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AN ECOLOGICAL STUDY OF THE FEEDING HABITS OF THE ENGLISH TITMICE

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(With 16 Figures in the Text)

INTRODUCTION

Problems of the interaction between predatory animals and the species whereon they feed may be attacked in two ways. When the predator species is sufficiently numerous and the prey is amenable to accurate sampling the advance may be direct. But when the predator is scarce or its foods are diverse; when the prey species are so inaccessibly or unevenly dispersed that they cannot be quantitatively surveyed, then indirect methods of investigation must be used.

Early in 1947, at the request of the Agricultural Research Council, the Edward Grey Institute of Field Ornithology began an investigation of the dual problem of the influence of bird predation upon the numbers of the prey species and of the influence of the stocks of prey upon the population level of the carnivores. It was agreed that species of economic importance should not be studied, so that the work should not be done upon birds directly dependent on man's activities for a major part of their food supply. The species selected for study must be resident throughout the year, and must be abundant. Here a difficulty was found, for few bird species, even those usually described as 'common' or 'abundant' are represented in any habitat in such numbers that adequate sampling will not sensibly modify, or even destroy the stock in the course of the investigation. This difficulty in choice of species suitable for a direct approach was especially marked after the decimation of the stocks of so many passerine birds in the great frost of early 1947 (Ticehurst & Hartley 1948). It was therefore decided to make an indirect attack upon the problem by the application of a principle enunciated by Charles Darwin (1859): 'As the species of the same genus usually have, though by no means invariably, much similarity in habits and constitution, and always in structure, the struggle will generally be more severe between them, if they come into competition with each other, than between the species of distinct genera.'

A group of closely related species, all reasonably abundant, was needed for work on the implication of this principle. In the English Midlands the Paridae (titmice) were an obvious choice. Four species were to be found regularly feeding in the same habitats: great tit, *Parus major* L.; blue tit, *P. caeruleus* L.; coal tit, *P. ater* L.; marsh tit, *P. palustris* L. Certain ecological conclusions could be drawn from the results of study of the feeding habits of four congeneric species living side by side. If no distinctions could be made between the foods, feeding places and feeding methods of the four species it might reasonably be assumed that food supply was not the factor limiting their numbers. Conversely, a measure of ecological separation between the species would justify the assumption of some degree of interspecific pressure. Lack

(1944), summarizing the almost invariable occurrence of ecological differences between closely allied species of passerine birds in the British Isles, remarked on the scanty knowledge of distinctions between the titmice and wrote: 'Hence in the British forms of *Parus* there is wide overlap in habitat, but detailed study of food and feeding habits might perhaps show a greater degree of ecological separation than this summary suggests.'

Studies of stomach contents alone, without data on sources of supply cannot solve the problems of interspecific feeding relationships with finality, even if adequate sampling be possible. The discovery of the same food organisms in all the species examined does not prove interspecific competition, unless it be also proven that all the predator species have investigated all the sources of supply with equal diligence and that the stock of food is inadequate for their needs. The finding of different foods in different species is not irrefutable proof of the absence of competition, unless it be shown that all selection of foods is by choice and choice alone from diverse super-abundant food stocks, all equally accessible to all the species studied.

After some preliminary trials of methods, the feeding habits of the four species of titmice already listed and those of two other birds—the willow tit, *P. atricapillus* Hellm. and the long-tailed tit, *Aegithalos caudatus* (L.)—were studied over a period of two and a half years, from the early summer of 1947 to the end of January 1950. A record was made for each feeding bird of the height from the ground at which it was at work, the species of tree or bush wherein it was and of the feeding 'site'. In trees and shrubs the 'sites' were classified into: trunk; limb—any main member more than 1 ft. in diameter; branch—any member between 1 ft. and 2 in. in diameter; twig—less than 2 in. in diameter; leaves, flowers, buds, fruits, etc. The heights of the feeding activities were sometimes measured with a simple level; sometimes ascertained by comparison with objects of known height; and sometimes estimated. A check of estimates against measured heights showed that they gave the accuracy needed—± 5 ft.

An arbitrary rule was adopted of 'One tree—one record'. So long as a titmouse continued in one tree, only one record was made, that of the height whereat the bird first alighted or was first seen. Titmice have no set method of working a tree, comparable with the steady ascent of the treecreeper, *Certhia familiaris* L., so that the 'height when first seen' rule does not weight the records in favour of the lower levels. The 'one tree—one record' rule has the disadvantage of emphasizing small shrubs of one species visited in rapid succession as compared with the large tree wherein hunting may be prolonged. But the alternative, timing by stop-watch the period spent in each tree, would be impossible in high summer, when a feeding bird may be glimpsed for a few seconds after minutes of scrutiny of the foliage. Timing would also reduce the number of records which could be made from a flock, since attention would be confined to a single bird. This would be a disadvantage in the post-breeding season; then a couple of empty hours may be followed by a few crowded minutes when a tit flock is at last encountered.

This study was made within an area in south Oxfordshire and north Berkshire. The boundary runs from Eynsham south-south-east to Abingdon east-south-east to Wallingford and thence north-west to Oxford and so to Eynsham, enclosing a wedge of country some 15 miles long and 5 miles wide at the base. In the north-west corner

of the area is the Wytham estate, owned by the University of Oxford, containing two woods. Wytham Great Wood, the scene of the most intensive study of the feeding titmice, stands on a bluff of Jurassic clay, capped with coralline crag, fronting the Midland Plain. It is a mixed deciduous wood; the predominant trees of the canopy are oak, *Quercus robur* L., sycamore, *Acer pseudo-platanus* L., and ash, *Fraxinus excelsior* L., with sallow, *Salix caprea* L., hawthorn, *Crataegus oxyacantha* L., black thorn, *Prunus spinosa* L., hazel, *Corylus avellana* L. and elder, *Sambucus nigra* L., in the shrub layer, and bracken, *Pteridium aquilinum* (L.) Kuhn, and brambles, *Rubus* sp. in the undergrowth. There are two plantations of spruce, *Picea abies* (L.) Karsten, larch, *Larix* sp., and Douglas fir, *Pseudotsuga taxifolia* (Poir.) Britt., and a few clumps of spruce and Scots pine, *Pinus sylvestris* L. Marley Wood, the smaller wood of the estate, where some observations were made, stands on clay, and has more hazel and birch, *Betula* sp., and fewer conifers.

Near the southward tip of the area is the village of Brightwell-cum-Sotwell, a second scene of close study. The long, narrow village stands north of the Berkshire Downs, and has large orchards, many walnut trees, *Juglans regia* L., and big hedgerow elms, *Ulmus* spp. Many records were made in north Oxford, where there are large gardens and big trees, including beech, *Fagus sylvatica* L., and horse chestnuts, *Aesculus hippocastanum* L., and variety of ornamental shrubs. Observations were made at many other places in the well-timbered agricultural country between Oxford and Wallingford.

A concentration upon the birds of a single habitat would give results certainly partial and probably misleading. The distribution of the titmice varied greatly with the seasons. Many woodland-bred birds wandered in late summer to the hedgerows of the farmed land. In winter the titmouse populations of village and town gardens were notably bigger than in the breeding season. This is illustrated by the seasonal variations in the number of records from Brightwell and from north Oxford, where occasions of observation were, by and large, equal from month to month. Birds ringed at Wytham have been recovered in north Oxford, and a great tit ringed in Wytham Great Wood traversed the whole area, being recovered in Brightwell two years later (Gibb 1950). To the study the titmice of one habitat would be to study only a part of the natural history of the species.

A word may be said about the extremely simple statistical treatment of the results. This never goes beyond the demonstration of significance in differences between the numbers of birds feeding at certain levels. The reasons for the simplicity of treatment are three.

(1) The sampling was very far from uniform. The uneven and frequently changing distribution of the titmice defeated any neat scheme of patrols of defined duration, timing and direction. The path which one day led to a gathering of feeding titmice might, within a week, lead directly away from it. The birds had to be sought where their wanderings led, or where temporary abundances of supply had assembled them.

(2) The titmice were not equally visible in all their feeding stations. A blue tit at 60 ft. in a bare oak was more easily seen than a coal tit in a nearby conifer or a great tit feeding among fallen leaves and brambles. It is fortunate that this hindrance of observation tended to minimize differences of distribution, since any ecological

distinctions between the species which emerge are proven in the face of a difficulty of technique tending to mask their appearance.

(3) The distribution of feeding niches was not itself 'normal' about any one level. In an acre of wood the whole of the woodland floor (saving the space taken by the actual boles of trees) was available to feeding birds. At 1 ft. the number of places to stand was reduced, and at each succeeding level the area of surface where titmice might cling and search varied not only with the species of trees and shrubs but also with their mode of growth and the closeness of the stand.

The statement that a difference is 'significant' implies a probability of 0·01 or less. Probabilities between 0·01 and 0·05 are stated.

Owing to lack of space it has been impossible to print the full results of this investigation here, but a copy has been placed in the library of the Edward Grey Institute. Duplicated sets of tables showing the height-frequency distributions of feeding activities have been prepared; copies may be obtained from the Secretary, Edward Grey Institute, Department of Zoological Field Studies, Oxford.

THE HEIGHT DISTRIBUTION OF FEEDING ACTIVITIES

(a) *The great tit*

Observations began during the intense frost of February 1947. The ground was snow-covered for most of the month. Great tits hunted chiefly at heights of less than 20 ft.—75 records of 90, including nine instances of feeding on the ground. In March the great tits fed more on the ground than at any other level (25% of 228 records) and there was a slight increase in activity at heights of over 20 ft. There was some evidence that the amount of ground feeding would have been greater had there been less snow (Fig. 1). In 51 records from six days with complete snow cover only one bird was at work on the ground; but in the two days before and the three days after the snow 49 of 112 observations of great tits were of ground feeding. In April feeding activity was fairly evenly distributed up to a height of 24 ft.; there were as many birds feeding on the ground as at any other level.

