SPECIFIC DIVERSITY IN WOODLAND BIRDS

By W. B. YAPP

Department of Biological Sciences, Ahmadu Bello University, Zaria, Nigeria. *

ABSTRACT

Three measures of specific diversity are considered: the logarithmic index, α; Shannon's index, H; and Yule's index, Y. Reasons are given for preferring the last for bird populations.

Values of Y for the avifaunas of different types of British woodland, both planted and semi-natural, are discussed. The lowest index for deciduous woods during the breeding season is given by birch, and the highest by pedunculate oak. For English and Welsh coniferous plantations the index increases from that of bare moorland up to the stage just before the trees are brashed, after which it falls off. Even in the oldest trees examined it is higher than on the open moor.

The correlation coefficient between the index and the number of bird species is 0.38 for deciduous woods and 0.58 for conifers. The index fluctuates with density in coniferous plantations but not in deciduous woods.

In winter the index is generally lower than in summer, with more geographical variation. Density is higher in coniferous plantations than in deciduous woods.

Density of woodland bird populations in various parts of Britain was higher in the 1960s and 1970s than in the 1950s.

INTRODUCTION TO MEASURES OF DIVERSITY

IN some recent ornithological papers, for example Batten (1972) and many read at the XVIth International Ornithological Congress in 1974, the number of species (S) in a habitat has been used as a measure of its diversity. This may be reasonable for "everyday" purposes, but it has the great disadvantage of being highly dependent on sample size: the larger the area investigated and the longer the time spent, the greater the number of species you are likely to find. Moreover S, by itself, gives no information about the pattern of distribution. To take a simple example, a red cloth with one small spot each of yellow, green and blue is not as diverse in coloration as a tartan composed of the same four colours in a more or less even mixture. Similarly, a wood containing 97 breeding territories of one species of bird, and one each of three others, does not have so diverse a community of birds as a wood containing roughly 25 territories of each of the same four species.

The Logarithmic Series

Various suggestions have been made for formulae that can be used to measure diversity. One of the earliest was the Index of Diversity α, derived from the logarithmic series:

$$S = \alpha \ln \left[1 + \frac{N}{\alpha} \right]$$

where S is the total number of species recorded, and N the total number of individuals; α is independent of both density and sample size. This assumes that, in

* Present address: Church End House, Twyning, Tewkesbury, Gloucestershire GL20 6DA.

any sample, the number of species with 1, 2, 3 . . . . individuals is

$$\alpha x, \frac{\alpha x^2}{2}, \frac{\alpha x^3}{3}, \ldots \text{ where } x = \frac{N}{N + \alpha}$$

and so must be less than unity.

Tucker (1952) applied the logarithmic index of diversity to some of his own counts of British birds, and also to some of the figures published by Lack and Venables (1939). So far as I know, these are the only measurements of diversity for British birds other than my own. The habitats of Tucker's own counts were too poorly defined botanically to be of much use. The values of α obtained from Lack and Venables are as shown in Table 1. The range is small and I do not think that any experienced observer would agree that the diversity of the beechwood avifauna is

Table 1. *Values of the logarithmic index of diversity (α) for birds of British woodlands in the breeding season. From Tucker (1952)*

	α
Oakwoods	5.8
Beechwoods with shrubs	6.7
Beechwoods without shrubs	3.6
Scots pine, England	5.1
Scots pine, Scotland	4.1

really higher than that of oakwoods. There are two possible reasons for the discrepancy:

First, the original data may not be reliable. The counts were made by a mixed group of volunteer observers, and, on the whole, woods of different types were done by different people. There is always a personal error and, as the counts were made without preliminary practice, it is likely that those made by different observers are not closely comparable. Nevertheless, I should have expected greater differences between the values of α for the different habitats than are shown.

Secondly, the data for bird communities only approximate to a logarithmic series. For my own birchwood counts (Yapp, 1974), with $\alpha = 7.97$ and $x \ (= \frac{N}{N + \alpha}) = 0.996$, the first six terms of the series, $\alpha x, \frac{\alpha x^2}{2}$, etc., are thus 7.94, 3.95, 2.62, 1.96, 1.57, and 1.30. In practice all these terms must be whole numbers (there cannot be half a species), so that the smoothed series is as shown in Table 2, matched against the actual distribution. The fit is reasonably good for the first few figures, but thereafter the two diverge widely. The early figures are those for rare species. In terms of biomass these contribute little to the community and, except for a few predators such as the raven (*Corvus corax*) and tawny owl (*Strix aluco*), they have little influence on the other members. Some indeed, such as the pied wagtail (*Motacilla alba*) and heron (*Ardea cinerea*), are transients that do not properly belong in the community at all. For the ecologically important species the actual value of S is unity (or, very occasionally, 2, and an extra sample would probably separate any two species with the same value of N); S calculated to the nearest whole number is zero. The string of ones matched by a string of noughts conveys no useful information.

