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Some aspects of the feeding ecology of four small insectivorous birds in Hamsterley Forest, County Durham

by Steve Moon, BSc (East Anglia)

A dissertation submitted as part of the requirements for the degree of Master of Science.

University of Durham.

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Part One: Introduction

The field observations summarised below were made between April and July 1974 at Hamsterley Forest, County Durham, during an investigation into the use made of a small area of deciduous woodland by four species of insectivorous bird. The aim of this study is to consider the various ways in which coexisting bird-species differ from each other in their use of resources. These differences evolved by species were termed 'ecological isolation' by Moreau (1948), and a qualitative study of them has been made by Lack (1971).

Charles Darwin (1859) discussed in detail some of the implications of coexistence between ecologically related forms:

> '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.'

The theoretical development of the concept of the 'niche' (Steere 1894; Grinnell 1904, 1917) gradually led to the realisation that the interactions between species are potentially independent of phylogenetic affiliation. Elton (1927) stressed that the niche was comparable to the role of a species in a community:

> 'When an ecologist says "there goes a badger", he should include in his thoughts some definite idea of the animal's place in the community to which it belongs, just as if he had said "there goes the vicar".'

Later, the niche concept was firmly welded with ideas on competitive exclusion after Gause (1935) had carried out his experiments to test the competition-equations formulated by Volterra (1926):

> '...as a result of competition two similar species scarcely ever occupy similar niches, but displace each other in such a manner that each takes possession of certain peculiar kinds of food and modes of life in which it has an advantage over its competitor.'

The basis for considerable development of the niche concept was provided by Hutchinson (1958). He defined the niche as a multi-dimensional space, with each dimension corresponding to a different requirement of a species.

Ecological isolation is most obvious among groups of related species that show non-overlapping ranges on a resource parameter such as vertical feeding range, or size of food-items. If ecologically similar species can be arranged in a series of partially overlapping distributions on some resources parameter they form what Cody (1974) terms a 'displacement pattern'. These patterns, he argues, are circumstancial evidence for the importance of competition as a factor in community composition and organisation. In addition they are pointers to the sorts of resources for which bird species compete.

Most studies aiming to describe the circumstances in which similar species are able to coexist in the same general habitat, have tended to stress the importance of spatial and temporal patterns relating to food-supply or foraging-behaviour which minimise competition for food and so avoid local extinction (Edington 1972; Morse 1970, 1971). Spatial separation is not, however, the only mechanism that would allow coexistence. Species may use the same space, but take different food - a situation often closely linked with differences in bill-size (Schoener 1965). It is also theoretically possible for two species that share the same food, and show no spatial separation, to coexist if their numbers are regulated below their food-resource level (Marshall 1960).

The present study concentrates on the identification of differences in the utilisation of a mixed woodland for feeding by redstart (*Phoenicurus phoenicurus* (L.)), pied flycatcher (*Ficedula hypoleuca* (Pall.)), willow warbler (*Phylloscopus trochilus* (L.)) and wood warbler (*Phylloscopus sibilatrix* (Bechst.)).

Part Two: Description of Study Area

Hamsterley Forest consists of approximately fifteen square kilometres of Forestry Commission conifer-plantation in Weardale, County Durham. In altitude the forest extends from 160 to 425 m., stretching up onto moorland on the edge of the Northern Pennine range. The study area extends over 6.9 ha. and lies at 200 m. near the north-east boundary of the forest in the valley of Euden Beck.

The site is in two main sections divided by Euden Beck. The woodland section lies on the north side of the beck, its damp floor rising steeply to meet the ranks of conifers that hem it in on this side. On the south side of the stream the site is open, resembling parkland. A belt of mature trees, mainly oak (Quercus robur L.), with scattered hawthorn (Crataegus sp.) and birch (Betula pubescens Ehrh.), forms the southern boundary of this section, and this is backed by dense birch-scrub mixed with young Norway spruce (Picea abies (L.)), about one to three metres in height.

The heterogeneous nature of the woodland habitat is shown well in the accompanying air-photograph of the site (Figure 1). The main area, Grove Wood, is a birch-ash wood with oak standards. There is no grazing-pressure from domestic animals, and the ground vegetation is dominated by grasses. Bracken (Pteridium aquilinum L.) is important in the drier parts of the wood. The shrub layer is only locally dense, and dominated by ash (Fraxinus excelsior L.), birch and alder (Alnus glutinosa L.), with scattered rowan (Sorbus aucuparia L.), hawthorn and holly (Ilex aquifolium L.).

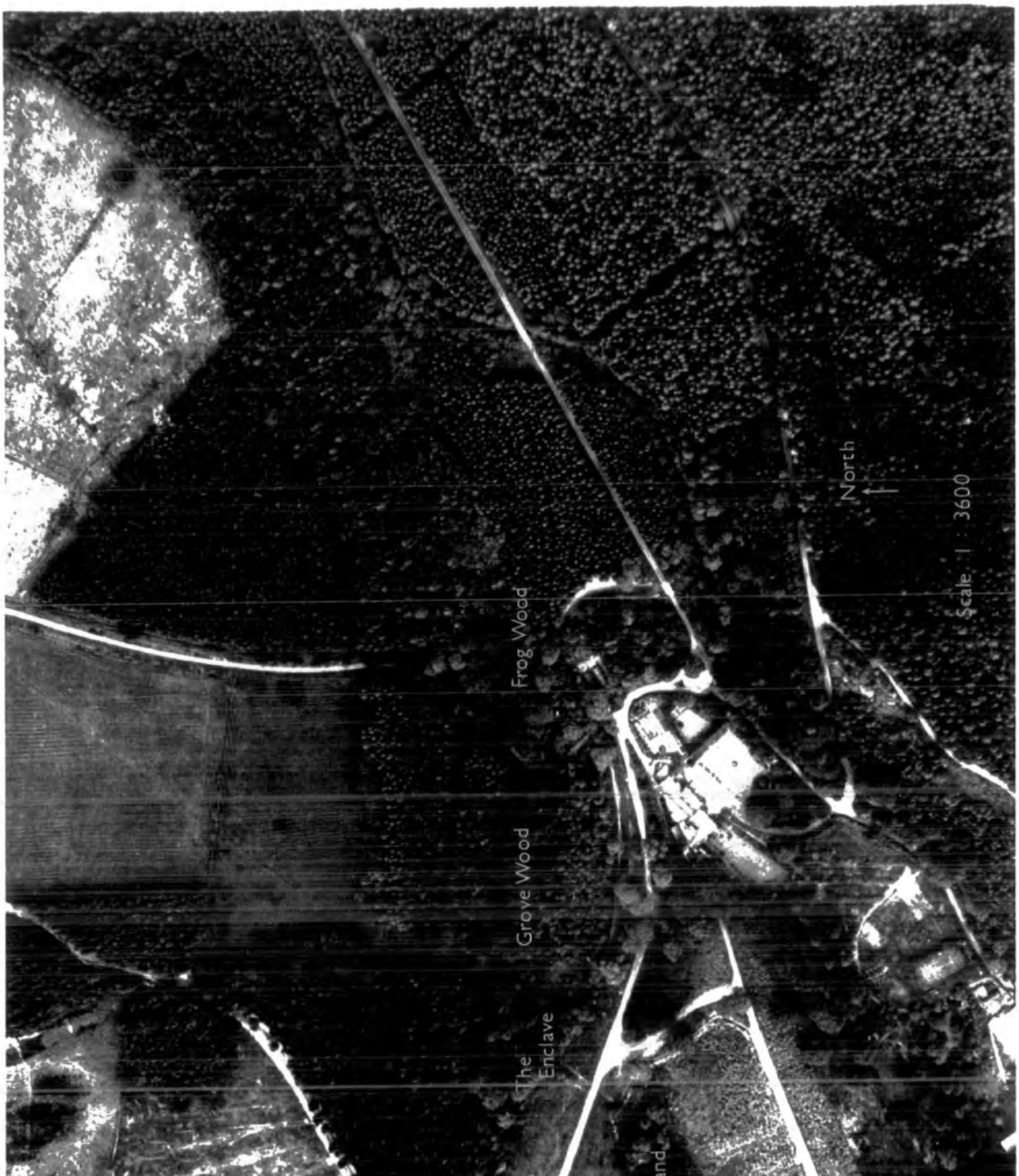


Figure 1 Air-photograph of study area

The canopy is dominated by birch, with ash, alder, sallow (Salix spp.), and a number of large oaks (Plate 1a).

A broad firebreak, colonised by birch-shrub, grasses and bracken, separates Grove Wood from a small enclave of mature trees to the west. The shrub layer here is very sparse, with birch and ash predominating, but consists of a variety of plants, including sallow, oak, rowan, beech (Fagus sylvatica L.), and hazel (Corylus avellana L.). The canopy is made up of large oaks and limes (Tilia X europaea L.), Scots pine (Pinus sylvestris L.) and the occasional yew (Taxus baccata L.) and horse chestnut (Aesculus hippocastanum L.). Frog Wood (Plate 2a) marks the eastern boundary of the study site, and is similar, with the canopy dominated by large oaks, limes and Scots pines. Sycamore (Acer pseudoplatanus L.), ash and horse chestnut also occur as canopy-trees, and the shrub layer has a good number of hawthorn, rowan and holly among the birch and ash saplings. The ground vegetation of Frog Wood is again dominated by grasses, but bilberry (Vaccinium myrtillus (L.)), ferns and mosses occur as local dominants.

A number of nest boxes have been put up in the study area as part of a ringing scheme in the forest, and these supplement the few natural holes afforded by mature and senile trees on the site. The take-up rate of these boxes was very low in 1974. Only three pairs of pied flycatcher were found in Hamsterley Forest (P. Yeoman, pers. comm.) and one pair's nest was destroyed. One pair of pied flycatchers nested successfully in a brand new box in the study area. This box had been placed

Plate 1 (a) Part of Grove Wood

(b) Wood warblers nest in Grove Wood

Plate 2 (a) Frog Wood ground vegetation

(b) Wood warblers nest in Grove Wood

ten feet above the ground, on the trunk of a large oak in the western 'enclave'. A pair of redstarts used a rickety old box, eight feet above ground on the trunk of an oak, across the stream. Two wood warbler nests were located, both on the ground, one in Grove Wood (Plate 1b), the other in Frog Wood (Plate 2b); and a pair of willow warblers betrayed the presence of their nest beneath the canopy of the redstarts' oak, while feeding their nestlings.

The small number of individual birds watched imposes some restriction on the interpretation and application of the results of this study. Conversely, this small number allows the use of more intensive methods of study which would be impracticable if the population under scrutiny was large.

Part Three: Methods of Study

3.1 The basic feeding observations

The field technique employed in this study to assess the utilisation of trees for feeding by a number of different birds, is similar to the 'repeated standard observations' described by Gibb (1954). Once located, a bird was watched until it moved to a new position - identified by the use of flight to reach it. The next feeding action that the bird made (successful or not) was recorded as one of ten parameters making up a standard observation:

(i) species of bird
(ii) species of tree
(iii) the vertical zone in which bird feeding
(iv) the horizontal zone in which bird feeding
(v) the perch used
(vi) the feeding action
(vii) the source of food
(viii) the foliage density at (v)
(ix) time of day (GMT)
(x) cloud cover

Similarly, the next standard observation could be made only after the bird flew to a new position. In this way each feeding action, each new situation, was as independent as it could be in practice of the one before. 140 hours were spent in the field and approximately 1,000 observations were recorded. 37 day-visits were made between 10 April and 9 July. Most of the fieldwork was done between 07.00 and 18.00 hours G.M.T., but special efforts were made to collect data in the few hours after sunrise, and just before sunset. In addition to the observations made on the four species named in the introduction, a limited amount of comparable data was collected for great tit (Parus major L.), blue tit (Parus caeruleus L.), and marsh tit (Parus palustris L.).

For each observation, a bird's position in a tree was delineated by the use of vertical and horizontal zones corresponding to convenient divisions of a 'typical' tree. The vertical zones are (1) ground-level, (2) trunk or shrub-level, (3) lower branches of tree, (4) upper branches, and (5) canopy, while the horizontal zones refer to (1) trunk or bole, (2) inner tree (base of branches), (3) outer tree, (4) the outermost twigs, and (5) outside of tree volume. This scheme allowed data to be collected for 25 'V-H' cells to describe each bird's feeding zone.

One serious problem associated with this sort of measurement concerns the fact that in some V-H cells the birds' behaviour, or the denseness of the foliage, randered them very difficult to watch; this was most noticeable with goldcrest (Regulus regulus (L.)) and coal tit (Parus ater L.), two species in the study area which predominantly used conifers and were therefore really only observed in the open zones of trees. In the same way, the male pied flycatcher's black and white plumage rendered him more conspicuous than his brownish mate. The only way that these problems could be minimised was to keep birds in view for as long as possible. This often meant that the observer had to move his position - a manoeuvre that would sometimes disturb the birds being watched. As no observation was recorded where a bird's behaviour was possibly affected by the presence of an observer, this compounded the difficulty, and a large number of hours of watching rarely turned up a large number of worthwhile observations (cf MacArthur 1958).

The birds were observed with 8 x 30 binoculars, and a portable tape-recorder was used in an attempt to record moment-by-moment observations of feeding behaviour. By timing these recordings with a stop-watch, a limited amount of data was collected on the feeding intensity of the birds - limited, because on transcription it was found that a fault in the recording device often left parts of the tape blank.

3.2 Home range and feeding areas

Initially, considerable time was spent in becoming familiar with the area, and the birds using the area. It was never possible to predict the birds' activity patterns, but a large amount of incidental information was recorded relating to inter- and intra-specific encounters, singing, courtship, etc., and a good general picture of territorial activity was built up.

The basic observational data described in the preceding section were supplemented by detailed information on the pied flycatcher, redstart, wood warbler and willow warbler nests during the period when the parents were bringing food to their young. The number of visits made to the nest were recorded over a twenty-four hour period, and attempts were made to identify the food items brought, at least to broad categories such as larva, pupa, etc. A telescope (25-40 x 40) was appropriate for the pied flycatcher pair, while the wood warblers allowed the use of a hide close to the nest.

In addition, the areas used by the parents for feeding during this nestling phase were mapped. The directions taken by the birds, and how far they went on leaving the nest, were recorded. Intensive observations were made on the five nests over a period of several days, and well-defined patterns of use emerged. Wherever possible, the food items brought to the nest were linked to the areas in which they were collected.

To avoid any a priori assumptions about the distributions of the data collected, non-parametric statistics have been used throughout the analysis of the study. In a behavioural study of this nature, it is arguable that observations are not wholly independent of one another, and so wherever the data allows its use, a rank correlation technique has been used in preference to chi-squared (Kendall 1948). Where a normal distribution of data has been assumed, as in the multivariate analysis described in Section 4.1.5, this has been noted in the relevant discussion. The comparative nature of the interpretation minimises any difficulties that may have arisen as a result of the problems of conspicuity described earlier.

TABLE 1: SUMMARY OF BASIC FEEDING OBSERVATION DATA

Absolute and Relative (percent) frequencies of data on seven variables.

Variable: Tree-Species Used

	Wood Warbler	Willow Warbler	Pied flycatcher	Redstart (male)
Ground vegetation (1)	2 (1.0)	0	15 (6.0)	76 (29.2)
Ash (2)	5 (2.4)	7 (5.4)	11 (4.4)	11 (4.2)
Birch (3)	100 (48.5)	52 (40.3)	7 (2.8)	33 (12.7)
Alder (4)	7 (3.4)	0	0	0
Sallow (5)	12 (5.8)	0	9 (3.6)	0
Hawthorn (6)	0	4 (3.1)	0	30 (11.5)
Copper Beech (7)	0	0	0	2 (0.8)
Beech (8)	22 (10.7)	0	2 (0.8)	0
Oak (9)	22 (10.7)	66 (51.2)	118 (47.0)	90 (34.6)
Elm (10)	2 (1.0)	0	0	1 (0.4)
Sycamore (11)	21 (10.2)	0	0	0
Lime (12)	0	0	58 (23.1)	0
Holly (13)	5 (2.4)	0	0	0
Scots Pine (14)	4 (1.9)	0	8 (3.2)	0
Sitka Spruce (15)	4 (1.9)	0	5 (2.0)	0
Douglas Fir (16)	0	0	2 (0.8)	0
Norway Spruce (17)	0	0	3 (1.2)	17 (6.5)
Yew (18)	0	0	13 (5.2)	0
	206	129	251	260

TABLE 2: BASIC FEEDING OBSERVATION DATA (Contd.)