In May 1947 there was a marked change in the height distribution of feeding great tits. The modal feeding level was now 15–19 ft., and 45% of the records were of birds at a height of over 20 ft. In this month caterpillars—chiefly the larvae of *Operophtera brumata* (L.) and *Hybernia* spp.—were abundant in the woods, in densities up to 37 per 100 oak leaves. In June, the abundance of caterpillars being ended by the 12th of the month, the higher levels were abandoned. In June, July and August feeding great tits were fairly evenly distributed between the lowest undergrowth and about 20 ft. But few birds fed on the ground.

In September 1947, when 25 of 116 records were of ground feeding, there were significant differences between the great tits of north Oxford on the one hand (37% of

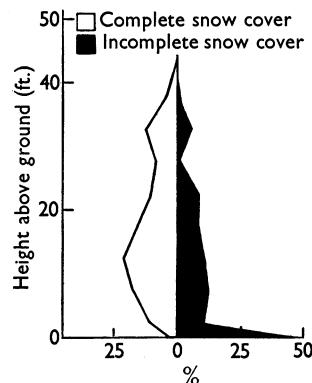


Fig. 1. The effect of complete snow cover on the height-frequency distribution of the feeding stations of great tits, March 1947. In this and the following figures birds feeding clear of the ground but below 5 ft. are grouped at 2½ ft., birds at 5–9 ft. at 7½ ft., and so upward.

74 records being of birds on the ground) and, on the other, Wytham Great Wood with no birds at work at ground-level and Brightwell with one record of ground foraging out of 27. The Great Wood and Brightwell had many elders in fruit and great tits feeding therein; but this food was not available in the Oxford gardens. In October north Oxford still differed from Wytham Great Wood and Brightwell in the significantly larger proportion of activity on the ground. The Wytham great tits fed much on aphids from the leaves of sycamore and oak, a food abundant in the autumn of this year (Table 1). In November 1947 there was much feeding on the ground in Oxford and Brightwell, but very little in Wytham Great Wood, where aphids were still abundant in the earlier part of the month. This general distribution of feeding birds continued until the end of the year.

1948 opened with the ground as the most frequented feeding place of great tits—35% of the records in January and 37% in February. In Wytham Great Wood 45 and 41% of the observations were of birds on the ground as against only 3 and 2% in November and December 1947. In March the proportion of ground foraging was 26% in the Great Wood, 22% in Brightwell and 34% in Oxford. In Wytham Great Wood the proportion of birds at or above 30 ft. showed a significant increase over that in the previous month. In April 1948 the feeding levels suddenly rose. In Wytham Great Wood the ground was deserted, 20–24 ft. was the modal height and 54% of all foraging was at heights above 19 ft. This sudden change in the habits of the feeding

Table 1. Numbers of aphids on the leaves of sycamores in Wytham Great Wood

	No. of leaves	No. of aphids	Aphids per leaf
23–28 Oct. 1947	82	538	6.55
6 Nov. 1947	49	195	3.97
1–15 Oct. 1948	114	32	0.28
7 Oct. 1949	7	58	8.26
3 Nov. 1949	90	185	2.06

great tits coincided with the spring outbreak of defoliating caterpillars, which began nearly a month earlier than in 1947. In May the foraging level most often recorded had dropped a little, but 53% of records were still at or above 20 ft. In June the percentage of activity above 19 ft. had dropped to 43%—the difference is not statistically significant. In July the modal height was 25–29 ft., and the percentage of records of birds foraging above 19 ft. had risen to 57%. (The increase over the proportion in June is not significant.) While the great tits of Wytham were feeding in the trees the few birds which were observed in Oxford in high summer continued to feed much upon the ground. In the four months April to July, 18 of 43 records from north Oxford were of birds foraging on the ground as compared with 12 of 492 records from the Great Wood.

In August 1948 ground hunting was seen in 14 out of the 54 observations in Wytham Great Wood, in statistically significant contrast to July. Only 22% of the records were of birds feeding at 20 ft. or more. In this month a number of great tits were seen feeding in big umbellifers growing beside country roads. In September, 17 of 64 records were of foraging on the ground.

In October 1948 the great tits in the Wytham woods were very differently employed from those at Brightwell. In this year of abundant beech-mast and few aphids

(Table 1) the birds in the Great Wood fed more in beeches than in the previous year (19% of records as against nil in 1947) and less in sycamores and oaks (16·5 and 1·5% of records as compared with 47·5 and 22% in 1947). Only 6 of 106 records are of birds on the ground. In Marley Wood all the observations were of birds in trees bearing nuts or fruit (beech, hazel, elder, hawthorn) and there was no ground feeding. But at Brightwell, where the bulk of a large walnut crop had fallen, 39 of 99 records were of great tits at work on the ground. In November the beech-mast crop had fallen. In Wytham Great Wood, with its few beeches there was little ground feeding, and 56% of the records were very evenly distributed between 10 and 50 ft. At Brightwell also most of the great tits were feeding above ground-level, the proportion of records of ground feeding differing significantly from that in October. In Marley Wood, 10 of 35 records were of ground hunting, and in north Oxford, where great tits had been few in October there were 131 records of ground feeding in a total of 189. December 1948 saw the establishment of ground feeding as the dominating habit in all the habitats: 50% of the records in Wytham Great Wood, 58% at Brightwell, 70% in Oxford.

In the first quarter of 1949 ground foraging predominated in the area as a whole, with 48, 40 and 46% of the records for the three months. In January the Wytham Great Wood birds showed a significant decrease in activity on the ground as compared with the previous month (23% of 35 records). Work in the Great Wood in February

Table 2. *Feeding activities of the great tit in Wytham Great Wood,
June 1947–49*

	June 1947	June 1948	June 1949
Number of records	65	165	82
Percentage of records of ground feeding	0	2	1
Percentage of records of feeding between 0 and 24 ft.	85	66	65

and March was restricted, and only a few great tit records were made in these two months. At Brightwell there was a significant increase from February to March in the proportion of birds active at or over 20 ft.

In Wytham Great Wood in April 1949, 20% of 64 records were of birds feeding on the ground, and another 48% of the records were of activity between the lowest undergrowth and 19 ft. The defoliating caterpillars had hatched—on 18 April a density of 21·95 caterpillars per 100 leaves had been found in one oak—but the great tits, even as late as 26 April, were not determinedly seeking them. May was given to observations on the foods of nestlings. In June 1949 the height distribution of feeding great tits resembled that in June 1948 (Table 2).

In October and November 1949 the great tits of Wytham fed but little (7 and 7·5% of records) on the ground. 1949 was a year of abundant aphids (Table 1), in the Great Wood, and a light crop of beech-mast. As in 1947 the great tits fed much in sycamores (27 and 30% of records in the two months) and in oaks (11 and 20% of records) and not at all in beeches. In Brightwell and in Oxford the records of ground feeding in each month exceeded 50% of the total.

In December 1949 the winter routine of ground feeding was again generally established: 56% of the records from Wytham Great Wood, 51% of 189 records from Bagley Wood, and 81% in north Oxford. In January 1950, 20 of 28 records from the

Great Wood, and 57% of the records from the area as a whole were of birds foraging at ground level.

To sum up, great tits are ground-feeding birds in winter quarters and in the mid-winter months (December to March) in the areas where the species is resident. Great tits go up into the trees for the caterpillar harvest of early summer, work the lower woodland foliage in high summer, and in autumn feed high or low as supplies dictate.

(b) *The blue tit*

At all seasons of the year the distribution in height of feeding blue tits was characterized by its wide range. Visits to the modal feeding levels usually exceeded the visits to the levels next in frequency (but not necessarily nearest in level) by only a small percentage of the total for the month.

In February 1947 blue tits were feeding at all heights from the ground to more than 60 ft., 15–19 and 25–34 ft. being the levels most frequented. In March and in April, 10–19 ft. was the modal level; and in May, 10–24 ft. In June, many observations were made in north Oxford: there the blue tits were most active at low levels—76% of the records were of birds at less than 20 ft. In July and August foraging was fairly evenly dispersed between the lowest scrub and 34 ft.

In September 1947 the blue tits at Brightwell fed relatively more ($P < 0.02$) at heights of 20 ft. and more than did the birds of the Great Wood; in the latter place there was significantly more foraging in the fruiting elders. In October this difference between the foraging habits of the blue tits of Brightwell and the Great Wood had vanished. The titmice of both localities differed significantly from the birds of north Oxford in the smaller proportion of ground feeding (one record of 70 in the Great Wood, nil of 44 at Brightwell, seven of 21 in Oxford).

In November 1947 the most frequented level in Wytham Great Wood was 30–34 ft., the proportion of birds at or over 20 ft. being 63%, a marked increase over the October proportion ($P < 0.02$). In Oxford ground foraging by blue tits had almost ceased, and 45% of 40 records were of birds at more than 19 ft. In December 72% of the Wytham Great Wood records were of blue tits at or above 20 ft., 18% of them being birds at 50 ft. or more, a highly significant increase over the 3% of records at such heights in the November sample.

In January 1948, 20–24 ft. was the most frequented level in the Great Wood and also in the area as a whole. There was no feeding on the ground. In Wytham Great Wood 30% of the records were of birds at 50 ft. or more. February was remarkable in Wytham Great Wood for the even height distribution of feeding activity: in the seven stages between 10 and 45 ft. the percentages of records were 10, 10, 10, 11, 11. Foraging at or above 50 ft. contributed only 11% of the records. At Brightwell the blue tits were active at much lower levels, 76% of records being less than 20 ft., as against 31% in the Great Wood. Oxford showed an intermediate distribution, with 54% of the feeding below 20 ft. There was little ground feeding anywhere.

