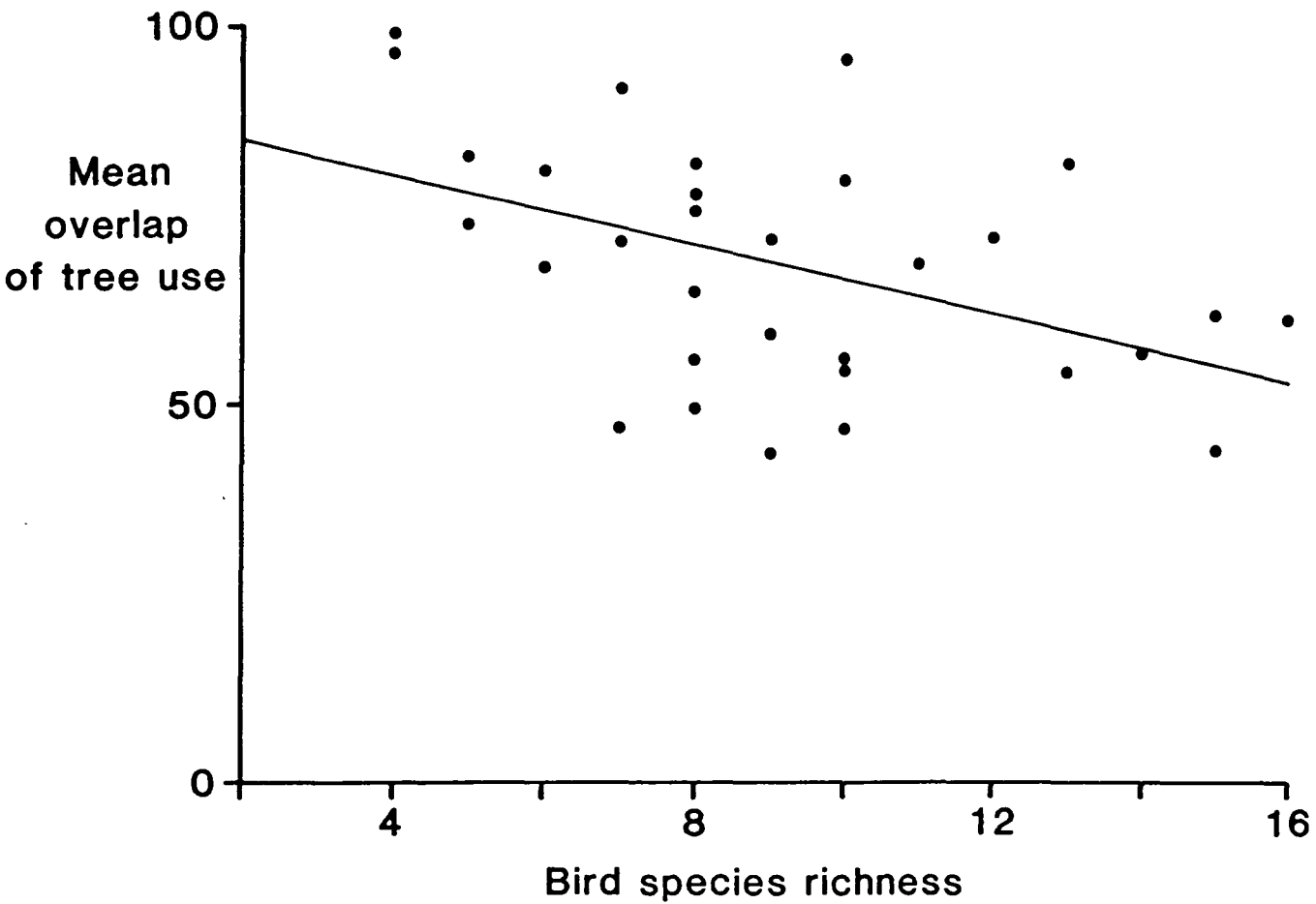Fig 5.2: The relationship between mean overlap in tree
species use between pairs of bird species and bird
species richness in compartments in Hamsterley
Forest, 1984-86.
Y = -2.26(+/-0.81)X + 89.54, r = -0.46, 29 d.f.

species present. No relationship was found between any of the four niche dimensions and the bird density in compartments.

Since the overlap in position, substrate and foraging height were not affected by differences between the compartments, they can be considered to be fixed. It is possible that the size and shape of individual bird species limited the variation of the response to these niche dimensions, ie. the dimensions were to all purposes rigid and non-changeable. It may also be that these niche dimensions were already fully expanded (see Morse, 1978, on expansion and contraction of niche dimensions), or that they were totally uncorrelated with and unaffected by the factors investigated in this study.

The negative correlation of the overlap in tree species use with bird and tree species richness (Figs 5.1 & 5.2), and through them indirectly with bird density, shows that the lower overlap of tree species choice allows greater species packing and greater bird densities in compartments with higher tree species richness and diversity. Since the tree species is the only niche dimension that allows the reduction in overlap between bird species, it can be regarded as the most important dimension of the foraging niche.

Birds were not distributed at random within Hamsterley Forest, but bird densities were higher than expected in some compartments and lower in others (section 4.9). Calculation of percent similarity of bird distribution within the forest (Table 5.7) shows that there were large differences in the distribution of each bird species. The blue tit and great tit were distributed in the most similar fashion (overlap 83%), and the great tit and goldcrest were

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Table 5.7

Percentage overlap in the use of different compartments by pairs of
bird species in Hamsterley Forest, March - October 1984-86

Bird species	1984	1985	1986	3 yrs
Blue tit - great tit	71	79	71	83
Blue tit - coal tit	30	53	52	49
Blue tit - goldcrest	24	41	34	40
Blue tit - chaffinch	43	52	54	55
Great tit - coal tit	25	54	39	42
Great tit - goldcrest	19	40	25	34
Great tit - chaffinch	41	51	45	50
Coal tit - goldcrest	61	77	63	75
Coal tit - chaffinch	60	66	69	70
Goldcrest - chaffinch	46	62	59	61
Blue tit - treecreeper	53	61	50	63
Great tit - treecreeper	53	65	42	65
Coal tit - treecreeper	33	61	61	62
Goldcrest - treecreeper	35	48	39	49
Chaffinch - treecreeper	39	50	64	59
mean+/-se	42$\pm$3.9	57$\pm$3.0	51$\pm$3.5	57$\pm$3.5

the most different (overlap 34%). There was also a tendency of each pair of bird species to use more similar areas in 1985 than in the other years (cf. Table 5.4 of similarity in tree choices). A plot (Fig 5.3) of overlap in tree choice against similarity of distribution between the compartments ($Y = 1.11X - 2.62$, $r = +0.93$, 13 d.f. $p < 0.001$) for each bird species pair shows that the similarity in the choice of compartments was the same as the similarity of tree species choice. Therefore, it is reasonable to conclude that the distribution of birds within the wood was determined by the distribution of tree species within it, and as each bird species searched out their preferred tree species, their distribution came to reflect the similarity of their tree choices.

5.4 Discussion

The similarity in the tree species choice for foraging site between pairs of bird species was the most important of the five dimensions of the foraging niche that were investigated. Since almost all bird species pairs overlapped less in their choice of tree species than in the combination of the position within a tree and foraging height, the similarity in tree species use should be considered as equally or more important than the spatial criteria that are commonly used to define the partitioning of the bird species' feeding niche. However, the blue and great tits formed an exception. Their tree choice overlapped by 89% in both woods. The similarity in the tree choice was so high that the birds had to partition their niche by spatial means, resulting in the
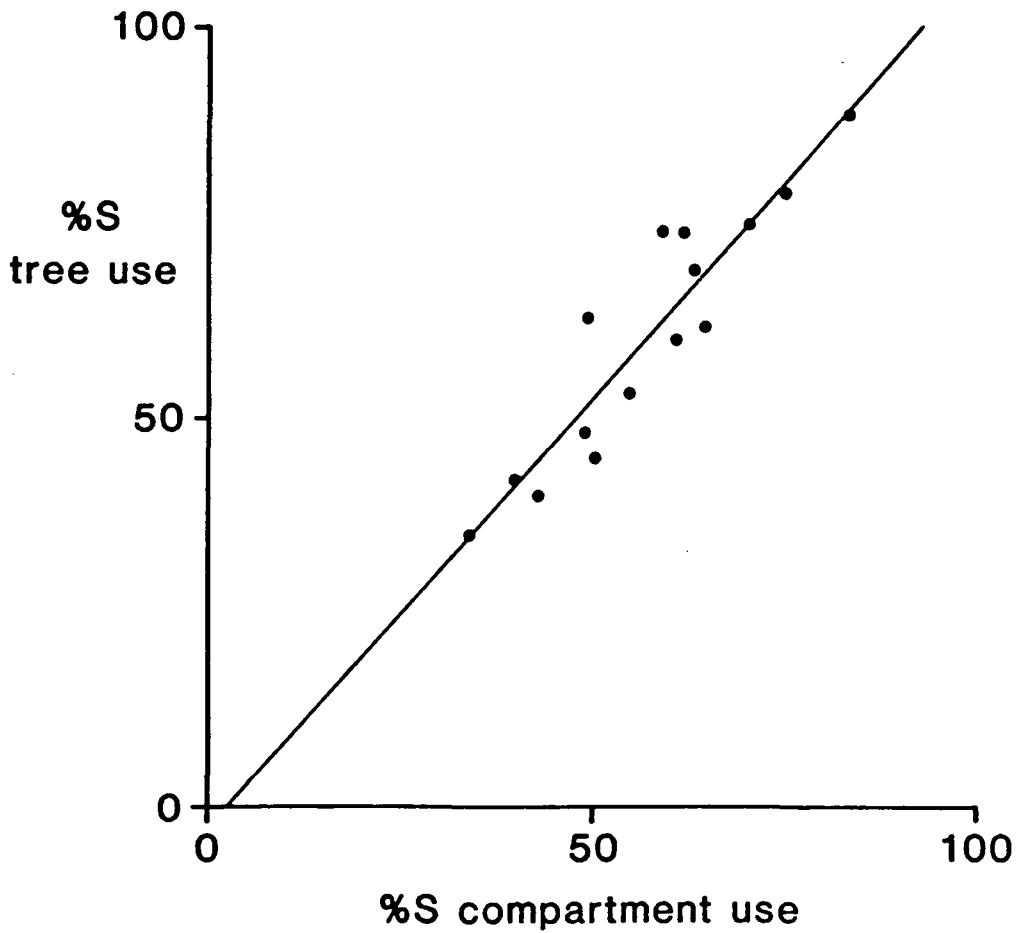
Fig 5.3: The relationship between the similarity in tree
         species use and the similarity in compartment use
         for pairs of bird species in Hamsterley Forest,
         1984-86.
         Y = 1.11(+/-0.13)X - 2.62, r = +0.93, 13 d.f.

combination of position and foraging height to be more important than the tree species. It appears from the results that tree species choice was the primary means of niche partitioning, with spatial criteria used only as a secondary measure.

The validity of spatial niche dimensions separating the birds' foraging niche has been under some doubt in recent years (e.g. Erdelen, 1984), since the spatial features of a wood are determined by the tree species composition in the wood. Therefore an observed difference in the spatial distribution of bird species in the canopy may simply be caused by the birds foraging in different tree species with no spatial separation within these tree species. In this study the similarity in tree species choice and both spatial dimensions of the feeding niche were found to change in the same way in the course of the year (Table 5.6), which indicates that spatial differences between bird species were largely determined by their choice of tree species.

Trees can be considered as foraging patches available to the birds, with each tree species representing a different patch type that provides configuration and foraging opportunities that are unique to that tree species. Therefore, an area containing a larger number of tree species will have a greater horizontal heterogeneity and patch diversity than species poor areas. Roth (1976) suggested two alternative ways of accommodating additional bird species to an area of woodland. Firstly, if bird species overlap does not increase proportionally with species richness, additional patches present in the habitat are used to partition the foraging opportunities. Secondly, if the overlap increases proportionally

with the species richness, patches do not permit horizontal segregation of bird species, but birds either partition the habitat vertically, or segregate ecologically in other ways. In this study the foraging niche was partitioned according to the first principle of Roth, because of the lack of positive relationship between overlap in the choice of tree species and bird species richness.

Niche overlap is known to be related to the predictability of resources. It varies dramatically in one component and only slightly (in the opposite direction) in the other components (Cody 1974). Each tree species support high densities of prey insects and other foods at different times of the year (Gibb & Betts, 1963), and the insect communities on the tree species are likely to react to environmental and weather changes in a different manner. Therefore the total food resource in an area containing a large number of tree species can be said to be more predictable and stable than in an area with few tree species. Because of this, the numbers of tree species in an area can be used as an indicator of the predictability of the food supply in the area, with high predictability in a species rich area and low predictability in a monoculture. Of the five dimensions of a feeding niche measured in this study, the overlap in the tree species choice was the only one that varied with the numbers of tree species in an area (Fig 5.1). The correlation of the tree species richness with the overlap in the other niche dimensions was either small positive or about zero indicating no relationship between the variables. This shows that the only change in the birds' feeding niche and the similarity of that niche between bird species comes from the change in the choice

of tree species for foraging site. The negative correlation between the overlap in tree species choice by birds and tree species richness indicates a relationship between niche overlap and resource predictability.

Cody (1974) reported that under conditions both of unusual abundance and unusual scarcity of food resources, bird species fail to evolve competitive displacement patterns. In systems where these displacement patterns occur normally, they can be temporarily or locally broken down by a superabundant food source or food shortage. The changes in the overlap of tree species use between pairs of bird species (Table 5.4) from one year to the next showed that the overlap was greatest in 1985, in which year the food availability was low in the second half of the year. This food shortage caused the partial breakdown of the differences in the choice of foraging site, and hence the tree species choice of the birds was more similar in 1985. Birds differed less from each other when foraging in sycamore than in any of the other tree species. This reduction of the differences between the bird species was caused by the superabundance of aphids on sycamore, whereby birds did not need to avoid competition from other species when foraging in sycamore.

CHAPTER 6

THE DENSITY OF ARTHROPOD PREY ON TREE SPECIES

6.1 Sampling times

    The terminal branches of each common tree species in the study
areas were sampled for arthropods in 1985 and 1986 at intervals of
one to two months during the field season. The sampling dates were
as follows. Great High Wood: 18 April, 21 May, 20 June and 20
September in 1985, and 22 April, 26 May, 30 June, 22 July and 1
September in 1986. Hamsterley Forest: 29 May and 26 September in
1985, and 23 April, 28 May, 2 July, 29 July and 4 September in
1986. Details of the sampling and the extraction of the animals
from the samples are given in the Methods. The length of the
arthropods in the samples was measured and the animals were
classified as small (0-2mm), medium (2.1-4mm) or large (>4mm).

    The geometric mean was calculated for all measures of density
(numbers per standard sample) in order to normalise the
distribution. In all of the tables the geometric mean (antilog of
the mean after the log-transformation) is presented, but since the
standard error is distributed symmetrically around the logarithm
of the mean and not its antilog, the logarithm of the standard
error is given. The logarithmic value of the mean and standard
error were used for all significance tests. The arithmetic mean was
applied for the estimates of biomass. The t-test was used to
establish significance in observed differences. Unless otherwise

stated, degrees of freedom is large and t equal to or greater than 1.96 indicates significance.

6.2   The density of arthropods on each tree species in Great High Wood

The density of arthropods varied greatly from one tree species to another (Table 6.1). Sycamore contained significantly greater density of arthropods than any other tree species (Table 6.1 & 6.6). This was mainly due to the large numbers of aphids on sycamore (over 90% of arthropods on sycamore were aphids), but other groups were also present, including lepidopterous caterpillars and spiders (Table 6.4). Birch, larch and oak also supported high densities of arthropods (Table 6.1). The fauna on beech was the poorest, albeit not significantly different from the density on holly and on elm. The arthropod density on larch and birch was significantly lower in 1986 than in 1985, but there were no significant changes from one year to the next in any other tree species (Table 6.1), despite the decrease in the arthropod density on oak of 24% and on sycamore of 44% and increase on holly of 27%. The sampling was not adequate to allow the change on these tree species to be confirmed, but more extensive sampling was not possible.

Table 6.1

Mean numbers of arthropods in samples of 50cm lengths of terminal branches
and an estimation of the proportion of arthropods on each tree
species in Great High Wood in 1985 and 1986

Tree species		1985 mean/ sample	se (log)	rel. abun.	N	1986 mean/ sample	se (log)	rel. abun.	N
Oak		7.8	0.07	7.8%	22	5.8	0.09	9.9%	27
Beech		3.2	0.09	3.0%	16	3.2	0.07	5.2%	25
Sycamore		97.7	0.14	79.1%	22	55.0	0.11	76.2%	24
Larch	*	13.5	0.04	5.3%	24	6.0	0.05	4.0%	42
Birch	*	14.5	0.16	3.8%	17	6.2	0.11	2.8%	23
Holly		4.5	0.17	0.7%	6	4.6	0.10	1.3%	24
Elm		4.5	0.13	0.3%	5	4.8	0.08	0.6%	21
Index of overall abundance		25.8				15.1			
Index excl. sycamore		5.4				3.6			

notes: N = number of samples
          Mean/sample is the geometric mean; the standard error refers to
          the logarithm of this mean.
          * = significant difference between the years

The formula

$$
\text{Index of abundance} = \frac{\sum \text{mean arthropods/sample X \%age of tree}}{100}
$$

was used to calculate an estimate of the overall abundance of insects in the wood in each year. The index of overall abundance in 1986 was half of that in 1985 (Table 6.1), thus the reduction in the food availability in Great High Wood in 1986 was severe.

The relative abundance of arthropods on each tree species was calculated in order to obtain an estimate of the proportion of all foliar invertebrates available in the wood that were on each tree species. This was calculated by multiplying the arthropod densities obtained from the samples by the frequency of the tree species in the wood and working out the percentage of arthropods in each tree species from this (Table 6.1). Sycamore accounted for almost 80% of all arboreal foliar arthropods, and a third of the remainder was found on oak. The changes in the relative abundance of arthropods on each tree species from 1985 to 1986 were small (0-4%) and non-significant, which shows that the above-mentioned reduction in the arthropod abundance in the wood was due to a general reduction in the wood and not restricted to only a few tree species. These small changes in the relative abundance are unlikely to have any effect on the tree choices by the birds.

The small arthropods were the most common size class in all trees in both years, except on sycamore and beech in 1986 (Table 6.2). The large arthropods were the least abundant throughout. There was a significant reduction in the density of the small arthropods on sycamore from 1985 to 1986, despite the overall change in density not being significant. There was a reduction in density of small arthropods on birch, while on larch both the small and medium sizes declined significantly.

There was no change in the density of large arthropods on any tree species (Table 6.2) but the species composition did change. For instance, most of the large arthropods on oak were lepidopterous caterpillars in 1985, but there were fewer caterpillars on oak in 1986, and they were replaced by the presence of a higher density of Diptera. These changes in the specific composition of arthropod fauna on trees is a possible reason for changes in birds' use of the tree species.