I conclude that it is misleading to try to explain the real distribution in terms of

Table 2. *Comparison of the number of species* (S) *and the number of individuals of each species* (N) *in birchwoods. Actual values of* S *are compared with those calculated on the assumption that the distribution follows the logarithmic series*

N	S actual	S calculated
1	9	8
2	4	4
3	3	3
4	2	2
5	4	2
6	2	1
7	0	1
8	1	1
9	1	1
10	0	1
11	0	1
12	0	1
13	1	1
14	0	1
15	1	0
16	2	0
22	2	etc.
24	1	
30	1	
44	1	
45	1	
55	1	
58	1	
70	1	
86	1	
127	1	
151	1	
175	1	
374	1	
799	1	

the logarithmic series. It is noteworthy that most of the counts in Williams (1964) that appear to give a fairly good fit are from random collections, such as of insects caught in a light trap, not of natural communities. Nevertheless, I have worked out α for four of my series of counts and the values are given in Table 3. These counts were all made by one man under controlled conditions, and are thus free from my objection to Lack and Venables' figures. It will be seen that α is higher than for most of Tucker's results, and that, in general, it matches the other indices (to be discussed later) fairly well. The values for the two birchwood series are rather different, and that for birchwoods in 1970–71 approaches that for sessile oak. Both of these points are contrary to what one observes on the ground, and tend to confirm that the logarthmic series does not apply to counts of this sort.

Table 3. *A comparison of four indices of diversity for the bird populations of different woodlands:* α = *the logarithmic index,* H = *Shannon's,* Y = *Yule's, and* d = *Simpson's*

Dominant Tree Species	Place and Date	α	H	Y	d
Birch, *Betula pubescens*	NW Highlands 1951–52	5.89	2.29	5.46	5.45
Birch, *Betula pubescens*	NW Highlands 1970–71	7.97	2.31	5.77	5.77
Sessile Oak, *Quercus petraea*	England 1951–67	8.96	2.95	12.65	12.65
Pedunculate Oak, *Quercus robur*	England 1951–67	12.09	3.13	16.81	16.81

Shannon's H

In recent years American ornithologists have used an index derived from communication theory (MacArthur and MacArthur, 1961; Shannon and Weaver, 1949; see also Varley, 1974).

$$H = - K \sum_{i=1}^{n} p_i \log p_i$$

In this formula p_i is the probability of the occurrence of the *i*th event; n is the number of events; and K is a positive constant depending on the choice of units. The logarithms may be to any base, since the change from one to another will merely alter H (or K) by a constant factor; for example $\log_2 x = 1.45 \ln x$. In practice ornithologists have mostly used natural logarithms, and taken K as unity, so that the formula is simplified to:

$$H = - \sum p \ln p$$

For bird populations it is simplest, but not necessary, to take p as the proportion of individuals belonging to any given species, so that $\sum p = 1$.

Mathematically, H is a measure of the degree of randomness, and is formally identical with entropy as calculated in statistical mechanics. There is no doubt that it makes the sort of distinction that we are looking for between bird communities. For instance, a population of 99 individuals of one species and one of another give:

$$H = - (0.99 \ln 0.99 + 0.01 \ln 0.01)$$
$$= - (- 0.010 - 0.046)$$
$$= 0.056$$

For two species, each of 50 individuals:

$$H = - (0.5 \ln 0.5 + 0.5 \ln 0.5)$$
$$= - (- 0.347 - 0.347)$$
$$= 0.69$$

For one species of 75 individuals and another of 25 $H = 0.56$.

Shannon (in Shannon and Weaver, 1949) derives his formula by stating three conditions that the measure must fulfil—and then says that H does so. If this were all, it would be like saying: "The man who committed the robbery was tall and dark, and carried a gun: this man is tall and dark, and has a gun, therefore he was the robber." But Shannon goes further and claims to prove that H is the only measure that satisfies the conditions. This seems philosophically unsound, since it is impossible to prove a negative of this sort; if there are things in existence of which we do not know we cannot prove that they do not exist.

Since H began to be used by ecologists, several discussions of it from a mathematical point of view have appeared. The best and clearest that I have read is that by Pielou (1969). All suffer from the defect that they have little relation to the real world, and, indeed, most of them give me the impression that their authors have never actually counted animals in their lives. The observational errors inherent in fieldwork render the mathematical refinements irrelevant and misleading. One

mathematical point that no one seems to have noticed, is, that by a theorem of Ramanujan (Hardy, 1940)

$$p_n \approx n \log n$$

where p_n is the nth prime number. In this formula n is an integer—but so is p_i in Shannon's formula if it is taken straight from field counts. It is only for convenience that people usually convert it first to a fraction. I find it difficult to believe that the distribution of birds has any important relationship to the sum of prime numbers.

