

HABITAT CORRELATES OF BIRD DISTRIBUTION IN BRITISH CENSUS PLOTS

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ABSTRACT.—Recent studies based on the British Trust for Ornithology's Common Birds Census scheme are reviewed in relation to theories of habitat distribution. Studies of the Wren, Chiffchaff, and Kestrel provide evidence for a hierarchy of preferences between the available habitats, with less preferred ones coming into use at high population densities. For two additional species, the Great Tit and Yellowhammer, increased use of secondary habitats is associated with density-dependent reduction of reproductive success in the primary habitat. Bird species diversity in English woodlands is, as elsewhere, positively correlated with foliage height diversity, but populations of individual species are most stable in woodlands with species-specific vegetation profiles. These studies support theoretical models of population density as a determinant of habitat use and indicate a need to consider population levels in determining habitat preferences for individual species.

The dynamics of habitat use is currently one of the least studied areas of avian population ecology, presumably because few investigators have been able to afford to dedicate many years to the censusing of individual plots or habitats required for such investigations. Important theoretical work on the dynamics of bird populations between different habitats has consequently gone largely untested. Lidicker (1962) suggested that emigration from crowded habitats was an important component of population dynamics, as migrant individuals could expect to achieve greater fitness in other areas. Brown (1969) considered the implications of models in which exclusion from preferred habitats was the outcome of territorial behaviour by males successfully established in those habitats. These population models predicted that at certain densities in a preferred habitat, individuals should begin to move into an alternative habitat, a pattern found in Chaffinch (*Fringilla coelebs*) censuses by Glas (1960). The models also indicated that population densities should fluctuate more in less preferred habitats, a feature of titmice (Paridae) populations showing the buffer effect between secondary and primary habitats (Kluyver and Tinbergen 1953). However it is not necessary that birds in a secondary habitat be excluded from the preferred one through territorial behaviour as such: any form of scramble competition by which the breeding success of birds nesting in the preferred but crowded primary habitat could induce breeding in a secondary, less crowded habitat yielding a net gain in fitness (Fretwell and Lucas 1969) suffices.

The present paper uses the long-running Common Birds Census of the British Trust for Ornithology (BTO) to examine these ideas in the light of field data.

MATERIALS AND METHODS

The BTO commenced a programme of monitoring bird populations on farmland using a mapping method, in 1961 at the request of the then Nature Conservancy (now the Nature Conservancy Council). In 1963 fieldwork was extended to encompass woodland studies. Currently some 300 to 350 sites (approximately 100 farmland, 100 woodland, and the remainder mixed habitats of various sorts) are sampled annually by volunteer observers. The maps prepared by the fieldworkers are returned to Beech Grove, the Trust's headquarters, for central analysis, and the resulting counts of territories are summarised into a national index for (where possible) farmland and woodland separately or as a pooled national index where the individual samples for farmland and woodland are too scarce. Material from a particular observer is included in the index calculation each year only if the observer has contributed a census from the previous year; this procedure eliminates the effects of observer bias in the calculation of the index. Various tests have been conducted and confirm that differences between analysts have been largely eliminated by the training these professional workers receive before undertaking routine analysis of the Common Birds Census returns.

Each individual census worker submits a habitat map for his census plot when he first enters the Common Birds Census scheme. These maps are minimally marked to indicate location of general landscape features—copses and spinneys and other small woods, hedgerows, ponds, crops, etc.—and may run to great detail (pesticides and fertilizer applications, winter treatment, felling regime, etc.). He subsequently reports any habitat changes on a year-to-year basis, either by correspondence or by submitting a revised habitat map. In this way the results from any census plot for individual species or for all species can be related to the habitat of the census plot.

Several census workers are still surveying plots that they commenced in the early 1960s, but the majority of census workers contribute information from individual plots only for a matter of some years and then leave the scheme for a variety of reasons. With this information a very large number of plots have both habitat and bird data available for analysis. In using this information, however, it is necessary to allow for differences in censusing efficiency between observers. Results in preparation show that as much as 20% vari-

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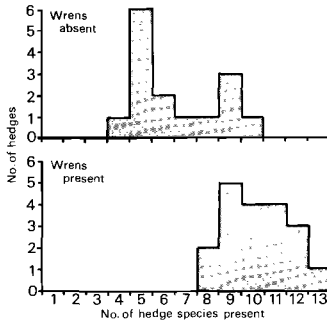


FIGURE 1. Wren habitat preferences in respect of arboreal species richness in field hedgerows. Data from P. Osborne.

ation between individual census workers can occur on the same census plot (see Enemar 1962). This error does not affect the index calculations but is a source of error in the use of the census information in relation to habitat studies.