Variable: Vertical Zones used by bird

	Wood Warbler	Willow Warbler	Pied flycatcher	Redstart
1. Ground or herb layer	2 (1.0)	4 (3.1)	26 (10.4)	88 (33.8)
2. Trunk or shrub layer	11 (5.3)	21 (16.3)	68 (27.1)	61 (23.5)
3. Lower branches of tree	85 (41.3)	47 (36.4)	84 (33.5)	87 (33.5)
4. Upper branches of tree	93 (45.1)	48 (37.2)	69 (27.5)	20 (7.7)
5. Canopy	15 (7.3)	9 (7.0)	4 (1.6)	4 (1.5)
	206	129	251	260

Variable: Horizontal Zones used by bird

	Wood Warbler	Willow Warbler	Pied flycatcher	Redstart
1. Trunk or bole	6 (2.9)	14 (10.9)	26 (10.4)	11 (4.2)
2. Inner tree	41 (19.9)	22 (17.1)	82 (32.7)	7 (2.7)
3. Outer tree	119 (57.8)	29 (22.5)	111 (44.2)	112 (43.0)
4. Outermost twigs	38 (18.4)	64 (49.6)	25 (10.0)	53 (20.4)
5. Outside of tree	2 (1.0)	0	7 (2.8)	77 (29.6)
	206	129	251	260

TABLE 3: BASIC FEEDING OBSERVATION DATA (Contd.)

Variable: Feeding Perch used by bird

	Wood Warbler	Willow Warbler	Pied flycatcher	Redstart (male)
1. Not using branch:				
(a) ground	2 (1.0)	2 (1.6)	22 (8.8)	40 (15.4)
(b) air	2 (1.0)	0	4 (1.6)	24 (9.2)
2. Large branch 50 mm +	4 (1.9)	14 (10.9)	16 (6.4)	11 (4.2)
3. Small branch 50-8 mm	17 (8.3)	21 (16.3)	84 (33.5)	37 (14.2)
4. Twigs less than 8 mm	181 (87.9)	92 (71.3)	125 (49.8)	148 (56.9)
	206	129	251	260

Variable: Stance used to take food

	Wood Warbler	Willow Warbler	Pied flycatcher	Redstart
1. Standing position	59 (28.6)	42 (32.6)	18 (7.2)	48 (18.5)
2. Reach up	18 (8.7)	5 (3.9)	2 (0.8)	0
3. Reach down	6 (2.9)	8 (6.2)	1 (0.4)	1 (0.4)
4. Reach forward	9 (4.4)	4 (3.1)	2 (0.8)	0
6. Cling to vertical stem	3 (1.5)	6 (4.7)	7 (2.8)	5 (1.9)
7. Hover	85 (41.3)	58 (45.0)	28 (11.2)	31 (11.9)
8. Hawk	24 (11.7)	6 (4.7)	193 (76.9)	175 (67.3)
9. Running glean	2 (1.0)	0	0	0
	206	129	251	260

Stance category 5 (Hang inverted) was only applicable in the case of blue, marsh and great tit.

TABLE 4: BASIC FEEDING OBSERVATION DATA (Contd.)

Variable: Source of food taken by bird

	Wood Warbler	Willow Warbler	Pied flycatcher	Redstart (male)
1. *Ground (a)	0	2 (1.6)	36 (14.3)	82 (31.5)
(b)	2 (1.0)	1 (0.8)	9 (3.6)	36 (13.9)
2. Large branch 50 mm +	5 (2.4)	12 (9.3)	9 (3.6)	11 (4.2)
3. Small branch 50-8 mm	7 (3.4)	7 (5.4)	2 (0.8)	1 (0.4)
4. Twigs, less than 8 mm	31 (15.0)	14 (10.9)	3 (1.2)	3 (1.2)
5. Leaves	127 (61.7)	71 (55.0)	35 (13.9)	64 (24.6)
6. Air	34 (16.5)	22 (17.1)	157 (62.5)	63 (24.2)
	206	129	251	260

*(a) bird alights on ground to take food

(b) bird in flight hawks through ground vegetation

Variable: Density of Foliage

	Wood Warbler	Willow Warbler	Pied flycatcher	Redstart
1. No leaves (dead, or bare twigs)	25 (12.1)	27 (20.9)	104 (41.4)	113 (43.5)
2. Intermediate foliage	42 (20.4)	11 (8.5)	63 (25.1)	107 (41.2)
3. Full foliage	139 (67.5)	91 (70.5)	84 (33.5)	40 (15.3)
	206	129	251	260

TABLE 5: FEEDING-ZONES OF REDSTART, PIED FLYCATCHER, WOOD WARBLER AND WILLOW WARBLER

Spread of Vertical-Horizontal Cells

	All tree-species				Oak				Birch		
*V-H cell	R	Pf	Wo	Wi	R	Pf	Wo	Wi	R	Wo	Wi
1.1	4	1	0	0	2	0	0	1	0	0	0
1.2	2	12	0	2	0	0	0	0	1	0	0
1.3	27	6	1	0	15	0	0	0	7	0	0
1.4	4	2	0	2	1	0	0	0	1	0	2
1.5	50	5	1	0	0	0	0	0	0	0	0
2.1	7	20	3	11	2	17	1	7	5	1	0
2.2	1	32	4	1	0	16	2	0	1	3	0
2.3	18	13	3	1	3	0	1	0	8	1	1
2.4	10	2	0	8	5	1	0	0	3	0	8
2.5	25	1	1	0	1	0	0	0	0	0	0
3.1	1	4	3	2	1	0	0	1	0	3	1
3.2	1	23	30	16	1	8	7	5	0	17	10
3.3	60	49	37	11	41	29	6	1	2	18	9
3.4	24	8	15	18	14	5	2	12	3	8	5
3.5	2	0	0	0	0	0	0	0	0	0	0
4.1	0	1	0	1	0	0	0	0	0	0	1
4.2	2	12	6	1	0	5	0	0	0	6	1
4.3	7	43	68	16	4	24	2	12	0	22	4
4.4	11	12	19	30	0	9	1	25	2	10	5
4.5	0	1	0	0	0	0	0	0	0	0	0
5.1	0	0	0	0	0	0	0	0	0	0	0
5.2	0	3	1	2	0	3	0	0	0	1	2
5.3	0	0	10	1	0	0	0	0	0	7	1
5.4	4	1	4	6	0	1	0	2	0	3	2
5.5	0	0	0	0	0	0	0	0	0	0	0
	260	251	206	129	90	118	22	66	33	100	52

*refer to Figure 3.

TABLE 6: CALCULATION OF THE SOURCE-STANCE DIVERSITY INDICES

	All tree-species				Oak				Birch		
*S-S category	R	Pf	Wo	Wi	R	Pf	Wo	Wi	R	Wo	Wi
1a	2	2	23	10	2	0	6	2	0	10	8
1b	1	1	4	6	1	0	0	1	0	3	5
1c	4	0	1	2	3	0	0	1	0	1	0
1d	5	6	29	22	4	4	5	13	0	14	10
1f	36	9	2	1	12	0	0	1	7	0	0
2a	0	0	4	0	0	0	0	0	0	4	0
2c	0	0	1	0	0	0	0	0	0	1	0
2d	0	2	13	5	0	1	0	4	0	7	1
3a	0	1	0	3	0	1	0	0	0	0	3
3b	0	0	0	1	0	0	0	0	0	0	1
3d	1	0	5	5	1	0	1	2	0	2	2
3e	0	0	1	0	0	0	0	0	0	0	0
4b	0	1	0	0	0	0	0	0	0	0	0
4d	0	1	9	4	0	0	0	2	0	5	2
6a	0	0	1	0	0	0	0	0	0	1	0
6c	5	7	1	5	2	6	0	3	3	0	0
6d	0	0	1	1	0	0	0	0	0	1	1
7a	1	0	2	1	0	0	0	1	0	1	0
7b	0	0	2	0	0	0	0	0	0	1	0
7c	2	1	2	5	1	0	1	4	1	1	0
7d	24	21	70	34	2	12	5	14	5	32	16
7e	4	5	9	16	1	2	2	14	0	1	2
7f	0	1	0	2	0	0	0	0	0	0	1
8c	0	1	0	0	0	1	0	0	0	0	0
8d	34	5	0	0	4	2	0	0	3	0	0
8e	59	152	24	6	28	87	2	4	6	13	0
8f	82	35	0	0	29	2	0	0	8	0	0
9a	0	0	1	0	0	0	0	0	0	1	0
9b	0	0	1	0	0	0	0	0	0	1	0
	260	251	206	129	90	118	22	66	33	100	52

* a = twig b = small branch c = large branch
d = leaves e = air f = ground 1-9 refers to coding of STANCE (Table 3)

Part Four: Results

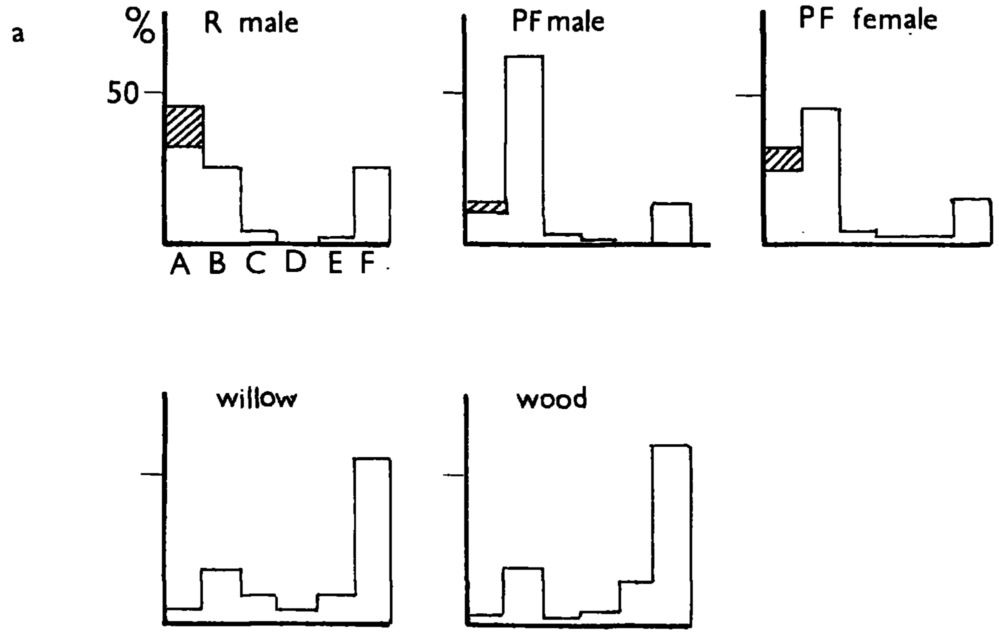
4.1 The basic feeding observation data

Data concerning the foraging behaviour of male redstart, pied flycatcher, wood warbler and willow warbler in the study area are presented in Tables 1 to 4. The female redstart deserted her mate at the end of the incubation period, and only 17 standard observations were collected for her. These data did not correlate with the data collected for the male, and have been omitted from the analysis. The data concerning male and female pied flycatchers have been aggregated on the basis of significant correlation coefficients (see Tables 7 to 9). The sexes of the wood warblers and willow warblers could rarely be distinguished in the field, and so the data for these two species are also in an aggregated form.

4.1.1 Food-source and feeding-perch

In Figure 2 the data on two of the parameters incorporated into the standard observation are summarised in the form of histograms. These feeding-sites have been arranged in a sequence, from the ground, through the trunk and large branches to the peripheral twigs and leaves. Because the category 'air' often represented the inter-trunk space (cf Edington 1972) it has been placed between ground and trunk and large branches. It is clear from these histograms, and from Table 7, that the four species fall into two pairs, wood warbler and willow warbler; redstart and pied flycatcher.

The two warblers take their food from the same places - mostly from the terminal leaves and twigs, but also to some



Key:

% = Percentage of observations made

A = Ground

B = Air

C = Large branches

D = Small branches

E = Twigs

F = Leaves

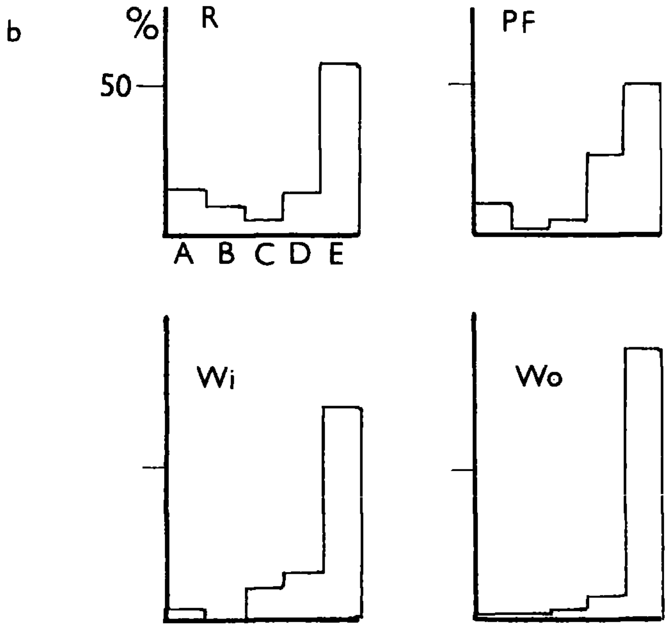


Figure 2: (a) Food-source (b) Feeding-perch for redstart, pied flycatcher, wood warbler and willow warbler.

extent from the air. The chi-squared value calculated on the original data is 10.8, which means that the similarity between wood warbler and willow warbler in the places used by them to take food is significant ($p < 0.05$).

These two warblers also use the same substrate or size of perch, but the relative use of these stations differs significantly between the two species ($p < 0.001$). This difference is due to the wood warbler restricting itself mainly to small twigs (less than 8 mm. diameter). However, when only the data on oak is compared (wood warbler 22 standard observations; willow warbler 66) the chi-squared value of 4.2 (three degrees of freedom) requires acceptance of the null hypothesis that there is no difference between them.

In the case of both redstart and pied flycatcher the most frequently used feeding-sites are the ground, the air and the leaves. Male and female pied flycatcher show no difference in their relative use of these sites as sources of food, although the calculated chi-squared value is only just smaller than the chi-squared ($p = 0.05$) value of 12.59 (see Table 7). (There is a tendency for the female to make more use of the ground vegetation than the male.)

In contrast, the difference between redstart and pied flycatcher in where they take their food is highly significant ($p < 0.001$). Redstart and pied flycatcher also differ in their use of various substrates, the flycatchers often using small branches (up to 50 mm. in diameter), and the redstart restricting itself to the twigs ($p < 0.001$).

TABLE 7:1.BETWEEN SPECIES COMPARISONS: PERCH USED

(a) Chi-squared matrix, data on all tree species:

	R	Pf	Wood	Willow
Redstart (male)	-	37.0^{***}	61.6^{***}	35.4^{***}
Pied flycatcher		-	74.3^{***}	27.1^{***}
Wood warbler			-	19.1^{***}
Willow warbler				-

Degrees of freedom = 3

Pied flycatcher male vs. female,
chi-squared = 4.1

(b) Chi-squared matrix, data on oak only:

	R	Pf	Wood	Willow
Redstart (male)	-	21.5^{***}	10.8^{*}	28.2^{***}
Pied flycatcher		-	13.5^{**}	16.3^{***}
Wood warbler			-	4.2
Willow warbler				-

Degrees of freedom = 3

2. BETWEEN SPECIES COMPARISONS: FOOD-SOURCE

Pied flycatcher male vs. female,
chi-squared (6 degrees of freedom) = 12.1

Pied flycatcher vs. Redstart,
chi-squared (6 d.f.) = 83.1^{***}

Wood warbler vs. Willow warbler,
chi-squared (6 d.f.) = 10.8

Null hypothesis of no significant difference between the data, rejected at $p < 0.05,^{*}$ $p < 0.01,^{**}$ $p < 0.001.^{***}$

TABLE 8: BETWEEN SPECIES COMPARISONS: VERTICAL-HORIZONTAL CELLS

(a) Spearman's rank correlation matrix, data on all tree-species:

	R	Pf	Wood	Willow
Redstart (male)	-	0.455^{*}	0.312	0.238
Pied flycatcher		-	0.645^{***}	0.597^{**}
Wood warbler			-	0.610^{**}
Willow warbler				-

Degrees of freedom = 23

Pied flycatcher male vs. female,

$r_s = 0.677^{***}$

(b) Rank correlation matrix, data on oak only:

	R	Pf	Wood	Willow
Redstart (male)	-	0.238	0.358	0.306
Pied flycatcher		-	0.577^{**}	0.493^{*}
Wood warbler			-	0.448^{*}
Willow warbler				-

Degrees of freedom = 23

(c) Rank correlation matrix, data on birch only:

	R	Wood	Willow
Redstart (male)	-	0.075	0.148
Wood warbler		-	0.587^{**}
Willow warbler			-

Degrees of freedom = 23

Null hypothesis of no association between the data, rejected at $p < 0.05,^{*}$ $p < 0.01,^{**}$ $p < 0.001.^{***}$

TABLE 9: BETWEEN SPECIES COMPARISONS: SOURCE-STANCE

(a) Spearman's rank correlation matrix, data on all tree-species:

	R	Pf	Wood	Willow
Redstart (male)	-	0.626***	0.297	0.393*
Pied flycatcher		-	0.260	0.450*
Wood warbler			-	0.632***
Willow warbler				-

Degrees of freedom = 27

Pied flycatcher male vs. female,

$r_s = 0.567^{**}$

(b) Rank correlation matrix, data on oak only:

	R	Pf	Wood	Willow
Redstart (male)	-	0.366	0.220	0.031
Pied flycatcher		-	0.234	0.319
Wood warbler			-	0.613**
Willow warbler				-

Degrees of freedom = 16

(c) Rank correlation matrix, data on birch only:

	R	Wood	Willow
Redstart (male)	-	-0.146	-0.144
Wood warbler		-	0.391*
Willow warbler			-

Degrees of freedom = 24

<u>Null hypothesis</u> of no association between the data,
rejected at $p < 0.05$,* $p < 0.01$,** $p < 0.001$.***

4.1.2 Feeding zones of redstart, pied flycatcher, wood warbler and willow warbler

Table 5 presents the V-H cells (incorporating the 'vertical' and 'horizontal' parameters of the standard observation) used by each of the four species. The resulting feeding 'zones' have been graphed in Figure 3. For each species, the four cells representing the most frequented parts of the tree (expressed as a percentage of the number of observations made) have been shaded. It is interesting to note that the four cells shaded for the wood warbler account for 74.8 percent of the observations made on this species. The figure for the other three species is approximately sixty percent, indicating the possibility that the wood warbler is specialised in its use of different parts of a tree.