In March 1948 blue tits in the Great Wood were evenly distributed between 20 and 44 ft. Only 17% of the records were of birds at less than 20 ft., a significant decrease from the degree of activity in the lower levels in February. But in Oxford the proportion of birds below 20 ft. had slightly increased. In April the level most frequented

was 15–29 ft. In Wytham Great Wood, whence the majority of the records came, the distribution of foraging activity through a wide range of levels had vanished, for the blue tits were deserting the higher twigs. This desertion of the upper levels continued in May: the modal foraging level in the Great Wood had fallen to 10–24 ft., and only 1% of the records were at 50 ft. or more. In the months of high summer the blue tits tended to forage lower and lower, the records of birds below 20 ft. in June, July and August 1948 being 41, 46 and 53% of the monthly totals. In July and August there were no observations of activity at or over 50 ft. Meanwhile, outside the Great Wood, blue tits fed at low levels in bushes and roadside weeds. In June, July and August the percentages of birds active at less than 20 ft. were 96, 65 and 81%. In and around Brightwell 29% of 83 feeding places recorded were on hogweed, *Heracleum sphondylium* L.

In September 1948 ground feeding (24% of 163) predominated among the blue titmice for the first time since observation began. This was the result of a very large crop of walnuts. At Brightwell 30 of 117 records (26%) were of birds on the ground, hacking into fallen nuts. There was no ground feeding in Wytham, but the titmice were in general in the lower levels, 55% of foraging being below 20 ft. In October the walnut harvest continued to affect the habits of the Brightwell blue tits; 66 of 214 records were of ground feeding. The effect of this temporarily super-abundant food supply on the routine of blue titmice is illustrated in Fig. 2. In Oxford, where the blue tits had arrived for the winter, there was also much ground feeding on fallen beech-mast (nine of 21 records). In Wytham Great Wood the beginning of a return to higher levels was seen; the percentage of birds at or over 35 ft. (23%) was the highest since March, and blue tits were seen foraging above the 50 ft. level for the first time since June. In Marley Wood the distribution of feeding activity was similar to that in the Great Wood. In both woods the birds were busy in elders and beeches.

In November 1948 there were but slight changes in the feeding habits of the blue tits in the Great Wood. In Oxford ground feeding was still predominant (41% of 76 records). At Brightwell, with the end of the walnut harvest, there was less ground feeding. The blue tits were active in low shrubs and bushes, and so continued through the winter. In Wytham Great Wood blue tits maintained the tendency to feed at higher levels as the winter advanced. In December the percentage of birds feeding at or above 35 ft. had increased from 25% in November to 30%, with 8% of the records at 50 ft. or more—the largest proportion of activity at these heights since March. In north Oxford in December ground foraging had ceased.

In January 1949 the feeding activities of the blue tits of the Great Wood differed

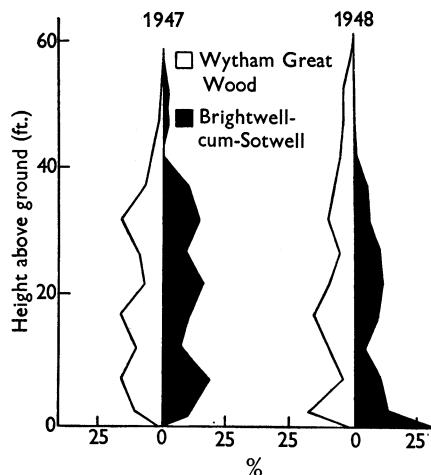


Fig. 2. Height-frequency distributions of the feeding stations of blue tits in Wytham Great Wood and at Brightwell-cum-Sotwell, October 1947 and October 1948.

a little from those of the previous month. The percentages of birds at or above 35 ft. (20%) and at or above 52 ft. (4%) were both less than in December, and the proportion of birds below 20 ft. (59%) showed a marked increase in low-level feeding ($P < 0.02$). In north Oxford there was a fairly even height distribution up to 55 ft.

In February the blue tits of Wytham Great Wood moved upward again. There was no feeding on the ground, only 18% of the observations were of birds at work at heights of less than 20 ft., 48% were at 35 ft. or more and 22% at 50 ft. or more. March in the Great Wood showed no significant differences from February, and April showed little difference from March, save that the proportion of birds foraging below 20 ft. was significantly less—10% as compared with 26%. While Wytham Great Wood showed a marked rise in feeding levels in the early spring months, in north Oxford there was a tendency for the blue tits to feed at lower levels as the spring advanced (Table 3).

Table 3. *Height distribution of feeding blue tits in north Oxford, 1949*

	January	February	March	April
Number of records	65	63	27	19
Percentage at or above 35 ft.	22	8	4	16
Percentage below 20 ft.	39	47	56	68

May 1949 was given to work on the food of nestlings. The few Wytham observations were of birds feeding high—11 of 18 foraging places were at heights of 35 ft. or more. The disposition of feeding blue tits in Wytham in June 1949, with 23% of the observations at or above 35 ft. and 32% below 20 ft. did not differ significantly from those observed in June 1948.

September 1949 saw most of the blue tits of the area feeding below 20 ft. Elder berries in Wytham and elder berries and pears at Brightwell attracted the birds to low levels. There was little ground foraging: the walnut crop was smaller than in 1948, and the nuts were thicker shelled and did not fall so soon. In October 1949 blue tits in Wytham Great Wood had begun to move upward. This general rise in feeding levels was continued until the end of the year (Table 4). Differences between October and

Table 4. *Height distribution of feeding blue tits in Wytham Great Wood, 1949–50*

	October	November	December	January
Number of records	170	166	106	193
Percentage at or over 50 ft.	4	2	10	7
Percentage at or over 35 ft.	15	13	32	17
Percentage below 20 ft.	53	44	29	58

November are not significant, but when December is compared with November, the increase in activity at or above 35 ft. and the decrease in activity below 20 ft. are both statistically significant. (In the increase in the proportion of birds feeding at or over 50 ft. $P < 0.02$.) In December 1949 a sample of 372 records was obtained in Bagley Wood. The percentage of birds foraging below 20 ft. (42%) was significantly larger than the 29% in the Great Wood, but the proportion of activity at 35 ft. and above (25%) did not differ significantly from that in Wytham.

While the blue tits in the Great Wood showed a rise in feeding levels during the last months of 1949, the birds at Brightwell showed a descent, the proportions of

birds hunting below 20 ft. being 81% in October, 84% in November and 100% in December. In this last month 8 of 29 records were of ground feeding. There were few observations in Oxford before December. In that month 18 of 25 records were of birds below 20 ft.—a proportion significantly less than that at Brightwell as it is higher than that in the Great Wood.

In January 1950 there was a general drop in the height of the feeding blue tits in Wytham Great Wood. The percentage of birds at or over 35 ft. (18%) was significantly less than the 32% in December and the proportion of birds below 20 ft. (58%) was twice that in the previous month. A similar, but less marked drop was recorded in January 1949. At Brightwell, by contrast, there was a rise in general level; 11% of the birds observed were at work at 35 ft. or more, the first records at such heights since October. Records of feeding below 20 ft. were 82% of the total, a decrease in low-level feeding, as compared with the previous month of $P < 0.02$. January of 1948 had shown a similar slight lift in height distribution. Oxford also showed a rise in feeding levels, with 28% of the observations of birds at or above 35 ft., as against 4% in December ($P < 0.05$) and 32% at less than 20 ft. as against 72%, a statistically significant difference.

Feeding blue tits range through a diversity of heights. In the winter months especially they are scattered from the lowest shrubs to the tops of the highest trees. In the mid-summer months the highest levels are deserted. Only when there is an abundant harvest of fallen nuts or fruits do blue tits feed on the ground with any frequency.

(c) *The coal tit*

In 1947 coal tits were seen in numbers only in Wytham and in north Oxford. In March they were fairly evenly distributed between the ground (12% of all records) and 44 ft., with a few birds feeding up to 65 ft. In April 92% of the records were distributed rather less evenly between 5 and 39 ft.

In June 1947 the dispositions of feeding coal tits in Oxford and in Wytham Great Wood were very different. In Oxford 53 of 57 records were of birds at work below 20 ft. In the Great Wood 14 of 15 records were of birds at 20 ft. or more. In July there was a significant rise in the feeding levels of the Oxford coal tits, half the 18 records being of activity at 20 ft. or above. In the Great Wood the lift was even more remarkable, 22 of 25 observations being of birds between 35 and 69 ft., compared with two records out of 15 above 35 ft. in June. In September 1947, 25 of 26 records from the Great Wood were of birds at or above 20 ft., while in north Oxford 16 of 26 records were of birds at 19 ft. or less. In September, in the Great Wood, 88% of the records lay between the levels 20 and 44 ft.; in November 68% of the records were between these levels, and in December 62%.

In 1948 most of the records (700 out of 869) came from Wytham Great Wood; discussion will be confined to the results from this area. In January records were few. During the next eight months the levels 20 and 44 ft. contained a remarkably even percentage of the monthly records, varying between 62% in April and 84% in July (Table 5). There were minor differences from month to month, including general descents in April and in July and some very high-level foraging in August. The months of high summer showed a concentration of activities between 25 and 34 ft.—51% of

records in June, 51% in July and 54% in August. In October and November 1948 there was a fairly even dispersal of foraging between the ground and about 60 ft. In December there was much feeding on the ground (12 or 40 records) and hunting in the trees up to about 50 ft.

In 1949, 305 records were obtained in Wytham Great Wood. In January, 13 of 22 observations were of birds between 20 and 44 ft., and the rest at lower levels. March, April and June generally resembled the spring and summer of the previous year, having 78, 68 and 77% of the records between 20 and 44 ft. But April 1949 differed from April 1948 in a general rise in the foraging levels, as compared with March. In October 66% of 52 observations were of birds between 20 and 44 ft.; by November the proportion within these levels had dropped to 58%, and in January 1950 it was 35%. In January 1950, as in January 1949, the bulk of the records outside the 20–44 ft. limits came from lower heights; but there was no ground feeding. In December 1949 a sample of 154 observations was obtained in Bagley Wood. Of the records 38% came from between the 20 and 44 ft. levels, and 57% from below. These figures are comparable with those obtained in Wytham Great Wood in December 1948 and January 1950.