Carl Pantin taught us nearly 50 years ago that the converting of figures to logarithms could be dangerous unless you understand why you are doing so. I think this a case where his warning should be heeded. Shannon's formula works well for his purpose, but it should not be applied to other problems where the same conditions do not hold. I know of no paper in which Shannon's three postulates are considered in relation to the distribution of animals. The product of a number and its logarithm does not mean anything to any biologist that I have consulted, and even three teachers of university mathematics, with whom I have discussed it, have been unable to regard it as anything but the result of a mathematical operation. Unless there are properties of an animal community that can be shown to vary linearly with the logarithm of the proportion of a species within the community, I would prefer an algebraic measure of diversity which can have a physical and biological meaning and which does not ignore the semantic properties of the community.

Since H has been widely used by other people, I have worked it out for four of my longest series of counts and the results are shown in Table 3. It does not make as good a discrimination between woodland avifaunas as does the third measure of diversity, Y, which is discussed below, but it appears to be better than the logarithmic index. There would 'clearly be no point in carrying out all the mathematics necessary to derive H (or any other index) unless the result were different from S (the total number of species), and one of the more surprising statements in the literature is that of Tramer (1969), that for bird populations in general the correlation between H and S is $+ 0.972$! For my four types of woodland it is $+0.65$.[*]

Yule's Index of Diversity

Fortunately there is available a suitable algebraic expression which gives us all that we want, has a physical meaning, and is readily understood. Williams (1946; 1964; 1970) has published a measure, Y, which he calls Yule's index of diversity.

$$Y = \frac{N^2}{\sum n(n-1)}$$

N is the total number of "occurrences" (this word will be explained below) and n_1, n_2, n_3, etc., are the number of occurrences of the first, second, third, etc., species so that $\sum n(n-1)$ is the sum of all the products $n_1(n_1-1)$, $n_2(n_2-1)$, $n_3(n_3-1)$ for as

---

[*] *Editor's note:* I am told that the *real* meaning of H is that it measures the probability of the next species you see being a particular one. This is just not quite the same as Y which is based on the probability that the next and the next plus one species will *not* be the same. There is a worked example of the use of Shannon's H in connection with Lack's (1933) data for Breckland birds on pp. 6–10 of Varley (1974).

many species as there may be. Yule worked out the original mathematics of this, but Williams' expression is simpler, and gives sensible values of Y that are easy to print and remember. Since Williams modestly named the index after Yule, I follow him.

Both Yule and Williams applied the formula to the comparison of prose written by various authors, and, except for a brief application to insects by Williams, it does not seem to have been used for animal populations. For any size of sample likely to be used Y differs little from another index, d, proposed by Simpson (1949).

$$d = \frac{N(N-1)}{\sum n(n-1)}$$

As is shown by Table 3, the difference between d and Y is well within the practical error of the observations, but, since d is slightly more tedious to calculate, I do not consider it further. For larger samples the Y formula can be further simplified to:

$$Y = \frac{N^2}{\sum n^2}$$

The use of this approximate expression changes the index for highland birches (all years) from 5.77 to 5.75; for *Quercus robur* from 16.83 to 16.55; and for Norway Spruce 26–32 ft (which is a small sample) from 4.52 to 4.38. The discussion below shows that the errors thus introduced are small in comparison with others that cannot be avoided and, since $\sum n^2$ can be obtained much more quickly than $\sum (n-1)^2$, it might well be used in future.

Unlike the Shannon index, Yule's has a real meaning; it is a measure of the chance that, if two occurrences are taken at random, they will *not* be of the same species. The more diverse the community, the greater this will be. Like most indices of this sort, Yule's depends on sample size. But if N is greater than 100 (which it always should be for other reasons) the variation of Y with N is small, and may be neglected. The number of species observed, S, increases with N in an approximately logarithmic manner, but the rare species, that are added in long counts, have little influence on the index. For my pedunculate oakwoods, with $N = 629$, the effect of doubling the sample and adding ten new species at one individual each, whilst keeping the proportions of the other species constant, is to raise the index from 16.8 to 17.0. The same operation on the larger sample of Highland birches, where $N = 2243$, only raises the index from 5.78 to 5.79. Both these changes are well within the observational error of the field method.

I have used the non-committal word "occurrence" because the formula can be used for measuring diversity in many different things and ways. In ornithological ecology, occurrences may be breeding territories, contacts in a line transect, individuals in a mixed roost, and so on. Measurements based on one type of occurrence must not be directly compared with those based on another. And, since in all counting of birds there is an unknown, but probably large, personal error, it is best to make comparisons on one person's figures.