The extent to which the four feeding zones overlapped was assessed using a rank correlation method. Table 5 summarises the between species comparisons based on the 25 V-H cells.

Spearman's coefficient of rank correlation has the formula:

$$r_s = 1 - \frac{6(\Sigma d^2 + \frac{t^3-t}{12})}{n(n^2-1)}$$

where d is equal to the difference between the ranks of the paired observations, and n the number of pairs of observations. The term $\frac{t^3-t}{12}$ is a correction factor that has to be added to Σd^2 when there is a tie in the ranks, where t is the number of tied observations (Kendall 1948).

From Table 8, it is clear that wood warbler, willow warbler and pied flycatcher have similar feeding zones ($p < 0.002$, except

Redstart

V5				4	
V4		2	7	11	
V3	1	1	60	24	2
V2	7	1	18	10	25
V1	4	2	27	4	50
	H1	H2	H3	H4	H5

Pied flycatcher

V5		3		1	
V4	1	12	43	12	1
V3	4	23	49	8	
V2	20	32	13	2	1
V1	1	12	6	2	5
	H1	H2	H3	H4	H5

Wood warbler

V5		1	10	4	
V4		6	68	19	
V3	3	30	37	15	
V2	3	4	3		1
V1			1		1
	H1	H2	H3	H4	H5

Willow warbler

V5		2	1	6	
V4	1	1	16	30	
V3	2	16	11	18	
V2	11	1	1	8	
V1		2		2	
	H1	H2	H3	H4	H5

Figure 3: Feeding-zones of redstart, pied flycatcher, wood warbler and willow warbler. For key to V-H cells refer to Table 2.

for pied flycatcher versus wood warbler, where $p < 0.001$). The data for the redstart correlates with the data for pied flycatcher - but the coefficient obtained is only significant statistically at $p = 0.05$. This overlapping of feeding zones is apparent in Figure 3. The redstart differs from the other species in that a high proportion of its feeding activity takes place on the ground beneath the branches, or away from the tree-volume altogether.

Significant correlations at tree-specific level are between pied flycatcher and wood warbler on oak ($p < 0.01$); between pied flycatcher and willow warbler on oak ($p < 0.02$); and between wood warbler and willow warbler on oak ($p < 0.05$) and on birch ($p < 0.002$). It must be pointed out however that this division of the data produces smaller sample sizes, which might, as is probable in the case of the wood warbler (only 22 standard observations), make interpretation of the coefficients doubtful.

4.1.3 Methods of obtaining food: the source-stance categories

Table 6 presents the spread of source-stance categories among the four species. This parameter is a composite of (a) the method used by a bird to obtain food, and (b) the source, or place from which the food is gleaned. In this scheme any differences between birds using the same feeding action (for example, hovering) but taking food from different places (hovering at leaves, compared with hovering at insects in the air) are elucidated.

The matrices of correlation coefficients presented in Table 9 clearly indicate the close similarity in feeding methods (all tree species data) between redstart and pied flycatcher on the one hand, and wood warbler and willow warbler on the other ($p < 0.001$).

While the redstart and pied flycatcher predominantly hawk or pounce, the warblers take most of their food by hovering, or gleaning twigs and leaves from a foothold.

At tree-specific level, wood warbler and willow warbler are again similar in feeding methods ($p < 0.01$ for oak, $p < 0.05$ for birch). In contrast, the correlation coefficients between redstart and pied flycatcher are not significant, indicating that despite their overall similarity in feeding methods, these two species differ from each other in their use of particular trees.

The willow warbler data, (unlike the wood warbler data), are comparable with both redstart ($p < 0.05$) and pied flycatcher ($p < 0.02$), but only when the data for all trees are considered together. At tree-specific level there are no significant correlations; and for oak, in particular, the correlation coefficient of 0.031 between redstart and willow warbler is the lowest value in the matrices.

It is evident from the above results that the four species fall naturally into two pairs. The wood warbler and willow warbler overlap strongly in both the parts of the tree used for feeding and in the methods used to obtain food. The redstart and pied flycatcher obtain food in very much the same manner as each other, but only partially overlap in their use of space.

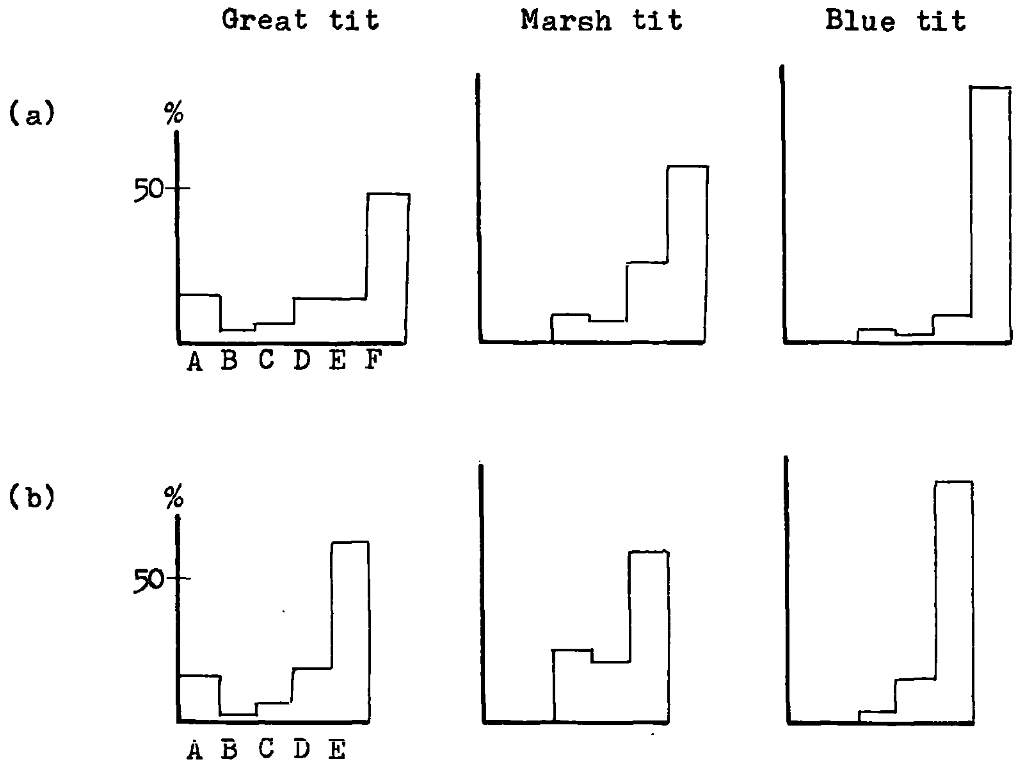
4.1.4 The foraging behaviour of blue, marsh and great tit

A limited number of feeding observations on blue tit, marsh tit, and great tit were made at the same time as the data for pied flycatcher, redstart, wood warbler and willow warbler were collected.

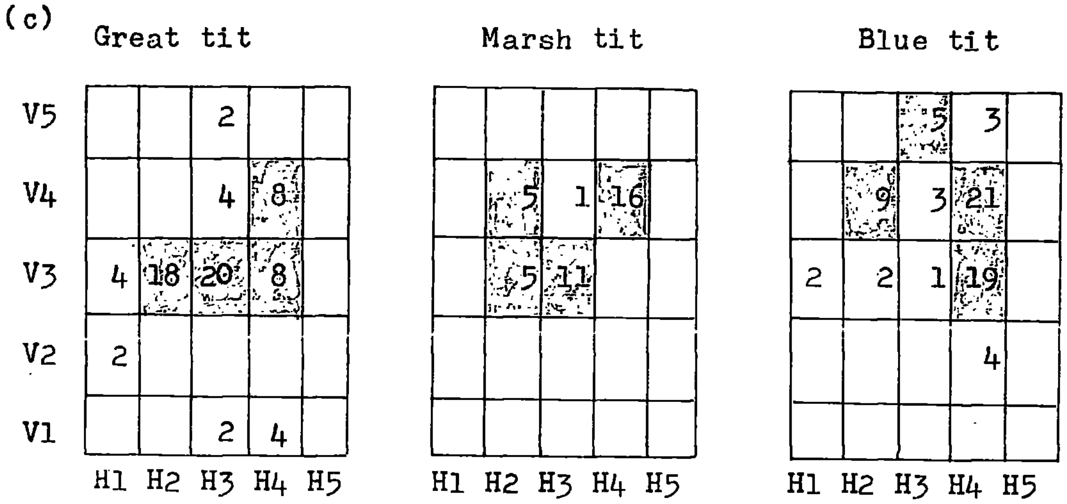
The sites used by the three tits as perches prior to the taking of food, and the places from where this food was then taken, are summarised in the form of histograms in Figure 4. Also shown in Figure 4, in graphical form, are the feeding zones used by the birds. This data is directly comparable with the data for the other four species (see Figures 2 and 3).

It is evident from the histograms that the blue tit makes predominant use of the terminal twigs and leaves of a tree when feeding, while the great tit makes relatively frequent use of both the ground and the branches. The marsh tit data have to be treated with caution since they comprise only 38 observations (compared with 69 for blue tit and 72 for great tit).

Table 10 gives the between species comparisons for the three tits with respect to their feeding zones and their methods of obtaining food. Great tit and blue tit appear to use similar feeding zones, but the correlation coefficient of 0.4 is only significant at $p < 0.05$ and suggests that this relationship is weak (perhaps due to the great tit's use of the ground). In contrast, there is no significant overlap between blue and great tit in the methods they use to take food (r_s of only 0.082), and the marsh tit shows no overlap with these two species in either feeding zone or method of obtaining food.



For key, see Figure 2



Great tit

	H1	H2	H3	H4	H5
V5			2		
V4			4	8	
V3	4	18	20	8	
V2	2				
V1			2	4	

Marsh tit

	H1	H2	H3	H4	H5
V5					
V4		5	1	16	
V3		5	11		
V2					
V1					

Blue tit

	H1	H2	H3	H4	H5
V5			5	3	
V4		9	3	21	
V3	2	2	1	19	
V2				4	
V1					

For key, see Figure 3

Figure 4: (a) Food-source (b) Feeding perch
(c) Feeding-zone for blue, marsh and great tit

TABLE 10: BETWEEN SPECIES COMPARISONS FOR BLUE, MARSH AND GREAT TIT

(a) Vertical-horizontal cells, rank correlation coefficients.

	G	M	B
Great tit	-	0.343	0.400*
Marsh tit		-	0.351
Blue tit			-

Degrees of freedom = 23

(b) Source-stance categories, rank correlation coefficients:

	G	M	B
Great tit	-	0.232	0.082
Marsh tit		-	0.368
Blue tit			-

Degrees of freedom = 18

*Null hypothesis of no association between the data, just rejected at $p = 0.05$.

These results are in agreement with those of Gibb (1954) and Hartley (1953) who both demonstrated that ecological differences of this kind between blue, marsh and great tit allowed these similar species to coexist in the same habitat.

4.1.5 A Components Analysis of the feeding observation data

Factor analysis defines the patterns of common variation among a set of variables, and variation unique to any one variable is ignored. In contrast, principal components analysis (the statistical technique employed in this study) is concerned with patterning all the variation in a set of variables, whether common or unique.

A principal components analysis can be used in several ways, but the most helpful characteristic of this technique is the way it reduces a mass of information to an economical description. It is necessary to bridge a conceptual gap and consider n variables as vectors in an n-dimensional space; it is clear that highly interrelated variables or characteristics will form clusters in this 'hyperspace', while unrelated variables will be at right angles to one another. These clusters are analogous to patterns of relationship in the data (Rummel). Each rotated factor delineated by a component analysis defines a distinct cluster of variables, and discussion can then centre, without much loss of information, on a fewer number of 'composite-variables', each of which can be given a label of biological significance.

Appendix 1 lists the four main components delineated by the multivariate technique. These represent four independent patterns of relationships among the variables. Each intersection of row and column of the matrix in Appendix 1 gives a loading for the row variable on the column component. The loadings, which are the component score coefficients, measure which variables are involved in which component pattern and to what degree. In this respect they are very like correlation coefficients. The square of the loading multiplied by 100 is equal to the percentage variation that a variable has in common with a pattern.

In this study, a pattern has been arbitrarily limited to those variables with at least 10 percent of their variation involved in the pattern (that is, a loading of 0.316).

While the component score coefficient matrix in Appendix 1 summarises the loadings by which the existence of a pattern for the variables can be ascertained, Appendix 7 lists a score for each case (each standard observation) on these patterns. Each variable is weighted in proportion to its involvement in a pattern - the more involved a variable, the higher its weighting. Each case's score on each variable is multiplied by the pattern weight for that variable, and the sum of these products is equal to the case's component score. Component scores can be interpreted in the same way as data on any variable since, as already explained, a component can be regarded as a composite-variable.

From Appendix 1 it is evident that 3 variables are involved in the pattern of relationships identified by Component 1. These are (a) the vertical zone used, (b) the foliage-density and (c) the source of the food taken. All three incorporate a strong height element, (as can be seen from the section on coding, 4.1.6) and Component 1 can be looked upon as a means of measuring the spread of cases along a space-resource axis.

Component 2 can be regarded as the horizontal complement of Component 1, since the two variables that load significantly onto this pattern are (a) the horizontal zone used, and (b) the size and type of perch used. In each case the variables have approximately 20 percent of their variation involved in the pattern.

Only single variables load significantly on to Components 3 and 4. The variable stance, describing the type of feeding actions used to take food, has almost 60 percent of its variation in common with Component 3, while Component 4 is clearly very closely related to the variable time of day.

In Figure 5 the basic feeding observation data has been platted on a graph of Component 1 (vertical axis) against Component 3 (horizontal axis) on the basis of their scores on these components. The colour of each co-ordinate identifies which of the four species (redstart, pied flycatcher, wood warbler or willow warbler) the observation refers to.

The resulting point-configuration is a two-dimensional portrayal of a multi-dimensional phenomenon - ecological overlap (Cody's 'displacement pattern'). While the vertical axis of the graph can be seen to have spatial significance, the horizontal axis accounts for variation in feeding behaviour.

The close overlap of component scores for wood warbler and willow warbler indicates just how similar these two species are in both their spatial requirements and their behaviour. Pied flycatcher and redstart have a similar spread of scores along the horizontal axis - they use the same feeding methods - but there is only a partial overlapping of their scores on the vertical axis. Figure 5 implies that while the redstart favours hawking near the ground, the pied flycatcher tends to hawk among the higher branches. The graph also shows that there are areas of overlap between the pied flycatcher and the warblers, while the redstart is to a very large extent ecologically isolated.

The displacement pattern described by Figure 5 provides striking confirmation of the results obtained in Sections 4.1.2 and 4.1.3 using rank correlation methods.

4.1.6 Coding and transformations of the data

The basic feeding observations collected in this study consist of data on nine parameters, or variables, for 863 cases. The data on two of these variables were collected in a continuous form, since time of day was expressed as Greenwich Mean Time and cloud cover was scored from 0 to 8 on the conventional scale. Three other variables comprise data that is in a semi-continuous form. The vertical and horizontal parameters were scored from 1 to 5 as described in Section 3.1, and density of foliage was scored 1 to 3 on the basis of 1 = no leaves, bare or dead twigs, 2 = intermediate, 3 = full leaf.

The remaining four variables were coded as follows:

(a) Tree-species used by bird. It was impossible to be objective in the scaling of this 'variable' and it was decided to rank the tree-species used by a bird for feeding along a gradient incorporating both overall size of tree and density of foliage. The result of this subjective ranking is recorded in Table 1.

(b) Stance. Feeding actions were scored on the basis of how well a bird could recover after performing a particular movement. The scaling is inevitably highly subjective; a glean in a standing position receives a score of 1, while a hawk scores 8 (Table 3).

(c) Perch used and (d) Source of food. The coding of these feeding-sites was straightforward. Scores were 1 for the ground, 2 for large branches, 3 for small branches, 4 for twigs, 5 for leaves and 6 for the air, incorporating in (d) especially, an 'upwards and outwards' component.

The first step in the principal components analysis was the generation of a matrix of correlation coefficients between the 9 variables. Caution had to be exercised in the interpretation of these values of r since it is clear from Appendices 2 - 4, and from the last few paragraphs, that the data collected on the nine feeding-observation parameters are in some cases far from normal, and r is invalid as a measure of the degree of linear relationship between these variables.