Table 5. Coal tit. Wytham Great Wood 1948. Percentages of records of feeding activity at different levels

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
20–44 ft.	(57)	71	70	62	82	83	76	84	65	49	39	37.5
> 44 ft.	—	13	12	12	2	2	2	10	4	22	24	10
< 20 ft.	—	15	17	24	15	15	21	4	31	28	39	52

The general disposition of feeding coal tits in Wytham is one of fairly high level activity in spring and summer, with a wider dispersal in autumn through a big range of heights and a drop to lower levels in mid-winter.

(d) *The marsh tit*

The marsh tit is not a bird of gardens and orchards. Of the 1819 records available 88% were made in Wytham Great Wood, 6.7% in Marley Wood and 2.5% in Bagley Wood. The marsh tits of Wytham were much reduced by the hard weather of early 1947. Records were few for the first half of that year. Throughout the period of observation the uniformity of the height distribution of the feeding marsh tits was in marked contrast to the changing dispositions of the great tit. In 21 of the 23 months for which there are adequate figures more than 50% of the feeding records were of birds foraging between < 5 and 19 ft.; in 16 of the 23 months more than 60% of the records lay within them, with maxima of 40 of 45 records in October 1947 and 38 of 44 records in November 1949. Of the records collected in Marley Wood in 1948, 81% in May, 100% in June, 92% in August and 68% in November were within the limits < 5 to 19 ft.

In the winter 1947–48 the proportion of marsh tits recorded as feeding above 19 ft. increased significantly from October to November. There was then no marked change in this proportion until a slight drop in February and a further drop in March. When the 50% of 'high' birds in January is compared with the 29% in March, the decrease

is sufficient to give $P < 0.02$. Through the spring and summer months of 1948 the general height distribution of feeding birds varied only a little. May saw a partial desertion of the lower levels. The percentage of birds feeding below 15 ft. (36%) was less than the 54% of April ($P < 0.05$) and less than the 52% of June ($P < 0.02$). This slight rise to higher levels coincided with the month of greatest abundance of defoliating caterpillars. In July and August there was a little ground feeding, and in August and September the population fed at its lowest levels for the year, 63 and 62% of the records being below 15 ft. In October the feeding level had begun to rise again, and it rose much more sharply in November, when 58% of the records were of birds at 20 ft. or more. Hunting for beech-mast may have accounted for some of this high-level feeding, just as the hunt for fallen mast may have brought some birds to the ground. (There was practically no ground feeding in the mastless autumn of 1947.) In December 1948 there was an unusually large amount of ground feeding, 23 records of 104. Of these 23 records of marsh tits on the ground, 15 were noted as under beech trees.

In January 1949, 56% of 48 records were of birds between < 5 and 19 ft., and there were 8 observations of hunting on the ground. In March the percentage of records between < 5 and 19 ft. had risen to 70%. April showed an increase in the proportion of birds feeding above 20 ft., but the figures are not sufficient to show statistical significance. In June 76% of the records were between < 5 and 19 ft., and no birds hunting on the ground or above 30 ft. The autumn of 1949 showed a concentration of marsh tits below 20 ft., with very little ground feeding. The beech-mast crop of 1949 was markedly smaller than that of 1948. In December 1949 a sample of 47 records was made in Bagley Wood; 43% of the observations were of birds foraging between < 5 and 19 ft., and 15% were of birds on the ground. There are only 18 Wytham records for this month; the proportion of birds between < 5 and 19 ft. (13 of 18) differs from the proportion within these limits in Bagley Wood ($P < 0.05$). But the figures obtained in Bagley Wood in December 1949 do not differ from those collected in the Great Wood in December 1948.

January 1950 closely resembled January 1949 in the disposition of feeding marsh tits. The percentages of records of ground feeding and of foraging between < 5 and 19 ft. were 19 and 58% as against 17 and 56% in 1949.

The marsh tit has the most clearly defined height-distribution of the four titmice. It is the titmouse of the shrub layer and the lowest limbs of big trees.

(e) *The long-tailed tit*

Since long-tailed tits were greatly reduced in numbers by the frosts of early 1947, only casual records of their activities were obtained during the rest of that year. Out of the breeding season long-tailed tits seem to be more nomadic in their habits than the other titmice. Long-tailed tits showed a considerable range of feeding levels. They were rarely recorded as foraging on the ground and not often in the highest twigs (Table 6). In the 13 months for which adequate figures are available (Table 7), more than 50% of the records were at or over 20 ft. in 10 months; more than 60% in seven; and less than 40% in one only, June 1948.

In Marley Wood in 1948, June with 94% of feeding records at less than 20 ft.

showed the least general feeding height recorded, and August with 70% of the observations at or over 20 ft. showed an intensity of upper levels foraging only twice surpassed in the Great Wood. In Bagley Wood in December 1949, 22 of 26 records (86%) were at 20 ft. or more; none was over 44 ft.

The long-tailed tit is, in general, a hunter in the top of the shrub layer and the lower strata of the woodland canopy.

Table 6. *Records of feeding at or above and below the 50 ft. level in blue, coal and long-tailed tits, 1948 and 1949*

	Blue tit	Coal tit	Long-tailed tit
Records of feeding at or above 50 ft.	220	63	22
Records of feeding below 50 ft.	2738	942	555
Total	2958	1005	577

χ^2 values: blue tit:long-tailed tit, -9.96; coal tit:long-tailed tit, -4.37; blue tit:coal tit, less than 2.

Table 7. *Percentages of long-tailed tits feeding at or above the 20 ft. level*

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1948	—	67.5	65	40	—	16	72.5	52.5	96	—	69	52
1949	40	—	—	—	—	—	—	—	—	69	61	—
1950	57.5	—	—	—	—	—	—	—	—	—	—	—

INTER-SPECIFIC COMPARISONS

A survey has been made of the height-distribution of food-seeking activity in each species. The survey suggests that a mechanism of ecological separation exists in differences of vertical distribution. But it is in the single habitat, rather than over several square miles of varied country, that interspecific competition may be actual rather than potential; and in the single habitat comparisons may be made with most reality. The first basis of comparison in the discussion which follows is in the proportions wherein birds of two species were feeding at or above, and below, 20 ft. This level was chosen for two reasons. In many months, and in more than one species, the 20 ft. level patently divided an abundant from a scanty distribution. In addition, and perhaps in explanation of this fact of observation, the dominant species of the 'shrub layer' (blackthorn, elder, hazel, sallow) appear largely as specimens something under 20 ft. tall. The 20 ft. level is, therefore, a rough boundary between the 'shrub layer' and the canopy.

In the first four months of the survey the figures are not separable into the localities of collection. Practically none of the February records came from Wytham; the woods were almost empty of titmice by the end of that most rigorous month (Gibb 1950). In February 1947, despite the snow cover which often prevented the great tits from feeding on the ground, blue tits were recorded feeding at or above 20 ft. significantly more frequently than were great tits. In March and in April blue tits continued significantly more active in the higher levels than were great tits, and were significantly less often recorded foraging on the ground. In these two months coal tits showed relatively more activity at or over 20 ft. than did great tits in March ($P < 0.02$) and relatively less feeding on the ground than did great tits in April ($P < 0.02$). In May 1947 blue tits were still relatively more abundant at or above the 20 ft. level than were great tits, but the difference was much less ($P < 0.05$). This reduction in the difference

between the feeding habits of great and blue tits coincided with the upward movement of the great tits in search of defoliating caterpillars. In this month coal tits did not differ from blue tits in height distribution, but fed significantly more often in the higher levels than did great tits.