The arthropod data were divided into two time periods to coincide with the seasons used for analysis of the bird data: March - June and July - October, which will be referred to as the 'early' and the 'late' season. The mean numbers of arthropods per sample calculated for these two seasons showed that the seasonal density in the two years was different (Table 6.3). The density on each tree species declined between the early and the late season in 1985 but increased in 1986. The decline in 1985 was significant on sycamore (t=4.74), birch (t=2.72) and elm (t=3.01), while oak (t=4.12), larch (t=2.09), birch (t=2.11) and holly (t=5.54) increased significantly in 1986. There was little change in the

Table 6.2

Mean numbers of arthropods in samples of 50cm lengths of terminal
branches in each size class in Great High Wood in 1985 and 1986

1985	0-2mm	se(log)	2.1-4mm	se(log)	>4mm	se(log)
Oak	4.7	0.09	2.5	0.06	1.7	0.06
Beech	2.0	0.08	2.0	0.08	1.2	0.04
Sycamore	41.7	0.15	16.2	0.19	2.0	0.06
Larch	9.6	0.05	3.6	0.07	1.6	0.04
Birch	10.0	0.15	3.3	0.14	1.5	0.05
Holly	3.5	0.15	2.0	0.11	1.1	0.05
Elm	2.5	0.13	2.6	0.13	1.7	0.09
1986	**0-2mm**	**se(log)**	**2.1-4mm**	**se(log)**	**>4mm**	**se(log)**
Oak	3.6	0.08	2.5	0.06	1.7	0.05
Beech	1.9	0.05	2.2	0.06	1.3	0.04
Sycamore	10.7	0.12	21.4	0.17	1.7	0.05
Larch	3.6	0.06	2.3	0.25	1.5	0.03
Birch	4.1	0.10	2.5	0.08	1.4	0.04
Holly	3.3	0.09	2.0	0.07	1.3	0.03
Elm	2.5	0.06	2.9	0.08	1.3	0.04

notes: Mean/sample is the geometric mean; the standard error refers to
          the logarithm of this mean

Table 6.3

Mean numbers of arthropods in samples of 50cm lengths of terminal branches in each season on tree species of Great High Wood in 1985 and 1986

Tree species	Early 1985 mean	se(log)	N		Late 1985 mean	se(log)	N		Early 1986 mean	se(log)	N		Late 1986 mean	se(log)	N
Oak	8.1	0.09	17		6.8	0.08	5	*	2.7	0.13	12	*	10.5	0.06	15
Beech	3.5	0.12	11		2.8	0.14	5		2.2	0.11	10	*	4.3	0.10	15
Sycamore	182.0	0.10	17	*	11.7	0.23	5		46.8	0.23	9		60.3	0.13	15
Larch	14.1	0.05	20		11.5	0.08	4	*	3.6	0.14	12	*	7.4	0.05	30
Birch	23.4	0.14	13	*	3.0	0.30	4		2.9	0.22	8	*	9.3	0.10	15
Holly	4.5	0.17	6						1.5	0.12	9	*	8.9	0.07	15
Elm	9.3	0.12	2	*	3.2	0.10	3		3.9	0.16	8		5.5	0.08	13

notes: N = number of samples
         * = significant change in the arthropod density between the adjacent seasons (t-test)

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arthropod density during the winter of 1985-86, with a significant change only on oak (t=2.62) and larch (t=3.10), on both of which the density declined during the course of the winter.

The taxonomic composition of the fauna on each tree species was different (Table 6.4). The most abundant groups were Hemiptera (especially Aphidae), Lepidoptera, Hymenoptera, Diptera and Arachnidae, and therefore the presence and abundance of these groups can be expected to be particularly important to the foraging birds. Lepidopterous caterpillars were common on oak, sycamore, larch and birch, with higher densities in 1985 than in 1986. The reduction in 1986 (based on the means) was 53% on oak, 61% on sycamore, 67% on larch and 79% on birch, of which the reduction on larch and birch was significant.

Aphids made up 93% of the arthropod fauna on sycamore. If aphids were excluded, the arthropod density on sycamore was similar to that on oak: 7.4 and 4.8 per sample on oak, and 9.8 and 5.0 per sample on sycamore in 1985 and 1986 respectively. The density on the two tree species did not differ significantly in either year. The only other tree species with large numbers of aphids was birch, where ca. 65% of arthropods were found to be aphids. Hemiptera, other than aphids, were most abundant on sycamore and larch.

Of the few arthropods on beech, the most numerous were Aphidae, Curculionidae and small Diptera (Table 6.4). Curculionidae were the most common group of Coleoptera found on any tree species, but all beetles were present at very low densities. Coleopteran larvae were more numerous than adults, and more numerous in 1985 than in 1986.

Table 6.4

Mean numbers of arthropods in each taxonomic group in samples of 50cm
lengths of terminal branches in Great High Wood in 1985 and 1986

1985	Oak	Beech	Sycamore	Larch	Birch	Holly	Elm
Hemiptera:							
Aphidae	0.45	0.38	69.79	1.19	6.59	-	0.26
Psyllidae	0.07	0.05	-	0.02	-	-	-
Psocoptera	0.02	-	0.17	0.23	0.05	-	0.26
Heteroptera	0.10	-	0.17	0.29	0.23	-	0.15
Homoptera	0.02	-	0.07	-	-	-	-
nymphs	0.48	-	0.82	0.82	0.35	0.12	0.15
Coleoptera:							
Curculionidae	0.02	0.29	0.07	0.35	0.05	0.12	-
Coccinellidae	0.10	-	0.10	0.02	-	-	-
other Coleopt.	0.17	-	0.32	0.15	-	-	-
larvae	0.20	0.05	0.35	0.15	0.23	-	-
Lepidoptera:							
imagos	-	-	-	-	-	-	-
caterpillars	0.55	0.15	0.51	0.70	0.82	-	0.15
Hymenoptera	0.23	0.23	0.51	0.15	0.23	0.26	0.15
sawfly (larvae)	-	-	-	-	-	-	-
Diptera	0.70	0.51	0.78	1.09	0.41	0.62	1.40
Collembola	0.20	0.23	0.10	0.48	-	0.32	-
Thysanoptera	0.74	0.12	1.24	0.45	0.20	0.45	0.74
Neuroptera	-	-	0.10	-	-	-	-
Plecoptera	-	-	-	0.05	-	-	-
Dermaptera	0.10	-	0.07	-	-	-	-
Arachnidae	0.70	0.20	0.58	1.40	0.48	1.69	-
Acarina	0.02	-	0.02	-	0.10	-	-
Cocoons	0.12	0.05	-	0.07	0.05	-	0.15

Table 6.4 contd...

1986	Oak	Beech	Sycamore	Larch	Birch	Holly	Elm
Hemiptera:							
Aphidae	1.04	0.51	45.71	0.48	3.63	0.48	0.91
Psyllidae	0.02	0.02	0.10	0.20	0.02	-	0.02
Psocoptera	0.26	0.10	0.48	0.48	0.35	0.62	0.02
Heteroptera	0.26	0.07	0.32	0.07	0.12	0.15	0.32
Homoptera	0.05	0.12	0.15	0.29	-	-	0.26
nymphs	0.35	0.10	0.38	0.07	0.48	0.62	0.32
Coleoptera:							
Curculionidae	0.32	0.45	0.07	0.10	0.10	0.02	0.07
Coccinellidae	-	0.02	0.12	0.02	0.07	-	0.02
other Coleopt.	0.05	0.05	0.12	0.07	0.02	0.02	0.07
larvae	0.05	0.02	0.26	0.12	0.12	0.07	0.02
Lepidoptera:							
imagos	0.02	0.02	-	0.01	-	-	-
caterpillars	0.26	0.10	0.20	0.23	0.17	0.15	0.10
Hymenoptera	0.58	0.12	0.23	0.10	0.10	0.10	0.26
sawfly (larvae)	-	-	-	0.07	-	-	-
Diptera	0.62	0.29	0.32	0.66	0.12	0.32	0.48
Collembola	0.10	-	-	0.05	0.02	0.23	0.02
Thysanoptera	0.12	-	0.32	-	-	-	0.17
Neuroptera	0.05	0.02	0.07	-	-	-	-
Plecoptera	-	-	-	0.01	-	-	-
Trichoptera	-	-	-	0.01	-	-	0.02
Dermaptera	0.02	-	-	-	0.02	-	-
Arachnidae	0.29	0.12	0.23	0.45	0.26	0.48	0.32
Opiliones	0.07	-	-	-	0.02	0.02	-
Araneiae	0.05	0.02	0.02	-	0.02	0.10	-
Cocoon/							
chrysalis	0.02	-	0.02	0.10	-	0.02	-

Spiders were most numerous on holly and larch, with considerable numbers also on oak, sycamore and birch (Table 6.4). Other groups of arthropods were recorded in the samples, but they were infrequent in both years. Data in Table 6.4 shows that the reduction in arthropod numbers from 1985 to 1986 was due to a general reduction in the density of each taxonomic group.

An estimate of the dry weight of the arthropods sampled was obtained by applying the formula $W = (0.0305L)^{2.62}$, where W = dry weight in mg and L = length of the animal in mm (Rogers et al. 1976). The results are presented in Table 6.5. The large arthropods made up the bulk of the biomass in most cases - about 50% of the total on oak and larch. The only significant change in the biomass from 1985 to 1986 was the 50% reduction of biomass on birch. Figures 6.1.a and 6.1.b show the relationships between arthropod density and biomass in the two years in Great High Wood. They both show that the tree species, which supported the greatest density of arthropods also supported the largest biomass. These correlations approached total agreement with r almost 1.00. It can therefore be concluded that in the current context the arthropod density reflected the biomass, and their possible influence on the birds could not be separated. Therefore density only was used for assessing the arthropod distribution on trees and the effect this had on the bird fauna.

The changes in arthropod density between years and seasons did not affect the rank order of tree species by the arthropod density on them (Table 6.6). This rank order was independent of the season or of the year. Table 6.7 summarises the changes in arthropod

Table 6.5

Mean arthropod biomass (in mg) in samples of 50cm lengths of
terminal branches in Great High Wood in 1985 and 1986

Tree species	1985				1986			
	0-2mm	2.1-4mm	>4mm	total	0-2mm	2.1-4mm	>4mm	total
Oak	0.7	1.5	3.4	5.6	0.7	1.5	3.8	6.0
Beech	0.2	1.2	1.7	3.1	0.2	1.3	1.6	3.1
Sycamore	11.1	47.9	6.5	65.5	4.1	36.7	3.2	44.1
Larch	1.0	2.7	3.8	7.4	0.6	1.5	2.9	5.0
Birch	2.1	4.4	3.2	9.6	0.8	1.8	2.2	4.9
Holly	0.3	1.0	1.2	2.5	0.7	1.3	1.6	3.5
Elm	0.2	1.7	4.7	6.5	0.3	1.8	1.8	3.9

notes: number of samples as per Table 6.1
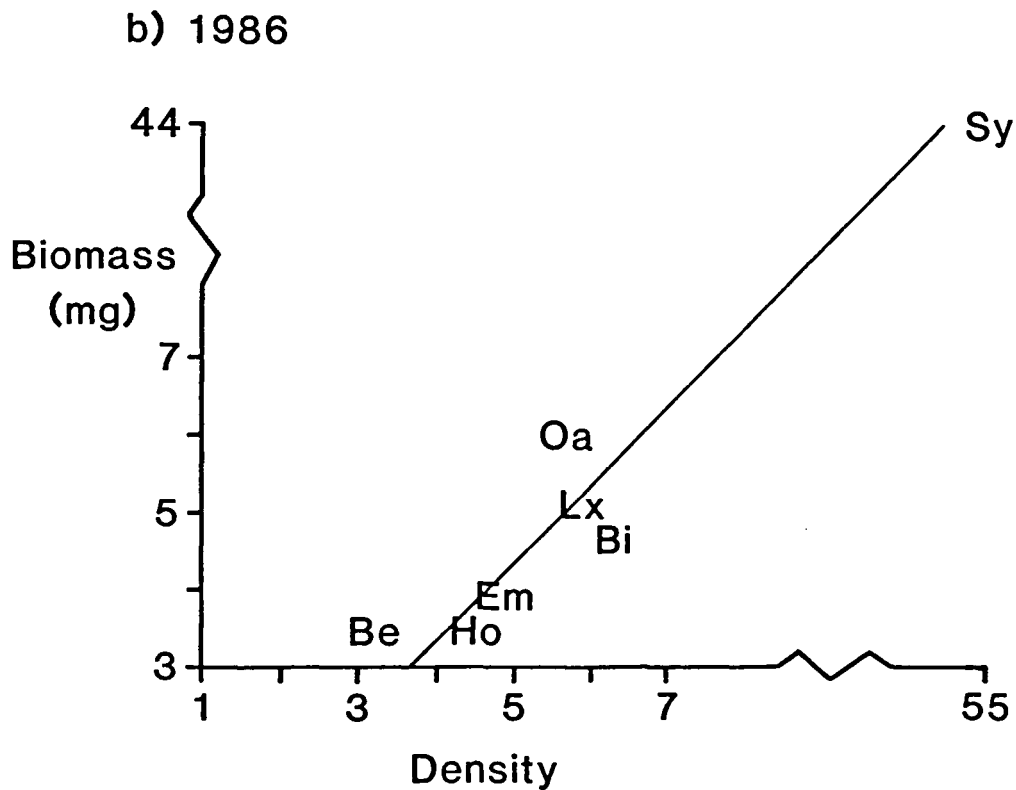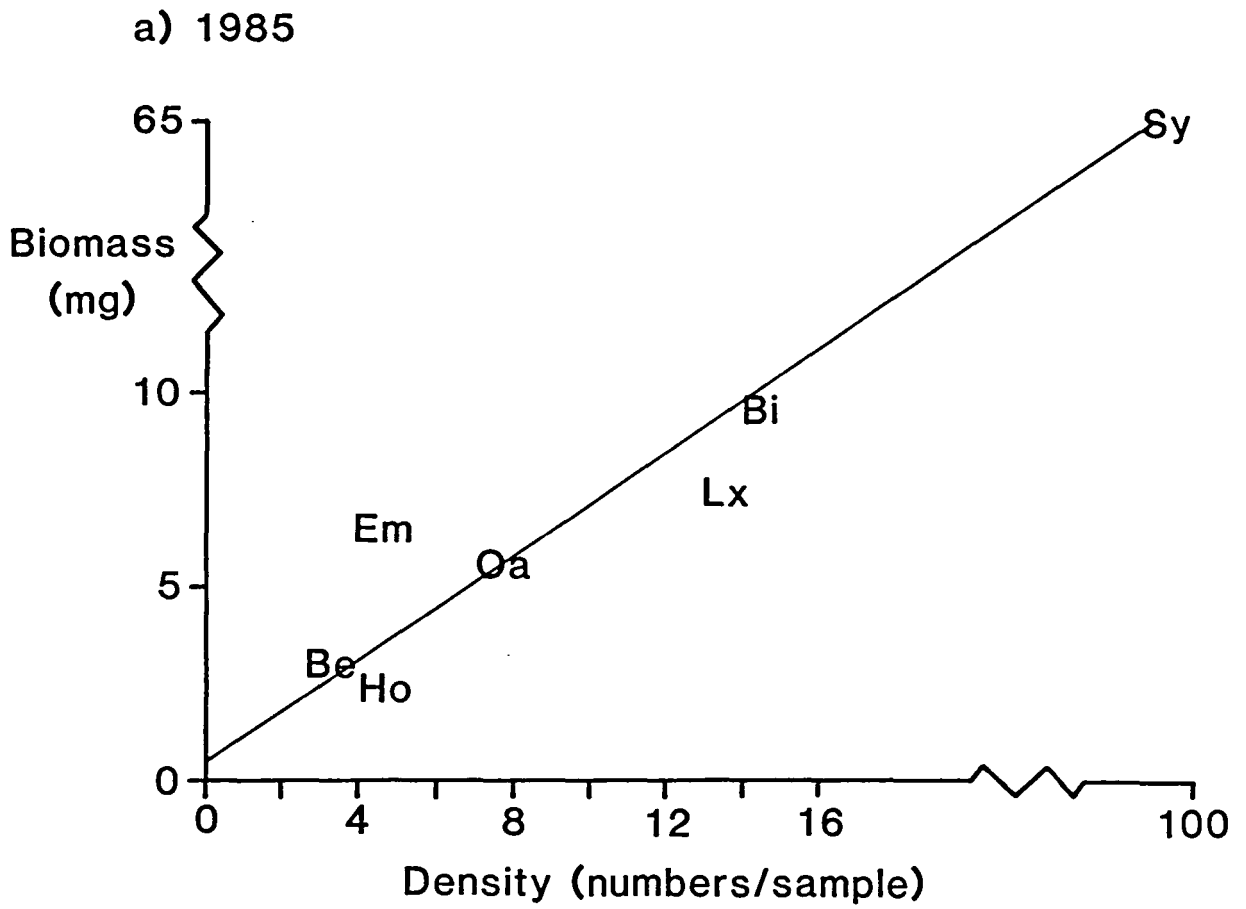
a) 1985

b) 1986

Fig 6.1: The relationship between arthropod density and
biomass in Great High Wood in
a) 1985; Y = 0.66X + 0.56, r = 0.99, 5 d.f. and
b) 1986; Y = 0.80X + 0.34, r = + 0.999, 5 d.f.

Table 6.6

Rank order of tree species by arthropod density on them in Great High
Wood. Species on the same line did not differ significantly in
arthropod density. Tree species are arranged in declining
order of arthropod density. There was some overlap in
the ranks, except the top one.

Early 85	Late 85	All 85
sycamore	sycamore, larch	sycamore
birch, larch	oak	birch, larch, oak
elm, oak, holly	elm, beech, birch	elm, holly
beech		beech
Early 86	Late 86	All 86
sycamore	sycamore	sycamore
elm, larch	oak, birch, holly, larch	birch, larch, oak
birch, oak, beech, holly	elm, beech	elm, holly
		beech

Table 6.7

Percentage change in the arthropod density on trees in Great High
Wood between years and seasons in 1985 and 1986

Tree species	Small 85-86	Medium 85-86	Large 85-86	Total 85-86	Total e/l 85	Total e/l 86	Total e85-86	Total l85-86
Oak	-22	0	0	-26	-16	+289*	-67*	+54
Beech	- 7	+12	+10	0	-20	+ 95	-37	+54
Sycamore	-74*	+32	-17	-44	-94*	+ 29	-74*	+415*
Larch	-63*	-34*	- 9	-55*	-18	+106*	-74*	-36*
Birch	-59*	-24	- 5	-57*	-87*	+221*	-88*	+210
Holly	- 5	+ 2	+15	+ 2		+493*	-67*	
Elm	-2	+12	-24	- 2	-66*	+ 41	-58	+ 72

notes: the figures are calculated from $\frac{\text{mean/sample } 86 - \text{mean/sample } 85}{\text{mean/sample } 85} \times 100$

* = significant change (t-test)
e = early season
l = late season

density between years and seasons. The changes in density from one
year to the next were primarily due to changes in the small size
class. The seasonal changes were more extensive than the overall
yearly changes. A general reduction in density in. 1985 was
accompanied by a significant change on sycamore, birch and elm, and
an increase in 1986 with oak, larch, birch and holly changing
significantly. The lowest arthropod density on all tree species was
in the first half of 1986. The density was significantly lower than
in the same period of 1985 in all tree species except beech and
elm. The density in the second half of 1986 tended to be higher
than in 1985, but a significant difference was found only on
sycamore. The arthropod density on larch was significantly lower in
the late season in 1986 than in 1985.