The amount of skewness in a population is given by a coefficient of skewness $\sqrt{\beta_1}$ based on 'the third moment about the mean'. The sample estimate of this coefficient is denoted $\sqrt{b_1}$. Simply, if the sample comes from a normal population, $\sqrt{b_1}$ is approximately normally distributed with mean zero and standard deviation $\sqrt{\frac{6}{n}}$ (Snedecor and Cochran 1967).

In this case the standard deviation of $\sqrt{b_1} = \sqrt{\frac{6}{863}} = 0.083$. As a rough estimation, skewness is confirmed if $\sqrt{b_1}$ lies outside of the range of values between $\pm 3 \times 0.083 = \pm 0.249$. The data on 5 of the 9 parameters described in Appendices 2 - 4 therefore have significantly skewed distributions.

An attempt was made to minimise skewness by means of ten different transformations of the data; the details of the transformations used, and the resulting values of $\sqrt{b_1}$ are tabulated in Appendix 5. It is clear from this table that the minimum values of $\sqrt{b_1}$ for three of the variables (perch, source of food, and stance used to take food) still lie outside the range ± 0.249.

Appendix 6 presents a modified version of the correlation matrix output by the principal components analysis computer-programme. The correlation coefficients in this matrix were computed using the variable scores obtained from the transformations generating the smallest coefficients of skewness (and therefore most closely approximating a normal distribution). The significant values of r (863 pairs of observations on each variable) are as follows:

TABLE 11

SIGNIFICANT ($p < 0.01$) CORRELATION COEFFICIENTS BETWEEN VARIABLES

Variables			r
Cloud	vs	Treespecies	-0.21
"	vs	Vertical zone	-0.31
"	vs	Perch	-0.16
"	vs	Stance	0.17
"	vs	Source	-0.22
"	vs	Foliage	-0.23
Treespecies	vs	Vertical zone	0.28
"	vs	Horizontal zone	-0.32
"	vs	Perch	0.35
"	vs	Stance	0.14
"	vs	Source	0.21
Vertical zone	vs	Perch	0.24
"	vs	Source	0.41
"	vs	Foliage	0.51
Horizontal zone	vs	Perch	-0.59
"	vs	Foliage	0.21
Perch	vs	Source	0.13
"	vs	Foliage	-0.13
Stance	vs	Source	0.28
"	vs	Foliage	0.18
Source	vs	Foliage	0.31

4.2 Territory, home range and feeding areas

4.2.1 The incubation period

The parts of the study area used by redstart and pied flycatcher during the incubation period are shown in Figure 6. The delineated areas are territories, although in this situation 'home range' is a more useful term. The areas were not limited in extent by territorial defence and often large distances were traversed by the males, especially the male pied flycatcher, during the courtship and incubation stages. On one occasion while his mate was incubating, the male pied flycatcher was seen to fly in the direction of Frog Wood. Later he was located singing on the edge of this area, above an old box situated on a yew fifty yards from the wood warblers' nest. I am confident that no other individuals were involved, and this may have been a brief attempt by the male to attract a second mate, as discussed by Haartman (1956).

One other redstart male sang in the study area while the female of the established pair was incubating, but he apparently left the same day after one encounter with the resident male. This bird was never seen to bring food to his mate while she was sitting on eggs; she was noted leaving the box for a few minutes at a time to search for food in the immediate area (the nest-oak or those oaks just across the path). The male, on the other hand, ranged over a large area. He frequently sang from the top of a dead hawthorn on the northern side of the belt of oaks, and would usually be found among the adjacent large trees. Few feeding observations were made on the male during the incubation period, as he was extremely difficult to watch among the branches of the oak. On several occasions when he was kept in view for up to half an hour, his main activities were clearly singing or preening.

The pied flycatcher was more conspicuous, and his behaviour made him relatively easy to find. He assiduously brought food-items to his mate while she was incubating. On the occasions when he returned to the box to find that the female had left it, he would sit on a nearby twig and sing softly until she returned. Invariably she would alight next to him and be fed before disappearing back into the box. For this reason few feeding observations were made on the female during this period, for she began incubating very soon after her arrival in the area. On the other hand, the male was conspicuous, and his home range could be mapped in some detail.

In contrast to the redstart and pied flycatcher the two pairs of wood warblers defended quite small territories (see Figure 6). The Grove Wood pair were especially active in the defence of the south-east boundary of their territory against willow warblers. Whenever the observer's approach disturbed a member of either pair, the alarm note or song given by it invariably drew response from its neighbours and territorial activity ensued. Usually bouts of vigorous song were adequate in marking a boundary, but on a number of occasions a willow warbler was chivvied and finally chased back after a particularly persistent sortie into the wood warblers' area.

On the western side of the wood warblers' territory, the firebreak marked a sort of 'no man's land'. The male wood warbler crossed this area on two occasions when observations were being made, but this was exceptional, and the area was almost certainly part of the territory of a second pair of willow warblers. There was however none of the aggression associated with the south east boundary on this side. The other sides of the territory appeared to be undisputed, natural barriers to foraging. On the south side lay the stream, and on the north side the dense stands of conifers.

The male of the Frog Wood pair could usually be located singing on the western edge of his territory, the only boundary that appeared to be actively defended. As in the case of the Grove Wood territory, the other sides of the Frog Wood territory were to a large extent delimited by natural barriers.

Figure 6 also shows the areas used by three pairs of willow warblers on the study site. Of particular interest is the mutual exclusion of the wood and willow warblers in Grove Wood from each other's territories. This situation is in contrast with the extensive overlapping of the areas used by the redstarts and willow warblers in the parkland section of the site.

4.2.2 <u>The areas used for feeding during the nestling stage</u>

The feeding areas of the five breeding pairs selected for study have been mapped, in the form of star-diagrams, in Figure 6. Each ray delineates a particular feeding area, and the numbers against each ray correspond to the visits that the parent-birds

Figure 6: The territories and feeding areas

Key to nests:

Redstart	○
Pied flycatcher	○
Wood warbler	●
Willow warbler	⊖

White numerals refer to the number of feeding trips made to each area.

Scale of map 1 : 1800

made to each area, usually over a twenty-four hour period, while they were feeding young in the nest. These data have been summarised in Tables 12-15.

It is clear from Figure 6 that the pied flycatchers collected the majority of their food-items from a small area around the nest-site. A number of visits were made outside of this core-area but these were exceptional (less than 1 percent of the total number of excursions). These long-distance trips were often associated with the removal of faecal sacs from the nest. Nine of the thirteen trips that the male pied flycatcher made to the edge of the firebreak between 04.30 and 12.30 on June 27th, were for this purpose. This in itself is remarkable for the majority of the droppings removed were deposited high in adjacent trees.

The overall association between the areas visited and the time of day was estimated using Kendall's coefficient of concordance, W.

W is defined as follows:

$$W = \frac{12\,\Sigma\left\{\Sigma r_a - \frac{\Sigma\Sigma r_a}{n}\right\}^2}{k^2(n^3-n) - \Sigma\left\{\frac{t^3-t}{12}\right\}}$$

(Kendall 1948)

Σr_a is the sum of the ranks given to each feeding area, while $\Sigma\Sigma r_a$ is the sum of these sums; k is the number of sets of ranks (corresponding to 8 two-hour periods), and n is the number of ranks in each set (corresponding to 11 feeding areas). In the eventuality of tied ranks the same correction $\frac{t^3-t}{12}$ used for

TABLE 12: FEEDING AREAS OF PIED FLYCATCHERS

The number of visits made to each area over two-hour periods.*

Male	Areas:	1	2	3	4	5	6	7	8	9	10	11	
	0430 - 0630	0	10	2	1	0	0	16	1	5	2	0	37
	0630 - 0830	4	7	2	20	7	3	1	0	5	1	0	50
	0830 - 1030	1	5	29	19	2	0	1	0	0	2	1	60
	1030 - 1230	2	14	13	13	4	2	1	0	1	11	0	61
	1230 - 1430	9	8	10	5	1	0	13	0	5	6	3	60
	1430 - 1630	8	10	0	4	3	0	16	1	6	6	2	56
	1630 - 1830	11	6	0	13	1	0	5	0	4	11	1	52
	1830 - 2030	3	2	0	3	2	0	4	0	10	13	4	41
	Totals:	38	62	56	78	20	5	57	2	36	52	11	417

Female	Areas:	1	2	3	4	5	6	7	8	9	10	11	
	0430 - 0630	1	13	3	1	1	0	2	0	0	4	1	26
	0630 - 0830	0	5	3	9	0	2	6	1	4	3	0	33
	0830 - 1030	1	9	5	8	0	0	5	0	0	4	1	33
	1030 - 1230	0	14	2	0	0	0	8	1	0	7	0	32
	1230 - 1430	2	13	1	1	0	0	6	0	1	4	2	30
	1430 - 1630	2	8	0	0	0	0	10	0	4	6	1	31
	1630 - 1830	1	9	1	1	0	0	5	0	0	6	3	26
	1830 - 2030	5	4	1	1	3	0	5	0	4	1	0	24
	Totals:	12	75	16	21	4	2	47	2	13	35	8	235

*0430 - 1230 June 27th, 1230 - 2030 June 28th.

TABLE 13: FEEDING AREAS OF WOOD WARBLERS

(a) Frog Wood pair: limited data over one 3-hour period, June 21st.

Areas:	N	S	E	W	*	
	25	10	4	7	5	(Total no of visits = 51)

(b) Grove Wood pair: food items brought to nest, by feeding areas and times of day.

Areas:	1	2	3	4	5	6	7	8	9		Totals
0430-0830 (July 4)	1	5	1	14	2	6	2	2	0	Adult	33
	2	2	0	5	0	0	2	0	0	Larva	11
	0	2	0	0	0	0	0	0	0	Pupa	2
	1	0	0	3	0	3	2	1	0	Unidentified	10
0830-1230 (July 3)	1	0	0	9	3	4	4	6	0		27
	3	0	0	4	2	5	7	1	0		22
	0	0	0	0	0	0	0	0	0		0
	0	0	0	2	1	1	0	1	1		6
1230-1630 (July 4)	2	2	0	7	3	1	4	4	1		24
	1	3	3	3	1	0	2	3	3		19
	1	0	0	0	0	0	0	0	0		1
	0	1	0	0	1	0	2	0	2		6
1630-2030 (July 5)	0	0	0	7	0	5	2	2	0		16
	1	1	0	6	1	2	2	2	1		16
	0	0	0	0	0	0	0	0	0		0
	0	0	0	0	0	2	3	1	2		8
	4	7	1	37	8	16	12	14	1	Adult	100
	7	6	3	18	4	7	13	6	4	Larva	68
	1	2	0	0	0	0	0	0	0	Pupa	3
	12	15	4	55	12	23	25	20	5		171

Total unidentified: 30

16 hr total visits: 201

TABLE 14: FEEDING AREAS OF REDSTART AND WILLOW WARBLER

(a) Redstart: the number of visits made to each area over four-hour periods,* plus additional data.

Areas:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Totals
June 21-24	5	14	0	3	3	5	0	1	0	0	0	0	0	0	0	31
*0430-0830	9	18	7	5	5	6	0	8	4	0	0	0	0	0	3	
0830-1230	5	29	5	11	5	1	1	5	4	0	1	0	0	2	8	
1230-1630	1	9	4	3	4	3	0	11	12	1	4	0	11	0	14	
1630-2030	0	2	1	1	2	0	0	10	7	1	4	7	20	0	2	
16 hr totals	15	58	17	20	16	10	1	34	27	2	9	7	31	2	27	276

*0430-1230 June 25th, 1230-1630 June 26th, 1630-2030 June 27th.

(b) Willow Warbler: limited data on two occasions.

Areas:	1	2	3	4	5	
June 13	3	5	47	17	0	between 0829 and 1029 GMT.
June 14	5	2	0	3	10	between 1600 and 1620 GMT.

Spearman's rank correlation coefficient is applied to the denominator of the expression.

The test of significance for W is based upon the sampling distribution of the sum of squared deviations of the $\sum r_a$'s round $\sum r_a$. If n is larger than 7, this sampling distribution is approximated by the chi-squared distribution with n - 1 degrees of freedom.

The W calculated for the male pied flycatcher's data is 0.391, and the calculated value of chi-squared is 31.2. This is just larger than the chi-squared value of 29.6 ($p = 0.001$) and therefore we can reject the null hypothesis that there is no association between the areas visited at different times of the day. As W is significant and there is some agreement between the feeding areas used over a 24-hour period, these areas can be ranked in order of importance according to their sums of ranks (Kendall 1948). This results in the series 2, 4, 10, 7, 1, 9, 3, 5, 11, 6, 8 where feeding area 2 (see Table 12) is the most consistently favoured site for the collection of food, and conversely, feeding area 8 is the least consistently favoured site.

The female pied flycatcher's data generate a W of 0.576 which suggests even stronger agreement between the feeding areas used over a 24-hour period than in the case of the male. The feeding areas used by the female are ranked 2, 7, 10, 3, 4, 1, 9 and 11, 5, 8, 6. There is in fact a close association between these two series, and a Spearman's rank correlation coefficient calculated on the original data has the value of 0.829 which is significant at $p < 0.002$ (Student't $t = 4.46$).

Overall analysis indicates that the male and female pied flycatchers are using the same feeding areas, and in addition are using them consistently over a 24-hour period. However, a closer inspection of the data in Table 12 suggests that there are differences that may be detected at a larger scale. There are three main directional components in the star-diagrams shown in Figure 6, and if the number of visits to the 11 feeding areas are aggregated into these broader categories and compared, 04.30 hrs - 12.30 hrs against 12.30 hrs - 20.30 hrs, the following obtains:

TABLE 16: FEEDING VISITS OF MALE AND FEMALE PIED FLYCATCHERS GROUPED INTO DIRECTIONAL COMPONENTS

	Time-period	East (1,2,3,4 and 5)	West (6,7 and 8)	North (9,10 and 11)
Male	0430-1230	155	25	28
	1230-2030	99	39	71
Female	0430-1230	75	25	24
	1230-2030	53	26	32

The chi-squared value calculated for the male pied flycatcher's data is 34.1 and is significant at $p < 0.001$, while the female's data gives a chi-squared value of 4.1 which is not significant. This confirms the earlier demonstration that the female pied flycatcher is more consistent in her use of feeding areas throughout the 24-hour period than the male. It is clear that the male pied flycatcher altered his foraging area during the period of observation, suggesting that feeding areas are not necessarily fixed or invariable.

Plate 3 Upslope of the Pied flycatchers nest - the limit to the deciduous fringe.

A clearer indication of this is given by the male redstart. The female redstart deserted her mate at the end of the incubation period and he alone fed the three nestlings (three eggs failed to hatch). Table 14 summarises the visits that he made to the nest over a 24-hour period of observation. For comparison, the table also includes a number of casual observations that were made over a period of three days before the main watch. Efficient observation could not be maintained for more than eight hours without a break. At the same time different nests, at a similar stage of nestling development, had to be covered simultaneously. This practical difficulty resulted in the implementation of a shift-system, and a '24-hour' watch usually spread over two or more days. In the case of the redstart an eight-hour watch was made between dawn and mid-day on June 25, and two further watches, each of four hours' length, were made on the afternoon of June 26 and through the evening of June 27. The feeding areas used by the redstart are once again plotted in the form of a star-diagram in Figure 6.

An inspection of the data in Table 14 suggests that there was a fundamental change in the areas being used by the male redstart for collecting food during these observation periods. The data for 04.30-08.30 and 08.30-12.30 are associated (the Spearman's rank correlation coefficient of $r_s = 0.713$ is significant at $p < 0.01$), and in addition the pattern of visits over this eight-hour period is in close agreement with the data collected between June 21 and June 24 (a W of 0.726 for the three sets of observations is significant at $p < 0.01$). Over these five days the male redstart concentrated his foraging activities around the ground and shrub vegetation on the edge of the belt of trees along the southern boundary of the study area (areas 1-5), and at this point in time it was apparent that the areas used for feeding were a small, predictable fraction of the male's original home range. A further period of observation, however, showed that the situation was far more complex.

On the 26th and 27th of June the male redstart unexpectedly began to make long flights across to the firebreak and (on the 27th) even into the pied flycatchers' territory. In the four hours before dusk on June 27th these new areas outside the bird's original range accounted for 47.7 percent of the feeding trips that it made. Only 10.5 percent of the redstart's excursions were made to the areas 1-5 during this period, compared with approximately 70% during the first eight-hour watch. The data for June 26th (1230-1630 hrs) and June 27th (1630-2030 hrs) are associated, the r_s value of 0.618 being significant at $p < 0.02$. In constrast the correlation coefficient of -0.108 between the data for 0430-0830 on June 25th, and the data for June 27th is a good indication of the redstart's altered behaviour.

A willow warblers' nest was found on the ground beneath the canopy of the redstarts' oak. Only a limited number of observations (92 on June 13th and 14th) were made on the parent-birds while they were feeding their well-grown young (see Table 14), but it is clear from Figure 6 that the area that was used for the collection of food over this period closely coincides with part of the feeding area that was later used by the male redstart. A fairly accurate boundary was drawn for the territory of this pair of willow warblers while the basic feeding observation data were being collected; and there was very little contraction of this territorial area during the nestling stage.