Against this background the present paper examines the habitat correlates of birds on the census plots studied in Britain. The extended time series information of bird populations available as a result of the running of the Common Birds Census scheme since the early 1960s allows rather more consideration to be given to temporal changes in habitat use than has been possible in previously reported short-term habitat studies.

RESULTS

Since 1961 bird populations in Britain have shown considerable variation, due largely to the occurrence of an exceptionally severe winter in 1962–63 and an only slightly less severe winter in 1978–79. Statistical analysis of the 1961–1978 population changes shows that for the majority of species winter conditions are limiting, though a few species are sensitive to summer weather (O'Connor unpublished data). For most species, population densities have varied two-to-three-fold over the two decades studied (Williamson and Batten 1977).

Williamson (1969) documented the changing habitat usage of the Wren (*Troglodytes troglodytes*) as it recovered in the immediate aftermath of the 1962–63 winter. In 1964 the commonest habitat element within Wren territories was woodland, but the use of this habitat rapidly saturated as the population grew. As the available woods were filled the second most common habitat used in 1964—streamside vegetation—began to fill up and saturate. Similarly, the third most popular habitat in 1964, gardens, began to fill up as the first two preferred habitats were less available. The least used habitat in 1964 was that of field hedgerows, and this clearly remained in a poor position throughout the 1964–67 population increase.

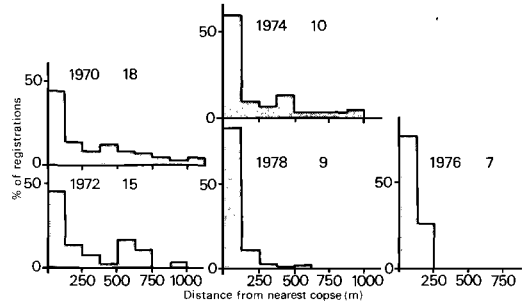


FIGURE 2. Distribution of Chiffchaff registrations with respect to copses in farmland, showing use of more remote song posts as population density increased. The figures to the right of each date give the species population level on the census plot in that year. Data from P. Osborne.

Even within this category of habitat it is possible to show the existence of more detailed microhabitat preference: Figure 1 shows that the Wren preferentially colonised those hedgerows that were rich in tree species, and were largely absent from those hedges containing rather few trees (P. Osborne, unpublished data). As these data were obtained in the late 1970s when Wren populations were rather high, they indicate that Wrens are showing considerable resistance to using species-poor hedgerows. There thus exists a distinct hierarchy of habitat preferences among the Wrens breeding in Britain, with the inferior habitats being colonised only under increasing population pressures.

Migrant species in Britain were, of course, less subject to population variation, escaping as they did the effects of the severe winters mentioned. Nevertheless, there is convincing evidence available that even migrant species show a similar hierarchy of habitat preferences. Figure 2 shows some data obtained for the Chiffchaff (*Phylloscopus collybita*) on a farm in Dorset: when the population of Chiffchaffs on the farm was low, as in 1976, practically all bird registrations were obtained within 250 m of a copse (a type of small wood) on the farm. At high population densities, on the other hand, much of the population was recorded on trees and hedgerows extending out from these copses at distances of up to 1 km from the nearest copse. The figure suggests that the Chiffchaff decreased on the farm during the study period and one might argue that this was due to habitat changes around the copses. In detail, however, the correlation of Chiffchaff positions with population density is greater than with time, both in the figure and within the full time series of data.

Why do these species show these population-dependent preferences in habitat usage? O'Connor (In press) has argued that resident species in Britain are largely *K*-selected in their population behaviour, in contrast to migrant species that are generally *r*-selected. On such a premise, the habitat use variations shown by resident species should be closely related to their reproductive fitness in the different habitats, and in some cases it has been possible to demonstrate that these exist. In the case of the Great Tit (*Parus major*) the long-running Wytham Woods study by the Oxford ecologists has shown that the Great Tit utilises farmland largely as a result of territorial exclusion from the preferred deciduous wood. Associated with this is a density-dependent reduction in clutch size within the woods themselves. The Common Birds Census data have been examined in conjunction with the BTO Nest Records scheme data on clutch size and breeding success, and the BTO Ringing Scheme data on dispersal and survival, to show that Great Tits nationally suffer similar clutch size and rearing success depressions in conditions of high population densities, and that the birds survive less well and disperse more widely under these conditions (O'Connor 1980d). These effects are also reflected for the Great Tit in apparent density-dependence within the woodland populations monitored by the Common Birds Census scheme, and are suggested for a number of other species (Williamson and Batten 1977).