In addition to invertebrate prey, certain vegetable foods were
available to foraging birds. The most important of these were the
cones on larch, which were more abundant in 1986 (a good cone crop
in contrast with the poor cone year of 1985). Birch seeded well in
both years, but beechmast production failed in both. Birch catkins
were available for the birds in each spring.

6.3 The density of arthropods on each tree species in Hamsterley
Forest

Arthropod density on different tree species in Hamsterley
Forest varied tenfold (Table 6.8). The poorest tree species was
beech, on average with three arthropods per sampling unit, which in

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Table 6.8

Mean numbers of arthropods in samples of 50cm lengths of terminal
branches and an estimation of the proportion of arthropods on each tree
species in the study compartments in Hamsterley Forest in
1985 and 1986

| Tree species | 1985 | | | | 1986 | | | |
	mean/ sample	se (log)	rel. abun.	N	mean/ sample	se (log)	rel. abun.	N
W. hemlock	9.8	0.12	1.7%	11	5.5	0.09	2.5%	24
E. larch *	17.0	0.06	20.5%	16	6.2	0.09	13.9%	23
J. larch	7.8	0.15	1.6%	3	6.8	0.10	5.0%	24
S. pine	7.8	0.11	9.5%	11	8.1	0.10	16.0%	23
S. spruce *	29.5	0.16	9.3%	11	9.1	0.06	4.9%	23
N. spruce	17.0	0.11	6.2%	11	14.8	0.09	8.5%	23
Birch	9.3	0.12	4.8%	11	8.1	0.12	6.0%	24
Oak	21.4	0.05	41.0%	16	12.6	0.11	35.9%	24
Beech	3.5	0.07	1.5%	11	2.6	0.06	1.6%	24
Alder	6.2	0.09	2.0%	16	6.6	0.10	2.3%	24
Sycamore	24.0	0.34	2.0%	2	30.9	0.12	3.5%	24
Index of overall abundance	14.3				8.7			

notes: N = number of samples
       Mean/sample is the geometric mean; the standard error refers to the
       logarithm of this mean.
       * = significant difference between years

both years was significantly less than the density on any other tree species. Sycamore harboured significantly higher densities of arthropods than the other tree species in 1986. In 1985 the mean arthropod density on sycamore was less than that on sitka spruce, but this difference was not statistically significant. In addition to sycamore, high arthropod densities were found on oak, birch, Norway and sitka spruce, European larch and Scots pine.

The arthropod density changed significantly between the years only on European larch and sitka spruce, where it declined from 1985 to 1986 - there was no significant change in the density between the years on any other tree species (Table 6.8).

A calculation of the relative abundance of foliar arthropods on each tree species in Hamsterley Forest (Table 6.8) revealed that a third of all arthropods in the study area were on oak, with European larch and Scots pine together making up another third. The relative abundance of arthropods on each tree species differed by as much as 7% between the years (Table 6.8). The biggest differences were on Scots pine and on European larch. The relative abundance on the former doubled, and on the latter fell by a third. However, on most tree species the relative abundance did not change. Calculation of the index of overall arthropod abundance in the wood as described in section 6.2 showed that the overall abundance in Hamsterley Forest declined by 38% from 1985 to 1986, which is similar to the 42% reduction in Great High Wood. Despite the differences in the tree species composition of the two sites, the changes in the arthropod abundance were very similar.

The small arthropods were the most common size class in 1985 (Table 6.9), but in 1986 the density of small and medium arthropods did not differ significantly. In both years the large size class was the least abundant, which was also the case in Great High Wood.

The arthropod data were divided into 'early' and 'late' seasons each year as described in section 6.2. The mean numbers of arthropods per standard sample in each season are presented in Table 6.10. The changes in arthropod density from early to the late season were greater and more numerous in 1986 than in 1985. The arthropod density on half of the tree species increased from early to late season in 1985 and decreased on the remainder, with a significant increase only on western hemlock ($t=4.04$) and Norway spruce ($t=3.50$) and a significant decline on Scots pine ($t=2.43$). In 1986, the density increased significantly on western hemlock ($t=4.02$), European larch ($t=4.54$), Japanese larch ($t=4.36$), Scots pine ($t=4.29$), birch ($t=4.82$), oak ($t=5.07$), beech ($t=2.90$), and alder ($t=4.27$). A number of changes took place during the winter of 1985-86, with a significant decline in the arthropod density on western hemlock ($t=5.95$), European larch ($t=4.27$), sitka spruce ($t=2.84$), Norway spruce ($t=2.32$), oak ($t=5.08$), beech ($t=3.53$) and alder ($t=3.00$). An equivalent drop in the arthropod density during the winter did not take place in Great High Wood.

The rank order of the tree species according to the arthropod density on them (Table 6.11), was independent of the season or of the year; the rank order of the tree species remained similar throughout the study. Therefore, a tree species that was a better or worse than average foraging site at one point in time, could be

Table 6.9

Mean numbers of arthropods in each size class in samples of 50cm
lengths of terminal branch in Hamsterley Forest in
1985 and 1986

1985	0-2mm	se(log)	2.1-4mm	se(log)	>4mm	se(log)
W. hemlock	2.8	0.10	4.9	0.19	1.3	0.05
E. larch	10.5	0.08	4.1	0.09	2.1	0.07
J. larch	5.6	0.23	1.8	0.14	1.5	0.16
S. pine	5.9	0.13	1.7	0.06	1.6	0.06
S. spruce	20.4	0.20	3.5	0.13	1.4	0.06
N. spruce	12.6	0.11	3.9	0.11	2.0	0.10
Birch	6.5	0.12	2.6	0.08	1.5	0.05
Oak	11.8	0.09	3.4	0.13	3.0	0.06
Beech	2.0	0.09	1.7	0.06	1.4	0.06
Alder	3.9	0.11	1.8	0.06	1.7	0.05
Sycamore	15.9	0.42	8.5	0.15	0.0	0.00

1986	0-2mm	se(log)	2.1-4mm	se(log)	>4mm	se(log)
W. hemlock	2.9	0.06	2.9	0.09	1.1	0.02
E. larch	3.0	0.07	3.0	0.08	2.0	0.07
J. larch	2.2	0.07	3.5	0.10	2.2	0.08
S. pine	4.2	0.11	4.0	0.08	1.3	0.04
S. spruce	5.6	0.05	3.0	0.09	1.2	0.03
N. spruce	8.1	0.10	4.4	0.11	1.4	0.05
Birch	4.6	0.12	3.6	0.08	1.6	0.05
Oak	11.0	0.11	2.0	0.06	1.5	0.05
Beech	1.8	0.06	1.4	0.04	1.2	0.04
Alder	2.5	0.08	3.3	0.13	1.8	0.05
Sycamore	6.2	0.13	13.8	0.15	1.7	0.05

Table 6.10

Mean numbers of arthropods in samples of 50cm lengths of terminal branches
in each season on tree species in Hamsterley Forest in 1985 and 1986

Tree species	Early 1985 mean	se(log)	N		Late 1985 mean	se(log)	N		Early 1986 mean	se(log)	N		Late 1986 mean	se(log)	N
W.hemlock	5.1	0.11	6	*	20.4	0.10	5	*	2.4	0.12	9	*	9.1	0.08	15
E.larch	19.5	0.07	11		12.6	0.10	5	*	2.5	0.13	9	*	11.2	0.06	14
J.larch	7.8	0.15	3						2.5	0.13	9	*	12.3	0.09	15
S.pine	12.3	0.12	6	*	4.6	0.13	5		2.6	0.16	8	*	14.8	0.07	15
S.spruce	49.0	0.28	6		15.8	0.09	5	*	8.3	0.09	8		9.5	0.08	15
N.spruce	10.0	0.10	6	*	33.1	0.11	5	*	9.8	0.20	8		18.2	0.09	15
Birch	10.0	0.09	6		8.5	0.25	5		2.2	0.16	9	*	18.2	0.10	15
Oak	20.0	0.07	11		24.5	0.06	5	*	3.7	0.15	9	*	25.7	0.07	15
Beech	2.8	0.11	6		4.6	0.07	5	*	1.6	0.11	9	*	3.5	0.05	15
Alder	5.9	0.13	11		7.1	0.07	5	*	2.4	0.14	9	*	12.3	0.09	15
Sycamore					24.0	0.34	2		27.5	0.18	9		33.1	0.16	15

notes: * = significant change in the arthropod abundance between adjacent
seasons (t-test)

Table 6.11

Rank order of tree species by arthropod density on them in Hamsterley
Forest. Species on the same line did not differ significantly in
arthropod density. Species are listed in declining
order of arthropod density. There was some overlap in
the ranks.

Early 85   Early 86

s. spruce, oak, E. larch   sycamore, N. spruce
S. pine, N. spruce, birch, J. larch s. spruce, oak
alder, w. hemlock, beech   S.pine, E.larch, J.larch, w.heml,
                                        alder, birch
                                     beech

Late 85   Late 86

N. spruce, oak, sycamore, w. hemlock sycamore, oak, birch, N. spruce
s. spruce, E. Larch, birch   S. pine, J. larch, alder, E. Larch
alder, S. pine, beech   w. hemlock, s. spruce
                                      beech

All 85   All 86

s.spruce,sycam,oak, E.Larch, N.spruce sycamore
w. hemlock, birch   N.spruce,oak,s.spruce, S.pine, birch
S.pine, J.larch, alder   J.larch, alder, E.larch, w.hemlock
beech   beech

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expected to be so throughout. Since the ranking was largely fixed despite the fluctuations in prey density, birds can use this information when choosing foraging sites.

As in Great High Wood, the taxonomic composition of the arthropod fauna differed on the tree species. Table 6.12 lists the mean numbers of arthropods per standard sampling unit in each taxonomic group that were found on the tree species. The commonest groups here, as in Great High Wood, were Hemiptera (especially Aphidae), Coleoptera, Lepidoptera, Diptera and Arachnidae.

Psyllids were common on the conifers and alder (Table 6.12), and were more abundant in 1986 than in 1985 (increase of 9 fold on European larch, 17 fold on Scots pine, 17 fold on Norway spruce, and more than doubled on alder). Most aphids were found on the two species of spruce, oak, birch and sycamore. 65% of all arthropods on sycamore in 1985 were aphids, and 90% in 1986. The 1986 figure is comparable in the two woods, but the percentage of aphids was considerably lower in Hamsterley Forest than in Great High Wood in 1985. Psocoptera were present in large numbers only on larches in 1985. Other Hemiptera were uncommon, with nymphs found mainly on larches in 1985 and on alder and sycamore in 1986. There were few Coleoptera on any of the tree species.

Most lepidopterous caterpillars were found on the broadleaves with the highest density on oak and sycamore (Table 6.12). Caterpillar density was lower in 1986 than in 1985 - a reduction (based on the means) of 57% on birch, 90% on oak, 93% on European larch, 47% on Scots pine, and 80% on sitka spruce, but due to the small sample sizes a significant change was detected only on oak

Mean numbers of arthropods in each taxonomic group in samples of 50cm

lengths of terminal branches in Hamsterley Forest in 1985 and 1986

1985	W.heml	E.larch	J.larch	S.pine	S.spruce	N.spruce	Birch	Oak	Beech	Alder	Sycam.
Hemiptera:											
Aphidae	0.20	0.32	5.03	1.19	9.00	4.01	3.07	4.25	0.17	1.24	12.49
Psyllidae	2.72	0.12	-	0.12	1.34	0.17	-	0.20	-	0.38	0.74
Psocoptera	0.20	0.62	0.82	0.07	0.29	0.12	-	0.05	-	0.12	-
Heteroptera	-	0.66	-	0.07	-	-	0.07	0.17	-	0.10	0.74
Homoptera	-	-	-	-	-	-	-	0.05	-	0.05	-
nymphs	-	2.24	0.82	0.23	0.20	0.07	0.51	0.86	0.07	0.48	-
Coleoptera:											
Curculionidae	0.10	0.32	-	-	0.12	-	0.48	0.48	0.17	0.12	-
Coccinellidae	0.07	0.32	-	0.29	0.12	0.17	-	0.15	0.10	0.05	-
other Coleopt.	-	0.10	0.26	0.07	0.07	0.12	-	0.05	-	-	-
larvae	-	0.32	-	-	0.20	0.07	0.12	0.20	0.07	0.10	-
Lepidoptera:											
imagos	-	0.05	-	-	-	-	-	-	-	-	-
caterpillars	0.07	0.95	0.26	0.38	0.35	-	0.35	1.51	0.29	0.23	0.41
Hymenoptera	0.12	0.35	-	0.07	0.29	1.14	0.07	0.48	0.12	0.05	-
sawfly (larvae)	-	-	-	-	-	-	-	-	-	-	-
Diptera	0.86	0.74	0.26	0.41	1.04	1.69	0.12	0.66	0.48	0.23	2.16
larvae	-	0.05	-	-	-	-	0.07	0.29	-	-	-
Collembola	0.32	0.20	-	0.55	0.07	1.14	0.12	0.45	0.12	0.32	-
Plecoptera	-	-	-	-	-	0.07	-	-	-	0.10	-
Neuroptera	-	-	-	-	-	-	-	0.05	-	-	-
Trichoptera	0.07	-	-	-	-	-	-	-	-	-	-
Thysanoptera	-	-	-	0.95	0.10	-	0.07	0.23	0.07	-	-
Ephemeroptera	-	-	-	-	-	-	0.07	-	-	-	-
Formicidae	-	-	-	-	-	0.07	-	0.10	-	-	-
Arachnidae	1.00	2.47	1.63	0.70	1.45	2.02	0.55	1.63	0.26	0.38	2.82
Opiliones	0.07	0.05	-	-	-	-	0.12	0.05	-	-	-
Acarina	-	-	-	-	0.10	0.07	0.07	0.10	-	0.12	-
Chrysalis/ cocoon	-	0.20	-	0.20	0.07	-	0.07	0.17	-	-	-

1986	W.heml	E.larch	J.larch	S.pine	S.spruce	N.spruce	Birch	Oak	Beech	Alder	Sycam.
Hemiptera:											
Aphidae	0.07	0.07	0.10	1.69	1.09	1.69	4.01	6.41	0.10	0.48	19.05
Psyllidae	2.24	1.19	2.02	2.16	1.63	3.07	0.12	0.07	0.10	1.29	0.10
Psocoptera	0.41	0.23	0.20	0.17	0.41	0.20	-	0.29	0.10	0.05	-
Heteroptera	-	0.02	-	0.02	-	0.07	0.10	0.02	0.02	0.15	-
Homoptera	-	0.26	0.10	-	-	-	0.26	0.02	-	0.17	0.05
nymphs	-	-	0.02	0.15	-	0.02	0.86	0.23	0.26	1.14	0.51
Coleoptera:											
Curculionidae	0.07	0.07	0.20	-	0.07	0.17	0.10	0.12	0.10	0.02	0.07
Coccinellidae	-	-	-	0.07	0.07	0.07	-	-	-	-	-
other Coleopt.	-	0.07	-	0.07	0.07	0.07	0.12	0.12	0.02	0.07	-
larvae	-	0.10	-	0.07	0.07	0.10	0.02	0.26	0.02	0.17	0.07
Lepidoptera:											
imagos	-	-	0.02	-	-	-	-	-	-	-	-
caterpillars	0.02	0.07	0.17	0.20	0.07	0.02	0.15	0.15	-	0.23	0.38
Hymenoptera	0.02	0.02	-	0.12	0.07	0.29	0.02	0.38	0.10	0.10	0.07
sawfly (larvae)	-	1.04	1.19	-	-	-	-	-	-	-	-
Diptera	0.51	0.38	0.35	0.35	0.45	1.19	0.23	0.41	0.32	0.38	0.41
Collembola	0.20	0.10	0.12	0.02	0.41	1.29	-	0.10	0.02	-	0.02
Plecoptera	-	0.02	-	-	0.02	0.10	0.10	-	0.10	0.07	0.26
Trichoptera	-	-	-	0.02	-	-	-	-	-	-	-
Ephemeroptera	-	-	-	-	-	-	-	-	-	0.02	-
Thysanoptera	-	-	-	-	-	-	-	0.23	-	-	0.02
Arachnidae	0.32	0.66	0.48	0.66	0.82	0.74	0.12	0.66	0.17	0.20	0.17
Opiliones	-	0.02	0.02	0.05	-	-	0.02	0.02	-	-	-
Acarina	0.02	-	-	-	0.07	0.17	-	-	-	0.02	-
Chrysalis/ cocoon	0.02	0.02	0.10	0.10	0.07	0.02	0.02	0.02	0.02	0.02	0.02

and European larch. The caterpillar density was comparable in the two woods. Sawfly larvae were only found on the two species of larch, and in considerably larger numbers than in Great High Wood.

Spider densities were considerably lower in 1986 (reduction of 68% on western hemlock, 73% on European larch, 71% on Japanese larch, 43% on sitka spruce, 63% on Norway spruce, 78% on birch, 60% on oak, 47% on alder and 94% on sycamore; densities on all except sitka spruce, birch and alder changed significantly) with high density in all tree species except on birch, beech and alder, where spider densities were low (Table 6.12). A number of other groups of arthropods were recorded in the samples, but they were uncommon. The changes in the arthropod density on trees in the two woods were similar, and the same groups of arthropods (Hemiptera, Coleoptera, Lepidoptera, Diptera and Arachnidae) were common on the trees in both.

The total estimated biomass on the trees was similar (Table 6.13) in the two years on most trees. However, on Japanese larch and oak the changes in the density of the large arthropods resulted in a pronounced change in the biomass. The large arthropods made up the bulk of the biomass in most cases - in half of the cases over 50% of the biomass was due to the large arthropods (primarily caterpillars, beetles, Diptera; different groups tended to prevail on different tree species). A linear relationship between the arthropod density and biomass in Hamsterley Forest (Fig 6.2.a+b) corresponded to the relationship found between these variables in Great High Wood (section 6.2).