(a) *Wytham Great Wood*

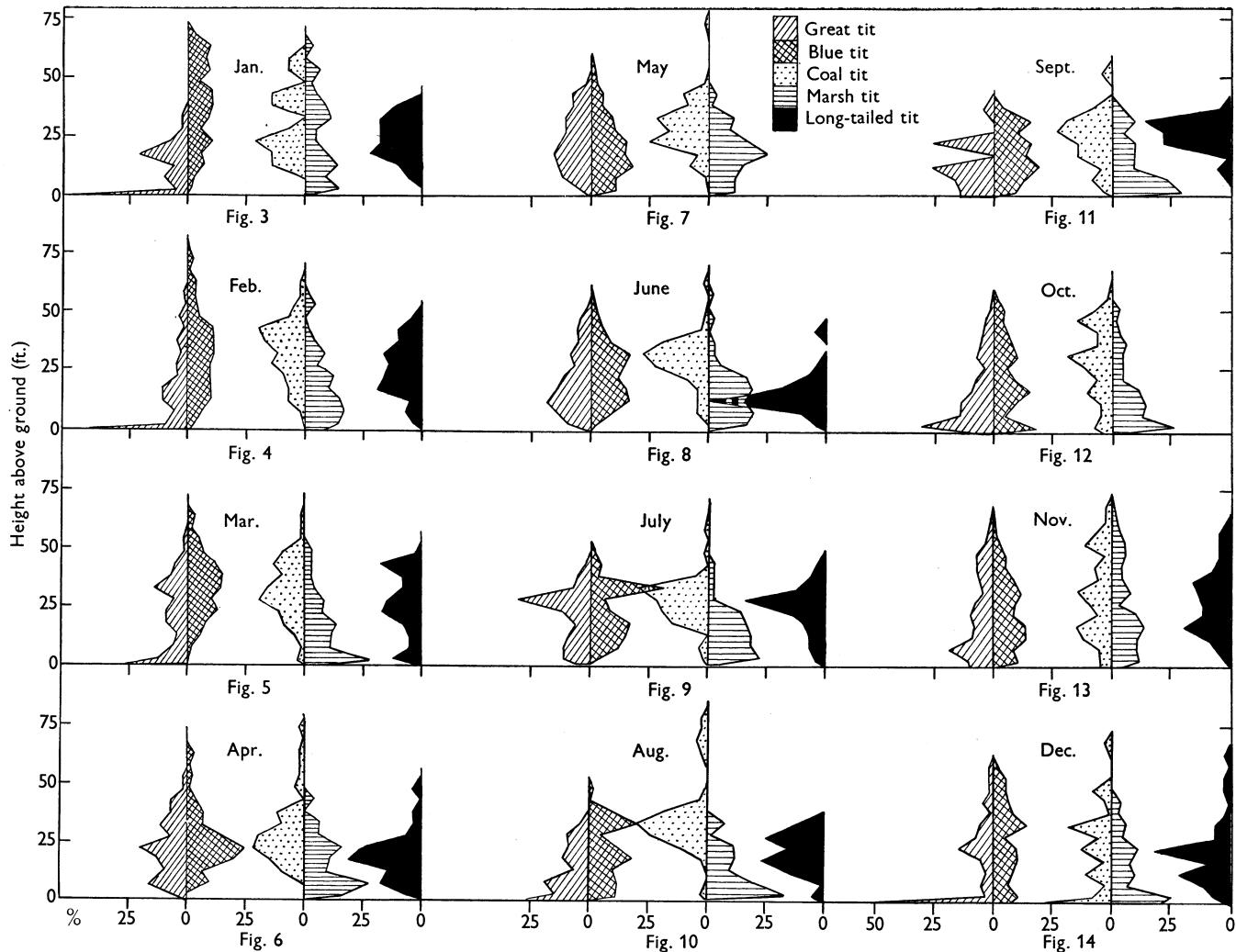
Wytham Great Wood has been selected for discussion in detail for two reasons: all five species of titmice, and also some willow tits, were regularly met there, and the numbers of records for all species greatly exceeded those from any other site. It has already been suggested that difference in height distribution is not the only possible mechanism of ecological separation among species which live intermingled. Birds may feed in trees of different species, or in different parts of the same trees, and the discussion of the feeding behaviour of the Wytham titmice is extended to include these two possibilities.

In October 1947 the number of coal tit records from Wytham Great Wood was too small to give data comparable with those for the other three parids. There was no difference between the height distributions of great and blue tits, but both species were feeding significantly more in the higher levels than were marsh tits. In November all four species were adequately sampled. There was no important difference in the vertical distributions of great and marsh tits, but blue tits were significantly more active in the higher levels than these two species, and coal tits were relatively more numerous at and over 20 ft. than were blue tits ($P < 0.02$). In December the dispositions of great and marsh tits had not much altered. Blue and coal tits were both significantly more active in the higher levels. The blue tit population had shifted a little upward; there was no significant difference in the degrees of activity of blue and coal tits above the 20 ft. level.

In January 1948 (Fig. 3) there was still no difference between blue and coal tits in the general occupation of the higher levels. But now great tits with 22 of 49 records as the proportion of ground-feeding were significantly more abundant below 20 ft. than marsh tits. Marsh tits in turn were significantly more active in the shrub layer (below 20 ft.) than blue tits. In this month long-tailed tits did not differ markedly from blue or coal tits in the proportion of feeding activity above 19 ft.

In February 1948 (Fig. 4) the four Paridae were yet more sharply separated. Great tits fed at the lowest level with 41% of all effort on the ground, significantly exceeding marsh tits in the proportion of birds below 20 ft. Marsh tits were the birds of the shrub layer being significantly more numerous than blue tits below 20 ft. Blue tits came next in the ascending order, and coal tits highest of all: the percentage of coal tits at or over 20 ft. was significantly greater than the percentage of blue tits. The vertical distribution of long-tailed tits closely resembled that of blue tits. In March (Fig. 5) conditions were little altered, save that there was now no significant difference between the proportions of blue and of coal tits foraging at or above 20 ft.

In April (Fig. 6) came a sudden change. The great tits had gone upward, leaving the ground, and did not now differ in feeding levels from blue tits. Marsh and long-tailed tits were the species of the lower levels. Coal tits differed ($P < 0.02$) from great tits in the higher proportion of birds hunting at or above 20 ft.; they were a little, but



Figs. 3-14. Height-frequency distributions of the feeding stations of titmice in Wytham Great Wood, 1948.

not significantly, higher than blue tits. In May (Fig. 7) conditions were not much altered, save that coal tits had moved notably upward, and differed highly significantly from the other three parid species in the proportion of birds recorded at over 19 ft. Great tits slightly exceeded marsh tits in the relative numbers of birds in the upper levels ($P=0.05$), but there was no significant difference in the dispositions of blue and marsh tits. These disappearances or reductions of ecological separations coincided with the summer caterpillar outbreak of 1948. The plague was severe, many oaks being completely defoliated before the end of May.

In June 1948, the caterpillar abundance being over (by 8 June the caterpillars per 100 leaves of oak in two trees were 0.66 and 2.55, as against 48.2, 49.5 and 15.2 caterpillars per 100 leaves on 7 May) the ecological separation of the titmice reappeared (Fig. 8). The coal tit was the species most strongly represented in the upper levels, with blue tits significantly less abundant there. Great tits were more frequent below 20 ft. than were blue tits, and marsh and long-tailed tits were more active in the lower levels than were great tits. The differences between great tits and blue tits, and between great tits and long-tailed tits were both statistically significant (i.e. $P < 0.01$). In the comparison of great and marsh tits, $P < 0.02$). In July (Fig. 9) coal tits still showed the biggest proportion of birds active at or above 20 ft., and marsh tits still the smallest. Long-tailed tits had risen suddenly; the proportion of the sample above 19 ft. did not differ significantly from the proportion in coal tits. The sudden rise in hunting level of great tits in this month has been already mentioned. The cause of this activity in the canopy, which made equal the proportions of the blue and great tit samples above and below the 20 ft. level, could not be ascertained. There remained a significant difference between blue and great tits in the higher proportion of the latter species feeding on the ground.

In August (Fig. 10) coal tits were still more numerous in the higher levels than any other species. Blue and long-tailed tits came next, differing significantly from both great and marsh tits in percentages of birds over 19 ft. There was no difference between the proportions of great and marsh tits recorded below 20 ft., but there were significantly more great tits on the ground. In September (Fig. 11) there was no difference between the percentages of birds below 20 ft. in the blue, great and marsh tit records, but the proportion of great tits hunting on the ground slightly exceeded ($P < 0.05$) the proportion of ground-feeding blue tits. Coal tits were at work at slightly higher levels than the other parids, differing significantly from great and marsh tits. Long-tailed tits were now feeding notably higher than the other species, 24 of 25 records being of birds at or above 20 ft. In October 1948 (Fig. 12) coal tits were significantly more active in the higher levels than the other species, and blue tits significantly higher than great and marsh tits. No long-tailed tits were seen in Wytham. In November (Fig. 13) there were no very striking differences in height distributions. Great tits were at a rather lower level than blue tits ($P < 0.05$) and coal tits ($P < 0.02$). Long-tailed tits showed the highest percentage (69%) of feeding records at heights of over 19 ft. This autumnal period of reduced ecological separation coincided with an abundant beech-mast harvest, and a notable gathering of titmice around the beeches. In December (Fig. 14) blue tits were the species most active above 19 ft. (59% of records). Long-tailed and coal tits were also busy in the higher levels, but

with ground foraging contributing 30% of the coal tit records, that species differed significantly from both blue and long-tailed titmice. Great tits, with ground feeding in half the month's observations, differed significantly from both coal and marsh tits.

In January 1949 there was still some gleaning under beeches, and no very marked ecological separations. Marsh and great tits did not significantly differ, nor did blue, coal, marsh and long-tailed tits. Blue tits showed significantly less ground-feeding than did great tits, and coal tits significantly more birds at or above 20 ft. than great tits did. February records were few. In March blue, coal and long-tailed tits were feeding significantly more above the 20 ft. level than were great tits. In 1949 the 'caterpillar outbreak' was a little later and not quite so large as in 1948. In April considerable ecological separations were still in force. Blue and coal tits were feeding significantly higher than great and marsh tits, and the proportion of ground feeding in great tits exceeded the proportion in marsh tits ($P < 0.05$).

In June 1949, the caterpillar abundance being ended, the dispositions resembled those of June 1948. Coal tits were most frequently found at or above 20 ft., with blue tits next in order, great tits lower than blue tits and marsh tits showing the highest proportion of birds active in the 'shrub layer'.

The height distributions of the titmice in October 1949 resembled those of October of the previous year. Coal tits showed the greatest activity at or above 20 ft., blue tits being significantly less frequent in the upper levels than coal tits, and significantly more frequent there than either great tits or marsh tits. Great tits were more active on the ground than marsh tits ($P < 0.02$). The hunting levels of long-tailed tits were similar to those of coal tits. November 1949 repeated the conditions of November 1948. Blue, coal and long-tailed tits did not differ in the proportions of records at or above 20 ft., and all showed a significantly greater activity in the 'high levels' than did great and marsh tits. Marsh tits fed rather less on the ground than did great tits ($P < 0.05$). December 1949 showed much the same situation as November, but the difference between the amount of ground foraging by great tits and marsh tits had significantly increased. In January 1950 the same general dispositions of feeding birds continued—blue, coal and long-tailed tits fairly high, marsh tits in the 'shrub layer' and great tits largely on the ground.