YULE'S INDEX APPLIED TO THE BIRDS OF BRITISH WOODLANDS

METHODS

Tables 4–8 give values for Y calculated from my own line transects in British

woods. The counting method, species and proportions of bird recorded, and the types of woodland are described in my book *Birds and Woods* (Yapp, 1962). In many instances I have included additional data, which increase the sample size without making any great difference to anything else. For birchwoods of the Northwest Highlands I have a much longer series of counts than in 1962, which have been published separately (Yapp, 1974). The tables also show the number of species, S, and the density in contacts per hour (Nh^{-1}).

CRITICISM

It is necessary to consider the reliability of these figures. The first question that arises is "Do the raw figures, the actual counts, correspond in some meaningful way with reality?" They are not exact; it is inherently impossible to make exact statements about bird populations. Even if one could recognise every breeding territory in a wood without mistake, by the time one had walked to its far end predators

Table 4. *Native British woodlands in summer (April, May and June)* $N = number\ of\ contacts$, $S = number\ of\ species$, $Nh^{-1} = Density\ in\ contacts\ per\ hour$, $and\ Y = Yule's\ Index\ of\ Diversity$. *Where dates are not shown in this and later tables counts were made in various years between 1950 and 1972, chiefly in the 1950s*

Dominant species of Tree in the woodland	Place and Date	N	S	Nh^{-1}	Y
Birch, *Betula pubescens*	NW Highlands 1951–52	681 ⎫ 2243	28 ⎫ 45	42	5.5 ⎫ 5.8
Birch, *B. pubescens*	NW Highlands 1970–71	1562 ⎭	42 ⎭	61	5.8 ⎭
Birch, *B. pubescens*	England and Wales	159 ⎫ 742	21 ⎫ 39	60 ⎫ 69	9.5 ⎫ 10.4
Birch, *B. verrucosa*	England and Wales	583 ⎭	36 ⎭	72 ⎭	10.3 ⎭
Birch, *B. pubescens*	Kilpisjarvi, Finland 1958	238	17	48	6.4
Birch-and-oak	Wyre Forest 1950–59	451	29	58	9.5
Birch-and-oak	Wyre Forest 1960–69	471	34	74	9.7
Sessile Oak, *Quercus petraea*	England and Wales	1207	44	55	12.7
Sessile Oak, *Q. petraea*	Lake District	378	27	28	8.2
Sessile Oak, *Q. petraea*	Wales	502	29	52	11.4
Sessile Oak, *Q. petraea*	Devon and Somerset	305	27	68	12.7
Oak-and-beech	Wyre Forest 1950–59	1221	37	58	13.9
Oak-and-beech	Wyre Forest 1960–69	1772	43	88	14.8
Pedunculate Oak, *Q. robur*	England	629	48	79	16.8
Beech, *Fagus sylvatica*	England	210	26	47	11.3
Ash, *Fraxinus excelsior*	England and Wales	355	32	73	14.6
Scots Pine, *Pinus sylvestris*	Scottish Highlands	567	45	38	7.5

Table 5. *The transition from open moorland to newly planted coniferous woodland up to 3 ft high. Summer. Symbols as in Table 4*

Vegetation	N	S	Nh^{-1}	Y
Unplanted moor, omitting species known to nest in woodland	79	9	19	3.4
Unplanted moor: all species seen	103	22	24	6.4
Unplanted or newly planted, with the trees not showing above the surrounding vegetation: omitting species known to nest only in woodland	92	9	17	3.8
Ditto: all species	148 ⎫ 301	22 ⎫ 24	27 ⎫ 45	7.0 ⎫ 4.2
Trees up to 3 ft high, all species (excluding data in line 4)	153 ⎭	13 ⎭	54 ⎭	2.8 ⎭
Unplanted, and newly planted, to 3 ft: excluding woodland nesters	229	10	27	2.7