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Table 6.13

Mean arthropod biomass (in mg) in samples of 50cm lengths of
terminal branches in Hamsterley Forest in 1985 and 1986

| Tree species	1985 0-2mm	2.1-4mm	>4mm	total	1986 0-2mm	2.1-4mm	>4mm	total
W.hemlock	0.4	5.4	1.1	6.9	0.5	2.6	0.3	3.4
E.larch	1.0	2.9	7.9	11.9	0.4	2.1	9.1	11.7
J.larch	0.3	0.8	1.4	2.4	0.4	4.0	10.2	14.6
S.pine	0.8	0.8	3.8	5.4	1.0	3.0	2.2	6.2
S.spruce	2.4	2.8	1.6	6.8	0.7	2.5	1.1	4.3
N.spruce	1.6	2.9	4.7	9.2	1.6	3.8	2.6	8.1
Birch	0.8	1.4	1.8	4.0	0.8	3.3	3.0	7.0
Oak	1.6	4.1	10.3	16.0	2.9	1.0	2.7	6.5
Beech	0.2	0.7	1.8	2.7	0.2	0.4	1.7	2.3
Alder	0.4	0.9	3.1	4.4	0.5	6.7	4.0	11.2
Sycamore	1.6	5.0	0.0	6.6	2.8	24.0	3.8	30.6

notes: number of samples as per Table 6.8
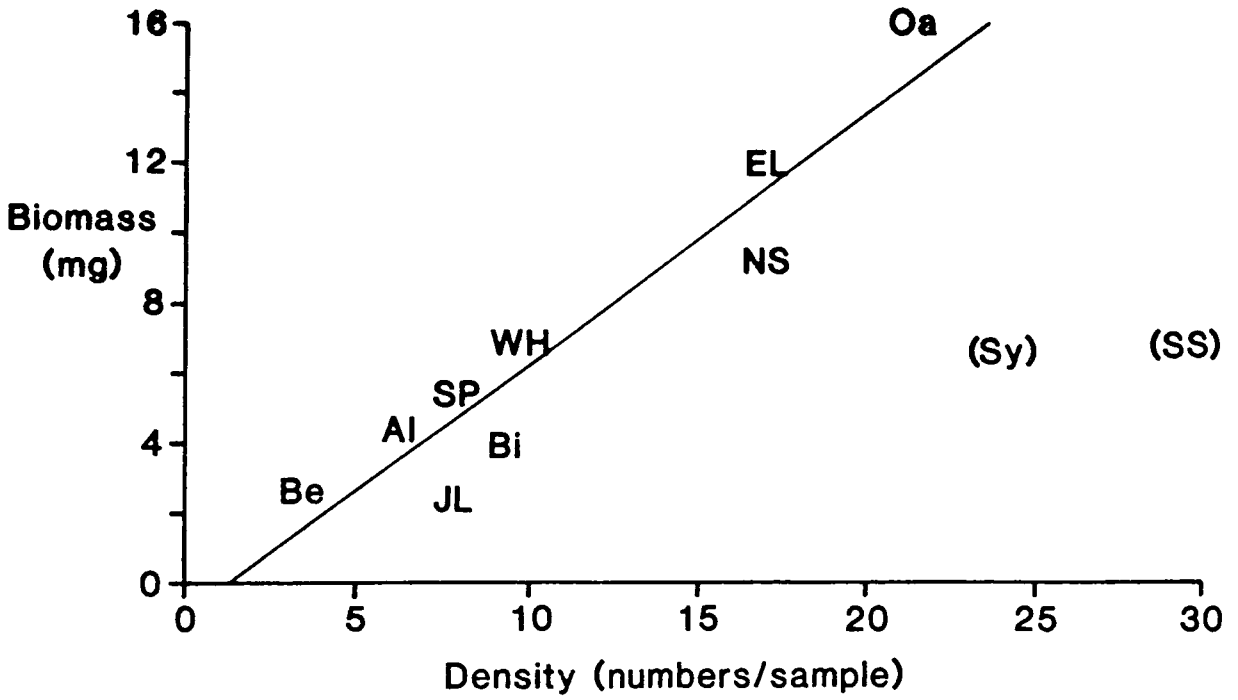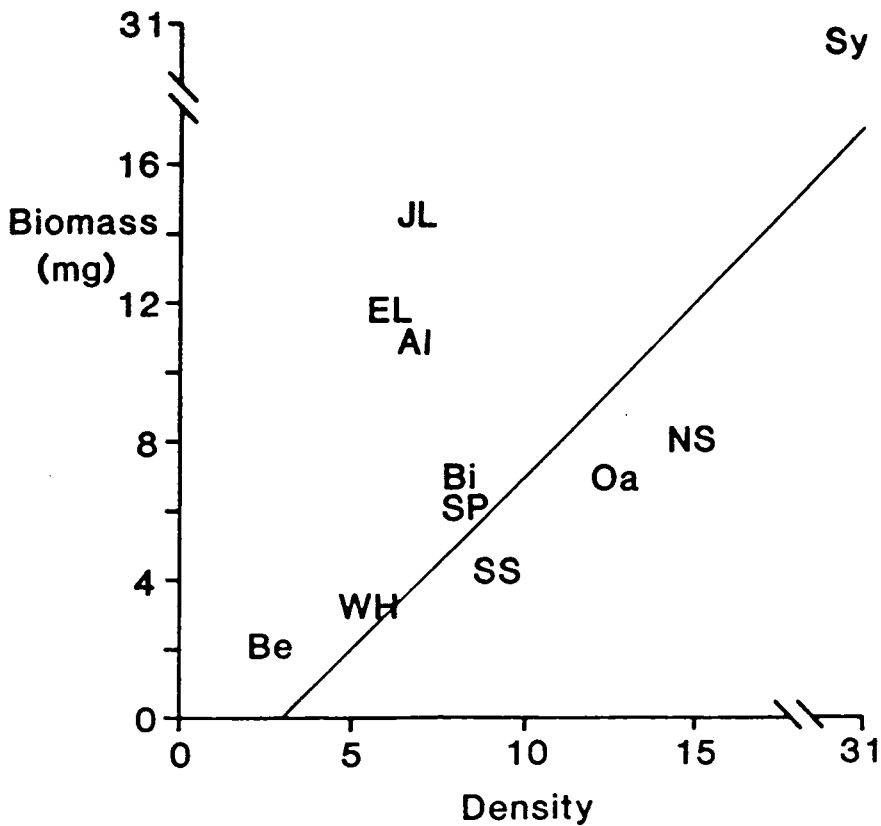
Fig 6.2: The relationship between arthropod density and
biomass in Hamsterley Forest in
a) 1985; Y = 0.72X - 1.01, r = + 0.94, 7 d.f. if
sycamore and sitka spruce are excluded (see
text), and Y = 0.28X + 2.99, r = +0.58, 9 d.f.
including sycamore and sitka spruce
b) 1986; Y = 0.84X + 1.13, r = +0.81, 9 d.f.

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Table 6.14 summarises the changes in arthropod density between years and seasons. As in Great High Wood, the observed changes in density from one year to the next were primarily due to the changes in the small size class, whereas changes in the medium and large arthropods were not detected in the overall change. There was a significant reduction in the small size class on European larch and sitka spruce in 1986, which resulted in the observed reduction in the overall density on these tree species. However, the increase in the medium size class on Scots pine and the decrease in the large size class on oak were not reflected in an overall change in arthropod density.

There were more changes in density between seasons in one year than from one year to the next (Table 6.14), which corresponds to findings in Great High Wood. Arthropod density on western hemlock and Norway spruce increased and that on Scots pine decreased significantly in the course of 1985. There were also some differences in the arthropod density in the late seasons of 1985 and 1986. However, the significant increase in the density in the course of 1986 and the significantly lower density in the early season in 1986 than in 1985 on most tree species shows that the arthropod density was fairly constant throughout the study period, except that the density was significantly depressed in the spring and early summer of 1986.

Table 6.14

Percentage change in the arthropod density on trees in Hamsterley
Forest between years and seasons in 1985 and 1986

Tree species	Small 85-86	Medium 85-86	Large 85-86	Total 85-86	Total e/l 85	Total e/l 86	Total e85-86	Total l85-86
W.hemlock	+2	-41	-13	-44	+298*	+280*	-53*	-55*
E.larch	-72*	-28	- 7	-64*	-35	+347*	-87*	-11
J.larch	-60	+91	+51	-13		+390*	-68*	
S.pine	-29	+134*	-21	+ 5	-63*	+462*	-79*	+224*
S.spruce	-72*	-13	-11	-69*	-68	+ 15	-83*	- 40*
N.spruce	-35	+12	-29	-13	+231*	+ 86	- 2	- 45
Birch	-29	+41	+ 2	-13	-15	+713*	-78*	+114
Oak	- 7	-41	-51*	-41	+23	+592*	-81*	+ 5
Beech	- 7	-21	-11	-24	+62	+124*	-44	- 22
Alder	-37	+82	+ 5	+ 7	+20	+413*	-59*	+ 74*
Sycamore	-61	+62	inf.	+29		+ 20		+ 38

notes: the figures are calculated from $\dfrac{\text{mean/sample 86 - mean/sample 85}}{\text{mean/sample 85}} \times 100$

* = significant change (t-test)
e = early season
l = late season

6.4 Discussion

It has been established in this chapter that the composition and structure of the arthropod fauna was similar in the two study sites. In each wood, the relative abundance of arthropods on trees remained similar in both years, and the overall abundance decreased by the same amount from 1985 to 1986 despite the differences in the tree species composition of the sites. The arthropod density differed on the tree species in both study sites. Oak, sycamore, birch, larch, and sitka and Norway spruces supported high densities of arthropods, and beech contained the poorest fauna in both woods. Arthropod densities tended to be higher on trees in Hamsterley Forest than in Great High Wood (up to three times higher for tree species that were present in both woods). The only exceptions were birch and sycamore, the former of which supported higher arthropod densities in 1985 and the latter in both years in Great High Wood, and beech, which did not differ in the two sites. The exclusion of sycamore in Great High Wood, because of the extreme density of aphids on it, revealed that the arthropod abundance on trees in Hamsterley Forest, as shown by the index of overall abundance, was twice that in Great High Wood in both years. Despite the higher arthropod density, the mean bird density was lower in Hamsterley Forest than in Great High Wood, and it can be speculated that predation pressure may be one of the factors causing the difference in the arthropod density between the two areas. The changes in the arthropod density between years and seasons were similar in the two sites, but there was little change during winter in Great High

Wood, whereas the change in density was large and significant on most tree species during winter in Hamsterley Forest. Vast majority of the observed changes in arthropod density apparently arose from the low densities in the early part of 1986, while for the rest of the time the densities remained at a fairly constant level. The distribution of arthropods in the three size classes was similar in the two woods - the small arthropods were the most abundant and the large ones most scarce in both.

The methods of collecting the arthropod samples was found generally satisfactory, but some problems were encountered during the analysis. The arthropod density was found to be variable on each tree species, which resulted in large standard errors for the samples. This meant that the significance of some large changes (2 or 3 fold or greater) in the density of all arthropods or of some taxonomic or size groups was not detected by t-test. These larger changes in density can be taken as indicative, but not conclusive, of a change, and have been reported in this chapter alongside with the changes that were statistically significant (e.g. changes in the density of taxonomic groups of arthropods). The amount of sampling done for this study was the maximum possible within the limits of time and resources, and it was just adequate. However, any further study that involves the food of insectivorous birds would have to make provisions for more extensive sampling of the arboreal arthropods.

The findings in this chapter show that despite different species composition and structure in the two woods, the arthropod fauna displayed some striking similarities. The increases and

decreases in the densities of the major taxonomic groups were similar in the two sites. Similarly, the overall changes in the arthropod density and the changes in the size classes from one year to another and within a year were similar in the two woods. The similarity of these changes suggests that they were brought about by environmental factors that affected both sites in the same way. Therefore it seems possible that the results of arthropod sampling in one area can, with some caution, be used to predict the changes in another area of woodland in the same region. Another implication of this is that the insectivorous arboreal bird species ought to be affected in a similar way by these changes in prey density in each wood.

CHAPTER 7

DOES FOOD AVAILABILITY AFFECT WHERE BIRDS FEED?

7.1 Introduction

It was established in Chapter 6 that there were differences in the density of arthropods on different tree species. This chapter investigates whether these affected the bird fauna in any way. I have attempted to answer the following questions:

1. Did the differences in prey density affect the tree choices of foraging birds?

2. Were the tree preferences by birds associated with tree species with relatively high prey density, and if so, what was their relationship?

3. Did the birds respond to the overall prey density or only to some components of the total prey available?

4. Did any exceptions occur, and if so, why?

5. Is there a relationship between the distribution of birds among the tree species and the relative abundance of prey on each tree species?

6. Was the frequency of use of each tree species by the birds related to the relative abundance of prey on each tree species or to the frequency of each tree species in the wood?

7. Did changes in prey density affect the tree choices by birds, and if so, how?

7.2 Tree preference index and prey density on the tree species

Prey densities were often different on different tree species in both woods. If birds were attracted to some tree species by the presence of high prey densities on the tree, greater numbers of birds would be expected to be foraging in these trees. To establish whether this occurred, the overall tree preference index (calculated from combined data on the six bird species) was plotted against the prey density using data from Great High Wood in 1985. No relationship was found (r=0.02, 5 d.f., with a slope of 0.00). An inspection of the graph revealed that this was due to the position of sycamore in the correlation. Prey density on sycamore was much higher than on any of the other tree species, but the TPI was near zero. The other points appeared to fall on a line, and when the regression was recalculated without sycamore, a correlation was found between the remaining variables (y = 0.11x - 0.77, r = +0.75, 4 d.f.; Fig 7.1). A significant and similar relationship between tree preference index and prey density was found in Hamsterley Forest (y = 0.09x - 0.90, r = +0.75, 9 d.f. in 1986). These two regressions do not differ from each other statistically in either the slope or the intercept, and give a combined regression equation of y = 0.08x - 0.55, r = +0.61, 15 d.f. Therefore, it can be concluded from this that the same relationship between tree preference and prey density was operating
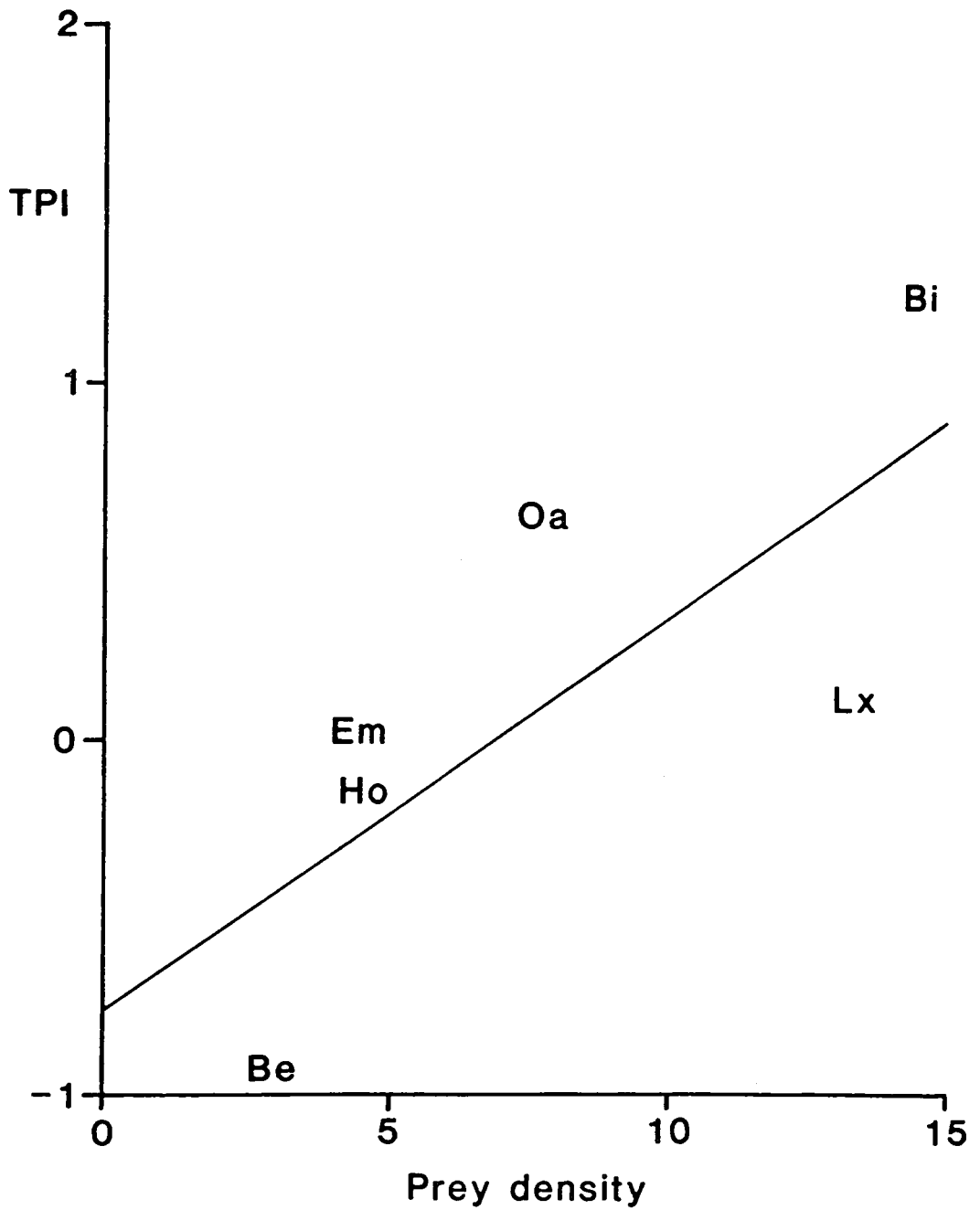
Fig 7.1: The relationship between the combined tree preference index (TPI) of six species of birds and prey density on tree species in Great High Wood in 1985. $Y = 0.11(+/-0.05)X - 0.77$, $r = +0.75$, 4 d.f.

in the two woods despite the different tree species composition. The relationship between these two variables is probably a general phenomenon rather than being specific to any one wood.

In order to investigate the relationship between the tree preference index and the prey density further, a plot of these two variables was made for each bird species separately. In all regression analyses sycamore was omitted for all bird species in Great High Wood. In Hamsterley Forest both species of spruce were omitted for blue and great tit, oak for coal tit and goldcrest, and Japanese larch for chaffinch. These tree species deviated greatly from the regression calculated for the other tree species, and are dealt with as special cases in section 7.4, where the reasons for their omission are also given.

Table 7.1 shows the regressions between tree preference index and prey density for Great High Wood, and Table 7.2 for Hamsterley Forest for each bird species. A positive relationship was found between the variables for each of the bird species. However, owing to the small number of points in each regression, most of the 8 relationships were not significant at the 5% level in Great High Wood, despite a high correlation coefficient. The majority of the 10 regressions in Hamsterley Forest were significant. Since each of a total of 18 correlations was positive, the trend for the birds to concentrate their foraging on tree species with high prey density was significant (sign test: chi-square = 18.00, 1 d.f., p<0.001).

When the relationship between the tree preference and prey density was compared in the two woods for each individual bird species, differences were found. However, many of the slopes and

Table 7.1

Regressions for plots of the tree preference of each bird species (y)
against the overall prey density (x) in Great High Wood in
1985 and 1986.