After the discussion of the height distributions of feeding activities, possible preferences of different species of titmice for different trees must be considered. No species of tree in the wood went unvisited, but four species and one group of species were worked far more intensively than the rest: these were ash, elder, oak, sycamore and 'conifers'. Table 8 shows the frequencies of visits by the five species of titmice to these five feeding places, and also the total numbers of trees visited, data being massed for the quarters of the year. The results are shown graphically in Fig. 15, in which it is seen that there were differences in the utilization of the five most frequently visited trees by the five species of birds. χ^2 tests were made, comparing each species with every other, of the statistical significance of these differences. Table 9 shows the results of these calculations, with a summary below, showing the number of quarters in which each species was significantly ($P < 0.01$) more often in each of the five trees than any one of its related species. A titmouse haunting one tree more frequently than the other

four species in every quarter would score a total of 16 'predominances'; and this the coal tit in conifers in fact did.

Fig. 15 and Table 9 show that, in Wytham Great Wood, of four members of the genus *Parus* the blue tit was the titmouse of oaks, the great tit the titmouse of sycamores, the coal tit the titmouse of conifers and the marsh tit the titmouse of elders.

Table 8. *Records of feeding activity of titmice in certain trees. Wytham Great Wood, 1947-50*

	Total	Jan.-Mar.	Apr.-June	July-Sept.	Oct.-Dec.
BLUE TIT					
Ash	294	72	108	20	94
Elder	259	38	29	43	149
Oak	1200	443	301	97	359
Sycamore	585	224	100	34	227
'Conifers'	260	48	78	32	102
Total trees	3484	1083	814	320	1267
GREAT TIT					
Ash	84	9	39	7	29
Elder	194	42	31	23	98
Oak	393	46	162	50	135
Sycamore	415	62	116	94	143
'Conifers'	91	22	28	20	21
Total trees	1642	247	538	236	621
COAL TIT					
Ash	113	39	33	13	28
Elder	31	3	3	4	21
Oak	231	80	69	21	61
Sycamore	99	42	17	7	33
'Conifers'	628	115	191	170	152
Total trees	1201	308	334	220	339
MARSH TIT					
Ash	103	31	23	14	35
Elder	293	77	68	28	120
Oak	372	120	97	36	119
Sycamore	187	45	31	25	86
'Conifers'	70	20	21	11	18
Total trees	1448	352	340	176	580
LONG-TAILED TIT					
Ash	64	10	8	5	41
Elder	47	24	3	5	15
Oak	112	59	9	16	28
Sycamore	134	70	16	15	33
'Conifers'	116	24	6	52	34
Total trees	620	231	67	123	199

The position of the long-tailed tit was less clear, but it seemed to be a bird of ashes, sycamores and conifers rather than oaks and elders. The long-tailed tit was the only species showing a marked seasonal change in choice of feeding trees. It was predominant in ashes only in the last quarter of the year. In sycamores it showed six predominances out of a possible eight in the first half of the year and only one in the second: in conifers it showed one predominance in the first half of the year and six out of a possible eight in the second. The disappearance of the predominance of marsh

tits over blue tits in elders during the third quarter, and the appearance of blue tit predominances over coal and long-tailed tits at the same season reflected the blue tit's fondness for elder berries.

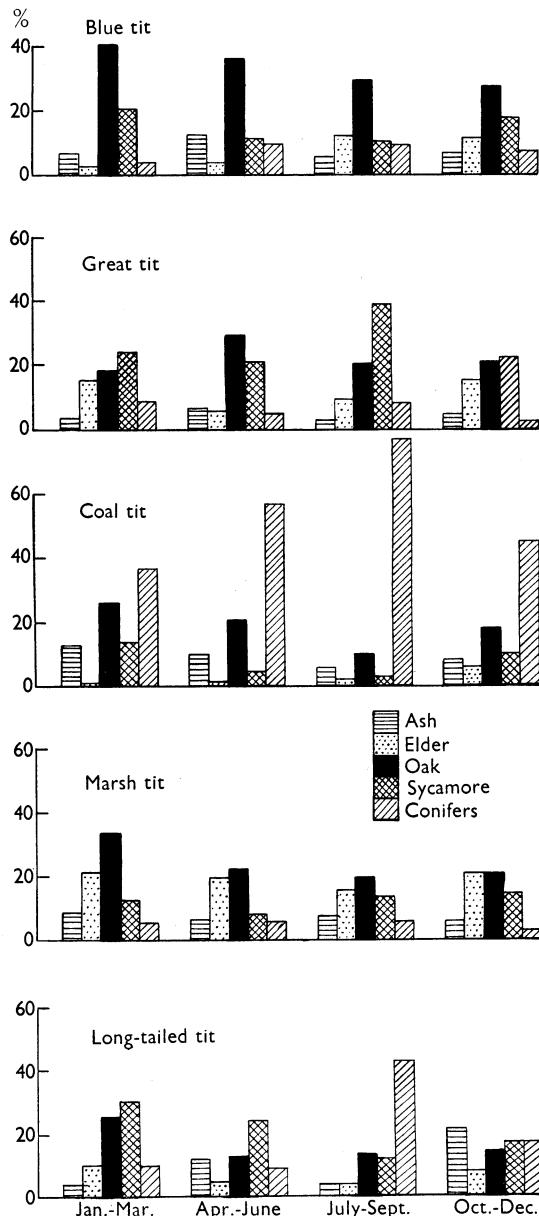


Fig. 15. Comparative frequencies of feeding visits of titmice to certain species of tree in Wytham Great Wood in the four quarters of the year, 1947 to 1950.

A third possible separation in feeding habits is in foraging in different parts of the trees—among leaves, along twigs or branches or on the trunks. Observations on this subject have been assembled in the same manner as those on utilization of different trees. Table 10 shows the frequencies of records of hunting by the five species of

Table 9. Values of χ^2 in comparisons of frequencies of feeding visits to different trees in Wytham Great Wood, 1947–50. Below—the ‘predominances’ in the different trees

Quarters of the year	... I	Ash				Elder				Oak				Sycamore				Conifers				
		II	III	IV	I	II	III	IV	I	II	III	IV	I	II	III	IV	I	II	III	IV		
Blue tit:																						
Great tit	—	12.11	—	5.9	—	—	—	—	43	6.88	5.82	8.99	—	—	—	—	—	8.54	—	15		
Coal tit	—	—	—	—	5.28	6.2	7.93	8.71	22.7	29	25.5	14.8	11.6	13.85	10.7	13.18	—	—	—	—		
Marsh tit	—	10.1	—	—	—	—	—	—	5.8	6.9	5.62	12.61	10.83	—	—	—	—	—	—	—	16	
Long-tailed tit	—	—	—	—	—	—	9.16	—	19	15.05	13.58	17.9	—	—	—	—	—	—	—	—	—	
Great tit:																						
Blue tit	—	—	—	—	63	—	—	—	5.92	—	—	—	—	21	66.6	6.88	8.04	—	—	—	—	
Coal tit	—	—	—	—	47.7	13	13.5	18.75	—	13.23	—	—	11.81	42.2	89	25.8	—	—	—	—	—	—
Marsh tit	—	—	—	—	—	—	—	—	—	—	—	—	15.1	23.2	5.38	13.1	—	—	—	—	—	—
Long-tailed tit	—	—	—	—	4.56	—	—	8.54	—	8.39	—	5.52	—	—	34.2	—	—	—	—	—	—	—
Coal tit:																						
Blue tit	12.49	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	24.9	276	250.5	271		
Great tit	17.6	—	20.78	3.8	—	—	—	—	3.86	—	6.1	—	—	—	—	—	—	59.2	371	218.2	256	
Marsh tit	3.95	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	107	202	198.6	248		
Long-tailed tit	11.05	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	50	519.5	42.2	42.3		
Marsh tit:																						
Blue tit	—	—	—	—	133.5	83.5	—	25.5	—	—	—	—	—	—	—	—	—	—	—	—	—	
Great tit	6.19	—	5.7	—	—	42	—	4.85	17.43	—	—	—	—	—	—	—	—	—	—	—	—	
Coal tit	—	—	—	—	67.4	64.5	39.3	34.55	5.12	5.6	8.44	—	—	—	4.14	16.02	4.9	—	—	—	—	
Long-tailed tit	4.89	—	—	—	12.72	9.37	10.33	17.9	—	6.46	—	—	—	—	—	—	—	—	—	—	—	
Long-tailed tit:																						
Blue tit	—	—	—	—	35.4	20	—	—	—	—	—	—	11.7	7.74	—	—	13.1	—	70	16.65		
Great tit	—	—	—	—	49	—	—	—	—	—	—	—	—	—	—	—	—	—	57.3	45.3		
Coal tit	—	—	—	—	39.96	25.4	4.86	—	—	—	—	—	14.7	27.1	10.64	5.49	—	—	—	—	—	
Marsh tit	—	5.12	—	36.1	—	—	—	—	—	—	—	—	26.88	11.84	—	—	—	—	56.3	46.6		
‘PREDOMINANCES’ (probability of 0.01)																						
Blue tit	—	2	—	—	3	—	—	—	13	—	—	—	5	—	—	—	—	3	—	—	—	—
Great tit	—	—	—	—	6	—	—	—	2	—	—	—	11	—	—	—	—	1	—	—	—	—
Coal tit	—	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	16	—	—	—	—
Marsh tit	—	—	—	—	12	—	—	—	2	—	—	—	—	—	—	—	—	1	—	—	—	—
Long-tailed tit	—	4	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	7	—	—	—	—

titmice in four different hunting places: leaf, twig, branch (and limb) and trunk. The data are masses for the four quarters of the year. Fig. 16 illustrates these data; Table 11 gives the results of calculations of significance of frequency differences, with a summary showing the number of quarters of the year where in each species of titmouse was predominant at work in any one hunting place over another species.