A particularly interesting example of hierarchical use of habitats has been established in the case of the Yellowhammer (*Emberiza citrinella*) (O'Connor 1980a). In this study, Yellowhammer populations on farmland were shown to have levelled off after a period of recovery from the effects of the 1962–63 winter; on the other hand, the population of Yellowhammers recorded in woodland habitats continue to increase, suggesting the occurrence of an overspill effect such as described above for the Great Tit. By examining the clutch sizes recorded for Yellowhammer in farmland and woodland habitats, O'Connor (1980a) showed that clutch size decreases with population pressure, both in woodland and farmland, but more steeply for the latter. In this way, Yellowhammers attempting to breed in farmland suffer increasing clutch size depression, thereby eroding the advantage of breeding on farmland (the preferred habitat) in the first place and thus making it reproductively advantageous to move into the "inferior" but less crowded woodland habitat. In this way, a balance of advantage between habitat quality and population pressure generates a situation of "equality of fitness" for the two habitats, thus

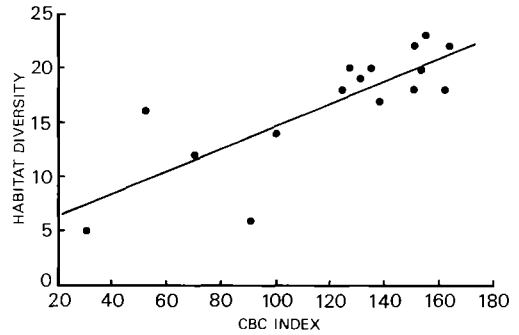


FIGURE 3. Diversity of breeding habitat use by Kestrels as a function of population density. Diversity assessed as number of standard nest record habitats cited in the annual sample. Data from British Trust for Ornithology nest record and Common Birds Census schemes.

accounting for the observed pattern of population movements.

A further example of changing habitat usage under increasing population pressures is provided by studies of the Kestrel (*Falco tinnunculus*) in Britain (O'Connor 1980b). This study showed that nonbreeding becomes increasingly frequent as the population rises, as might be expected for a carnivorous species subject to relatively little human persecution. This non-breeding is associated with an increasing use of a diversity of habitats, as recorded in the Nest Record cards for the species returned to the BTO since 1961 (Figure 3). Detailed examination of breeding performance by Kestrels in these different habitats showed that poorer habitats were increasingly used with the increase in population pressure. Thus, the hierarchy of habitat use by the Kestrel is directly linked to its breeding performance in the different habitats, providing a proximate explanation for the marked habitat preferences exhibited at low population densities. The increasing incidence of non-breeding demonstrated in this study at the highest Kestrel densities underlines this explanation.

Detailed study of the use made by Yellowhammers of particular "patches" on East Hammoon Farm in Dorset (see Williamson 1971) has shown an interesting trade-off between habitat quality, territory size, and population pressure. Under high population pressures, Yellowhammers can accept small territories provided they are of high quality, but can accept low quality territories only if they are extensive enough (O'Connor 1979 and unpublished data). Quite independent confirmation of this interpretation of the Dorset data comes from hedgerow cut-back studies on Pendley Farm, Hertfordshire,

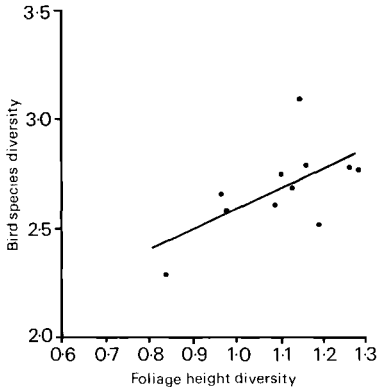


FIGURE 4. Bird species diversity in relation to foliage height diversity in 12 southern English woods censused by BTO members. Based on data in Pearson (1980). The regression equation is: $BSD = 0.92 FHD + 1.67$; with $r = 0.726$ ($P < 0.02$).

censused annually by BTO staff. Between 1975 and 1976 the internal hedgerows of the farm were severely pruned back to stump level. The Yellowhammers responded to the cut-back not by changing the location of the territories but by greatly enlarging their territory size on the farm (see Morgan and O'Connor 1980). Size and quality of territory are thus independent channels of adjustment to habitat quality and population pressure in Yellowhammers.