Bird	N	Slope	se	Interc.	se	r(4d.f.)
1985						
Blue tit	6	0.10	0.06	-0.62	0.57	0.62
Great tit	6	0.12	0.08	-0.86	0.72	0.61
Coal tit	6	0.22	0.11	-1.06	1.09	0.69
Chaffinch	6	0.06	0.06	-0.67	0.54	0.44
All birds	6	0.11	0.05	-0.77	0.46	0.75
1986						
Blue tit	6	0.35	0.21	-1.66	1.07	0.65
Great tit	6	0.44	0.30	-1.86	1.55	0.60
Coal tit	6	0.84	0.75	-3.91	3.87	0.49
Chaffinch	6	0.70	0.80	-3.26	4.16	0.40
All birds	6	0.44	0.15	-2.06	0.79	0.82*

* = significant correlation coefficient

Table 7.2

Regressions for plots of the tree preference of each bird
species (y) against the overall prey density (x) in
Hamsterley Forest in 1985 and 1986

Bird	N	Slope	se	Interc.	se	r	d.f.
1985							
Blue tit	9	0.22	0.08	-2.04	1.15	0.71	7*
Great tit	9	0.18	0.07	-1.82	0.91	0.71	7*
Coal tit	10	0.03	0.03	-0.26	0.43	0.37	8
Goldcrest	10	0.10	0.02	-0.90	0.29	0.88	8*
Chaffinch	10	0.07	0.08	-0.64	1.30	0.32	8
All birds	11	0.06	0.04	-0.52	0.62	0.43	9
1986							
Blue tit	9	0.30	0.04	-2.27	0.44	0.96	7*
Great tit	9	0.13	0.04	-1.09	0.50	0.76	7*
Coal tit	10	0.08	0.03	-0.74	0.40	0.66	8*
Goldcrest	10	0.13	0.04	-0.88	0.49	0.76	8*
Chaffinch	10	0.03	0.03	-0.54	0.39	0.32	8
All birds	11	0.09	0.03	-0.90	0.34	0.75	9*

* = significant correlation coefficient

intercepts in the two woods were not statistically different from each other. Combination of data for each bird species from both woods revealed that the relationship between tree preference and prey density was similar in the two woods for the blue and great tits (correlation coefficient remained about the same as for the two separate correlations). However, there was a reduction in the correlation for coal tit and chaffinch. This suggests that the relationship between tree preference and prey density remains the same, and is independent of the tree species composition in the wood for some but not all bird species. Therefore, there was no overall justification to combine the data from the two woods.

7.3 Do birds respond to different size classes of prey differently?

Each bird species is known to take different sized prey, which is best suited to the size of the bird and its bill (Betts 1955). This suggests that birds respond most to the presence and the density of prey in the preferred size range. To allow for the identification of the prey size that determined birds' tree preferences, the regression between tree preference and the prey density of each size class was calculated for each bird species.

Figure 7.2 shows the relationships between tree preference index for goldcrest and the prey density in each size class in Hamsterley Forest in 1985. Fig. 7.2.a shows that the overall prey density was correlated with the tree preference index (r = +0.88, 8 d.f.). When the data were divided into small (Fig 7.2.b), medium

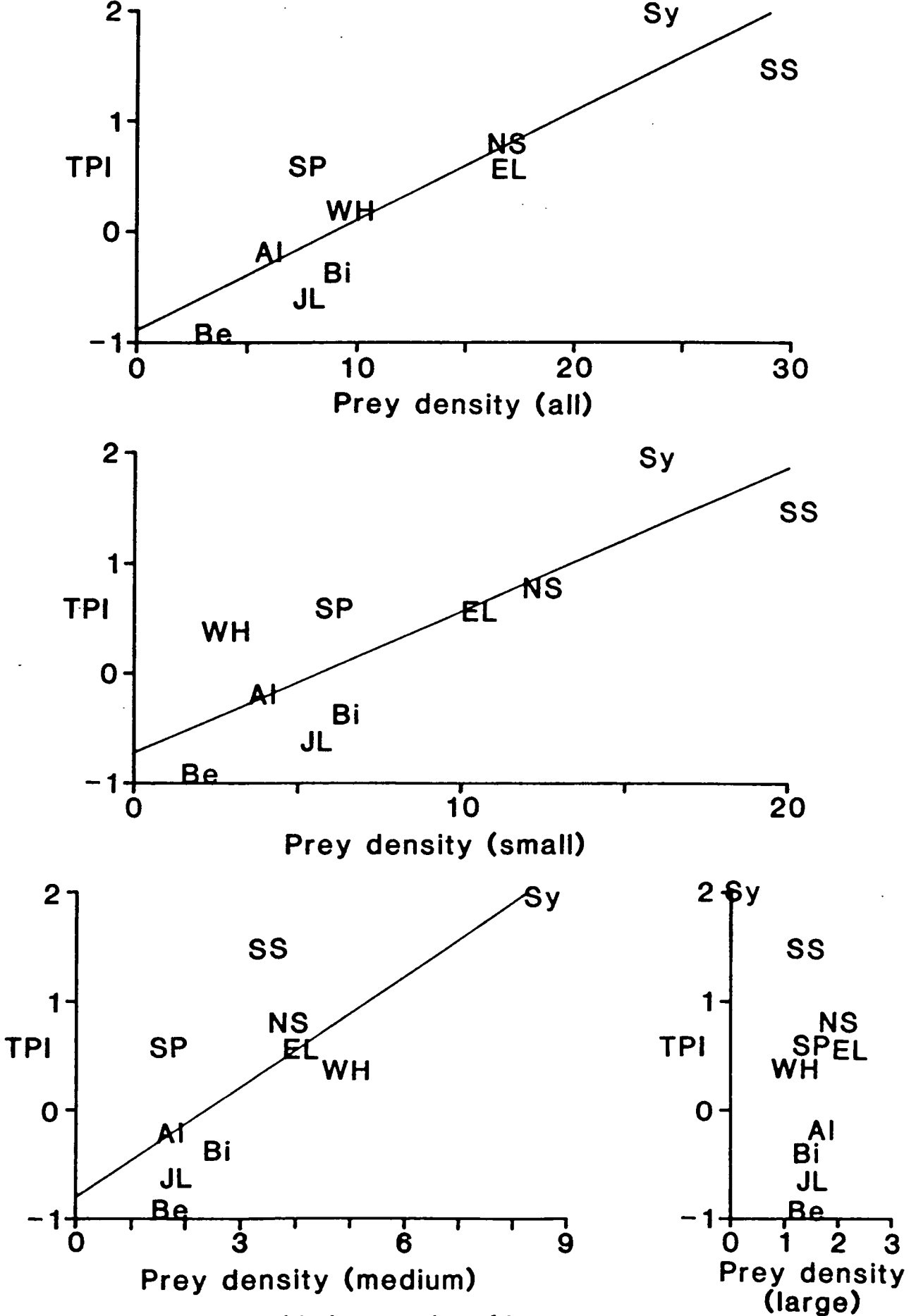Fig 7.2: The relationship between the goldcrest tree
preference (TPI) and the prey density overall and
in size classes in Hamsterley Forest in 1985.
a) overall prey density; Y = 0.1X - 0.9,
   r = +0.88, 8 d.f.
b) density of small prey; Y = 0.13X - 0.72,
   r = +0.83, 8 d.f.
c) density of medium prey; Y = 0.34X - 0.79,   186
   r = + 0.77, 8 d.f.
d) density of large prey; no correlation.

(Fig 7.2.c), and large (Fig 7.2.d) prey, a highly significant correlation was found between the tree preference and the density of the small prey items. A correlation was also found with the medium prey, but there was no relationship between tree preference of the goldcrest and the density of the large size class of prey. The closest agreement was with the density of small prey items.

Following this procedure (Fig 7.2), the relationship between the tree preference and the density of prey in each size class and combinations of size classes (i.e. small+medium and medium+large) was established for each bird species in 1985 and 1986. It was found that the tree preference index for each bird species was correlated with some, but not all, prey sizes. The best correlation between the tree preference and prey density for each bird species is tabulated in Table 7.3 for Great High Wood and in Table 7.4 for Hamsterley Forest. The results show that the tree preference of most bird species was correlated with the density of at least one size group of prey, which in most cases was the small or medium size, and that the strength of the relationship between the tree preference and prey density differed between the bird species.

The correlation coefficients for each size class of prey against tree preference index are tabulated in Table 7.5 (Great High Wood) and Table 7.6 (Hamsterley Forest). These tables show that the strength of the tree preference was normally distributed among the size classes, with a gradual decline in the strength of the correlation between tree preference and distribution of each size class as the prey size moved away from the optimum. The correlation with prey size was, on average, stronger in Hamsterley

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Table 7.3

Regressions for plots of tree preference index (y) and mean
number of arthropods (x) for the arthropod size class
that gives the best fit. Great High Wood, 1985
and 1986. Sycamore is excluded (see text).

Bird	Size	N	Slope	se	Interc.	se	r(4d.f.)
Blue tit 85	S	6	0.12	0.09	-0.51	0.56	0.57
Blue tit 86	M	6	1.46	0.77	-3.40	1.86	0.69
Great tit 85	S	6	0.16	0.11	-0.75	0.70	0.59
Great tit 86	S	6	0.71	0.34	-1.96	1.09	0.74
Coal tit 85	M	6	2.01	0.62	-4.66	1.68	0.86
Coal tit 86	S	6	0.71	1.10	-1.88	3.57	0.31
Chaffinch 85	L	6	2.67	0.19	-4.08	0.27	0.99
Chaffinch 86	M	6	1.57	3.32	-3.50	8.09	0.23
All birds 85	S	6	0.15	0.07	-0.63	0.46	0.71
All birds 86	S	6	0.46	0.28	-1.26	0.91	0.63

S = small, M = medium, L = large prey

Table 7.4

Regressions for plots of tree preference index (y) and mean
number of arthropods (x) for the arthropod size class
that gives the best fit. Hamsterley Forest, 1985
and 1986. Some tree species were excluded for
each species of bird as per description
in the text

Bird	Size	N	Slope	se	Interc.	se	r	d.f.
Blue tit 85	S+M	9	0.31	0.07	-2.63	0.83	0.86	7
Blue tit 86	M	9	0.67	0.10	-2.09	0.54	0.93	7
Great tit 85	S+M	9	0.24	0.06	-2.20	0.70	0.84	7
Great tit 86	S+M	9	0.22	0.06	-1.75	0.54	0.83	7
Coal tit 85	S	10	0.05	0.04	-0.29	0.39	0.44	8
Coal tit 86	M+L	10	0.21	0.06	-1.17	0.42	0.76	8
Goldcrest 85	S+M	10	0.11	0.02	-0.98	0.27	0.90	8
Goldcrest 86	S+M	10	0.22	0.06	-1.47	0.59	0.78	8
Chaffinch 85	M	10	0.75	0.23	-2.24	0.92	0.76	8
Chaffinch 86	L	10	2.04	0.49	-3.26	0.74	0.83	8
All birds 85	M	11	0.39	0.12	-1.08	0.49	0.72	9
All birds 86	M	11	0.24	0.05	-0.95	0.26	0.85	9

S = small, M = medium, L = large prey

Table 7.5

Summary table of the correlation coefficients of
regressions between tree preference by birds and prey
density in each size class in Great High Wood

1985	Blue tit	Great tit	Coal tit	Chaffinch	Total birds
S	0.57	0.59	0.70	0.25	0.71
S+M	0.56	0.57	0.73	0.38	0.70
M	0.49	0.42	0.86*	0.29	0.64
M+L	0.53	0.40	0.83*	0.76	0.66
L	0.48	0.26	0.52	0.91*	0.54
All	0.62	0.61	0.69	0.66	0.75

1986	Blue tit	Great tit	Coal tit	Chaffinch	Total birds
S	0.48	0.74	0.31	0.10	0.63
S+M	0.69	0.65	0.27	0.18	0.74
M	0.69	-0.19	-0.07	0.22	0.40
M+L	0.70	-0.21	-0.14	0.22	0.49
L	0.24	-0.11	0.24	0.03	0.31
All	0.65	0.60	0.49	0.40	0.82*

* = significant correlation coefficient
S = small, M = medium, L = large prey

Table 7.6

Summary table of the correlation coefficients of regressions
between tree preference by birds and prey density in
each size class in Hamsterley Forest

1985	Blue tit	Great tit	Coal tit	Gold-crest	Chaf-finch	Total birds
S	0.80*	0.79*	0.44	0.83*	0.35	0.47
S+M	0.86*	0.84*	0.36	0.90*	0.50	0.59
M	0.81*	0.77*	0.00	0.77*	0.76*	0.72*
M+L	0.69*	0.68*	0.03	0.78*	0.60	0.56
L	-0.62	-0.51	0.09	-0.44	-0.67*	-0.64*
All	0.71*	0.71*	0.37	0.88*	0.32	0.43

1986	Blue tit	Great tit	Coal tit	Gold-crest	Chaf-finch	Total birds
S	0.41	0.71*	0.22	0.60	-0.06	0.07
S+M	0.90*	0.83*	0.62	0.78*	0.25	0.63*
M	0.93*	0.60	0.73*	0.73*	0.39	0.85*
M+L	0.92*	0.60	0.76*	0.70*	0.44	0.88*
L	0.14	0.12	0.54	-0.15	0.83*	0.55
All	0.96*	0.76*	0.66*	0.76*	0.32	0.75*

* = significant correlation coefficient
S = small, M = medium, L = large prey

Forest than in Great High Wood. Most of these correlations were positive (45/50 in Great High Wood and 53/60 in Hamsterley Forest), giving further evidence for that birds' tree preferences are linked to prey density.

Table 7.7 summarises the relationships between the densities of different size classes of prey on each tree species and from one year to the next. There was a good correlation between all three size classes in both years in Great High Wood. Also a good correlation existed between the years for each size class and the overall prey density. Therefore, in Great High Wood each tree species provided similar size composition of prey, and hence the primary differences between tree species were prey density and the specific composition of prey. This suggests certain stability in the structure of the prey population and its distribution among the tree species in Great High Wood, with few changes in time. The birds showed strongest correlation with single size classes rather than with combinations of them (Table 7.3). The size class that in the analysis correlated strongest with the tree preference was most likely immaterial, and possibly due to chance because of the intercorrelation of the size classes.

In Hamsterley Forest (Table 7.7) the correlation between size classes was poor or non-existent in both years, which shows that the tree species provided a different size composition of prey. The densities of small and medium prey were correlated between the two years, but there was a lack of correlation with the large prey, and the correlation of the overall prey density between the years was weak. The low correlation of the size classes between the two years

Table 7.7

Summary table of the correlations of the densities between different
size classes of prey within and between years on trees in
Great High Wood and Hamsterley Forest

	N	Slope	se	Interc.	se	r	d.f.
Great High Wood:							
1985 S-M	7	0.36	0.02	0.77	0.36	0.99	5*
1985 M-L	7	0.04	0.02	1.33	0.12	0.74	5
1985 S-L	7	0.02	0.01	1.36	0.11	0.73	5
1986 S-M	7	2.34	0.28	-4.76	1.41	0.97	5*
1986 M-L	7	0.01	0.01	1.36	0.07	0.59	5
1986 S-L	7	0.04	0.02	1.27	0.09	0.69	5
Small 85-86	7	0.21	0.01	2.04	0.25	0.99	5*
Medium 85-86	7	1.38	0.07	-1.22	0.45	0.99	5*
Large 85-86	7	0.39	0.18	0.83	0.27	0.71	5
Total 85-86	7	0.55	0.02	0.78	0.82	1.00	5*
Rel. abun. 85-86	7	0.96	0.02	0.61	0.64	1.00	5*
Hamsterley Forest:							
1985 S-M	11	0.18	0.10	1.84	1.02	0.53	9
1985 M-L	11	-0.19	0.10	2.23	0.41	-0.52	9
1985 S-L	11	-0.01	0.04	1.67	0.43	-0.08	9
1986 S-M	11	0.21	0.39	3.09	2.10	0.18	9
1986 M-L	11	0.02	0.03	1.45	0.18	0.23	9
1986 S-L	11	-0.02	0.04	1.66	0.22	-0.19	9
Small 85-86	11	0.30	0.13	2.10	1.34	0.61	9*
Medium 85-86	11	1.35	0.32	-0.57	1.27	0.81	9*
Large 85-86	11	0.00	0.16	1.54	0.28	0.00	9
Total 85-86	11	0.54	0.24	2.56	3.92	0.59	9
Rel. abun. 85-86	11	0.80	0.09	1.83	1.24	0.95	9*

* = significant correlation coefficient
S = small, M = medium, L = large prey

suggests that the prey population in Hamsterley Forest was unstable from the point of view of a foraging birds. The relative importance of the size classes on any one tree species also changed from one year to the next. The tree preferences of the birds correlated best with combinations of size classes (Table 7.4), which tended to reflect their preferred size of prey better than any individual size class. This relaxed preference for a size range of prey was possibly accounted for by the variability in the size range of prey on the trees.

However, despite the differences in prey density in the size classes, the relative abundance of prey on each tree species remained unchanged in both woods from 1985 to 1986 (r=1.00 in Great High Wood, and r=0.95 in Hamsterley Forest, Table 7.7). This suggests that if the birds were to forage preferentially in tree species with higher prey density, little or no change in tree species choice would be expected between the two years. The changes in birds' tree use and reasons for these are dealt with in sections 7.6. - 7.8.

7.4 Exceptions to the relationship between tree preference index and prey density

The relationship between tree preference and prey density was not universal, but exceptions occurred. This section features tree species that did not comply with the general relationships, and attempts are made to explain the reasons why this should happen.

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In Great High Wood, sycamore contained about 80% of all arboreal arthropod prey in the wood, while the frequency of the tree species was 21%. Because of this, the birds would have been expected to forage most extensively in sycamore. However, this did not happen, and birds showed little preference for sycamore. In order to fit sycamore onto the regression line of tree preference index against prey density that was calculated for the other tree species in 1985, the tree preference index for sycamore would have to be 9.98. However, because of the frequency of sycamore in Great High Wood, the maximum possible preference index attainable by birds feeding on sycamore was 3.79. This shows that it was not possible to fit sycamore onto the same regression as the other tree species, but that factors, other than prey density, affected the foraging of birds in sycamore. In Hamsterley Forest the preference for sycamore, which was present at 1% frequency only, did not deviate from the regression based on other tree species.

Because of this difference in the response to sycamore in the two woods, the most likely reason for the lack of preference for sycamore in Great High Wood was predator saturation by the prey on sycamore, and therefore the prey could not be utilized to the full, while there were no such limitations in Hamsterley Forest. Numerous reports of prey saturation in many groups of animals have made this a well known phenomenon. Prey density on sycamore can be likened to insect outbreaks - as prey density increases beyond a certain level, there is no further increase in the exploitation of that food source by birds (e.g. Buckner & Turnock, 1965).

Another possible reason for the lower than expected use of sycamore in Great High Wood is the accessibility of prey. Most of the arthropods on sycamore are found on the leaves, and are therefore difficult to reach by a potential predator due to the long flattened petioles.

Some irregularities were discovered in the birds' response to larch in Great High Wood. The coal tit and the chaffinch lacked any correlation with prey size classes in 1986 in Great High Wood Table 7.3). This appeared to be due to the strong preference for larch by both these species in 1986. The preference by coal tit was caused by feeding on larch seeds, which, as a plant structure, was not included in the prey density data, and therefore biased the results. The explosion of the larch sawfly population in 1986 attracted the chaffinches to forage preferentially in larch, resulting in a higher than expected preference for larch due to a single prey species. Removal of the effect of larch from the regression for the coal tit and the chaffinch revealed a relationship between the tree preference index and prey density for the remaining tree species. For the coal tit the relationship remained weak with $r = +0.44$, but the regression for the chaffinch was significant with equation $y = 2.47x - 6.44$, $r = +0.87$, 3 d.f.