Table 6. *Coniferous plantations, with trees more than 3 ft high*

Tree, height and condition	N	S	Nh^{-1}	Y
All species, 3–6 ft	197	19	25	8.0
6–13 ft, not brashed				
Sitka *Picea sitchensis*	421 ⎫	32 ⎫	66 ⎫	8.7 ⎫
Norway *P. excelsa*	197 ⎪ 1063	22 ⎪ 36	74 ⎪ 70	12.6 ⎪ 8.6
Scots pine *Pinus sylvestris*	276 ⎪	24 ⎪	62 ⎪	9.0 ⎪
Others	169 ⎭	18 ⎭	98 ⎭	6.2 ⎭
13–19 ft, not brashed				
Sitka	165 ⎫	20 ⎫	63 ⎫	6.5 ⎫
Norway	134 ⎬ 349	17 ⎬ 26	155 ⎬ 80	7.4 ⎬ 7.8
Others	50 ⎭	18 ⎭		
19–26 ft, not brashed				
Sitka	237 ⎫ 378	20 ⎫ 24	94 ⎫ 94	7.3 ⎫ 9.7
Norway	141 ⎭	19 ⎭	95 ⎭	10.7 ⎭
19—26 ft, brashed				
Sitka	229 ⎫	23 ⎫	75 ⎫	4.7 ⎫
Norway	312 ⎬ 558	23 ⎬ 30	76 ⎬ 76	7.5 ⎬ 6.3
Others	17 ⎭	7 ⎭		
26–32 ft, brashed				
Sitka	173 ⎫	17 ⎫	59 ⎫	6.4 ⎫
Norway	142 ⎬ 368	14 ⎬ 22	42 ⎬ 52	4.5 ⎬ 5.7
Others	53 ⎭	11 ⎭		
32–40 ft, brashed				
Sitka	144 ⎫	16 ⎫	64 ⎫	4.2 ⎫
Norway	212 ⎬ 444	15 ⎬ 22	75 ⎬ 75	4.9 ⎬ 4.8
Others	88 ⎭	13 ⎭		
40–60 ft, brashed				
Sitka	39 ⎫ 177 ⎫	7 ⎫ 14 ⎫	68 ⎫ 65	5.1 ⎫ 4.9 ⎫ 4.9
Norway	138 ⎭ ⎬ 260	13 ⎭ ⎬ 16	⎭	⎭ ⎭
Others	83			
6–26 ft, not brashed, Sitka				
Cumberland	363 ⎫ 709	25 ⎫ 34	82 ⎫ 77	8.8 ⎫ 9
Devon	346 ⎭	27 ⎭	72 ⎭	8.3 ⎭

Table 7. *Winter (October–March), British Woodlands*

Dominant Tree	Place and Date	N	S	Nh^{-1}	Y
Birch	England and Wales	186	23	32	11.7
Quercus petraea	Devon and Somerset	107 ⎫ 298	17 ⎫ 27	34 ⎫ 26	9.5 ⎫ 11.3
Quercus petraea	Other England and Wales	191 ⎭	22 ⎭	23 ⎭	8.6 ⎭
Oak and Beech	Wyre Forest, 1951–53	1285	26	93	2.2
Oak and Beech	Wyre Forest, 1951–53 (excluding *Columba palumbus*)	419	25	30	12.3
Oak and Beech	Wyre Forest, 1953–60	263	23	32	9.3
Oak and Beech	Wyre Forest, 1960–65	562	24	52	10.8
Quercus robur	Dartmoor	99	12	38	7.2
Larch	Wyre Forest, 1951–56	476	25	73	8.7
Larch	Wyre Forest, 1956–66	545	24	84	7.1
Sitka	High level, all heights, Cumberland	545 ⎫	23 ⎫	86 ⎫	4.8 ⎫
Sitka	High level, all heights, Wales	190 ⎬ 952	12 ⎬ 32	42 ⎬ 60	3.7 ⎬ 8.9
Sitka	High level, all heights, Devon	217 ⎭	19 ⎭	43 ⎭	3.0 ⎭
Norway	High level, all heights, England and Wales	315	23	44	4.8
Larch	High level, all heights, England and Wales	51	13	24	7.0

Table 8. *Mid-season, British Woodlands*

Dominant Tree and month	Place and Date	N	S	Nh⁻¹	Y
Larch, April	Wyre Forest, 1951–64	223	25	92	9.6
Oak and Beech, April	Wyre Forest, 1951–59	329	29	40	12.7
Oak and Beech, April	Wyre Forest, 1960–70	580	37	81	13.9
Quercus petraea, September	England and Wales, high level	123	20	43	4.7

might have destroyed one of the birds already counted. What the counts give may be compared to a colour photograph, which exaggerates some colours and blurs others, but which gives much more information than a mere sketch. The line transect (like every other method) over-estimates conspicuous species and under-estimates quiet ones, but can give consistent results over the years, and estimates by different people can agree quite closely.

Secondly, the counts cannot claim to be more than samples. The theory of sampling depends on the assumption that the part can represent the whole. Chemists regularly base statements of the composition of a gas, or well-stirred liquid, on the analysis of a single sample. Communities of living organisms are very different. Almost every wood is different from every other one, and generalisation is impossible. If one refers to "oakwoods" there is enormous variation in terms of height and spacing of tree, field and shrub layers of the vegetation, aspect, latitude, altitude and so on. If one makes all the possible subdivisions there are so many small separate samples that one has a mass of meaningless figures. I have therefore grouped my counts for woods that appear fairly uniform on the ground. In this way it is possible to obtain grouped samples (with *N* greater than 100) from a number of counts that are too small to be of much value in themselves. The degree of homogeneity is fairly high in the birchwoods of the Northwest Highlands, but much lower in oakwoods of *Quercus petraea*. Although such woods in the Lake District, Wales and Exmoor have obvious resemblances they are recognisably different, for example, in their field layer, as well as being widely separated geographically. The three groups are thus tabled separately as well as together.