Table 13 summarises the data for the feeding areas of the two pairs of wood warblers. A three-hour watch of the Frog Wood pair on June 21st suggested that, as in the case of the willow warblers, the whole of the small territorial area was used by the parent birds for their excursions to collect food for their young. A chi-squared test of the data, however, shows that the birds display a strong preference, ($p < 0.001$) for particular parts of the area (see Figure 6).

These pilot findings were confirmed by a 24-hour watch of the Grove Wood pair of wood warblers. From Table 13, the visits made by the parent-birds to each of the nine sites are as follows:

Areas:	1	2	3	4	5	6	7	8	9	
0430-0830 (July 4)	4	9	1	22	2	9	6	3	0	56
0830-1230 (July 3)	4	0	0	15	6	10	11	8	1	55
1230-1630 (July 4)	4	6	3	10	5	1	8	7	6	50
1630-2030	1	1	0	13	1	9	7	5	3	40
	13	16	4	50	14	29	32	23	10	Totals

The W statistic calculated between the four sets of data is 0.714 and the corresponding chi-squared value of 22.8 for eight degrees of freedom requires rejection of the null hypothesis at $p < 0.01$. There is good agreement as to the areas visited by the parent-birds during the periods of observation, and they can be ranked in order of decreasing preference: 4, 7, 6, 8, 2, 1 and 5, 9, 3.

Despite this tendency for some parts of the territory to be used more often than others, Figure 6 clearly shows that once again there was no contraction in the territorial area during the nestling stage.

Tables 12, 13 and 14, in summarising the above data, conceal a number of preparatory observations on the movements made by the four species while they were collecting food during the nestling stage.

It was not always possible to see exactly how far a bird travelled in certain directions because of the topography of the area, or because of the screening effect of trees near the observer's position.

The difficulty was minimal in the case of the redstart (and the neighbouring willow warblers). The male redstart was watched from a car parked approximately thirty metres from the nest-box, and this position gave the observer an unobstructed view across the areas used by this bird for feeding. On a number of occasions a full repertoire of feeding actions could be monitored during the few minutes the bird was away from the nest.

Preliminary observations were required to assess the areas used by both pairs of wood warblers in order to position a hide satisfactorily for the main watches. In practice this proved to be straightforward; the small areas involved and the relative openness of the vegetation in both Grove Wood and Frog Wood allowed the birds to be followed through the trees without any real difficulty. A few casual observations on the boundaries of the territories confirmed the extent of the birds' travels.

The main frustrations were caused by the topography of the area around the pied flycatchers' nest. Not all of the feeding areas used by the parent-birds could be overlooked from the vantage point that gave the most unobstructed view of the nest-hole; if a member of the pair left in an eastwards direction it was impossible, from the observer's position upslope (north) of the box, to accurately record how far it flew. Did it stop among the saplings in the small glade (feeding area 4), or did it travel further, to the firebreak (area 5)?

These questions were largely answered by the observer concealing himself along the flightline east of the nest-box. 28 of the 32 feeding trips made by the male pied flycatcher over six hours' observation between June 18th and 24th stopped short at the glade-saplings. In any event, during the main period of observation on June 27th it was found that the bird's height as it left the nest, and the directness or otherwise of its flight, were very good indications of the bird's ultimate destination.

The main feature to emerge from watching the birds at this stage of the breeding season is that, in contrast to the wood and willow warblers, which used the whole of their territory for food-collecting, both the pied flycatchers and redstart displayed marked changes in the areas they used. The pied flycatchers were clearly using a fraction of the male's original home range; the redstart male, after concentrating his food-collection activities in a similar, contracted area, also used parts of the study area that he had never visited before.

4.2.3 Feeding rhythyms, and the food brought to the nestling

During the 24-hour periods of observations on the feeding areas used by the birds, the pied flycatchers, the male redstart and the wood warbler made the following visits to their nests to bring food to their nestlings.

TABLE 17: THE FEEDING-RHYTHYMS OF THREE BREEDING PAIRS

Number of visits between	Redstart	Pied flycatcher		Wood Warbler (Grove Wood)	
	(male)	(male)	(female)	(male)	(female)
04.30 - 05.30	22	20	16	16	1
05.30 - 06.30	24	25	13	12	0
06.30 - 07.30	16	24	14	12	1
07.30 - 08.30	15	26	19	16	0
08.30 - 09.30	17	31	16	12	1
09.30 - 10.30	14	29	17	15	1
10.30 - 11.30	24	26	19	16	2
11.30 - 12.30	21	35	13	12	0
12.30 - 13.30	17	28	17	15	2
13.30 - 14.30	17	32	13	13	2
14.30 - 15.30	15	31	17	11	3
15.30 - 16.30	19	25	14	11	4
16.30 - 17.30	18	29	10	11	2
17.30 - 18.30	14	23	16	9	5
18.30 - 19.30	10	19	10	10	4
19.30 - 20.30	10	22	14	10	3
20.30 - 21.30	3	15	12	11	6
	276	440	250	212	37

Number of infertile eggs	3	0	3
Number of pulli	3	5	2
Age of pulli (days)	8-10	9-10	7-9

These data are graphed in Figures 7, 8 and 9.

Figure 7: Visits made to the nestlings by the male redstart over a 24 hour period.

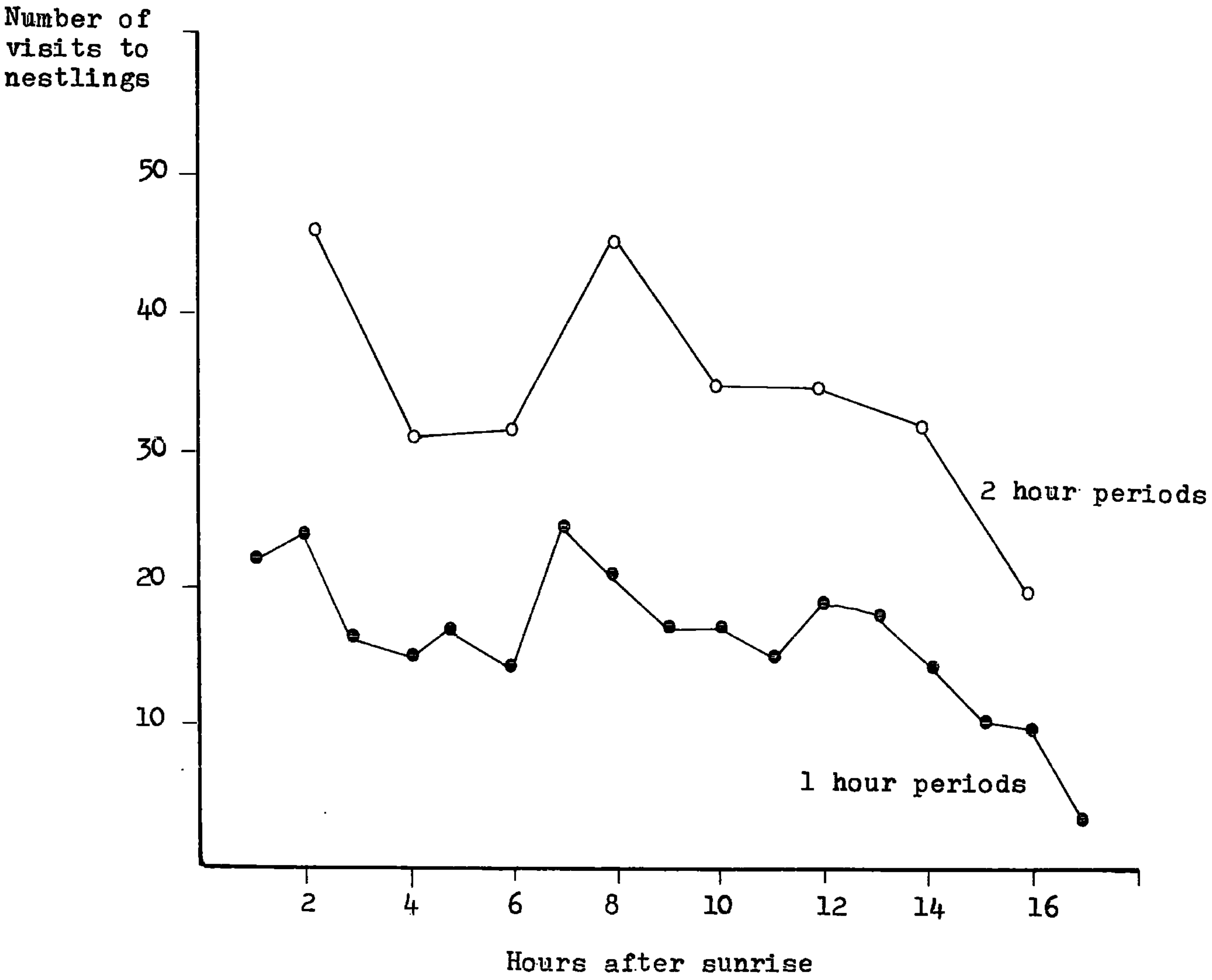


Figure 8: Visits made to the nestlings by the pied flycatcher over a 24 hour period.

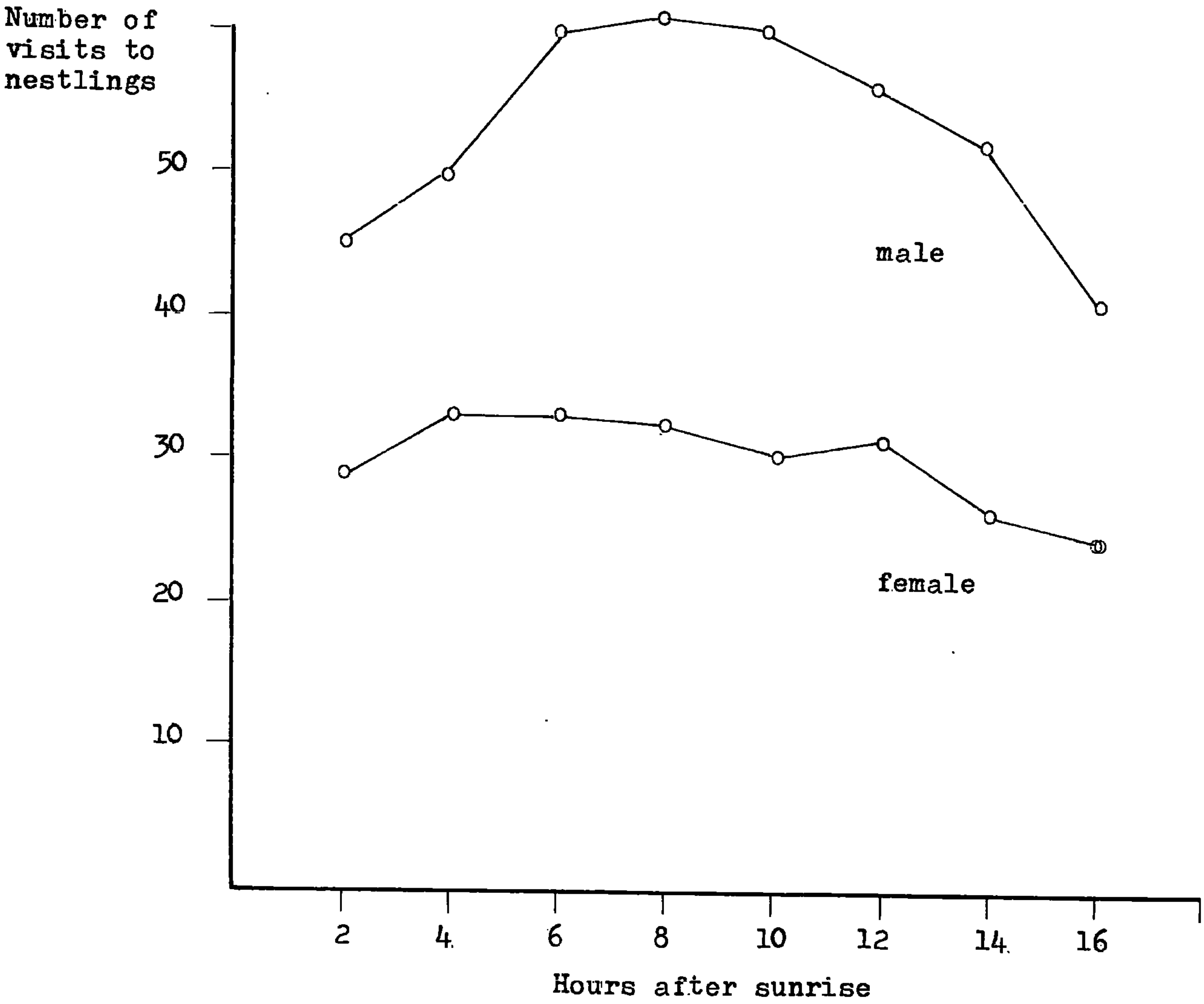
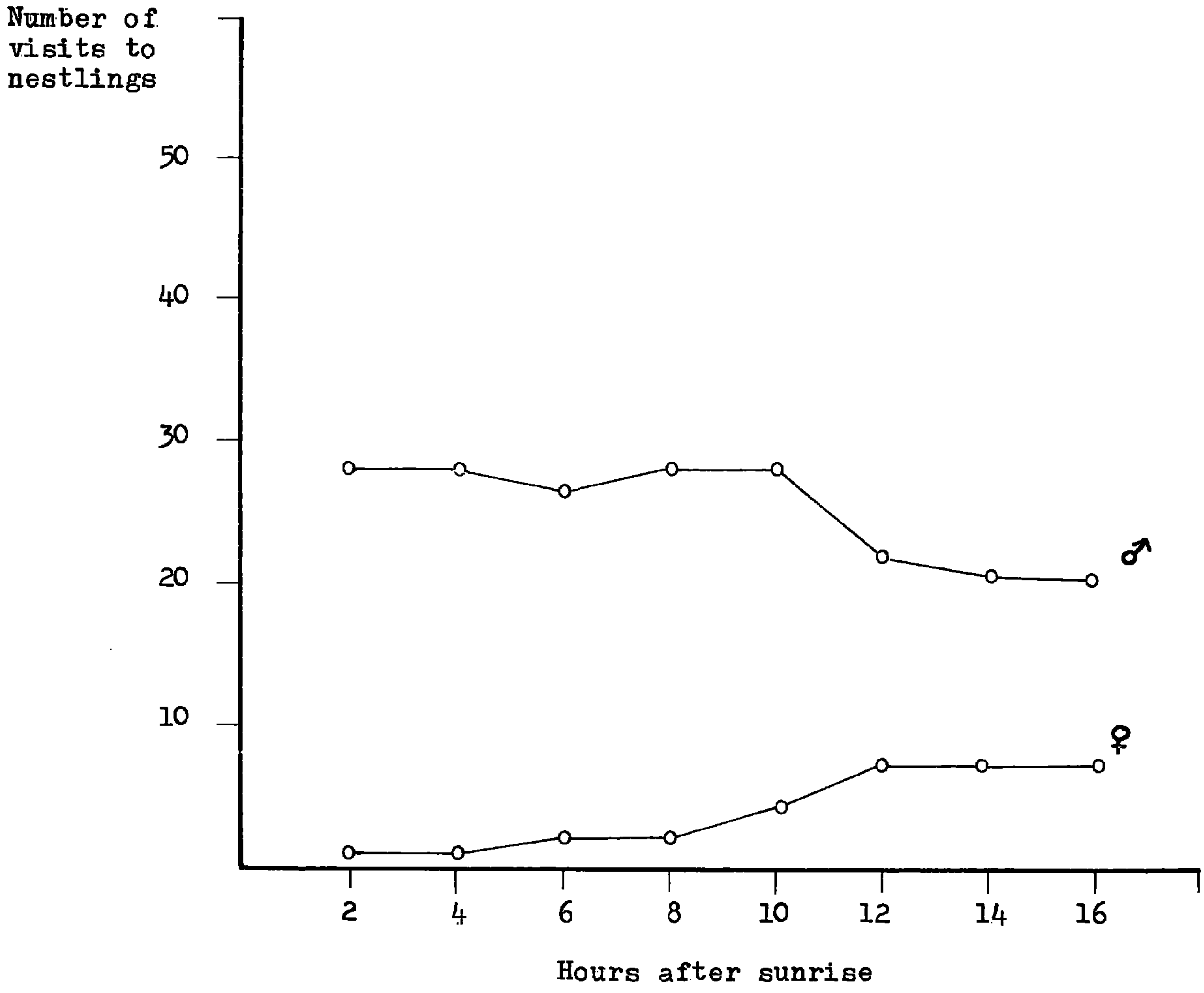


Figure 9: Visits made to the nestlings by the wood warblers in Grove Wood over a 24 hour period.



The redstart (Figure 7) was most active in the first hours after sunrise. During the morning the number of visits that he made to the nest decreased markedly, but peaked again at midday, only to fall away rapidly during the few hours before dusk. The graph for the male pied flycatcher (Figure 8) lacks an early morning peak, the number of visits to the nest increasing gradually to a plateau in the middle of the day, and then gradually falling away towards dusk. In contrast to her mate, the female pied flycatcher maintained a steady rate of feeding throughout the day. In addition her activity was much lower than the male's (chi-squared significant at $p < 0.001$). This result is at variance with Haartman's (1954) claim that during the last days of the nestling stage the female pied flycatcher takes the leading role in feeding the young, and it is possible that she had started to moult.