Table 10. *Utilization of different feeding places in the four quarters of the year. Wytham Great Wood, 1947–50*

	Total	Jan.–Mar.	Apr.–June	July–Sept.	Oct.–Dec.
BLUE-TIT					
Leaf	421	20	218	56	127
Twig	1884	763	257	153	711
Branch	209	64	37	9	99
Trunk	140	59	1	12	68
Total	2654	906	513	230	1005
GREAT TIT					
Leaf	193	3	118	28	44
Twig	746	175	150	108	313
Branch	169	24	40	17	88
Trunk	66	11	9	7	39
Total	1174	213	317	160	484
COAL TIT					
Leaf	170	25	48	46	51
Twig	624	199	175	81	169
Branch	122	31	24	11	56
Trunk	64	8	7	16	33
Total	980	263	254	154	309
MARSH TIT					
Leaf	143	1	87	20	35
Twig	570	204	84	55	227
Branch	206	74	24	20	88
Trunk	77	26	12	7	32
Total	996	305	207	102	382
LONG-TAILED TIT					
Leaf	12	—	5	6	1
Twig	481	162	33	114	172
Branch	16	10	2	2	2
Trunk	9	2	1	1	5
Total	518	174	41	123	180

Differences were less pronounced than in the visitation of different trees, but the long-tailed tit was markedly the titmouse of twigs, with fifteen out of sixteen possible predominances. The marsh tit, with nine out of a possible sixteen predominances, was the titmouse of branches, and the coal tit, with eight out of a possible sixteen, showed the highest number of predominances in leaves and needles. The blue tit was more often predominant as a hunter among leaves and along twigs than as a searcher of branches and boles. It has earlier been shown that the great tit was often predominant on the ground.

Fig. 16 shows that the proportionately small amount of leaf feeding by coal tits in the second quarter of the year, in comparison with the other four species, was not attributable to a decrease in leaf feeding by coal tits but to a very marked increase in

leaf searching by the other titmice. This increase in leaf searching coincided with the increase in the populations of leaf-feeding caterpillars in the early summer. The high frequency of leaf hunting by coal tits in the first and last quarters of the year resulted from the species' preference for coniferous trees. In the autumn of 1949 coal tits were active in probing between the thick-clustering keys of ash. Odum (1942) found con-

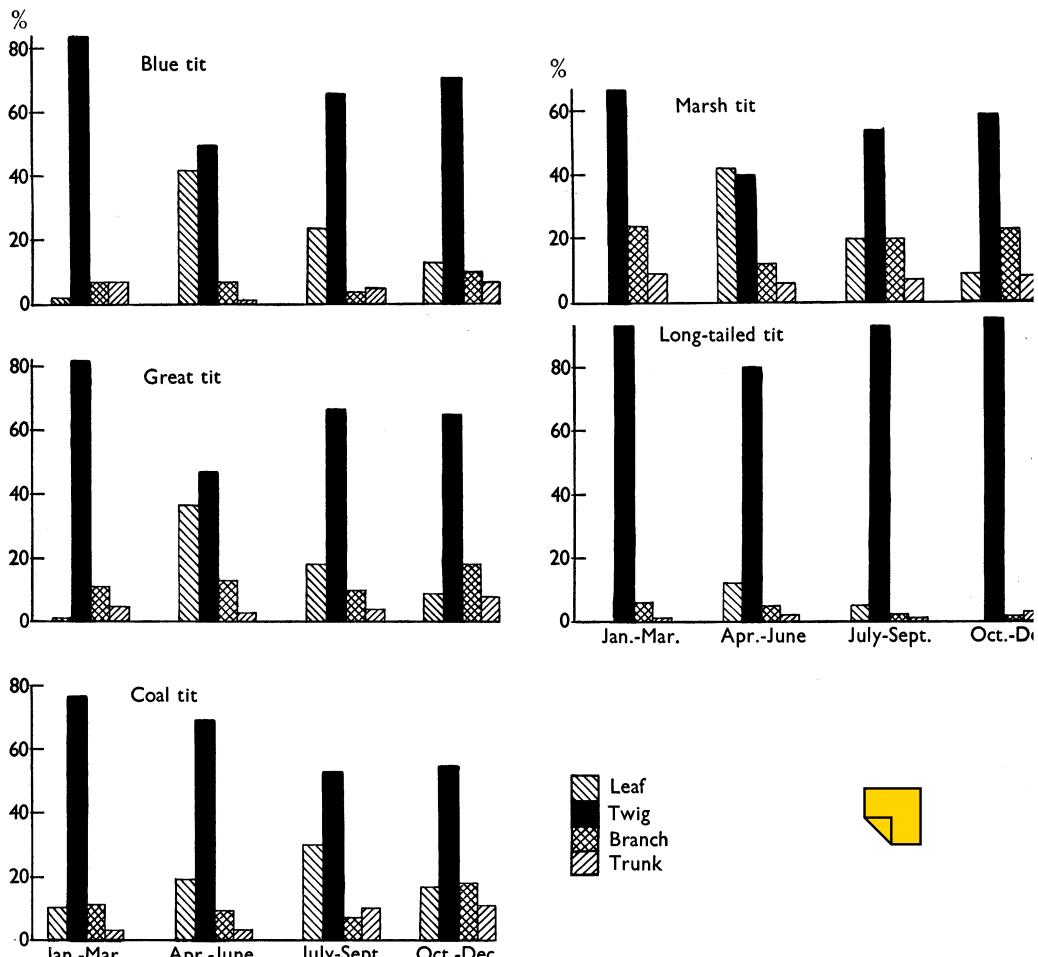


Fig. 16. Comparative frequencies of feeding visits of titmice to different parts of trees, Wytham Great Wood in the four quarters of the year, 1947 to 1950.

siderable seasonal variation in the feeding places of *Parus (Penthestes) a. atricapillus*. Fig. 16 also shows how little the flush of leaves in early summer affected the feeding place of the long-tailed tits.

It is not suggested that all the mechanisms of ecological separation between titmouse species have been explored. But it has been shown that in Wytham Great Wood the five species of titmouse there living intermingled are separated in three different ways—in foraging at different heights, in searching of different trees and in seeking food in different parts of those trees. Not all the species are separable all the time; but no two are identical in their feeding behaviour.

Table 11. *Values of χ^2 and 'predominances' in comparisons of frequencies of feeding visits to different parts of trees. Wytham Great Wood, 1947-50*

Quarters of the year	...	Leaf				Twig				Branch				Trunk			
		I	II	III	IV	I	II	III	IV	I	II	III	IV	I	II	III	IV
Blue tit:																	
Great tit		—	—	—	4.03	—	—	—	6.22	—	—	—	—	—	—	—	—
Coal tit		—	41.9	—	—	10.25	—	7.5	28.45	—	—	—	—	4.53	—	—	—
Marsh tit	4.73	—	—	—	—	42.2	5.16	4.53	16.4	—	—	—	—	—	—	—	—
Long-tailed tit	3.93	14.45	120.7	21.1	—	—	—	—	—	—	—	—	14.82	8.75	5.3	4.38	4.21
Great tit:																	
Blue tit		—	—	—	—	—	—	7.51	7.9	3.99	6.82	6.86	20.6	—	11.53	—	—
Coal tit		—	22.9	—	—	—	—	7.6	—	—	—	—	—	—	—	—	—
Marsh tit		—	—	—	—	14.8	—	—	—	—	—	—	—	—	—	—	—
Long-tailed tit		—	10	10.41	15.1	—	—	—	—	—	—	9.36	32.6	4.73	—	—	12.16
Coal tit:																	
Blue tit	32.7	—	—	—	—	24.6	—	—	5.6	—	—	—	17.2	—	11	—	5.16
Great tit	13.59	—	—	9.78	—	29.95	—	—	—	—	—	—	—	—	—	4.16	—
Marsh tit	24.65	—	—	8.5	—	37.3	—	—	—	—	—	—	—	—	—	—	—
Long-tailed tit	16.12	—	27.95	29.92	—	—	—	—	4.49	—	4.64	31.8	—	—	10.93	—	6.01
Marsh tit:																	
Blue tit	—	—	—	—	—	—	—	—	64.8	—	20.5	41.5	—	25.9	—	—	—
Great tit	—	—	—	—	—	—	—	—	13.78	—	4.16	—	21.4	—	—	—	—
Coal tit	—	29.4	—	—	6.9	—	—	—	14.65	—	8.95	—	—	—	—	—	—
Long-tailed tit	—	13.1	11.83	15.05	—	—	—	—	21	—	20.58	44	10.89	—	5.95	—	6.01
Long-tailed tit:																	
Blue tit	—	—	—	—	—	9.39	13.36	30.6	46.4	—	—	—	—	—	—	—	—
Great tit	—	—	—	—	—	10.25	16.1	26.2	64	—	—	—	—	—	—	—	—
Coal tit	—	—	—	—	—	22.6	—	52.6	89.5	—	—	—	—	—	—	—	—
Marsh tit	—	—	—	—	—	42.4	22	45	78.3	—	—	—	—	—	—	—	—
'PREDOMINANCES' (probability 0.01)																	
Blue tit		4				5				1				1			
Great tit		4				4				5				2			
Coal tit		8				3				2				2			
Marsh tit		4				1				9				3			
Long-tailed tit		—				15				—				—			

In the village of Brightwell-cum-Sotwell the summer titmouse population was small. The winter population consisted of many great and blue tits and a few coal tits.

In the autumn of 1947 there was no difference in the height dispersal of great and blue tits in September. In October and November blue tits were significantly more active at or above 20 ft. In December there were few observations of either species above 19 ft., but great tits were significantly the more occupied upon the ground.

In January 1948 there were few great tit observations, but blue tits were tending to seek higher levels, so that in February blue tits were more active ($P < 0.02$) than great tits at or above the 20 ft. level. There were no significant differences between the two species in March.