Thirdly, there is the general question of whether the figures are representative, meaningful or statistically respectable. They take a long time to collect, so that we often have only one grouped sample, and never have more than a few for each class. In these circumstances statistical methods are not necessarily more helpful than experience in interpreting one's data. It is necessary to be clear as to what statistics can, or cannot, do. They cannot make a bad observation into a good one, but they can sometimes suggest meanings in a large mass of data that are not, at first sight, obvious. They can also tell one that a certain result might be due to chance with a known degree of probability. They cannot tell one that a particular observation *is* due to chance. In practice, an experienced field worker may be able to make a shrewd guess as to how far a single pair of measurements, on two populations that he knows, may be relied upon as indicating a genuine difference.

Nobody who has spent much time observing and counting woodland birds can doubt that there are real differences between the bird communities of the different types of woodland, or that the transect counts give quantitative expression to these differences. Yule's index, calculated from the counts (Table 4), gives sensible results. The Highland birchwood samples give lower values than other deciduous woods;

oakwoods give the highest; whilst the English and Welsh birchwoods (and the birch-and-oak of Wyre Forest), which are intermediate in vegetation type, are inter-mediate in the index. The two indices for Highland birchwoods, although separated by 19 years, are very close, as are those for both parts of Wyre Forest in successive decades. The rise and fall of the index as a coniferous plantation grows up agrees with one's observations on the ground.

My guess is that, provided N is not less than a few hundreds, Y is reliable to about 20 per cent, and that if N is a thousand or more it is probably reliable to within 10 per cent. It will be most reliable in homogeneous habitats.

These provisional conclusions can be tested statistically on some of the samples.

1. I divided the counts for Highland birches (1970–1971), the largest series, into four parts of approximately equal size by taking the record cards as they came out of the file and working out Y for each part. The mean was 5.9 and its stan-dard deviation 1.27. Thus, assuming the mean to be reliable within twice its stan-dard deviation, $Y = 5.9 \pm 2.54$ which is not good, although it would distinguish birchwoods from oakwoods. Discarding one of the four groups whose mean was very different from that of the other three (it is reasonable to do this for a small series) the figure becomes $Y = 5.2 \pm 1.0$ which is close to my guess.
2. I repeated the exercise for the birchwoods of 1951–1952. For the four groups $Y = 6.1 \pm 3.2$, again a useful result. Here also there was one poor sample containing, by chance, data from two atypical woods. If this is omitted $Y = 5.3 \pm 1.6$.
3. I applied the same treatment to Sitka spruce of 6–13 ft (the only coniferous class for which N was large enough to be divided). $Y = 8.3 \pm 3.5$.
4. I tested six indices for birchwoods against six for other deciduous woods. By Student's t the differences are significant at the 5 per cent level, and by Snedecor's F they are significant at the 1 per cent level. The avifaunas of birchwoods appear to have a genuinely lower diversity than those of other deciduous woodlands.
5. I tested Norway Spruce against Sitka for all heights from 6 to 26 feet by Snedecor's F. The differences are just not significant at the 5 per cent level. How-ever, when only the unbrashed plantations of these heights are compared (i.e. those which still have their lower branches), the difference is significant at the 1 per cent level.

DISCUSSION

Several generalisations can be made about the figures in the tables. First, there is no close correlation between the index of diversity, Y, and the number of species, S. S may be high with a low index of diversity, as in Highland pinewoods. Less notably, high diversity may go with low numbers of species as in the oakwoods of Wales and the West Country (Table 4). There is, however, some connection and, leaving out the regional figures for *Quercus petraea* woodlands, the correlation coeffi-cient between Y and S is $+ 0.38$. The correlation for coniferous plantations, for which the connection is obviously closer (Tables 5 and 6) is $+ 0.58$.

Similarly, there is no close correlation between Y and density as measured by the "contacts per hour". Both may be high together (*Quercus robur* woodlands Table 4) or low together (Lake District *Q. petraea* woodlands Table 4), but in some of the birchwoods high densities go with relatively low diversity. In coniferous planta-tions, however, Y follows density fairly closely.

Thirdly, in every case where the figures for a later set of years can be compared with those for an earlier there has been an, sometimes substantial, increase in density. This surprised me, as I had no suspicion of the change until I had worked out the figures. It is unlikely that this can be explained as due to my becoming more observant over the years. One does become more expert in using the line-transect method for the first two seasons, but not thereafter. In any case, the vast majority of contacts in counting woodland birds are auditory, and the acuity of one's ear declines steadily with age, so that I should have expected any change caused by personal error to have led to a decline in the numbers recorded. I therefor conclude that the increases shown are genuine.