Figure 9 summarises the visits that the Grove Wood pair of wood warblers made to their nestlings over the 24-hour observation period. The female of this pair made very few excursions away from the nest to search for food, and these trips were nearly always close to the nest-site. Three of the clutch of five eggs failed to hatch, and this may be one of the reasons for her spending so much of her time incubating. A remarkable feature to emerge from Figure 9 is the complementary behaviour of the male and female wood warblers. As the period of observation progressed the female's activity increased, and the male's decreased. The net result was that the overall number of visits made to the nest remained approximately the same throughout the period.

The food items brought to the nest by pied flycatcher and wood warbler have been summarised in Tables 13 and 15. It was impossible, even with the aid of a telescope, to identify the food items that the male redstart brought to his three nestlings on more than a very small number of occasions, (they were mainly winged insects, and a few larvae), and for both the pied flycatcher and wood warbler, identification of the food items was limited to broad categories - larva, pupa, adult insect. In consequence, the discussion of these results can only be in general terms.

A derivation of Table 15 is the following summary of the food items brought by the male and female pied flycatchers:

	Male	Female	Total
Adult	94	47	141
Larva	26	12	38
Pupa	6	9	15
	126	68	194

The chi-squared calculated on this data is 4.48, and since this is less than the chi-squared ($p < 0.05$) value of 5.99 (2 degrees of freedom), the null hypothesis, that there is no difference between the sexes in the broad categories of food that they are taking, can be accepted. However, earlier (Figure 2), it was found that the female pied flycatcher showed a tendency to use the ground more than her mate (although this trend was not statistically significant). It is interesting to note here that she also displays a disproportionate (but not significant) preference for pupae.

TABLE 15: FOOD ITEMS BROUGHT TO NEST BY MALE AND FEMALE PIED FLYCATCHERS, BY FEEDING AREAS AND TIMES OF DAY.

425 ITEMS BROUGHT, JUNE 18-24 (231 UNIDENTIFIED)

Areas:	1		2		3		4		5		6		7		8		9		10		11		♂	♀	T
0430-0630 (GMT)	2	2	0	1	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	5	3	8
	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	3	0	3
	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
0630-0830	0	0	0	0	0	2	1	0	3	0	0	2	0	0	0	0	1	0	1	0	0	0	6	4	10
	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2	2
	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0830-1030	1	3	1	0	1	1	0	2	0	0	1	0	1	2	0	0	0	0	0	1	0	0	5	9	14
	0	1	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	3	3
	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2
1030-1230	1	3	1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	2	0	0	2	7	9
	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1230-1430	10	3	1	0	3	0	5	0	0	0	2	0	7	1	0	0	3	1	1	1	2	1	34	7	41
	9	0	0	0	2	1	4	0	0	0	1	0	0	1	0	0	1	1	0	0	1	0	18	3	21
	3	1	0	0	1	1	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1	4	5	9
1430-1630	3	0	1	0	0	0	2	0	1	0	1	0	2	4	1	0	3	0	2	0	1	0	17	4	21
	0	0	0	1	0	0	1	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	4	1	5
	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1630-1830	3	2	2	0	2	0	5	1	0	0	0	0	1	3	0	0	0	0	3	0	0	0	16	6	22
	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	3
	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	2	2
1830-2030	1	0	0	1	0	0	1	0	1	1	0	0	2	2	0	0	1	2	3	1	0	0	9	7	16
	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
	♂	♀																							
Adult	21	13	6	2	7	3	15	3	5	1	4	2	14	14	1	0	8	3	10	5	3	1	141		
Larva	10	2	0	3	2	1	7	1	0	0	2	0	2	4	0	0	1	1	1	0	1	0	38		
Pupa	3	2	0	0	2	2	0	0	0	0	0	0	0	2	0	0	0	2	1	0	0	1	15		
Total	34	17	6	5	11	6	22	4	5	1	6	2	16	20	1	0	9	6	12	5	4	2	194		

The coefficient of concordance W calculated for the data in Table 12 shows that there is good agreement with respect to what food items are brought during the eight 2-hour periods into which the observations are grouped. W is the same for both male and female, and is equal to 0.766 (significant at $p < 0.01$). Similarly, a between-sites analysis shows that there is no overall difference in the food items collected in the eleven different feeding areas. The W for the male pied flycatcher is 0.883, and a chi-squared value of 19.4 (2 degrees of freedom) shows that this value of W is significant at p very much less than 0.001. The coefficient of concordance calculated for the female pied flycatcher is rather lower, at 0.449, but this value is still significant (at $p < 0.01$).

72.7 percent of the identified food items brought by the pied flycatcher to their five nestlings comprised adult flying insects. Just under 20 percent were larvae, and nearly 8 percent were pupae ($n = 194$).

The data for the Grove Wood wood warblers in Table 13 were compared in the same way, but using the chi-squared statistic instead of W. It was found that the food items brought to the nest did not vary, either between the different times of day (chi-squared of 6.37 < chi-squared, $p = 0.05$, of 7.82), or between the different areas used to collect them (chi-squared of 12.7 < chi-squared, $p = 0.05$, of 15.5, and H_0 again accepted).

In the case of the Grove Wood wood warblers, 58.5 percent of the identified food items brought to the nestlings were adult flying insects, 39.8 percent were larvae, and only 1.8 percent were pupae (n = 171). For comparison, observations were made on the food brought by the wood warblers in Frog Wood:

Diptera	8
'Small winged insects'	17
'Large winged insects'	7
Moths	3
Beetles	1
Larvae	24
Pupae	2
Not identified	19

Of the 62 items identified, 56.5 percent were adult flying insects and 38.7 percent larvae.

It is not surprising that for the two species, redstart and pied flycatcher, that take a predominance of flying insects, the scores on the Density of Foliage variable are on the whole low. In contrast, the majority of the observations made on the two warblers show that their feeding sites are mainly in full leaf, and this is clearly associated with the higher number of larvae that is taken by them.

Part Five: Discussion of Results

The justification for the transformation of sets of data as a means of improving the interpretability of correlation coefficients is discussed by Gorusch (1974). He also summarises the effects of data (especially dis-continuous data) with skewed distributions on the component patterns identified by multivariate analysis.

Table 11 lists those parameters incorporated into the basic feeding observation that show significant inter-correlations. The figures are for all the species grouped.

Cloud-cover may be considered to have an effect on both air-temperature (which would be related to insect abundance and mobility), and 'visibility', which from the bird's point of view, might mean that it can feed in the shady interior parts of a tree when the sun is high. In these contexts, cloud-cover would be expected to have a number of influences on both the spatial and behavioural components of a bird's foraging behaviour, and it is not surprising that this parameter has significant (although small) correlations with nearly all the others.

In contrast, the time of day which might also be regarded as temperature- or prey activity-related, shows none of the inter-correlations that this might imply.

The species of tree in which a bird feeds will obviously dictate in part where a bird feeds in that particular tree, the food available to the bird, and the method a bird has to use to take this food, and Table 11 confirms that such correlations are significant.

Similarly one would expect correlations between the bird's feeding zone (the V-H cells) and factors such as the choice of perch, or substrate, and whether the bird is feeding in the open or the leafy parts of the tree. It follows that a bird's feeding zone will also influence the places where it takes its food, and these expected associations are demonstrated in the correlations shown in Table 11.

A bird's stance, or feeding action may be expected to be partially related to physical factors such as the tree-species being used, the openness or otherwise of the leaf canopy where the bird is feeding, and the source of its food items. Table 11 confirms that these are significant inter-correlations. One interesting point to emerge however, is that the feeding action a bird uses to take prey is not, in general, related to the feeding-zone being used. Because these observations are for several species grouped, any inter-species differences in feeding actions are highly significant. As a bird's feeding action is in general independent of where it is feeding, it may be that differences in feeding behaviour between species are adaptive.

It is obvious that a number of influences affect any one parameter. At the time an observation is made, all sorts of environmental factors are operating to modify a bird's foraging behaviour. Effects of this kind might be expected to blur distinctions between the species in this study, and it is notable that clearcut differences and similarities, like those described for aspects of foraging behaviour in Section 4.1, occur.

The importance of vertical feeding stations in ecological isolation of closely related bird-species was pointed out by Colquhoun and Morley in 1943. In fact there are many cases of stratification of species or specific differences in foraging behaviour, and especially in woodland birds (for example Lack 1944, 1954, 1966, 1971; Snow 1949; Hartley 1953; Gibb 1954, 1960; Betts 1955; MacArthur 1958; Morse 1967, 1968, 1970; Power 1971; Willson 1970; Williamson 1971; Edington 1972).

Gibb, whose work was largely paralleled by Hartley, studied the tits of the genus Parus in a wood near Oxford. He found that the small blue tit feeds high up in oaks, on the twigs, buds and leaves - and in addition it is more agile than the other species, readily hanging upside down. In contrast the heavier great tit feeds mainly on the ground, although it uses the leaf canopy to take caterpillars for its young. The marsh tit, which is intermediate in size between blue and great tit, tends to use the twigs and branches below twenty feet when feeding in large trees. Betts (1955) showed that, corresponding to these differences in feeding station, the species take mainly different food items. This difference is correlated with bill-size and shape. The great tit can take harder seeds than the other species (for example hazel nuts) and takes larger insects (in many cases over 6 mm in length). The blue tit takes few seeds and its insect prey is usually less than 2 mm long. The marsh tit, which takes a variety of seeds and fruits, mostly takes insects that are intermediate in length (3-4 mm).

MacArthur (1958) examined the ecology of five very similar species of parulid warblers that breed in boreal forest in north eastern USA, and feed on the same species of spruce-tree. Despite their overall similarity, MacArthur found that the warblers differ markedly in the parts of the tree they feed in, and their feeding methods.

Brownheaded nuthatches (Sitta pusilla) in mixed flocks of birds spend a large proportion of their foraging time on the distal parts of limbs, and on twigs, while pine warblers (Dendroica pinus) in the same flocks spend a large part of their time on the proximal parts of the limbs, regularly moving on to the trunk. In a study by Morse (1967) it was found that the two species, when not in one another's presence, have in fact, similar foraging distributions. Snow (1949) found in Scandinavia that when great tits were present in mixed flocks, crested tits (Parus cristatus L.) and willow tits (Parus montanus L.) foraged at a low level, but that when great tits were absent, the other two species foraged at all heights.

Recently, Edington (1972) confirmed that a number of co-existing species of insectivorous bird show this sort of spatial separation (with a strong vertical component) in an upland wood in South Wales. But not all of the species that he studied fitted into this scheme. In particular, two pairs of birds, (willow warbler and wood warbler; redstart and pied flycatcher), were described as having virtually complete overlap in their feeding stations.

In his study, Edington considered the 'feeding station' to be a composite of (a) the substrate or size of branch used by the bird, and (b) the part of the tree (leaf, twig, branch etc.), or ground, or air, from which the bird takes its food.

The present study, also made in an upland site, is in general agreement with Edington in that the wood warbler and willow warbler are alike, and that the redstart shows a number of similarities with the pied flycatcher, but there are contrasts.

First, it is clear from Figures 2-3 that while the pied flycatcher and redstart take food items from the same type of substrate, they use different places for perching, or launching a feeding action. More importantly, with respect to feeding zones (which were not considered by Edington) the two species show a very definite partial separation in space. The redstart mostly uses the lower layers of the vegetation for feeding, while the pied flycatcher spends a lot more of its time foraging higher up.

It is significant that the two species in this study that display no separation in vertical space, the wood warbler and willow warbler, also defend mutually exclusive territories - that is, they are separated horizontally (a fact that was also demonstrated by Edington in his Welsh study).

In addition, the redstart and pied flycatcher, the two species that do show vertical separation in their use of the habitat, hold territories that are much less exclusive in character. Edington presents evidence for the occurrence of overlap between the territories of adjacent redstart and pied flycatcher pairs (Edington 1972), and Haartman's (1956) contention, that a male pied flycatcher concentrates most of his territorial activity in a small area around the nest-hole, would suggest that the poorly defended boundaries of his territory would be in consequence only vaguely defined. In this situation, overlapping with adjacent territories would not be surprising.

The above observations indicate that species which are not separated vertically need to be separated on a horizontal basis, and that horizontal separation is less critical when a degree of vertical segregation between species is present.

Differences in foraging behaviour and the resulting partitioning of the habitat are often interpreted as being the result of interspecific competition for food (MacArthur 1958, Mayr 1963, Cody 1968) and the necessity to reduce this. MacArthur (1958) argues that birds avoid competition by behaving in such a way that they are exposed to different kinds of foods - they feed in different parts of the tree, use different feeding methods, etc..

Competition is usually defined in terms of a limiting resource. For example Miller (1967) describes biological competition as 'the active demand by two or more individuals of the same species population (intraspecies competition) or members of two or more species at the same trophic level (interspecies competition) for a common resource or requirement that is actually or potentially limiting.' Competition in fact appears to be not only possible but highly probable in the context of Elton's (1927) concept of the niche. If it is an organism's functional status in the trophic system that is important, then it is clear that any one functional role can be performed by several different species.

But it is not easy to identify the actual process of competition in nature. Despite numerous studies there is no direct evidence that competition occurs (Andrewartha and Birch 1954). Lack (1966), in agreeing with this, attributes the lack of evidence to 'competition having occurred mainly in the past'.

Most studies (with the exception of Gibb 1960, Pulliam 1971) do not attempt to present accurate estimates of how much food exists in a habitat, let alone how much of it is available to, or actually utilised by birds. The practical difficulties are very great. In addition there are a number of other questions that have to be answered before the assumption can be made that food is a limiting factor. For example, how much food can be exhausted before individuals can no longer search out food items efficiently enough to maintain a neutral or positive energy balance? What is the nutritive values of the different food items brought? (Morse 1971).

Because of the practical difficulties in measuring the food available in a habitat, most information supporting food-limitation is of an indirect nature, and Morse (1967) suggests that such limitation often exists for only a small part of the time. Gibb (1954) argued that food was in 'short' supply for tits during the winter and the breeding season, and there is circumstantial evidence to confirm this in the case of the redstart and pied flycatcher males in this study.

At the beginning of the breeding season, while his mate was incubating, the male redstart spent a large proportion of his time performing activities, such as singing and preening, that were not related to feeding. On a number of occasions he could be watched for half an hour without one feeding movement being made by him. In contrast, after the hatch, when he was bringing food to his three young, feeding became his major activity. During the few minutes he was away from the nest he usually made several consecutive feeding movements. The interesting point to emerge at this stage of the breeding season, was that, up to this time, the male redstart had not been seen feeding in the ground vegetation - his preferred layer during the urgent job of feeding young. The data collected for the male during the incubation phase are too limited to support this observation statistically, but the indications are that the male redstart altered his behaviour, perhaps to exploit the habitat more efficiently during a period when he was under some pressure (that is when food was 'short').

The pied flycatcher's behaviour also became more urgent during the nestling stage, but there were no significant differences in either the parts of the tree he used for feeding (rank correlation coefficient $r_s = 0.577$, $p < 0.01$) or in his methods of obtaining food ($r_s = 0.585$, $p < 0.02$) between the pre-hatch period (63 observations) and the post-hatch period (135 observations).

Root (1967) found marked changes in the feeding behaviour of a number of insectivorous birds which he claimed corresponded to the differing demands of feeding young and 'self-maintenance' feeding. He described alternations between overlap and discreteness in the 'exploitation patterns' (that is, a composite of feeding behaviour, feeding areas, and diets) of several coexisting species, resulting from changes in prey-availability from season to season, and from habitat to habitat (see also Lack 1946, Gibb 1954, and a study relating to fish by Nilsson 1960).

Root also demonstrated very obvious shifts of territorial boundaries, and of areas used for feeding, by the blue-grey gnatcatcher (Polioptila caerulea) as the breeding season progressed. Similar observations of an alteration in the area being used for feeding were made for the pied flycatcher male, the redstart male and the willow warblers, in this study. However, rather than a 'permanent' shift in habitat as described by Root for the gnatcatcher, these changes in area may have been associated with <u>daily</u> shifts in habitat preference corresponding to varying abundance of insects, as documented for certain species of North American blackbirds (Orians and Horn 1969).

Edington (1972) puts forward the reasonable hypothesis that the contraction, or alteration in the areas used for feeding by redstart and pied flycatcher during the nestling phase, is a mechanism by which the original, large overlapping territories are redefined as mutually exclusive feeding areas, similar to the mutually exclusive territories held by wood warbler and willow warbler (which do not alter in size or shape during the period when young are in the nest). This phenomenon can be regarded, once again, as indirect evidence for food-limitation; it can at least be inferred that competition for food is being reduced by subdivision of the food-resource.

A possible source of confusion is the argument that territoriality is a means by which individuals compete for the available food supply. The data are, in fact, incomplete, but the evidence at present available seems to indicate otherwise (Hinde 1956).