Examination of Common Birds Census data for a number of English woodlands has shown that their bird species diversities are correlated with foliage height diversity (Figure 4), in line with the results of previous studies (MacArthur and MacArthur 1961, Recher 1971, Moss 1978). However, the regression slope in Pearson's (1980) study is lower than those of the earlier studies. Whilst one may postulate several explanations, it is perhaps significant that the English data relate to years of generally high populations, when even poor habitats should be colonized if the models of Brown (1969) and Fretwell and Lucas (1969) are correct. To cope with such problems, Pearson (1980) has analyzed the variance of population densities in woods of different foliage structures and found that for individual species woods with structures either below or above some particular value contained more fluctuating populations than did woods at that value. Figure 5 illustrates the findings for the European Robin (*Turdus ericetorum*) and for the European Blackbird (*Turdus merula*) in relation to vegetation volumes within the 0–2 m and 2–3 m height zones, respectively. This approach identifies key characteristics of woods in which population densities are particularly stable, thus

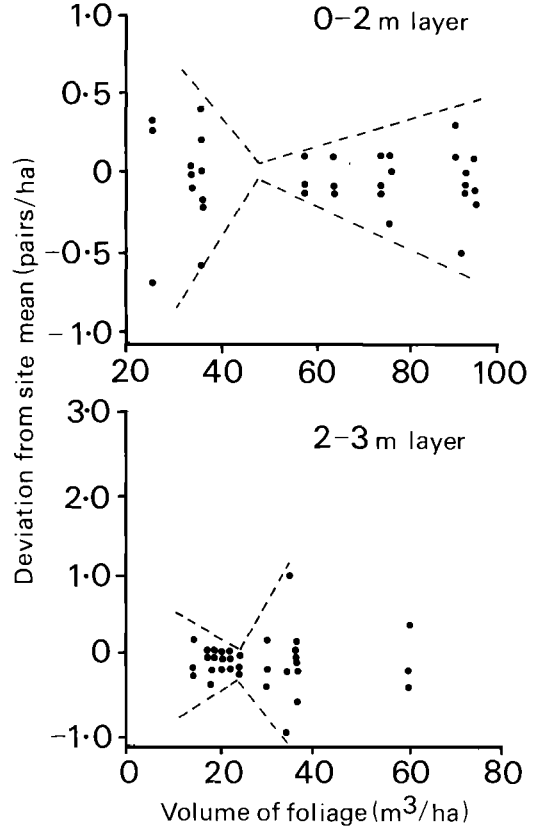


FIGURE 5. Population stability in relation to foliage volume in stated canopy layers for (top) European Robin and (bottom) European Blackbird. The vertical axis shows for each of the 12 woodland plots censused over three years the deviation of each annual population density from the three-year site mean. The dashed lines indicate the subjective limits of the data, to emphasize the reduction in the range of population densities apparent at particular foliage volumes (from Pearson 1980).

extending the analysis to take account of the population effects noted earlier.

DISCUSSION

The studies reviewed briefly here show that a variety of species display some form of hierarchical habitat preferences, as expected on the basis of Brown's (1969) theory. For some, such as Yellowhammer and Kestrel, the data suggest that utilization of the different habitats reflects the equality of fitness argument advanced by Fretwell and Lucas (1969). For others, such as the Great Tit, density-dependent reduction of clutch size and other components of reproductive success certainly occur within the preferred habitat (Krebs 1970, 1971; O'Connor 1980d), but

fitness in the alternative habitat has not been measured.

These findings are particularly important for the analysis of habitat utilization by means of census studies. They indicate that different results may be obtained from censuses conducted in different years. This risk is particularly significant when one of the habitats being censused is a secondary or tertiary one for the species concerned. The distribution of the birds between habitats will reflect the total population pressure for the region, and may be changed suddenly following sharp changes in that pressure. Cawthorne and Marchant (1980) found that many English woodland species showed proportionally larger population decreases on farmland census plots than on woodland plots between 1978 and 1979, the intervening winter being un-

usually severe. They suggest that vacancies in woodland due to the death of resident birds were filled differentially through birds previously on farmland moving into the preferred woodland. Ringing data indicate that this hypothesis has a good basis in fact (unpublished data). Attempts to correlate bird densities with habitat features must therefore take into account the intraspecific competition for preferred habitats documented here.

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