When we consider semi-natural native woodland (Table 4), it is seen that Y for birchwoods is consistently lower than for other deciduous woods. The native Scottish pinewoods also have a low Y, and there is an obvious possibility that high latitudes, with their accompanying harshness of climate and short summers, contribute to low diversity irrrespective of the dominant trees in the woodland. Lake District oakwoods are also lower than oakwoods further south. At the other end of the country, most field ornithologists would agree that *Quercus robur* oakwoods, which score the highest number of species and contacts per hour as well as the largest value of Y, are the richest of all British woodlands in terms of birds. Most of these woods are in the southeast of England.

Tables 5 and 6 deal with coniferous plantations on the hills in the north and west. Many people, for example, Ratcliffe (1970), have claimed that such planting is highly unfavourable to wildlife. This must always be a subjective judgement, but measurement of the index of diversity for different groups of animals and plants can help to provide the necessary facts on which such a judgement can reasonably be based.

Unfortunately my figures for bare moorland are rather thin, most of them being taken from areas adjacent to existing plantations. The Forestry Commission usually plants the lower slopes on newly-acquired land first and gradually extends upwards. It was thus convenient to count in established woodlands, that could be reached by car, and then proceed up onto the open or newly-planted moor. General observation showed that planting had very little effect on the birds at first, and even when the trees were 3 ft high there was not much. Table 5 shows figures for unplanted moor, newly-planted moor, and plantations with trees up to 3 ft high in various combinations. The figures given exclude the birds seen, or, from their nesting habits, presumed, to have flown out of the neighbouring woodland.

Table 6 shows figures for later stages, by height classes and, where the numbers are large enough, by tree species. Heights were estimated by eye so that the conversion of 3 ft = 1 m is probably good enough.

At 3–6 ft the index is just about trebled, at 8.0, and this is maintained or exceeded throughout the thicket stage. The maximum, 9.7, is given by the 19–26 ft stage, unbrashed, and the statistical test reported above suggests that the increase is significant. It is interesting that the maximum number of species is reached earlier, at 6–13 ft; at this stage the trees have not usually closed in so that woodland and heath birds co-exist with moorland species. The index is depressed by the small numbers of the latter.

After brashing (the removal of the lower branches to permit a man to walk easily through the wood), and with further growth of the trees, there is a slower but

probably progressive fall in the diversity, unaccompanied by any regular change in number of individuals, but with a fall in the number of species. These results confirm that brashing has no sudden or marked effect (Yapp, 1958).

In all the younger stages, up to 26 ft, both density and diversity are significantly higher for Norway Spruce than for Sitka. At greater heights the differences are irregular. This point deserves further attention: it may simply reflect the fact that Norway Spruce is generally planted on somewhat better soils, or that Sitka, a non-European tree, may be less extensively colonised by British invertebrates. There are no important differences between the number of bird species in the two types of woodland at any stage.

The figures show that the coniferous plantations on the hills of England and Wales have both a denser and more diverse avifauna than the moorlands they replaced. Even when the trees are 40 or more feet high and the diversity has fallen, it is still at least as high as on open moorland, and the density is greater. This con-clusion would not necessarily apply to Scotland, where it is my impression that the moorland has a richer avifauna than south of the border. Helliwell (1973) has shown that the number of species on a moor in southwest Scotland is indeed higher than I found in England; but that, nevertheless, planting with Sitka spruce and Lodgepole pine increased it. Calculation of Y from his figures shows that here too diversity is increased. I do not publish these values of Y because his counting was done by a different method and thus the figures are not comparable with mine.

The Index in Winter

There are interesting seasonal changes in the values of Y. Table 7 shows figures for the winter months of October through March. In almost every case where a comparison can be made the index is lower than in summer; this would be expected, with the absence of summer migrants and the presence of relatively high numbers of a few species in flocks. How these can distort the picture is best shown by the Wyre Forest oak-and-beech figures for 1951–1953, which included an excep-tionally good mast year in which flocks of woodpigeons (*Columba palumbus*) greatly outnumbered all the other species in the woods put together. The index is conse-quently at my lowest recorded value of 2.2. Re-calculation of the index without the pigeon raises it to a more normal value. The exceptionally low figure indicates a defect of sampling, not of the index. If woodpigeons were normally present in such numbers the diversity would be correctly expressed as $Y = 2$ or thereabouts. But as these big flocks only occur for a week or two about once a decade a small sample including some of those days is not representative and the index, although correct for the sample, is misleading if applied to the wood as a whole.

The highest winter index is that for English and Welsh birchwoods. These are the only woods to give a higher index in winter than summer. The difference is small but possibly genuine, since several species come into (or remain in) birchwoods that are absent from oakwoods in winter, no doubt attracted by the seeds.