In July 1948 there were more blue tits than great tits at work above 19 ft. ($P < 0.05$), and in August significantly more great tits were foraging on the ground. In the three autumn months, September, October, November, with the great harvest of walnuts, no marked differences were found between the two species. In December 1948 and in January and February 1949 great tits were significantly more active on the ground than were blue tits. In the two latter months there was also statistical significance in the larger percentages of blue tits above 19 ft. In March 1949 there were still significantly more great tits than blue tits feeding on the ground, but the great tits had extended their feeding range upward, and there was no important difference in the hunting activities of the two species above 19 ft.

In the four months October 1949 to January 1950 there were no significant differences in the proportions of great and blue tit records at 20 ft. and more, but in every month relatively more great tits were feeding on the ground (P in the first three months 0.01, in the fourth 0.05).

In 1947 there was no walnut crop, and as soon as the elder berries were eaten (October) ecological separation appeared between blue and great tits. In 1948 the elder harvest was followed by a bumper crop of walnuts, and there was no ecological separation between the two species until December. In 1949 there was an average walnut crop. In October and November (there were no September observations) there were no differences in high-level feeding but there was more ground-feeding in great tits than in blue tits. It would seem that the effect of the walnut harvest was to make some great tits work upward in search of nuts still on the twigs, and that many shattered nuts lying below the trees would bring the blue tits down to feed on them.

The number of coal tits observations from Brightwell was too small for more than a general statement. In the second half of 1947 and the first quarter of 1948 coal tits at Brightwell were more active than blue tits at or above 20 ft. In the first quarter of 1949 there was no significant difference from blue tits.

(c) *North Oxford*

In north Oxford the titmouse population was greatly augmented in winter, blue and great tits appearing in numbers. In 1947 figures sufficient for the comparison of these two species were obtained in June, July and September to December. In all these months, save October, blue tits were significantly the more active at heights of 20 ft. and above. In October, with some beech-mast, there was no significant difference

between the two species, either in the proportions of activity above and below 20 ft. or in relative frequency of ground-foraging.

From January to May 1948 blue tits showed a consistently higher proportion of records of birds feeding at or above 20 ft. than did great tits, and very much less activity on the ground. In September and October 1948 with a heavy crop of beech-mast there were no significant differences between blue and great tits either at 'high-levels' or on the ground. In November 1948, though many blue tits were still seeking fallen beech-mast, the proportion of ground-feeding birds was now significantly less than in the great tit and the proportion of 'high-level' birds was significantly more. In December 1948 there were no blue tits foraging on the ground as compared with 70% of the great tit records. January to March 1949 saw blue tits in north Oxford consistently more active in the higher levels than the great tits and far less active on the ground.

In the following winter there were few blue tits before December 1949: in that month and in January 1950 blue tits were again proportionately more frequent at or above 20 ft. and great tits more frequent upon the ground.

In general the height distribution of feeding coal tits in north Oxford differed little from that of the blue tits. May 1947 when coal tits were feeding unusually low was an exception to this generalization.

(d) Bagley Wood

In one month, December 1949, the titmice of Bagley Wood were sampled. The general relationship between four of the five species resembled the usual mid-winter situation in Wytham Great Wood. Great tits were feeding at the lowest levels. The proportion of records from below 20 ft. and the percentage of ground-feeding activity were significantly greater than in all the other species. Blue tits showed a significantly larger proportion of birds hunting at or above 20 ft. than did two other members of the genus *Parus* (great tit and coal tit) and some excess over the marsh tit ($P < 0.05$). Long-tailed tits were at the highest general level, significantly exceeding the other titmice in the proportion of records at or over 20 ft. Marsh tits and coal tits did not differ significantly in their distributions about the 20 ft. level, and occupied an intermediate position between the great tits and the blue tits.

DISCUSSION

The general ecological relationship between the titmice of English woodlands is very similar to that described by Lack (1947) in *Darwin's Finches of the Galapagos*: '...ecological divergence has mainly taken the form of difference in food habits, in which case the species are not forced to occupy separate habitats, but can exist side by side.' It has been shown that in an area of English country the species of titmice are ecologically separated by their feeding habits; that each species has its characteristic height distribution, fixed or varying seasonally; that each species has its favoured foraging trees, and a tendency to seek its food in different parts of those trees; and that no two species are identical or even consistently similar in their food-seeking behaviour.

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Palmgren (1930) found that in southern Finland, great, blue and long-tailed tits were the titmice of deciduous trees, and coal tits the titmice of spruce. In Holland, Kluijver (1951) describes great tits as preferring 'broadleaved deciduous woods to conifers'.

In July and August 1948, Snow (1949) investigated the height distribution of feeding titmice in the woods near Uppsala, Sweden. He found that

The great tit fed at all heights, and showed a slight preference for spruce. It dominated the mixed flocks, usually keeping high.

The blue tit was constantly high. The high proportion of records from pine was due to the preponderance of pine at the height preferred.

The coal tit strongly preferred spruce, feeding particularly on the twigs and needles...it was rather less social than the other tits.

The crested tit and the willow tit fed at all heights and showed no preference for pine or spruce. In flocks dominated by great tits they kept low, but when by themselves they were seen feeding at all heights.

The marsh tit showed a preference for feeding low down, especially in small trees. It preferred deciduous trees where they were available.

Snow observed the great tit to feed more frequently on the ground than any other titmouse species. Similarities to feeding habits in England are striking—ground feeding in great tits, high-level foraging in blue tits, the activities of coal tits in seeking among the needles of conifers, the preference of marsh tits for low levels.

Table 12. *Comparison of height distributions of feeding titmice in Wytham Great Wood and at Brightwell, 1947–50*

	Blue tit	Great tit
Number of months compared	22	16
Number of months with a difference in height distribution	17	10
Number of months with a higher proportion of Brightwell birds at or above 20 ft.	0	3
Number of months with a lower proportion of Brightwell birds at or above 20 ft.	17	7

Colquhoun & Morley (1943) surveyed the vertical zonation of twelve species of bird, including five titmice, in Bagley Wood in the winter of 1941–42. They arranged the titmice in the descending order blue tit, long-tailed tit, coal tit, marsh tit, great tit: but their records were not confined to feeding birds (only 56% of the great tits observed were feeding), and the observations of seven months were massed in a single calculation for each species. Their results are scarcely comparable with those above set forth in a degree which justifies detailed discussion.

The effect of the presence or absence of one species upon the feeding habits of another, such as that described by Snow (1949) in Sweden, is not easy to establish. Variations in the dispersals of the feeding birds may be seen in communities of different composition, but the casual connexion can only be assumed. When the feeding habits of the blue and great tits of Wytham Great Wood are compared with those of the Brightwell birds, the height distributions of the blue tits are seen to differ consistently in the two areas, whereas there is little consistent difference between the habits of the great tits (Table 12). Marsh tits were very rarely seen in Brightwell, and in that area blue tits fed notably more in the lower levels than they did in the Great Wood. Such differences in distribution are at least amenable to the explanation that in the Wytham woods blue tits were excluded from the lower levels by the pressure

of competition with marsh tits. But a second possible explanation must be noticed. In the village many people feed wild birds at bird tables, and the blue tits may have acquired the habit of seeking food at unusually low levels. Snow (1952) found that in arctic Lapland great tits are entirely dependent on human habitations for their livelihood.

It may be advanced that no proof has been given of the immediate ecological relevance of the differences of routine observed. The feeding habits as now seen may have had survival value in times past but may bear no present relation to the food supplies and requirements of the titmice. Were the feeding habits of each species fixed and unvarying, as for example are general patterns of song, this objection would be a serious one. But it has been shown that the feeding habits of the titmice are variable from season to season and from place to place, and that in the majority of cases a variation in feeding behaviour can be correlated with a variation in food supply. The upward movements of great tits and marsh tits at the time of appearance of the summer caterpillar harvest; the hunting in beeches in the good mast year of 1948 (Table 13); the effect of the Brightwell walnut harvest of 1948 on the blue tits of that village may be cited as striking examples of the adaptability of foraging behaviour.

Table 13. *Records of feeding in beeches (expressed as percentages of total numbers of trees visited) in Wytham Great Wood in October and November*

	Great tit	Blue tit	Coal tit	Marsh tit
1947	0	0·6	0	2·54
1948	19	6·3	4·2	8·7
1949	0	0	0	0

It has been shown that when, as in the early months of summer and in autumn, ecological separations between two or more species have disappeared there has been available in that period a temporarily superabundant supply of food. With the ending of that abundance the different species have returned, each after its kind, to the accustomed and separate foraging places. Were suitable foods always to be found in superabundant measure, the evolutionary significance of the segregation of the different species for so large a part of the year (and the temporary disappearance of these segregations) would be difficult to explain. But the regular appearance of separating mechanisms as soon as patently rich supplies of food are exhausted urges that pressure upon food stocks 'which gives the ultimate limit to which any species can increase' (Darwin 1859) is such that the force of intra- and interspecific competition working in combination must be avoided.

The influence of food supply upon the populations of the different species of titmice has not been proven. But the foraging habits here described are such that their survival value may be traced to the partial separation of each species from the others and the resulting diminution of interspecific competition. Only by the evolution of specialization of feeding habits are several closely allied species able to occupy and to exploit a single habitat. These specializations the English titmice show.

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SUMMARY

1. The feeding habits of five species of titmouse in an area in the English Midlands have been observed over a period of three years.
2. It is shown that each species of titmouse has a characteristic height distribution of foraging activities, and preferences for certain species of trees and parts of trees. The height distribution of some species varies from season to season, and may be modified by an unusual abundance or lack of some food.
3. It is shown that the height-frequency distribution of the foraging activities of each species, and also the favoured feeding tree, differ from those of the other four species.
4. From time to time the ecological separations between different species have been found to disappear. It has been possible to show that these extinctions of ecological separation have coincided with temporary superabundances of food.
5. The ecological implications of the differences in feeding habits are discussed.

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