In Hamsterley Forest both broadleaved and coniferous elements were present, and some division of tree use by birds that preferred broadleaves or conifers could be expected. It was discovered that some tree species were not used despite high prey density on them. The blue and great tits did not feed in either species of spruce. Similarly, the coal tit and goldcrest did not forage on oak,

despite an abundance of prey. These avoidances were clearly due to other factors than prey availability, and they resulted in the trees and potential food sources being neglected. In 1986, a population explosion of sawflies caused a sharp increase in the preference for larch by chaffinches, and a large deviation of Japanese larch from the other tree species in the relationship between tree preference and prey density.

All the above mentioned tree species deviated considerably from the regression line calculated for tree preference index and prey density for the other tree species, and their inclusion generally resulted in no relationship between the two variables to be apparent. In each case this was caused by a single well defined factor, the effect of which on the tree preference could be readily explained, which is why these tree species were treated as special cases separately from the main analysis of relationships between the birds' tree preference and prey density.

7.5 Relationships between the bird and prey distributions on tree species. Do birds choose their foraging sites by the relative abundance of prey on them?

Since birds chose their foraging sites by the prey density in the trees, as described in section 7.2, a correlation between bird and prey distribution among the trees can be expected. Because of the reasons given in section 7.4 on exclusion of certain tree species, sycamore was discounted in Great High Wood from all correlations, and sitka and Norway spruce were excluded for blue

and great tits, and oak was left out of the analysis for coal tit, goldcrest and chaffinch in Hamsterley Forest. A good relationship was found between the bird and prey distributions among the trees in both woods for each bird species. The summary of the regressions is presented in Table 7.8 for Great High Wood and in Table 7.9 for Hamsterley Forest. Most of the correlations were high, generally 0.8 and above. The only exceptions were coal tit and chaffinch in Great High Wood in 1986, when these species concentrated their foraging on the seeds and sawfly larvae on larches. This resulted in a higher than expected percentage of the birds foraging in larches and in a deviation from the regression line in the same manner as the tree preference of these birds (section 7.2). There was a linear relationship between the remaining points.

Because of this close relationship between the distribution of birds and arthropods among the tree species, it was suspected that the tree preferences established in Chapters 3 and 4 may be directly associated with the prey distribution, rather than with tree species frequencies. Therefore, a modification of the tree preference index was calculated for each bird species by calculating the expected number of birds in each tree species from the relative frequency of arthropods on the tree species (cf. Methods for calculation of the original tree preference index). A comparison of the modified and original tree preference indices gives insight into the extent to which the prey availability on the trees affected the tree species preferences. If a tree preference index that originally indicated significant preference or avoidance becomes non-significant when the index is modified, the bird

Table 7.8

Regressions for plots of bird percentage (y) against relative abundance
of prey (x) in each tree species to establish the existence of a
relationship between the two variables in Great High Wood.
Sycamore has not been considered (see text)

Bird	N	Slope	se	Interc.	se	r	d.f.
1985							
Blue tit	6	1.28	0.42	-5.19	8.62	0.84	4*
Great tit	6	1.24	0.47	-4.84	9.81	0.79	4
Coal tit	6	0.92	0.49	0.55	10.05	0.71	4
Chaffinch	6	1.61	0.45	-10.19	9.34	0.87	4*
All birds	6	1.27	0.36	-5.10	7.43	0.87	4*
Great tit							
excl. larch	5	1.48	0.37	-4.59	7.29	0.92	3*
Coal tit							
excl. larch	5	0.66	0.14	0.22	2.76	0.94	3*
1986							
Blue tit	6	1.16	0.36	-3.95	7.57	0.85	4*
Great tit	6	0.51	0.29	6.56	6.15	0.66	4
Coal tit	6	0.65	0.76	5.39	16.09	0.39	4
Chaffinch	6	0.30	0.97	11.30	20.42	0.15	4
All birds	6	1.00	0.33	-1.18	6.98	0.83	4*
Coal tit							
excl. larch	5	0.63	0.20	-2.87	4.41	0.87	3
Chaffinch							
excl. larch	5	0.27	0.12	0.58	2.57	0.80	3

notes: * = significant correlation coefficient

Table 7.9

Regressions for plots of bird percentage (y) against relative abundance
of prey (x) in each tree species to establish the existence of a
relationship between the two variables in Hamsterley Forest.
Oak has not been considered for some of the birds
(see text)

Bird	N	Slope	se	Interc.	se	r	d.f.
1985							
Blue tit	11	0.83	0.16	1.19	2.35	0.87	9*
Great tit	11	1.02	0.18	-0.79	2.56	0.89	9*
Coal tit	10	1.60	0.27	-0.53	2.22	0.90	8*
Goldcrest	10	1.48	0.29	0.47	2.36	0.88	8*
Chaffinch	10	0.92	0.35	2.78	2.85	0.68	8*
All birds	11	0.53	0.15	4.03	2.14	0.77	9*
1986							
Blue tit	11	1.11	0.19	-1.37	2.53	0.89	9*
Great tit	11	1.48	0.25	-4.40	3.36	0.89	9*
Coal tit	10	2.32	0.38	-5.84	3.04	0.91	8*
Goldcrest	10	2.42	0.45	-5.60	3.55	0.89	8*
Chaffinch	10	1.96	0.78	-3.52	6.17	0.66	8*
All birds	11	0.61	0.28	3.40	3.75	0.58	9

notes: * = significant correlation coefficient

species is most likely choosing to feed in the tree species according to the proportion of all prey that is available in that tree species. A lack of such change or a change from non-significant into significant suggests either that no such dependence exists or that the dependence exists only for some component of the prey and cannot be detected by the method used.

These modified preference indices are presented for Great High Wood in Table 7.10 and for Hamsterley Forest in Table 7.11. Preferences and avoidances were still evident for a large number of tree species over and above the prey availability on them. When the preference indices from Tables 3.13 and 4.18 were compared with the modified indices in Tables 7.10 and 7.11 in this section, it was discovered that some of the indices changed from significant to non-significant between the two treatments, suggesting that the birds chose to forage in the tree species in proportion to the amount of prey items on it. These changes are summarised in Table 7.12. Two out of the 15 significant combinations of bird and tree species in Great High Wood considered here, changed from significant to non-significant in 1985 and four out of 16 in 1986. A change in the opposite direction happened in two cases in 1985 and in three in 1986, and the status of most of the cases remained unchanged in both years. Therefore there is no evidence that tree preference index is directly associated with the prey distribution in Great High Wood, and other explanations are needed to account for the deviation from random tree use. However, in Hamsterley Forest 15 out of 39 significant bird-tree combinations in 1985 and 10 out of 35 in 1986 became non-significant when the

Table 7.10

Modified tree preference index for birds in Great High Wood.
Expected values are based on the relative abundance of
all prey present on each tree species

Tree	Blue tit	Great tit	Coal tit	Chaf-finch	Total birds
1985					
Oak	4.64*	4.36*	2.13*	3.95*	4.42*
Beech	-0.18	-0.90*	0.12	-0.64	-0.34
Sycamore	-0.74*	-0.70*	-0.89*	-0.48*	-0.73*
Larch	0.54*	0.08	7.61*	1.16*	1.13*
Birch	3.16*	4.00*	2.11*	0.50	3.00*
Holly	4.21*	5.03	3.66*	-1.00	3.93*
Elm	5.13*	3.19	9.97*	6.42*	4.81*
1986					
Oak	3.03*	1.40*	1.47*	-0.03	2.61*
Beech	-0.75*	-0.50	-0.73	-0.64	-0.64*
Sycamore	-0.66*	-0.71*	-0.84*	-0.60*	-0.70*
Larch	1.62*	4.36*	11.97*	11.38*	3.60*
Birch	2.13*	4.22*	0.01	-0.32	1.95*
Holly	2.41*	6.60*	1.17	-1.00	2.64*
Elm	4.71*	2.75	1.50	5.79*	3.82*

notes: * = significant preference or avoidance (chi-square)
       positive = preference, negative = avoidance,
       zero = no discrimination

Table 7.11

Modified tree preference index for birds in Hamsterley Forest.
Expected values are based on the relative abundance of all prey present
on each tree species

Tree	Blue tit	Great tit	Coal tit	Gold- crest	Chaf- finch	Total birds
1985						
W. heml.	-1.00*	-1.00	-0.53	1.05	-1.00	-0.55*
E. larch	0.11	-0.52*	0.56*	0.33*	0.13	0.23*
J. larch	0.84*	-0.62	3.37*	-0.30	6.66*	2.10*
S. pine	-0.57*	-0.42	1.52*	1.93*	1.17*	0.80*
S. spruce	-0.95*	-0.76*	-0.22	0.20	-0.86*	-0.47*
N. spruce	-0.87*	-1.00*	-0.21	0.50*	-0.21	-0.32*
Birch	2.60*	2.08*	0.90*	-0.01	-0.17	1.25*
Oak	-0.14*	0.16	-0.76*	-0.82*	-0.60*	-0.51*
Beech	-0.52	-1.00	-1.00*	-0.79	-0.11	-0.66*
Alder	0.71	2.07*	0.36	0.86	2.37*	1.06*
Sycamore	3.21*	18.41*	-0.31	0.73	2.96*	1.38*
1986						
W. heml.	-1.00*	-1.00	-0.80*	0.34	-0.72	-0.76*
E. larch	0.02	0.14	1.52*	0.49	2.42*	1.36*
J. larch	-0.66*	-1.00	1.38*	-0.33	2.47*	1.16*
S. pine	-0.46*	-0.89*	0.83*	1.73*	-0.25	0.40*
S. spruce	-1.00*	-1.00	-0.33	1.85*	-0.76*	-0.45*
N. spruce	-1.00*	-0.59	-0.65*	-0.32	-0.42*	-0.65*
Birch	1.78*	1.93*	-0.31	-0.31	-0.58*	-0.01
Oak	0.17	0.56*	-0.76*	-0.98*	-0.75*	-0.57*
Beech	0.78	-1.00	-1.00*	-1.00	-0.87	-0.68*
Alder	-0.56	-0.21	-0.87*	-1.00	0.10	-0.56*
Sycamore	1.46*	-0.01	-0.15	0.16	-0.58	-0.04

notes: * = significant preference or avoidance (chi-square)
positive = preference, negative = avoidance, zero = no discrimination

Table 7.12

Changes in the significance of tree preference when the baseline for
calculating expected frequencies is changed from tree frequencies
to prey distribution in Great High Wood and Hamsterley Forest

a) Number of significant TPIs to become non-significant

	BT	GT	CT	GC	CF	total	N
Great High 1985	1	0	1		0	2	15
Great High 1986	2	1	0		1	4	16
Hamsterley 1985	2	4	2	4	3	15	39
Hamsterley 1986	2	0	3	2	3	10	35

N = number of combinations of bird - tree pairs that were significant
     originally
BT = blue tit, GT = great tit, CT = coal tit, GC = goldcrest, CF = chaffinch

b) Number of non-significant TPIs to become significant

	BT	GT	CT	GC	CF	total	N
Great High 1985	0	1	1		0	2	9
Great High 1986	0	1	2		0	3	8
Hamsterley 1985	1	2	1	0	2	6	16
Hamsterley 1986	0	0	0	0	0	0	20

N = number of combinations of bird - tree pairs that were non-significant
     originally
BT = blue tit, GT = great tit, CT = coal tit, GC = goldcrest, CF = chaffinch

preference index was modified. There were only six changes in the opposite direction in 1985 and none in 1986. This result suggests that some degree of dependence of tree preference index on prey distribution did occur in Hamsterley Forest. However, this occurred in less than 30% of the cases, and therefore cannot be considered conclusive.

7.6   Changes in prey density and in the tree choices of birds between years

In order to investigate the changes in prey density between tree species, the prey density relative to other tree species was calculated. (Unless otherwise stated, the word density is used to refer to the relative density of prey on trees throughout the sections 7.6 - 7.8. Only significant changes in density are reported.) There were few changes in the relative density of prey on the tree species between years. In Great High Wood (Table 7.13) there was a significant change in the overall prey density only on beech. However, an increase in the density of the small size class of prey was detected on oak, beech, holly and elm, and a decrease in the medium class on larch. An overall decrease in prey density on European larch and sitka spruce was evident in Hamsterley Forest (Table 7.14). The density of small prey increased on western hemlock and beech, and declined on European larch, medium prey increased on Scots pine, and declined on oak and beech, and there was a decline in large prey on oak. As well as the differences in the relative prey density on a tree species from one year to the

Table 7.13

Percentage change in relative prey density on each tree species
in Great High Wood from 1985 to 1986

Tree species	Small prey	Medium prey	Large prey	Total prey
Oak	+ 95.5*	-10.9	+ 6.5	+27.0
Beech	+131.6*	0.0	+17.9	+68.8*
Sycamore	- 35.9	+18.1	-12.2	- 3.8
Larch	- 6.7	-40.3*	- 1.9	-24.6
Birch	+ 1.1	-31.9	+ 1.0	-26.1
Holly	+134.4*	- 9.1	+23.3	+76.2
Elm	+141.7*	0.0	-18.5	+69.6

notes: the figures are percent change in prey density calculated from

$$\frac{\%1986 - \%1985}{\%1985} \times 100$$

* = significant change (t-test)

Table 7.14

Percentage change in relative prey density on each tree species
in Hamsterley Forest from 1985 to 1986

Tree species	Small prey	Medium prey	Large prey	Total prey
Western hemlock	+90.6*	-50.0	-11.3	+62.2
European larch	-46.6*	-39.0	- 3.7	-50.0*
Japanese larch	-25.4	+60.4	+54.3	+19.6
Scots pine	+33.3	+100.0*	-18.0	+42.9
Sitka spruce	-48.3	-26.7	- 8.0	-57.5*
Norway spruce	+21.1	- 5.3	-27.6	+19.7
Birch	+32.9	+18.7	+ 5.2	+19.4
Oak	+75.8	-50.5*	-49.7*	-19.5
Beech	+77.3*	-33.3*	- 8.0	+ 4.0
Alder	+18.2	+52.8	+ 7.4	+47.7
Sycamore	-26.4	+37.2		+77.3

notes: the figures are percent change in prey density calculated from

$$\frac{\%1986 - \%1985}{\%1985} \times 100$$

* = significant change (t-test)

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next, the relative prey density between tree species changed in many cases without the rank order of trees being affected (i.e. prey density similar on two tree species became significantly different or vice versa).

The extent to which each tree species was used by the birds changed from one year to the next. In Great High Wood (Table 7.15) there was a significant decrease in the overall use of oak and birch and an increase in the use of larch from 1985 to 1986 with no change in the extent the other tree species were used. However, the individual bird species changed their patterns of tree use independently of each other. The blue tit increased its use of sycamore and decreased its use of birch, while the great tit increased its use of larch and holly and decreased its use of oak. The coal tit reduced its use of birch and the chaffinch reduced its use of oak and increased the use of larch.

There were more overall changes in the patterns of tree species use by birds in Hamsterley Forest. The overall use of European and Japanese larch, and Scots pine increased significantly from 1985 to 1986 (Table 7.16), while there was a significant decrease in the overall use of sitka spruce, birch, oak, alder and sycamore. The coal tit changed its pattern of tree species use most, and the great tit least from 1985 to 1986 (Table 7.16).

Since the bird species differed in their tree species choice and in the changes in them, it is likely that they were responding to different fractions of the available food supply.

Table 7.15

Percentage change in the frequency of visits to each tree species
by the birds in Great High Wood from 1985 to 1986

Tree species	Blue tit	Great tit	Coal tit	Chaf- finch	Total birds
Oak	- 9	- 43*	0	-75*	-15*
Beech	-48	+767	-59	+73	- 5
Sycamore	+22*	- 6	+42	-25	+ 8
Larch	+31	+209*	+15	+339*	+68*
Birch	-45*	-24	-76*	- 67	-46*
Holly	+16	+123*	-18	0	+31
Elm	+68	+ 62	-59	+ 65	+50

notes: the figures are percent change in the tree use calculated from

$$\frac{\%1986 - \%1985}{\%1985} \times 100$$

* = significant change (t-test)

Table 7.16

Percentage change in the frequency of visits to each tree species
by the birds in Hamsterley Forest from 1985 to 1986

Tree species	Blue tit	Great tit	Coal tit	Gold-crest	Chaf-finch	Total birds
W. hemlock	abs.	abs.	-38	- 6	abs.	- 33
E. larch	- 37*	+60	+ 9	- 24	+104*	+ 30*
J. larch	- 41	abs.	+71*	+200	+ 42	+118*
S. pine	+112*	-67	+24*	+ 58*	- 41*	+ 32*
S. spruce	abs.	abs.	-55*	+ 25	- 8	- 45*
N. spruce	abs.	abs.	-39	- 38	0	- 29
Birch	- 5	+17	-55*	- 15	- 38	- 46*
Oak	+ 19	+18	-12	- 89*	- 45*	- 23*
Beech	+300*	abs.	abs.	abs.	- 85	0
Alder	- 71	-70	-89*	abs.	- 63	- 76*
Sycamore	+ 2	-47	+114	+ 17	- 81*	- 29*

notes: the figures are percent change in the tree use calculated from

$$\frac{\%1986 - \%1985}{\%1985} \text{ x } 100$$

* = significant change (t-test)
abs. = no observations on the bird in the tree species

7.7   Factors influencing the changes in birds' tree species choice

The general finding in this chapter is that birds selected the trees in which they fed according to the density of arthropod prey on the tree species. There were exceptions to this generalization. In some cases, some tree species were avoided by a bird species irrespective of the food available, and in other instances superabundant prey caused predator saturation. There is also evidence that birds did not respond to changes in food on rare tree species, perhaps because such trees were visited too infrequently to allow for the evaluation of the food available.

With these factors qualifying the general trend, birds might be expected to respond to changes in prey density by changing their tree preference if

1. the rank order of the prey density on each tree species changes

2. there is no change in the rank order, but the difference in the prey density between two tree species changes magnitude.

The changes in tree choice can be caused by overall changes in prey density, the change in the density of one or more size classes (presumably those preferred by the bird), or even by the change in abundance of a single taxonomic group of prey, e.g. sawflies.

As a consequence of this the tree species choices of birds are not necessarily affected by changes in prey density on tree species that are used only a little or that are uncommon. A large change in the extent a tree species is used by birds that is caused by a change in the relative prey density on the tree species, will result in a converse trend in the use of one or more other tree

species, whether the prey density on these tree species has changed or not. This will be referred to as compensatory change in tree species use.

7.8 Do the changes in tree use and prey density agree with the predictions?

Tables 7.17 and 7.18 summarise the birds' tree preferences, and the significant changes in the tree use by the birds and in the prey density in the two woods. It was discovered that the changes in the tree use by birds in both woods could be explained in terms of the changes in the relative prey density as outlined in section 7.7. Birds primarily changed the extent of use of the tree species that were preferred or used extensively, and there was no response to changes in prey density in avoided or uncommon tree species. Thus the prey availability was a major reason for tree preferences by the bird species studied, and birds changed their tree species choices in response to the changing supply of arthropod prey, and seeds and berries when they were available.

In order to illustrate the changes in birds' tree choices and how these related to changes in prey density, the changes relating to each bird species are dealt with in detail below.