Murray (1971) argues that interspecific territoriality - that is, competition for space-is more frequently demonstrated than is competition for food, and he further argues that it is interspecific territoriality, not competition for food, that is the more frequent cause of differences in habitat or foraging behaviour. Willis (1966, 1968) for example, found cases of interspecific aggression resulting in changes in foraging behaviour. In particular, plain-brown woodcreepers (Dendrocincla fuliginosa) feed from higher perches at army ant swarms when ocellated ant-thrushes (Phaenostictus mcleannani) are nearby; and lunulated and Salvin's antbirds (Gymnopithys lunulata and G. salvini) feed from higher perches when larger antbirds and woodcreepers are present, than when they are absent. The changes in foraging height in these cases result from direct supplanting attacks by a larger bird, and Murray considers that if (a) the dominant species was common enough, and (b) the subordinate species was always supplanted, then one might expect the subordinate bird's behaviour to be permanently modified.

Hutchinson's (1958) concept of the niche as an 'n-dimensional hypervolume' has proved a useful tool in describing the overlap between species with respect to all of their ecological requirements, and the possibility of competition between them. But there is always a practical limit to the number of parameters which can be measured, and MacArthur (1968) points out that no matter how many variables have been measured without ecologically separating two species, the chance is always there that the consideration of one more might reduce the overlap markedly. Basically this means that in theory one can demonstrate that two species do not occupy the same niche, but it is not possible to demonstrate that they do occupy the same niche!

Despite these operational problems, Figure 5 can be regarded as an attempt to portray in two dimensions the realised feeding niches ('realised' in the sense of Hutchinson 1958) of four species of bird. The displacement pattern described by the point-configuration not only represents the extent to which the species overlap in their ecological requirements for feeding, but also makes clear the potential that exists for competition to be serious. Redstart and pied flycatcher have very different feeding niches from the warblers, and also differ between themselves to an extent that suggests that potential competition is minimised. In contrast, the wood warblers and willow warblers have very similar feeding niches, and the very large potential for competition between them might reasonably help to explain why they need to maintain mutually exclusive areas of the habitat for breeding.

It must however be borne in mind that overlap in resource use by two species in nature can be evidence both for and against the existence of competition between them. Competition may be operating, but if exclusion or displacement is incomplete, the observed niche overlap will be evidence <u>for</u> competition; while in a situation where the resource under consideration is in oversupply or is irrelevant to one or both species, niche overlap will be evidence against competition (Colwell 1971).

The existence of competition can only be demonstrated by comparing realised niche overlap to fundamental niche overlap between suspected competitors. Hutchinson's (1958) 'fundamental niche' includes all regions of niche space in which an organism has 'positive fitness', and if the fundamental niche overlap is greater than the realised niche overlap then the existence of competition has been domonstrated. Morse (1967, 1970) has shown that the absence of one species may allow another species to exploit a wider vertical range, and Miller (1968) has demonstrated that where they are sympatric, yellow headed blackbirds (Xanthocephalus xanthocephalus (Bonaparte)) exclude the more specialised redwing (Agelaius phoeniceus (L.)) from the former's niche. The realised niche of the redwing can be viewed as a physical refuge in the habitat.

In addition to the spatial aspects of separation between species that are described above, there are many accounts of species that coexist without spatial separation, apparently because each has become specialised to use a different food-source, often with associated differences in bill-size (Lack 1947, Schoener 1965, Newton 1967).

The length, width and depth of the bill of redstart, pied flycatcher, wood warbler, and willow warbler are given in Table 18. The measurements are of birds in the British Museum (Tring) and the Hancock Museum (Newcastle).

TABLE 18: THE BILL-STRUCTURE OF REDSTART, PIED FLYCATCHER, WOOD WARBLER AND WILLOW WARBLER

Species	No. measured	Length	Bill Width	Depth	Length/ Width	Length/ Depth
Redstart	5	13.3	5.68	4.12	2.34	3.23
Pied flycatcher male	5	11.8	5.85	4.25	2.01	2.78
Pied flycatcher female	5	11.3	5.75	4.12	1.97	2.74
Wood warbler	5	12.5	5.00	3.75	2.50	3.33
Willow warbler	6	12.2	4.91	3.87	2.48	3.15

It is clear that the wood warbler and willow warbler have similar bill-structure, and in fact, with respect to culmen length, they are more alike (the character difference ratio is 1.025, Hutchinson 1959) than the male and female pied flycatchers (a character difference of 1.044). This is evidence that the birds may be taking similar foods.

The redstart, on the other hand, has a relatively longer, more slender bill than the pied flycatcher (a character difference of 1.128 to 1.177), indicating possible separation between the two species in the food items they are taking. The pied flycatcher's shorter, but stouter bill is better adapted to catching flying insects (Williamson 1971) than the redstart's more warbler-like bill. These points would appear to have some relevance to the feeding rhythyms displayed by the birds at the nest in the present study (Figures 7-9).

The curve for the male pied flycatcher (Figure 8) may be related to the abundance of air-borne insects. The numbers available, and therefore the numbers of food items brought to the nest, would seem to be dependent on increasing air temperature throughout the morning, peaking around the middle of the day. In contrast, the redstart, with his finer bill and habit of sweeping through the ground vegetation, seems to be better adapted to picking sessile or 'cold' insects from the vegetation stems; and this could well be part of the reason for his early morning peak. The wood warblers' steady food-bringing activity (Figure 9) throughout the period of observation, may well be related to the sessile nature of their main prey (larvae).

Further measurements of body-structure are summarised below:

TABLE 19: BODY-WEIGHT AND LEG-STRUCTURE*

(Numbers of individuals measured are in brackets)

Species	Mean total leg-length (mm)	Mean percentage length			Mean Weight (gm)	Total leg-length / body wt.
		Femur	Tibia	Tarsus		
Redstart male	64.4 (12)	23.3	43.5	33.2	13.2 (66)	4.9
Pied flycatcher	53.0 (10)	24.5	43.8	32.6	11.6 (60)	4.6
Wood Warbler	58.3 (5)	24.5	44.9	30.5	8.4 (43)	6.9
Willow Warbler	58.4 (12)	22.4	44.2	33.4	7.9 (191)	7.4

*Weights taken from Ash (1969) are post-migratory lean weights. Bone measurements are of birds in the British Museum (Tring).

Newton (1967) in his detailed work on finches, found that those species that often used the ground for feeding either were relatively larger and heavier, or had relatively longer legs with respect to body-weight (for example, Chaffinch Fringilla coelebs (L.)).

Both of these points emerge from the above table. The redstart, which is heavier than the pied flycatcher, and has slightly longer legs in relation to its body-weight, has been shown by this study to use the ground-layer to a greater extent than the flycatcher. In particular, the redstart shows a certain likeness to the robin (Erithacus rubecula (L.)) in the way it will run a few paces along the ground, bend to pick up something, run a few more paces, etc., before taking flight. The pied flycatchers were never seen behaving in this manner.

The fact that the willow warbler has relatively longer legs than the wood warbler in relation to body-weight, may be one of the factors behind the willow warblers' more ready use of larger branches than the wood warblers. Conversely, there may be a relationship between the relative shortening of the tarsus in the wood warbler (Table 19) and this species' apparent adaptation to the use of twigs for perching.

Tendencies for any of the species to specialise in their methods of feeding in different trees were assessed by means of the Shannon + Weaver (1963) formula for H", an information theory index.

In the context of information theory, diversity is equated with the amount of uncertainty that exists regarding an individual selected at random from a population. The more individuals there are, and the more nearly even their representation in the population, the greater the uncertainty. Information content is a measure of uncertainty, and can therefore be used as a measure of diversity (Pielou 1966).

For samples, $$H'' = - \sum_{i=1}^{s} p_1 \log p_1$$

where H" is the maximum likelihood estimator of the unknown population diversity H'. H" is obtained by taking the observed $N_{i/N}$ values as estimates of the unknown p_1 values. N_i is the number of individuals found in category i and N the total number of individuals in the sample. H" reaches a maximum for a given s (the number of available feeding methods, or source-stance categories) when all the $N_{i/N}$ values are equal. In this way,

$$J'' = {}^{H''}/_{H''\ \mathrm{max}} \qquad \text{(Pielou 1966)}$$

can be used as an index of specialisation to a few categories. A small value of J" represents a relatively strong tendency to specialise. Between species comparisons are facilitated by calculating the J" values using the total number of categories recorded (i.e. i = s) (McNaughton 1970). This technique has been used by several workers (Orians 1966; Paine 1963; Root 1967; Willson 1970; Morse 1970, 1971) but has been criticised by Hurlbert (1971) who proposes alternative formulae.

Table 20 presents the calculated J" values for the feeding behaviour of redstart, pied flycatcher, wood warbler and willow warbler:

TABLE 20: FEEDING BAHAVIOUR DIVERSITY INDICES (J")

Species	All trees	Oak	Birch
Redstart	0.544	0.543	0.538
Pied flycatcher	0.415	0.249	N/A
Wood warbler	0.568	0.517	0.670
Willow warbler	0.687	0.629	0.675

It is clear from this table that the generalist among the four species is the willow warbler which consistently scores the highest J" values. In this event it is not surprising that it shows significant correlations with the other three species in the source-stance matrix (Table 9). The pied flycatcher consistently receives the lowest J" values (for lime J" = 0.393) and is clearly the specialist in this situation.

The tendency for specialisation is most notable where the flycatchers are feeding in oak (J" = 0.249). Some of the reasons for this difference in behaviour must be due to the morphology of the trees being used. Whereas the pied flycatchers mainly hawked about the branches of the large oaks in the Enclave, they were able to use limes both for hawking and for ground-feeding. The old limes have huge, low branches, and there are numerous twigs at the bases of their trunks, enabling the birds to perch only a little above the ground in readiness for pouncing or dropping onto prey, or sweeping through the ground vegetation.

The redstart was able to drop to the ground from the lower branches of oak, and this appears to be a real difference between these two species. The flycatchers were only seen to use this 'pouncing' or 'dropping' action from low ground-vegetation stems or branches hanging close to the ground (limes and yews).

It is interesting to note that both the wood warbler and the willow warbler, the two most strongly generalist species in Table 20, show differences in the feeding behaviour used in different trees. Spearman's rank correlation coefficient $r_s = 0.456$ for wood warbler in oak against wood warbler in birch ($p < 0.05$ only, 27 degrees of freedom), while for willow warbler in oak against willow warbler in birch $r_s = 0.208$, which is not significant. In the case of the willow warbler, there is a tendency for this species to use fewer hovering movements and correspondingly more gleaning movements when it is feeding in birch trees, indicating that it is able to respond to a differing food supply with a certain degree of plasticity.

However this difference, which is apparent in Table 21 below, is not statistically significant (the calculated chi-squared value for three degrees of freedom is 6.72):

TABLE 21: FEEDING ACTIONS OF WILLOW WARBLER

Tree-species	Glean	Cling to vertical Stem	Hover	Hawk	Total
Birch	32	1	18	1	52
Oak	26	4	34	4	68

The results of this study show that four similar species of insectivorous bird are able to coexist in the same general habitat because they differ in their use of space.

Wood warbler and willow warbler, which have similar foraging behaviour - they use the same feeding methods and hunt in the same parts of a tree as one another, defend mutually exclusive territories in the breeding season. Pied flycatcher and redstart differ in their relative use of the vertical layers in the woodland habitat, and consequently do not need to be so strictly separated horizontally.

This system of habitat partitioning involves both habitat selection and competitive exclusion, both in the vertical and the horizontal plane, and its significance might well lie in the resulting subdivision of the food resource. It can be seen that because of their behaviour, redstart and pied flycatcher are exposed to different kinds of food items, while the wood warbler and willow warbler take different portions of the same food items. In both cases interspecific competition for food would appear to be diminished.

Summary

The aim of this study, which was carried out in a small area of deciduous woodland on the edge of conifer-plantation in Hamsterley Forest, County Durham, was to identify differences in the utilisation of a mixed woodland for feeding by four small insectivorous birds.

The field technique used was that of repeated standard observations of feeding birds during the breeding season, each observation comprising a number of parameters describing several aspects of the bird's behaviour and use of space. These data were supplemented by detailed information on the four species during the period when the parents were bringing food to their young.

It was found that the four species fall naturally into two pairs. Two of the species, wood warbler and willow warbler, show extensive overlap in both their feeding behaviour and in the parts of a tree used by them for feeding. The other two species have similar feeding behaviour, but only partially overlap in their use of space, since the redstart uses the ground vegetation to a greater extent than the pied flycatcher.

The two warblers also defend mutually exclusive territories, in contrast to the far less well-defined home ranges used by the redstart and pied flycatcher.

The relationship between the vertical and horizontal components of habitat partitioning is discussed in relation to competition theory and the concept of the niche.

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APPENDIX 1

COMPONENT SCORE COEFFICIENTS DETERMINED BY MULTIVARIATE ANALYSIS

Variables	Components			
	1	2	3	4
Time of day	-0.007	-0.052	-0.009	0.910*
Cloud cover	-0.260	-0.073	0.250	-0.215
Treespecies used	0.085	0.277	0.229	-0.179
Vertical zone used	0.386*	0.088	-0.006	-0.123
Horizontal zone used	0.088	-0.452*	0.176	-0.004
Perch used	0.019	0.429*	-0.017	0.020
Stance used	-0.046	-0.037	0.769*	0.000
Source of food	0.337*	-0.038	0.292	0.130
Foliage density	0.372*	-0.206	-0.118	-0.136

* Variables that have at least 10 percent of their variation involved in a component-pattern, i.e. a loading of 0.316.

APPENDIX 2: BASIC FEEDING OBSERVATIONS

Variable characteristics: 863 valid observations

Variable: GMT (Time of Day)

Mean = 1,254.1
Standard error of mean = 13.23
Variance = 151,126.6
Standard deviation = 388.8
Range = 1,670
Kurtosis = -0.969
Minimum = 04.30
Maximum = 21.00

Skewness = -0.065

Variable: Cloud Cover

Mean = 5.386
Standard error of mean = 0.096
Variance = 7.996
Standard deviation = 2.828
Range = 8.0
Kurtosis = -1.132
Minimum = 0.0
Maximum = 8.0

Skewness = -0.564

Variable: Tree-species used

Mean = 6.976
Standard error of mean = 0.146
Variance = 18.40
Standard deviation = 4.289
Range = 17.0
Kurtosis = -0.468
Minimum = 1.0
Maximum = 18.0

Skewness = 0.377

APPENDIX 3: BASIC FEEDING OBSERVATIONS (Contd.)

Variable characteristics: 863 valid observations

Variable: Vertical Zones used by Bird

Mean = 2.879 Standard error of mean = 0.037
Variance = 1.162 Standard deviation = 1.078
Range = 4.0 Kurtosis = -0.724
Minimum = 1.0 Maximum = 5.0

Skewness = -0.249

Variable: Horizontal Zones used by Bird

Mean = 3.103 Standard error of mean = 0.035
Variance = 1.062 Standard deviation = 1.031
Range = 4.0 Kurtosis = -0.289
Minimum = 1.0 Maximum = 5.0

Skewness = -0.042

Variable: Feeding Perch used by Bird

Mean = 1.131 Standard error of mean = 0.025
Variance = 0.552 Standard deviation = 0.743
Range = 3.0 Kurtosis = 0.417
Minimum = 0.0 Maximum = 3.0

Skewness = 0.582

APPENDIX 4: BASIC FEEDING OBSERVATIONS (Contd.)

Variable Characteristics: 863 valid observations

Variable: Stance used to take food

Mean = 5.977 Standard error of mean = 0.095
Variance = 7.823 Standard deviation = 2.797
Range = 8.0 Kurtosis = -0.723
Minimum = 1.0 Maximum = 9.0
Skewness = -1.041

Variable: Source of food taken by bird

Mean = 4.311 Standard error of mean = 0.064
Variance = 3.539 Standard deviation = 1.881
Range = 5.0 Kurtosis = -0.783
Minimum = 1.0 Maximum = 6.0
Skewness = -0.906

Variable: Foliage Density

Mean = 2.1 Standard error of mean = 0.029
Variance = 0.733 Standard deviation = 0.856
Range = 2.0 Kurtosis = -1.607
Minimum = 1.0 Maximum = 3.0
Skewness = -0.192

APPENDIX 5: BASIC FEEDING OBSERVATIONS (Contd.)

Transformation of data to minimise skewness.

Table of coefficients of skewness $\sqrt{b_1}$

Trans-formation	Variables[+] 1	2	3	4	5	6	7	8	9
$y = x$	-0.07*	-0.56	0.38	-0.25	-0.04*	0.58*	-1.04	-0.91	-0.19
$y = \sqrt{x}$	-0.34	-1.35	-0.18	-0.63	-0.57	-0.92	-1.14	-1.07	-0.32
$y = \frac{1}{x}$	1.20	2.74	1.83	1.58	2.24	1.81	1.40	1.39	0.61
$y = \frac{1}{x^2}$	1.95	2.74	2.37	1.89	2.95	1.81	1.48	1.48	0.71
$y = \log x$	-2.77	-2.64	-0.73	-0.99	-1.12	-1.77	-1.24	-1.20	-0.43
$y = x^2$	0.42	-0.18*	1.66	0.47	0.75	2.06	-0.85*	-0.56*	0.02*
$y = x^{1.5}$	0.18	-0.30	1.00	0.12*	0.39	1.51	-0.94	-0.74	-0.07
$y=\sqrt{x}+\sqrt{x+1}$	-0.29	-1.15	-0.14*	-0.54	-0.43	-0.60	-1.13	-1.05	-0.28
$y = x^{1/3}$	-0.42	-1.84	-0.38	-0.81	-0.83	-1.37	-1.19	-1.12	-0.38
$y = \frac{1}{x^3}$	2.90	2.74	2.50	2.01	3.25	1.81	1.51	1.51	0.75

* Minimum value of $\sqrt{b_1}$

\+ For key, see Appendix 6

APPENDIX 6: CORRELATION MATRIX (VARIABLES)+

Correlations are computed using the standard scores of the transformation of smallest skewness.