Different geographical areas give different indices for woods of Sitka spruce and *Quercus robur*; and when the areas are grouped together the indices are higher than for any one section. For Sitka it is doubled. This suggests that superficially similar woods support different avifaunas, and an inspection of the cards bears this out. There is much less geographical variation in summer (Table 4 for oak and Table 6 for Sitka).

As in summer, the indices for broad-leaved woodlands are higher than those for conifers, with larches at the level of the lowest broad-leaved.

The number of contacts for high-altitude larch is too small for much reliance to be placed upon the index, but it is interesting that it has about the same value as for larches in Wyre Forest at only 400 ft. Larch, like most broad-leaved trees, is deciduous, and this relatively high index would not perhaps have been expected. Possibly the greater amount of sunlight is more important than the decreased shelter. Even when allowance is made for the inherent variability of density, it looks as though coniferous plantations hold rather more individuals, and about the same number of species, as deciduous woodlands in similar situations.

Table 8 shows a few figures for the transitional months. In April the larches in Wyre Forest have a lower index, but higher density, than the nearby oak-and-beech. This is because they are favoured by numbers of transitory and newly-arrived summer visitors. High level oakwoods have a poor fauna in September. Summer migrants have gone but the winter inhabitants have not yet arrived.

Birds and Woods

Attempts have been made to correlate the diversity of woodland birds (measured by H) with various measures of the structural diversity of the vegetation. One of the most interesting is that of Blondel, Ferry and Frochot (1973) who found a correlation coefficient of $+ 0.94$ between H and the diversity of vegetational layering in French woodlands. I have made no similar measurements in British woods, but my impression is that the correlation, if any, would be low. To judge by eye the diversity of layering in birchwoods is at least as great as that in upland sessile oak, and that in Highland pinewoods probably rather greater: yet Y is easily highest in oak. Some of the supposed correlations have been based on distressingly small samples—in one case $N = 41$ and in another 27. Since this paper was written, Moss (1978) has published correlations of Shannon's H for birds with that of the structure of some Scottish woodlands. Here also the samples were small. Although structural diversity may well be important, there are other factors, such as food supply, nest sites and climate that are likely to influence the composition of bird communities.

REFERENCES

BATTEN, L. A. (1972). Breeding bird species diversity in relation to increasing urbanisation. *Bird Study*, **19**, 157–166.

BLONDEL, J., FERRY, C. and FROCHOT, B. (1973). Avifaune et végétation: Essai d'analyse de la diversité. *Alauda*, **41**, 63–84.

HARDY, G. H. (1940). *Ramanujan.* Cambridge University Press.

HELLIWELL, D. R. (1973). Priorities and values in nature conservation. *Journal of environmental management*, **1**, 85–127.

LACK, D. (1933). Habitat selection in birds with special reference to the effects of afforestation on the Breckland avifauna. *Journal of Animal Ecology*, **2**, 239–262.

LACK, D. and VENABLES, L. S. V. (1939). The habitat distribution of British woodland birds. *Journal of Animal Ecology*, **8**, 39–71.

MACARTHUR, R. H. and MACARTHUR, J. (1961). On bird species diversity. *Ecology*, **42**, 594–598.

MOSS, D. (1978). Diversity of woodland song-bird populations. *Journal of Animal Ecology*, **47**, 521–527.

PIELOU, E. C. (1969). *An introduction to mathematical ecology.* John Wiley, Chichester and New York.

RATCLIFFE, D. A. (1970). Reported in *The Times,* 27th October.

SHANNON, C. E. and WEAVER, W. (1949). *The mathematical theory of communication.* University of Illinois Press, Urbana.

SIMPSON, E. H. (1949). Measurement of diversity. *Nature (London)*, **163**, p. 688 only.

TRAMER, E. J. (1969). Bird species diversity: components of Shannon's formula. *Ecology*, **50**, 927–929.

TUCKER, D. G. (1952). An application of the logarithmic series and the index of diversity to bird population studies. *London Naturalist*, **31**, 62–80.

VARLEY, M. E., ed. (1974). *Diversity in communities.* Open University S 323 Ecology course. Block C Unit 14. Open University Press.

WILLIAMS, C. B. (1964). *Patterns in the balance of nature.* Academic Press, London and New York. 482 only.

WILLIAMS, C. B. (1964). *Patterns in the balance of nature.* Academic Press, London and New York.

WILLIAMS, C. B. (1970). *Style and vocabulary: numerical studies.* Griffin, London.

YAPP, W. B. (1958). The colonisation of coniferous plantations by birds. *Proceedings of the XII International Ornithological Congress*, Helsinki.

YAPP, W. B. (1962). *Birds and Woods.* Oxford University Press.

YAPP, W. B. (1974). Birds of the northwest Highland birchwoods. *Scottish Birds*, **8**, 16–31.