1. Blue tit

The blue tit increased its use of sycamore and decreased its use of birch from 1985 to 1986 in Great High Wood (Table 7.17). In 1985 the prey density on birch was higher than on oak, but in 1986

Table 7.17

Significant preference shown by birds for each tree species, and
significant changes in the birds' use of tree species and in
the relative arthropod density on the tree species between
years in Great High Wood

	Oak	Beech	Sycam.	Larch	Birch	Holly	Elm
Blue tit							
TPI 1985	*				*		
TPI 1986	*		*		*		
changes 85-86	0	0	+	0	-	0	0
Great tit							
TPI 1985	*				*		
TPI 1986				*	*	*	
changes 85-86	-	0	0	+	0	+	0
Coal tit							
TPI 1985				*	*		
TPI 1986				*			
changes 85-86	0	0	0	0	-	0	0
Chaffinch							
TPI 1985	*		*				
TPI 1986	*		*	*			
changes 85-86	-	0	0	+	0	0	0
Arthropods							
85-86 (small)	+	+	0	0	0	+	+
85-86 (medium)	0	0	0	-	0	0	0
85-86 (large)	0	0	0	0	0	0	0
85-86 (total)	0	+	0	0	0	0	0

notes: *   = preference for the tree species
        TPI = tree preference index
        +   = significant increase
        -   = significant decrease
        0   = no significant change

Table 7.18

Significant preferences shown by birds for each tree species, and
significant changes in the birds' use of tree species and in
the relative arthropod density on the tree species
between years and seasons in Hamsterley Forest

	Al	Be	Bi	EL	JL	NS	Oa	SP	SS	Sy	WH
Blue tit											
TPI 1985			*	*			*			*	
TPI 1986			*				*			*	
changes 85-86	0	+	0	-	0	0	0	+	0	0	0
Great tit											
TPI 1985			*				*			*	
TPI 1986			*				*				
changes 85-86	0	0	0	0	0	0	0	0	0	0	0
Coal tit											
TPI 1985				*	*			*	*		
TPI 1986				*	*			*		*	
changes 85-86	-	0	-	0	+	0	0	+	-	0	0
Goldcrest											
TPI 1985				*		*		*	*	*	
TPI 1986								*	*	*	
changes 85-86	0	0	0	0	0	0	-	+	0	0	0
Chaffinch											
TPI 1985				*	*					*	
TPI 1986				*	*						
changes 85-86	0	0	0	+	0	0	-	-	0	-	0
Arthropods											
85-86 (small)	0	+	0	-	0	0	0	0	0	0	+
85-86 (medium)	0	-	0	0	0	0	-	+	0	0	0
85-86 (large)	0	0	0	0	0	0	-	0	0	0	0
85-86 (total)	0	0	0	-	0	0	0	0	-	0	0

notes: *   = preference for the tree species
        TPI = tree preference index
        +   = significant increase
        -   = significant decrease
        0   = no significant change
        see Table 2.1 for abbreviations of tree species

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there was no difference in prey density on the two tree species due to the increase in the small prey on oak. As the prey density on the two tree species became more similar, the preference the blue tit showed for these tree species became more similar. The prey abundance in Great High Wood was lower in 1986 than in 1985, which resulted in an increase in the use of sycamore by the blue tit in order to compensate for lower absolute prey densities, and thereby possibly lower prey capture rates, in other tree species.

In Hamsterley Forest there was no change in the prey density on oak and birch in the two years (Table 7.18), and hence the blue tit did not change its use of these tree species. The reduction in the overall prey density on larch was caused by a reduction in the density of the small prey. The prey density on oak and European larch were similar in 1985, but the density on European larch was significantly lower (t=2.17) in 1986. This resulted in the reduction in the use of European larch by the blue tit in 1986. The prey density on Scots pine was significantly lower than that on European larch in 1985 (t=2.70), but in 1986 the relative densities on the two tree species were similar, i.e. the relative density on Scots pine increased with respect to European larch. This, combined with the increase in the density of medium prey, resulted in increased use of Scots pine by the blue tit. The density of small prey increased significantly on beech, but there was no change in the overall prey density. The blue tit increased its use of beech in 1986, but this was most likely an artefact caused by low numbers of birds using beech, since beech was avoided each year.

2. Great tit

The great tit increased its use of larch and holly, and decreased the use of oak in Great High Wood in 1986 (Table 7.17). The increase in the use of larch was caused by the increased density of larch sawflies in 1986, which the great tits exploited. Similarly, the increase in the use of holly appears to be caused by the increased density of caterpillars. There was no change in the prey density on oak, and therefore the decrease in the use of oak was most likely compensatory.

There were no changes in the tree species choices by the great tit, in Hamsterley Forest (Table 7.18), which is predictable, since the prey density on the preferred oak and birch did not change.

3. Coal tit

Coal tits in Great High Wood used birch significantly less in 1986 (Table 7.17), despite the relative density of prey being same on birch and larch in both years. The good cone crop on larch in 1986 provided the coal tit with a supply of seeds. Since there was no comparable increase in vegetable foods on birch, the use of birch declined as the coal tit increased its use of larch.

The decrease in the use of sitka spruce by the coal tit in Hamsterley Forest in 1986 (Table 7.18) was caused by the decline in the relative prey density. The prey density on European larch declined and did not change on Japanese larch from 1985 to 1986. The increase in the use of Japanese larch by the coal tit and the lack of change in the use of European larch were caused by the good cone crop in 1986 on both tree species. The coal tit fed

extensively on the larch seeds. There was an increase in the density of medium prey on Scots pine in 1986. The relative prey density compared with sitka spruce and European larch also increased. In 1985 prey density on Scots pine was significantly lower than on sitka spruce (t=2.98) and on European larch (t=2.70), while in 1986 there were no significant differences between these three tree species. These factors caused the increase in the use of Scots pine in 1986. There were no changes in the relative prey densities on birch and alder, and hence the decline in the use of these tree species by the coal tit were probably compensatory.

4. Goldcrest

Data for the goldcrest was only available for Hamsterley Forest (Table 7.18). The goldcrest increased its use of Scots pine in response to the increase in the density of medium prey, and in response to the increased prey density relative to sitka spruce (Scots pine < sitka spruce in 1985, t=2.98; Scots pine = sitka spruce in 1986). There was a decline in the relative density of medium prey on oak in 1986. This together with a withdrawal of goldcrests from the secondary habitat of broadleaves as goldcrest population declined in winter 85-86, resulted in the reduction in the use of oak.

5. Chaffinch

The increase in the use of larch by the chaffinch in Great High Wood in 1986 (Table 7.17) was directly related to the increase in the density of sawfly larvae, which the chaffinch fed on

extensively. Since there was no change in the relative prey density on oak, the decline in the use of oak by the chaffinch was compensatory to the increased preference for larch.

In Hamsterley Forest there was a significant increase in the use of European larch by the chaffinch from 1985 to 1986 (Table 7.18). The use of Japanese larch increased by 42%, but this was not significant. The increase in the use of both species of larch was caused by the increase in the density of sawfly larvae, which the chaffinches fed on extensively. The chaffinches did not show a preference for oak, but the tree was used extensively, and therefore the decline in the density of medium and large prey on oak caused a reduction in the use of oak by the chaffinch. There was no change in the overall density of prey on Scots pine or sycamore, and therefore the decline in the use of these tree species by the chaffinch was compensatory and caused by the increase in the use of the larches.

7.9 Discussion

It has been established in this chapter that birds chose their foraging sites by the prey density on the tree species, and that they responded to the density of one or more size categories of prey items. This relationship was sometimes masked by the unexpectedly strong preference or avoidance of one or two tree species, which was found to be due to one of the following causes:

1 preference for one prey species (e.g. chaffinch in Japanese larch),

2 preference or avoidance of a type of tree independent of the prey density on it (e.g. blue tit & spruces),

3 the structure of the tree making prey unaccessible (e.g. sycamore), or

4 saturation of the predators by high prey density (sycamore).

The removal of these modifiers revealed an underlying relationship between the tree preference and the prey density on the trees in all cases.

The prey density was found to be correlated with the tree preference of the birds, and the bird and prey distributions in the trees were very similar. However, the tree preference could be directly explained in terms of the prey distribution between the tree species only in a small number of cases. Therefore, there is some indication that prey distribution on tree species influenced birds' tree preference, but that other factors were involved. It can be concluded that prey density is an important factor, which has a strong influence on the choice of foraging sites of insectivorous forest birds, but that other factors also affect where birds feed.

The changes in the relative prey density on trees were reflected in the changes in the tree choices by the birds. All changes in the tree species use by the birds could be explained in terms of changes in prey density or arising from these changes. Therefore it can be concluded that the tree use and the changes in the tree use of each bird species studied was largely influenced by prey density and changes in the prey density on the trees.

CHAPTER 8

FINAL DISCUSSION

Four main findings of passerine foraging ecology are revealed in this thesis. Firstly, each bird species was found to discriminate in favour of or against most of the tree species in both study sites. Moreover, these preferences were different for each bird species, which made them an effective means of niche partitioning between pairs of bird species. Secondly, the bird community structure in a wood was affected by these tree preferences. This was evident from the correlations between bird density and species richness with tree species richness. Similarly, the tree species choice by birds was the dimension of the foraging niche in which bird species overlapped least. Thirdly, a pronounced edge-effect resulted in a negative correlation between bird density and compartment size. Fourthly, the tree preferences were largely determined by food availability and changes in the food availability in each tree species.

8.1 Tree preferences and their importance

The tree use by bird species in this study fell roughly into the broad categories of broadleaved and coniferous trees, which is the only division that many workers have made over the years (Morse, 1967a,b; Sturman, 1968; Morse, 1970; Simms, 1971; Alerstam

et al. 1974; Morse, 1978; Moss, 1978b; Newton, 1982; Morrison, 1984; Hartley, 1987). However, the extent of use of each tree species within these categories was different (see also Gibb, 1954), and the tree use differed from one bird species to another (see also Hartley, 1953).

The tree preference index allowed the quantitative extent of preference or avoidance of each tree species to be established. It also facilitated the determination of significant differences between the bird species in their tree species choice. Large differences in the tree preferences were found between bird species. The concept of preferences for certain tree species was first introduced and investigated further by a number of ecologists in America for whole bird communities (Balda, 1969; Willson, 1970; Austin & Smith, 1972; Grubb, 1975; James, 1976; Holmes et al. 1979; Holmes & Robinson, 1981; Maurer & Whitmore, 1981; Franzreb, 1983b; Rice et al. 1984; Morrison, et al. 1985; Yahner, 1987) as well as in studies of one or two bird species (Kilham, 1970; Kisiel, 1972). Jackson (1970), Kisiel (1972) and Williams (1980) found differences in the tree species preferences between the sexes of individual species of woodpeckers, and Franzreb (1983c) between the sexes in warblers. The only European work on the topic was by Gibb (1960) and Ulfstrand (1975). Preferences for some foods or foraging sites over others is not restricted to birds, but food preferences have been reported from a number of animal groups. Webb (1959) demonstrated that white-tailed deer showed a distinct preference for the foliage of some tree species and avoided others, while Beyer & Saari (1977) showed that tree species affected the

distribution of slugs. Preference for some grasses over others was reported by Effer (1973) for bighorn sheep in Canada, and by Mirza & Waiz (1973) for blackbuck in Pakistan.

Heinrich & Collins (1983) demonstrated that wild caught black-capped chickadees were able to distinguish and discriminate between foliage of different broadleaved tree species by sight, and. choose the preferred ones. This is supported by observations in this study of the ability of flocking birds to reject some tree species without entering them. The preference for certain type of foliage was shown by Klopfer (1963) to be innate, albeit modifiable by experience early in the life of individual birds. These innate preferences and ability to recognize foliage are likely to play a large part in determining birds' tree preferences. The development of food preference by early experience and of this becoming partially hereditary was demonstrated by Wallin (1988) for fruitflies.

Each bird species changed their use of the tree species from one season to another, showing that the tree preferences were dynamic rather than static. Gibb (1954) reported that the extent of use of each tree species by three species of tits changed with seasons. He found that the peak use of sycamore was in the spring and autumn, which coincides with the peaks in this study. The use of beech concentrated in the autumn in both studies, when some birds fed on the beechmasts, but the tree was used only little at any time of the year. Hartley (1953), too, found that beech was not used by the birds. Seasonality in the tree species use by birds was also reported by Willson (1970,1971), Gaston (1973), Travis (1977),

Conner (1980,1981), Lewke (1982), Morrison et al. (1985) and Yahner (1987). Gaston (1973) found that the changes in tree species use by birds in the spring were associated with the leafing out of each tree species in succession. Hutto (1981) reported on the dependence of the temporal patterns of foraging activity on prey availability.

Only small differences were found between bird species in their foraging height, position, and substrate when they were feeding in trees. Overall, the difference between any two bird species was greater in their choice of tree species than spatial attributes of the foraging site. This agrees with the findings of Hartley (1953), Willson (1970), Austin & Smith (1972), Ulfstrand (1975), Williams (1980), Franzreb (1983a,b), Rice et al. (1984) and Hartley (1987). Holmes et al. (1979) did not emphasize a difference between the relative importance of tree species and spatial criteria, but concluded on the basis of their results that space related distribution of birds, as well as foraging opportunities, are secondary and caused by the presence and abundance of particular tree species. Some workers failed to demonstrate the importance of tree species and stressed the importance of spatial criteria in the choice of feeding site and ecological separation of the bird species (e.g. Morse, 1967a,b; Pearson, 1971; Simms, 1971; Morse, 1978).

Rice et al. (1984) working in North America found that tree species composition was the most important attribute in the habitat selection by birds. The same was established in this study. The niche overlap between pairs of bird species was significantly lower in the tree species choice than in either or a combination of the

two main spatial variables. The fact that niche overlap did not decline significantly as the effect of spatial variables were added one at a time to the tree species choice, shows that the primary determinant of overlap of foraging niches between pairs of bird species was the tree species used for foraging. Any other niche parametres were secondary and largely determined by the tree species chosen.

8.2   Tree preferences and bird community structure

The significantly lower overlap between pairs of bird species in tree species choice than any of the spatial or structural (inc. foraging substrate) variables displays the importance of the specific composition of a wood to the birds. A close correlation between bird and tree species richness was established in this study. Such correlation was also reported by Willson (1974), Ulfstrand (1975), James & Wamer (1982), Erdelen (1984), Osborne (1984), and Rice et al. (1984). This accounts for the observations of Williamson (1969, 1970, 1972) and Moss (1978a,b), that plantations of monoculture contain the lowest numbers of bird species and mixed woods are the richest. Lack & Venables (1939) contrasted planted and natural stands, and noted that a planted stand of any particular type had consistently poorer bird fauna than a comparable natural stand. However, a comparison of the two study sites in this project does not fully support this view. Simms (1971) showed that coniferous woods supported on average only half of the breeding density of birds than broadleaved woods (80/40 ha

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and 160/40 ha respectively), but he also observed that the lowest recorded breeding densities in Europe were from beechwoods. In this study stands of beech were found to be least acceptable to the birds.

Indices of species diversity and spatial variables have been widely used in bird community studies for the past 25-30 years. The commonest indices are bird species diversity, and foliage height diversity derived from the foliage profile. A relationship between these two indices was first proposed by MacArthur & MacArthur (1961), and it has been demonstrated in a number of studies since (e.g. MacArthur et al., 1966; Karr & Roth, 1971; Moss, 1978a). The principle was echoed in earlier work by Colquhoun (1941), who claimed that a strong vertical zonation with little overlap between zones exists in woodland bird communities. MacArthur & MacArthur (1961) claimed that foliage height diversity is the only variable needed to predict bird communities, and that tree species have no importance at all.

A number of researchers did not find a relationship between bird species diversity and foliage height diversity (Balda, 1969; Tomoff, 1974; Willson, 1974; James & Wamer, 1982; Erdelen, 1984; Osborne, 1984; Rice et al. 1984). This prompted Willson (1974) and Erdelen (1984) to investigate closer the properties of these diversity indices. They both found that the relationship between bird species diversity and foliage height diversity only exists if open ground habitats are included in the regression, and pointed out that this applied also to the original data of MacArthur & MacArthur (1961). Both Willson and Erdelen concluded that there

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were too many inconsistencies, both in the measuring of foliage height diversity and in the results, to allow foliage height diversity to be used as a predictive index. Willson stated that the mere existence of a correlation between bird species diversity and foliage height diversity is not enough to justify its repeated use in widely differing habitats.

The strongest criticism of the widespread use of complex habitat measures has so far come from Erdelen (1984) and Rice et al. (1984). Both of them stressed the importance of simpler, more direct, measures (e.g. absolute tree species abundance) instead of diversity indices, which are often plagued by interpretation difficulties. They also criticized that many other studies did not give tree species composition a valid and thorough assessment as a potential means of niche partitioning, which was the case a.o. with MacArthur et al. (1966), Dickson & Noble (1978), Ligon (1968), Morse (1968), Karr & Roth (1971),Pearson (1971), Williamson (1971), Moss (1978a) and Perrins (1979). Seidel & Whitmore (1982) identified differential use of tree species by birds but discounted it as unimportant without a reason.

Rice et al. (1984) found that tree species measures were the most frequently selected habitat attributes in multivariate analysis, and that vertical and horizontal foliage diversity were unimportant in avian habitat selection at the species level in woodlands. Bibby et al. (1985) reported that bird species richness was determined by the stage of succession and the variety of tree species in young plantations. It appears from the data provided by the different workers that characteristics relating to vertical

diversity affect different guilds of birds differently, but that they are unimportant when investigations concentrate within any one guild. Taxonomic variables take precedence over ones relying on height diversity when only one guild of birds is investigated (e.g. Rice et.al. 1984).

Patchiness of the habitat has been associated with habitat choice and bird species richness by some workers (e.g. Roth, 1976; Gerell, 1988). Patchiness can be taken to reflect tree species diversity and richness, and the structural patchiness in a forest canopy is often caused by the presence of a mixture of tree species. MacArthur (1966) recognized habitat patchiness as a means of resource partitioning between bird species (bird species pursue prey in different patches), but did not accept tree species as 'patches'.

The foliage height diversity was not measured in this study, but the percentage similarity in the use of each height interval by pairs of bird species can be taken as indicative of the importance of height diversity to the birds. The degree of similarity between pairs of bird species in their choice of foraging height and position was high, and bird species did not differ significantly from each other in either variable. Therefore, these two niche dimensions can be considered of equally low importance to the birds as a means of partitioning of the foraging niche. The significantly lower overlap between pairs of bird species in tree species choice shows that criteria relating to tree species are more important than spatial diversity. Tree species diversity was found to be a good predictor of bird species diversity, but the correlation was

higher if tree species richness was substituted for tree species diversity. The predictability of bird species diversity on bird species richness agrees with the findings of Kricher (1972). This study agrees with the views of Rice et al. (1984) and many others that within a guild, the plant species richness and diversity determine the structure of the bird community, not the spatial diversity.

Areas with different tree species composition were found to contain differing assemblages of bird species. This appeared to be caused by each tree species attracting different birds, an observation that was made also by Ulfstrand (1975). Some pairs of bird species chose the same woodland stands more often than other pairs. The fact that the choice of the foraging area was influenced primarily by the tree species composition in the area, was clearly demonstrated in Fig 5.3, which displays the identical overlap in the choice of tree species and area by each pair of the six bird species studied.