V	1	2	3	4	5	6	7	8	9
1	1.00	-0.06	0.00	-0.01	-0.05	0.08	0.05	0.13*	-0.06
2		1.00	-0.21*	-0.31*	0.09	-0.16*	0.17*	-0.22*	-0.23*
3			1.00	0.28*	-0.32*	0.35*	0.14*	0.21*	-0.01
4				1.00	-0.03	0.24*	-0.09	0.41*	0.51*
5					1.00	-0.59*	0.06	0.02	0.21*
6						1.00	0.06	0.13*	-0.13*
7							1.00	0.28*	0.18*
8								1.00	0.31*
9									1.00

* r, the correlation coefficient, is significant $p < 0.01$.

\+ 863 observations on each variable.

1 = GMT (Time of Day)

2 = Cloud Cover

3 = Tree-species used by bird

4 = Vertical zones used by bird

5 = Horizontal zones used by bird

6 = Feeding perch used by bird

7 = Stance used to take food

8 = Source of food taken by bird

9 = Density of foliage

Appendix 7

```
PRINCIPAL COMPONENTS ANALYSIS


   NORMAL END OF JOB.
   19 CONTROL CARDS WERE PROCESSED.
    0 ERRORS WERE DETECTED.
EXECUTION TERMINATED



$LIST FACSCORES  I             II           III          IV
       1      -0.380825  0.086977 -1.264595 -0.267214
       2      -0.555147  0.057545 -1.435237 -0.011989
       3      -0.037512  0.655403 -1.014220 -0.449564
       4       0.161541  0.220273 -1.446869 -0.229441
       5       0.388025 -0.163590 -0.183766  1.669906
       6       0.499236 -0.024071 -0.036608  1.692268
       7      -0.366825  1.211423 -2.200113  1.719784
       8       0.477471 -0.941321 -1.647502  1.591474
       9       0.473373 -0.601811 -0.013161  1.665733
      10       0.500159 -0.043822 -1.889385 -0.787033
      11       0.620691  0.867137 -0.330321  1.032957
      12       0.778190 -0.070279 -1.785851  1.001508
      13       0.445524  0.547795 -2.120028  0.889355
      14       0.598926 -0.050112 -1.941216  0.932164
      15       0.765526 -0.587045  0.034336  0.998077
      16      -0.043549  0.361369  0.085172  1.004918
      17       0.445524  0.547795 -2.120028  0.889355
      18       0.778190 -0.070279 -1.785851  1.001508
      19       0.684275 -0.488333 -1.770611  0.927991
      20       0.333391 -0.132737 -1.635309  1.878645
      21       0.853456 -0.209117 -0.663310  1.302203
      22       0.289784 -1.065722  0.431274  0.532108
      23       0.222528  0.793423  0.326308  0.640630
      24       0.200763 -0.123827 -1.284587  0.539836
      25       0.168092 -0.150009 -0.734727  0.540083
      26       0.119086 -0.189281  0.090064  0.540454
      27       0.204435 -0.627502  0.260669  0.536281
      28       0.367364 -0.660760  0.690965  0.605749
      29       0.367364 -0.660760  0.690965  0.605749
      30       0.119086 -0.189281  0.090064  0.540454
      31       0.631748 -0.441926 -0.516518  0.379497
      32       1.039143 -0.320955 -1.347065  0.264550
      33       1.026479 -0.837721  0.473121  0.261119
      34       0.115738 -0.658228 -0.966485  0.506170
      35       0.115738 -0.658228 -0.966485  0.506170
      36       0.176982 -0.266355 -0.431863  0.579935
      37      -0.230413 -0.387327  0.398685  0.694882
      38       0.480569 -0.454477 -1.551328  0.480324
      39       0.834861 -0.033269  0.077257  0.440007
      40       0.143945  0.381074  0.065324  0.695695
      41       0.268773 -0.582525 -0.840347  0.664492
      42       0.122180 -0.536176 -1.545570  0.594900
      43       0.203431 -0.634888  0.259376  0.664986
      44      -0.268033  0.080765 -0.598358  0.862490
      45      -0.219027  0.120038 -1.423148  0.862119
      46      -0.235362  0.106947 -1.148218  0.862243
      47      -0.443625 -0.402743  0.791535  0.789591
      48      -0.231690 -0.396728  0.397039  0.858688
      49      -0.231690 -0.396728  0.397039  0.858688
```

```
   50      0.668450 -0.593005 -1.093452  0.624621
   51      0.403837 -0.134617 -1.419422  0.559450
   52      1.051380 -0.325264  0.216151 -1.042224
   53      0.957466 -0.743318  0.231390 -1.115741
   54      0.953794 -0.239643 -1.313866 -1.112185
   55      0.742088 -0.922879  0.614082 -0.889862
   56     -0.234134 -0.673717 -0.042290 -0.897580
   57      1.383437 -0.309896 -1.758281  1.090798
   58      0.943371 -0.457050 -0.377873  1.205994
   59      1.383437 -0.309896 -1.758281  1.090798
   60      1.008712 -0.404686 -1.477594  1.205499
   61     -0.467855  0.579059 -0.455669  0.171715
   62      1.276824  0.261494 -1.117323 -1.205896
   63      1.276824  0.261494 -1.117323 -1.205896
   64      1.358076  0.162782  0.687624 -1.135812
   65      1.280496 -0.242181  0.427933 -1.209452
   66      1.195148  0.196039  0.257328 -1.205278
   67      1.195148  0.196039  0.257328 -1.205278
   68      1.195148  0.196039  0.257328 -1.205278
   69      1.260489  0.248403 -0.842394 -1.205773
   70      0.960495  0.892658 -1.726430 -1.318174
   71      1.383938  0.740523  0.664177 -1.109277
   72      0.875020 -0.000926 -1.546580 -0.965936
   73      1.150116  0.036987 -1.425182  0.240629
   74      1.389002 -0.268936 -1.751108  0.377076
   75      1.414864  0.308805 -1.774554  0.403612
   76      1.054111 -0.234519 -1.363698  0.408102
   77      1.063639  0.330131 -1.112214  0.434760
   78      0.972435 -0.299973  0.010954  0.408720
   79      1.389002 -0.268936 -1.751108  0.377076
   80      1.096310  0.356313 -1.662074  0.434513
   81      1.254866  0.054392  0.761418  0.227164
   82      1.091937  0.087650  0.331122  0.157696
   83      1.091937  0.087650  0.331122  0.157696
   84      0.912673  0.107816  0.175757  0.088352
   85      0.470519  0.096521  1.208055  0.540192
   86     -0.192599  0.536122 -2.062656  1.917506
   87      1.375751 -0.308208 -1.831803  1.627200
   88      1.379423 -0.811884 -0.286547  1.623645
   89      1.737811 -0.730184 -0.292304  1.509068
   90      1.737811 -0.730184 -0.292304  1.509068
   91      0.935685 -0.455362 -0.451395  1.742393
   92      1.021033 -0.893583 -0.280790  1.738220
   93      0.151338 -0.413233 -0.004758  2.055421
   94      1.517268 -0.604131 -1.829406  1.539228
   95      1.419256 -0.682676 -0.179824  1.539970
   96      1.333908 -0.244455 -0.350429  1.544144
   97      1.790308 -0.084211 -2.005768  1.428825
   98      1.790308 -0.084211 -2.005768  1.428825
   99     -0.214821  0.348251  0.090085  2.247810
  100      0.513501  0.301579 -2.133566  1.904424
  101     -0.366525 -1.741966  0.249451  2.406884
  102      1.455439  0.082635 -0.998673 -0.219795
  103      0.944809 -0.388214 -0.439635  0.572356
  104      0.944809 -0.388214 -0.439635  0.572356
  105      1.551475 -0.777994  0.155509  0.523074
  106      1.128170 -0.747890 -1.918612  0.567440
  107      1.499974  0.089006 -1.829225  0.353155
  108      0.717765  0.428432 -1.934955  0.544642
  109      0.837718 -0.028027 -0.665954  0.852374
```

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110      0.923067 -0.466248 -0.495348  0.848201
111      0.923067 -0.466248 -0.495348  0.848201
112      0.389873  1.258913  0.734073  0.695158
113      0.231042  0.952663 -1.330565  0.551431
114      0.491557  0.833784  0.629747  0.690861
115      0.488796 -0.479902 -1.562371  0.383677
116      0.972368 -0.707216 -1.290801  0.181254
117      0.789006 -0.347540  0.188176  0.186169
118      0.539101 -0.198170 -0.471127  0.209963
119      0.908235  0.038068  0.507991 -0.029754
120      1.125330 -0.331677  0.675316  0.926664
121      0.787435 -0.084701  0.144132  0.209813
122      0.885448 -0.006156 -1.505449  0.209071
123      1.111670 -0.828845 -0.011188  0.342088
124      0.680597  0.044442 -1.996222  0.464268
125      0.950837  0.442186  0.916605  0.506969
126      0.262774  0.226373  1.284226  0.745835
127      0.881732  0.892827  0.470951  0.522718
128      0.702468  0.912993  0.315586  0.453374
129      1.287650 -0.873185  0.139943  0.832648
130      0.764234 -0.173478  0.086537  0.672866
131      0.145190 -0.014266 -2.184505  0.394747
132      0.568773 -0.288435  0.522590  0.856910
133      1.171629 -0.052506 -0.744011  0.557919
134      1.176531 -0.257734 -1.082965 -0.759679
135      1.127524 -0.297007 -0.258174 -0.759308
136      1.127524 -0.297007 -0.258174 -0.759308
137      1.212873 -0.735228 -0.087569 -0.763481
138      1.310886 -0.656683 -1.737151 -0.764223
139      1.212873 -0.735228 -0.087569 -0.763481
140      0.936162 -0.751473 -1.456464 -0.649523
141      1.192866 -0.244643 -1.357896 -0.759802
142      0.936162 -0.751473 -1.456464 -0.649523
143      0.984758  0.098686 -1.260594 -0.236186
144      0.903081  0.033231  0.114057 -0.235567
145     -0.945517  2.601998 -0.679923  0.007632
146      0.948596 -0.534197  0.177939 -0.156066
147      0.863247 -0.095976  0.007334 -0.151893
148      0.867535 -0.064417  0.012861 -0.701812
149      1.225650  0.015268  0.006751 -0.781287
150      1.225468  0.013925  0.006516 -0.757886
151      1.274474  0.053198 -0.818276 -0.758258
152      1.225468  0.013925  0.006516 -0.757886
153      1.321930  0.081055 -1.645064 -0.559721
154      1.223643  0.000496  0.004164 -0.523878
155      0.950603 -0.519425  0.180526 -0.413475
156      1.223460 -0.000847  0.003929 -0.500477
157      1.223460 -0.000847  0.003929 -0.500477
158      1.321473  0.077698 -1.645653 -0.501219
159     -0.186808  1.119466 -0.069077 -0.498869
160     -0.512665  1.185981 -0.929667 -0.637805
161     -0.268485  1.054011  1.305575 -0.498251
162      0.762518 -0.137224  0.443927 -0.752644
163     -0.414972  0.756632 -0.715462  0.287320
164      0.818288 -0.549233  0.597655  0.497145
165      1.206503  0.667015  0.215183  0.681621
166      1.180640  0.089275  0.238630  0.655086
167      1.262318  0.154729 -1.136022  0.654467
168      0.722931  0.894328 -0.056387  0.884044
169      0.820944  0.972873 -1.705969  0.883302
```

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170        0.615817  0.415300 -1.837887  0.787423
171        0.697069  0.316589 -0.032941  0.857509
172        0.782144 -0.123647  0.137312  0.888436
173        0.965505 -0.483323 -1.341665  0.883521
174        0.786241 -0.463156 -1.497030  0.814178
175        1.484814 -0.241920  0.670970  0.671683
176        0.176065 -0.303561 -1.420738 -1.290636
177       -0.201810  0.515414 -0.228943 -1.081052
178       -0.180392  0.185628 -1.070923 -1.135579
179       -0.180392  0.185628 -1.070923 -1.135579
180       -1.128719  1.658785 -1.783657 -0.573395
181       -0.919930  0.384426  0.223549 -0.487035
182       -0.740665  0.364260  0.378914 -0.417691
183       -0.177738  0.574826  0.572121 -1.927153
184        0.577674  0.094182 -1.266472 -1.949923
185        0.398409  0.114349 -1.421837 -2.019267
186        0.578243 -0.432323  0.274786 -1.555662
187        0.578243 -0.432323  0.274786 -1.555662
188        0.741172 -0.465581  0.705082 -1.486195
189        0.172756  0.410533 -1.374840 -1.758024
190       -0.385828 -0.127611  0.752692 -1.371953
191       -0.300479 -0.565832  0.923297 -1.376125
192        0.569120 -0.499471  0.263026 -0.385623
193       -1.458588 -1.955429 -1.599499  0.355397
194       -0.274865  0.556701 -1.253287  0.038633
195       -1.205904  0.423066 -1.473593  0.543701
196       -0.488987  0.464432 -1.168619  0.567813
197       -1.561916  2.243807  0.007134  0.699123
198        0.722925 -0.599876  0.681562  0.853886
199        0.049190 -0.053778  1.145503  0.876039
200        0.842427 -0.212254  1.001730  0.602863
201        0.566747 -0.516929  0.259969 -0.081413
202        0.729676 -0.550187  0.690265 -0.011945
203       -0.421951 -0.473411  0.839795  0.375808
204       -0.507299 -0.035190  0.669190  0.379981
205       -0.507299 -0.035190  0.669190  0.379981
206       -1.676493  1.892445 -0.306684  0.318324
207        0.581236  0.013266 -1.557866 -0.311990
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825	0.783688	-1.606436	0.877260	0.659373
826	-1.218743	-1.996253	0.313847	0.779905
827	1.446778	-0.042544	1.595116	-0.014391
828	-1.420120	-0.155595	0.134810	0.816974
829	-1.665631	1.865246	-0.588671	1.020225

```
    830        -1.665631  1.865246 -0.588671  1.020225
    831        -1.665631  1.865246 -0.588671  1.020225
    832        -1.681967  1.852156 -0.313740  1.020348
    833         0.917693  0.752197  1.259663  0.108531
    834         0.511178  0.293189  0.985688  0.580168
    835        -1.340452  0.102820  0.348256  0.649625
    836        -1.340452  0.102820  0.348256  0.649625
    837        -0.384381  0.195797  1.285166  0.870833
    838        -0.384381  0.195797  1.285166  0.870833
    839        -1.297838  0.048678 -1.070463 -1.943710
    840        -1.516927 -0.661964 -1.657438 -1.483500
    841        -1.516927 -0.661964 -1.657438 -1.483500
    842        -1.578502 -0.869204 -1.819875 -1.123981
    843        -1.578502 -0.869204 -1.819875 -1.123981
    844        -1.459000 -0.481582 -1.499706 -1.375003
    845        -1.459000 -0.481582 -1.499706 -1.375003
    846        -1.459000 -0.481582 -1.499706 -1.375003
    847        -1.459000 -0.481582 -1.499706 -1.375003
    848        -1.459000 -0.481582 -1.499706 -1.375003
    849        -1.459000 -0.481582 -1.499706 -1.375003
    850        -1.429135 -0.667053 -1.751106 -0.869109
    851        -1.488887 -0.860864 -1.911190 -0.743597
    852        -1.488887 -0.860864 -1.911190 -0.743597
    853        -1.306189 -0.818669 -2.089354 -0.427443
    854        -1.306189 -0.818669 -2.089354 -0.427443
    855        -1.186686 -0.431046 -1.769185 -0.678467
    856        -1.464474 -0.521870 -1.506762 -0.672981
    857        -1.466846 -0.539329 -1.509819 -0.368770
    858        -1.468123 -0.548730 -1.511466 -0.204964
    859        -1.470496 -0.566188 -1.514524  0.099247
    860        -1.505927 -1.401430 -1.665733  0.509904
    861        -1.446176 -1.207619 -1.505649  0.384392
    862        -1.446176 -1.207619 -1.505649  0.384392
    863        -1.386424 -1.013808 -1.345565  0.258880
END OF FILE


$CREATE HEAD
 FILE "HEAD" HAS BEEN CREATED.
$NU
$UN
$RUN FAKAD 1=HEAD+FACSCORES
"FAKAD" DOES NOT EXIST.
NEXT CARD IS
GET NEW 1


$SIGNOFF
```