The positive correlation between bird species richness and bird density shows that the addition of new species is accompanied by an increase in the bird density, and does not come about by replacement of individuals of commoner species. Since bird density is also correlated with tree species richness, it is clear that the areas with greater tree species richness are capable of supporting a wider range of birds at a higher total density than species poor areas. This, together with the lower niche overlap between pairs of bird species in compartments with higher tree species richness, shows that woods that are taxonomically richer are capable of

supporting a larger and more varied avifauna than monocultures. The same interpretation can be arrived at from papers by James & Wamer (1982) and Osborne (1984). In some habitats the availability and abundance of certain tree species as nest sites rather than foraging sites determine the presence and abundance of bird species (Tomoff, 1974, on birds in desert scrub).

8.3 The effect of the size of the wooded area on the bird community

The negative correlation between bird density and area was caused by edge effect, which was strongest in the smallest compartments. Helliwell (1976) and Newton (1982) found a similar correlation, but Bibby et al. (1985) and Bibby et al. (1989, in press) found no relationship between area and bird density in the coniferous plantations in Wales. The distribution of birds within each area was not recorded in this study, but Yahner (1987) points out that bird species richness was higher at edges of stands than in the interiors. The bird density was found by Hansson (1983) to be higher in an outer forest belt of ca. 50m than deeper inside the forest. This edge effect was greatest for tree gleaning species, which probably were attracted to the edges by the richer insect fauna (Hansson, 1983). The difference in the abundance of insect fauna in the centre and edges of a wood plot appeared to be due to the higher primary productivity in the edge belts (Ranney et al. 1981; Hansson, 1983). Some bird species are known to be affected

more by the presence of edge than others. Robin is a well known example of an edge species.

In this study the study areas were part of a larger forest with many of the edges being an edge to a stand containing a different tree species rather than an edge to open area. However, this did not appear to affect the results. The important factor seemed to be a border to a different habitat, whether it was structurally similar or not. Ford (1987) found a similar area-density correlation for birds on forest islands of various sizes surrounded by fields. The correlation between the two variables was valid only in the small woods, not in the control areas chosen from within a large uniform forest. This is further evidence indicating that area related density is caused by edge effects. Ford found that the bird species richness was positively correlated with area, but that for a given area, small woods had significantly more species and greater densities than parts of a large wood. The results of Ford (1987) and of this study show that whether the woodland is in one large block or divided into a number of isolated woods, the heterogeneity within and between the wooded areas is of primary importance in determining the bird density and species richness. Therefore, plantation forests ought to be designed to contain small compartments with the maximum amount of edge of one kind or another.

8.4 Tree preferences and food availability

The tree species in the study areas were found to contain vastly different densities of invertebrates. Evidence of different invertebrate densities on tree species was also produced by Gibb (1960), Lack (1966), Claridge et.al. (1968), Claridge & Wilson (1976), Southwood et al. (1982), Kennedy & Southwood (1984) and Bevan (1987). The wide variability in the invertebrate density between samples in this study (cf. Gibb, 1960, Southwood et.al. 1982), was less than the variability between tree species, as was discovered also by Southwood et al. (1982). The invertebrate density was not correlated with the number of species on trees reported by Southwood (1961) and Kennedy & Southwood (1984). This lack of correlation between species richness and density was also demonstrated for leafhoppers by Claridge & Wilson (1981).

Klomp & Taernink (1973) showed that out of the ca. 70 species of insects on pine (_Pinus sylvestris_) in Holland, most species were represented by only few individuals, and only a small proportion of the total were abundant enough to be an important part of the birds' diet. This was found to be the case also in this study - a small number of invertebrate species was abundant on each tree species. The relative abundance of these prey species largely determined the total prey density on each tree species.

Positive correlations were found between the prey density on trees and the preference bird species showed for each tree species. Concentration of birds into areas with high prey availability was also recorded by Goss-Custard (1970) for redshanks feeding on

intertidal areas, Buckner & Turnock (1965) for forest birds in relation to sawfly densities in Canada, Graber & Graber (1983) for warblers and lepidopterous caterpillar densities in USA, and Smith & Sweatman (1974) for captive great tits. The effect of prey density on birds is also clear from work by Gibb (1960), who found a close association (r=0.987) between the decline in numbers of birds and the invertebrate stock during the winter. Newton (1972) suggested a possible link between breeding densities of chaffinches and food availability in the wood. Tricas (1989) found that the territory size and therefore the density of corallivorous butterflyfish was correlated with food availability allowing the highest fish densities in the densest areas of coral.

Southwood's (1961, also Southwood et al. 1982) work on the influence the abundance of a tree species and the length of time it has been in the country has on the accumulation of insect species, has been misinterpreted by a number of researchers (e.g. Peterken 1981; NCC, 1986), and in particular by various conservation organisations as a means of identifying the tree species that provide good foraging for birds. The reports by Claridge and Wilson (1981), Southwood (1961) and Kennedy & Southwood (1984) about the lack of correlation between the invertebrate densities and species richness, have gone unnoticed. This study has shown that birds respond primarily to prey densities when choosing their foraging site, not to prey species diversity or richness. The same appears from the work of Gibb & Betts (1963), Goss-Custard (1970), and Graber & Graber (1983). As a consequence, a re-evaluation of the value of each tree species for birds needs to be done, and any

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recommendations on structuring new woods or managing existing ones needs to be based on the new information.

Tree species supporting medium prey densities tended to have the highest adjusted tree preference indices and thereby the highest predation rate, whereas the preference for tree species with low and high prey densities was lower than expected. These results agree with Tinbergen (1960) and Gibb (1962), both of whom found that predation rate by birds at low prey densities was well below expected. Tinbergen explained this by the prey density being too low to allow a search image to be formed, and Gibb by that the birds sampled the prey density and abandoned it as uneconomic. The lower than expected predation rate at high prey densities was explained as abandonment of search image at high densities of prey, and as the prey density exceeding the density expected by birds hunting by expectation. Both Tinbergen and Gibb found that the highest predation rate occurred at intermediate prey densities.

This study concludes that prey density is one of the major factors affecting where birds choose to feed, but that other causes are involved. The taxonomic prey composition on the tree species differed, and preference for a certain type of prey (e.g. spiders and caterpillars over Coleoptera) may have acted as a major modifying factor of tree use. Preference for some foods over others was demonstrated by Betts (1955), Morris (1955), Prop (1960), Jansson & Bromssen (1981), Graber & Graber (1983), Moermond & Denslow (1983) and Levey et al. (1984).

The accessibility of potential food can also alter the extent to which a food source is exploited and their relative preference

(Moermond & Denslow, 1983, Levey, 1984). This is a likely reason for the reduction in the use of sycamore by great tits and chaffinches after the leaves have expanded. It may also have caused the replacement of the use of sycamore in the latter half of 1985 by the use of larch in 1986 by these two bird species, when sawflies on larch provided an alternative food source that was easier to reach.

All changes in the extent of tree species use recorded in this study could be attributed to changes in prey availability in the tree species. The change of foraging site with prey availability was demonstrated by Benkman (1987) for North-American crossbills, by Shettleworth et.al. (1988) for captive pigeons, and by Smith & Sweatman (1974) for captive great tits.

This study advances knowledge of the factors governing the structure of bird communities in woods. Tree species preferences were established quantitatively for a number of European passerines, and the causes and consequences of these preferences were evaluated for the first time. The results of this work will be particularly valuable in the design and management of woodlands to increase bird numbers and diversity. Further work on the topic could establish tree preferences for other bird species, cover a wider range of tree species, investigate the possibility of geographical differences in the tree preferences, and investigate the role tree preferences play in determining the territory size and breeding densities of woodland birds.

SUMMARY

1.   The tree species preferences of six species of arboreal
passerines (blue tit, great tit, coal tit, goldcrest, chaffinch and
treecreeper) were investigated in two sites in County Durham. Great
High Wood is a broadleaved seminatural wood, and Hamsterley Forest
a plantation of primarily coniferous trees. The effect the tree
composition of a wood had on the arboreal bird community was
investigated.

2.   The overall density of arboreal passerines throughout the
year was 4.18 birds/ha in Great High Wood, and 2.72 birds/ha in the
study area at Hamsterley Forest. The large differences in the bird
densities between compartments influenced the overall bird density
in Hamsterley Forest and resulted in the observed lower overall
density.

3.   Each bird species showed a preference for some tree species
and avoided others. The tree preferences shown by each bird species
differed significantly from those of all other bird species. Beech
was avoided by all bird species, whilst larch was universally
preferred. Sycamore appeared to be an important alternative food
source at times of food shortage. The strength of preference or
avoidance of a tree species varied from one year to the next, but
as a rule, if a tree species was preferred in one year, it was
likely to be preferred in following years.

4.   The four most extensively used tree species accounted for
ca. 70% of all foraging effort for the blue tit and great tit, and
80-90% for the remaining four bird species in Great High Wood, and

78-83% for all bird species in Hamsterley Forest. These tree species differed for each bird species in most instances. When the same tree species were chosen by two bird species, the relative importance of these tree species in the rank order differed.

5.   The greatest differences in the use of tree species between pairs of bird species occurred in oak, sycamore, larch, birch and holly, making these tree species important in partitioning the feeding niche of the six bird species in Great High Wood. In Hamsterley Forest, oak, birch, Scots pine, sitka spruce, Norway spruce, European larch and Japanese larch were the most important tree species in niche partitioning. Blue tits and great tits foraged most often in broadleaves, coal tits and goldcrests chose conifers more often than the other bird species, and chaffinch was intermediate to these groupings in both woods. Treecreepers were strongly associated with broadleaves in Great High Wood, but showed no affinity to a particular tree type in Hamsterley Forest.

6.   Large seasonal differences in tree preferences were found for each bird species. A greater number of tree species were preferred or avoided during July - October (late season) by the tits and goldcrests, while chaffinches showed stronger discrimination of tree species during March - June (early season). For example, in Hamsterley Forest the coal tit showed significant preference or avoidance for 7 tree species in the early season and for 12 in the late season. The peak use of many tree species was found to coincide between bird species, and are therefore thought to be caused by periods of peak food availability in those trees.

7.   It was found that as well as choosing to feed in different tree species, birds partitioned their feeding niche further by feeding in the same tree species at different times of the year, e.g. great tits fed in sycamore primarily in the early season and blue tits in the late season.

8.   The tree preferences by bird species were compared between the two study sites for the tree species that were present in both. Discrimination of a tree species (preference or avoidance) was stronger in the study site where the tree species was present at a lower frequency.

9.   The most commonly used height zone for feeding was the 4-8m zone in both woods, while only 3% of the birds foraged at heights above 12m. No significant difference was found in the height distribution between bird species. There was no significant difference in the mean foraging heights in the two woods (7.73m in Hamsterley Forest and 7.16m in Great High Wood).

10.   The feeding position within a tree was a potential means of niche partitioning. Blue tits foraged primarily in the outer canopy and on twigs, while goldcrests concentrated on branches in the inner canopy. Coal tits, great tits and chaffinches did not differ significantly from each other. Treecreepers occupied a different position within the trees and foraged almost exclusively on the trunk. The feeding positions of each bird species did not differ in the two woods.

11.   Bark and foliage were the main foraging substrates for the five canopy foraging bird species. The great tit used the foliage (67% of the time in both woods), and the goldcrest used bark (62%

of the time in Great High Wood and 54% in Hamsterley Forest) most extensively. Substrate choice between the bird species did not differ more during budburst than in the rest of the year. Because of its foraging location within the trees, the treecreeper foraged exclusively on the bark.

12.   Birds foraged for longer in tree species that they preferred most. However, up to 80% of the tree preference was found to be caused by active discrimination of tree species by the birds, leaving only a small part of the tree preference accountable by differences in the duration of foraging bouts in each tree species. The mean feeding rate and the mean duration of the foraging bout of blue tits did not differ in the two study sites. This suggests that adequate foraging sites were available in both woods, and therefore differences in the tree species composition and the structure of the wood between the two sites did not affect the foraging rate of the blue tit.

13.   Bird density was found to be negatively and significantly correlated with the logarithm of compartment size. This appeared to have been caused by an edge effect, which resulted in small compartments supporting disproportionately high bird densities. An increase in compartment size from one to ten hectares reduced the bird density by 5 birds/ha, but there was less reduction in bird density at larger compartment sizes. Compartment size was not correlated with any other parameter measured.

14.   Bird density and tree species richness were positively correlated. It was found that the highest bird densities were in small compartments rich in tree species. Medium densities occurred

in small compartments with lower tree species richness, and the lowest bird densities in large compartments with few tree species.

15.   The percentage of broadleaved trees in a compartment was only weakly, but significantly, correlated with bird density. The broadleaved content was more strongly correlated with bird species diversity and bird species richness. A 25% increase in broadleaves in the area increased the bird species diversity by 0.25 and the bird species richness by one bird.

16.   Tree species richness was found to be a good predictor of bird species richness. The bird species richness was increased by two by each three additional tree species. Bird species richness was also correlated with tree species diversity, but the relationship was weaker.

17.   The niche breadth, as measured from the tree species choice, did not differ between the bird species within either wood. The niche breadth of each bird species was greater in Hamsterley Forest than in Great High Wood, possibly because of the larger number of tree species present in the former.

18.   Of the five niche dimensions measured, the choice of tree species separated the bird species best in both woods. The mean overlap of tree use between the five canopy foraging bird species was 57% in Hamsterley Forest and 66% in Great High Wood, which was significantly lower than the overlap in the other dimensions. Position within a tree and height above ground were also identified as possible means of niche partitioning. These spatial variables were more important in Great High Wood than in Hamsterley Forest. The treecreeper overlapped, on average, equally with the other bird

species in the choice of tree species, but because of its mode of foraging the lowest overlap with other bird species was in the position within a tree.

19.   There were no significant differences in the degree of similarity of tree use between pairs of bird species from one season and year to another.

20.   Overlap in the tree species choice between pairs of bird species was lower in compartments with greater tree species richness. The mean overlap between pairs of bird species declined by 20% for every five additional tree species. Therefore, woodlands with greater tree species richness allow considerably greater niche partitioning of canopy foraging birds than species poor woods.

21.   Since the overlap in the use of tree species between pairs of bird species was negatively correlated with bird and tree species richness, indirectly, it was also negatively correlated with bird density. This suggests that the lower overlap of tree species choice allowed higher bird densities and greater species packing in compartments with higher tree species richness and diversity. The tree species was the only niche dimension which allowed this.

22.   Percentage overlap in the choice of tree species and in the distribution of birds between the compartments in Hamsterley Forest were identical between each pair of bird species. Therefore, it is reasonable to conclude that the distribution of birds within a wood was determined by the distribution of tree species within it.

23.   In both woods tree species were found to contain widely different densities of arthropods. In Great High Wood the densities

varied between 4.5-98 animals per sampling unit of 50cm of terminal branch, and in Hamsterley Forest between 2.6-31 animals per sampling unit.

24.   Arthropod densities were lower in 1986 than in 1985. In both woods the index of overall abundance fell by almost a half. Investigations of the seasonal arthropod density in both woods revealed lower density in the early season in 1986, whilst the densities were similar during the other periods.

25.   The rank order of tree species according to the arthropod density on them was independent of the season or the year, and remained similar throughout the study.

26.   There was a significant trend for each bird species to show the strongest preference for tree species with high prey density.

27.   The tree preference index of most bird species was correlated with at least one size group of prey, but never with all of them, suggesting an optimum food size. The strength of the correlation decreased progressively as the prey size considered moved further from the optimum. The correlation with prey size was, on average, stronger in Hamsterley Forest than in Great High Wood.

28.   Some tree species did not fit the relationships between tree preference index and prey density that were found for the majority of the tree species. The superabundance of prey on sycamore caused predator saturation in Great High Wood, where sycamore was a dominant tree species. This resulted in the lack of the expected strong preference for sycamore. In Hamsterley Forest Norway spruce, sitka spruce and oak fitted the regressions for some but not all

bird species due to the avoidance of these trees by some of the bird species irrespective of food availability.

29.   All temporal changes in the tree use by birds could be explained in terms of corresponding changes in relative prey density on tree species.

30.   This study has established that each bird species preferred to feed in different tree species, and that these differences formed the basis of niche partitioning independent of any structural characteristics of a wood. The tree preferences were correlated with prey density on the tree species, and the changes in the tree preferences were caused by changes in the prey available.

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Appendix 1

Scientific names and abbreviations of the
bird species in the study

Common name	Scientific name	Abbreviation
Blue tit	*Parus caeruleus*	BT
Great tit	*Parus major*	GT
Coal tit	*Parus ater*	CT
Willow tit	*Parus montanus*	WT
Long-tailed tit	*Aegithalos caudatus*	LT
Goldcrest	*Regulus regulus*	GC
Chaffinch	*Fringilla coelebs*	CF
Siskin	*Carduelis spinus*	SI
Crossbill	*Loxia curvirostra*	CB
Goldfinch	*Carduelis carduelis*	GF
Treecreeper	*Certhia familiaris*	TC
Phylloscopus warblers	*P. trochilus, P. collybita, P. sibilatrix*	PH
Blackcap	*Sylvia atricapilla*	BC
Nuthatch	*Sitta europaea*	NH
Spotted flycatcher	*Muscicapa striata*	SF
Pied flycatcher	*Ficedula hypoleuca*	PF

Appendix 2

Compartment size, bird and tree species diversity and richness,
and bird density in each compartment in Hamsterley Forest,
March - October, 1984-86

Comp. no.	Comp. size	Species bird	diversity tree	Species bird	richness tree	Bird density
0000	0.81	1.76	1.48	9	9	9.63
0011	4.05	1.49	0.00	1	8	1.30
0012	1.21	1.77	1.26	10	13	6.29
0014	2.43	1.61	0.10	6	13	5.52
0031	1.62	1.73	1.80	9	8	4.40
0041	4.86	1.31	1.57	5	8	4.34
0054	3.24	1.19	1.38	5	5	2.33
0101	3.24	1.71	1.39	6	10	3.72
0103	1.62	1.39	0.00	1	8	3.40
0111	4.45	1.78	0.98	5	9	5.62
0112	3.24	1.84	1.30	8	9	2.04
0113	1.21	1.69	0.00	1	8	2.88
1514	4.85	1.19	0.00	1	5	2.62
0403	4.86	1.63	0.56	2	6	0.50
0690	6.48	1.42	0.48	7	7	1.99
0712	4.05	0.70	0.00	1	4	2.39
1416	15.79	1.56	1.94	9	10	1.69
1435	1.62	2.35	1.73	9	15	9.47
1442	4.45	1.78	0.99	5	11	3.60
1445	1.21	2.41	2.29	12	15	10.56
1552	10.12	2.00	1.06	7	14	2.98
1562	4.05	1.06	1.30	5	6	1.73
1601	4.05	1.50	0.96	3	8	1.12
1602	10.12	0.98	1.11	6	7	1.09
1620	8.10	1.77	0.94	5	10	1.06
1630	10.12	2.02	1.17	9	16	3.52
1640	3.64	1.79	0.05	7	12	4.30
2163	3.64	1.00	0.00	1	4	1.03
2171	6.07	1.64	0.57	2	10	3.92
2181	4.86	1.91	0.40	2	10	2.61
4051	8.91	1.09	0.00	1	7	2.41

notes: compartment size is displayed in hectares
bird density is the overall numbers of birds per hectare