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Robert H. MacArthur; John W. MacArthur; James Preer

The American Naturalist, Vol. 96, No. 888. (May - Jun., 1962), pp. 167-174.

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Vol. XCVI, No. 888 The American Naturalist May-June, 1962

ON BIRD SPECIES DIVERSITY

II. Prediction of Bird Census from Habitat Measurements

ROBERT H. MACARTHUR, JOHN W. MACARTHUR AND JAMES PREER
Department of Zoology, University of Pennsylvania, Marlboro College
and Swarthmore College

A competent bird watcher can look at a habitat and correctly name the bird species which will breed there in abundance. This tells us that some properties of the general appearance of the habitat are sufficient to determine most of the breeding birds; it doesn't tell us just which measurable properties these are. In an earlier paper (MacArthur and MacArthur, 1961) the authors showed that in deciduous forests the diversity of breeding bird species depends upon foliage profile (foliage density plotted against height) and not upon plant species composition. Also, in this paper, it was suggested that each species requires a "patch" of vegetation with a particular profile for its selected habitat, and that the variety of "patches" of vegetation within a habitat determines the variety of bird species breeding there. In the present paper this hypothesis is tested; foliage profiles acceptable to many bird species are measured and compared with those available as patches in various habitats.

Plotting a profile as a point. Although it is doubtless more informative and more accurate to plot a complete profile as was done in the earlier paper, for our purposes it is easier and more picturesque to plot each profile as a point and then show the variety of profiles (representing the variety of "patches") as a cluster of points. This was done as follows: The vegetation was divided into three layers: that 0-2 ft from the ground, that 2-15 ft above ground, and that over 15 ft. (In the early paper 2-25' was used as the second layer; this was changed to 2-15 to improve the accuracy of the technique in brushy fields where most of the current work is being done). The proportion of the total foliage which is in each layer can be plotted in an equilateral triangle (see figure 1). From each point, imagine the three perpendicular lines dropped to the three sides. The lengths of these three lines are the proportions of foliage in the three layers, and the total length of the three combined is independent of the position of the point. Thus, a single point represents the proportions in the three layers and hence gives a crude picture of the profile. A 3-dimensional graph (in a tetrahedron instead of triangle) would allow us to represent a subdivision into four layers giving greater accuracy; in general it is possible with a point to represent the actual profile with any desired degree of accuracy if we are willing to plot (or imagine a plot!) in a space of enough dimension. The pictorial value of our triangle, which can actually be drawn, compensates for the crudeness of its detail. It would be nice to plot the density as well as the proportions, but this, too, would require an extra dimension.

Figures 1-3 show the variety of profiles found in five different habitats in Pennsylvania and Vermont. Figure 1 contains (as a bar graph) measurements from a recently abandoned Pennsylvania field and (as dots) from a Pennsylvania "slash" plot which is a recently cut forest which has scattered tall trees surrounded by dense ground cover, berries, and young trees. Each habitat was divided into 100 ft squares and each of these is plotted as a single point. Figure 2 shows, as plus signs, the foliage proportions in 100 ft square patches of a dense Pennsylvania second growth forest and, as dots, a brushy field grown up in spots to clumps of young trees up to 40 ft high. Figure 3 shows, as plus signs, 100 ft square patches of a Vermont second growth forest, and as dots, a Vermont slash plot. Imagine a horizontal line across these figures half way up; above this line the measurements are less accurate than below it. For, the techniques of measurement (measuring the horizontal distance at which leaves obscure just 1/2 of a board from view — see earlier paper) are most accurate in practice where one can stand on the ground. Hence, measurements in which a substantial part of the vegetation is above 15 ft may be somewhat dis-

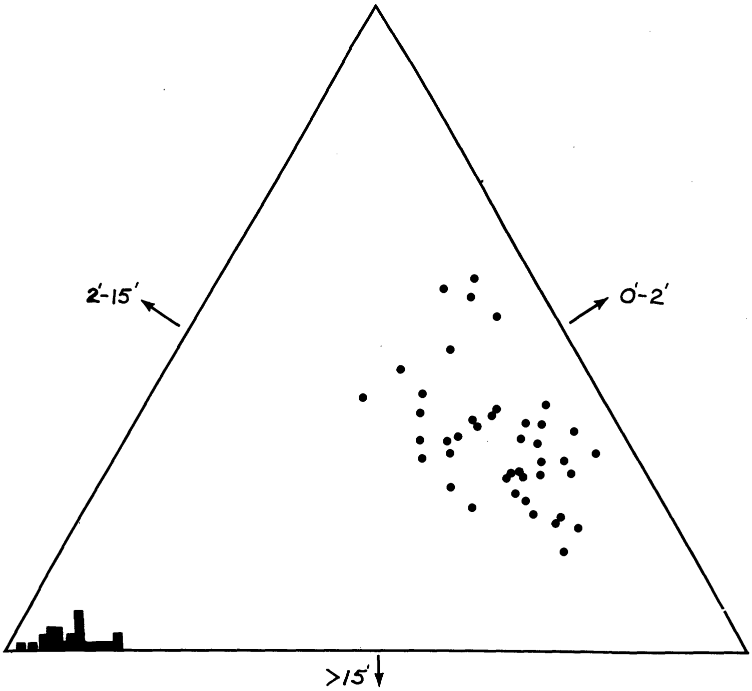

FIGURE 1. Each dot represents the proportions of foliage in each of the three horizontal layers (0-2', 2-15', over 15') in a 100 ft square of Pennsylvania slash plot. Each square (the squares adding into columns of a bar graph) represents the proportions of foliage in the three layers in 100 ft squares of a recently abandoned Pennsylvania field.

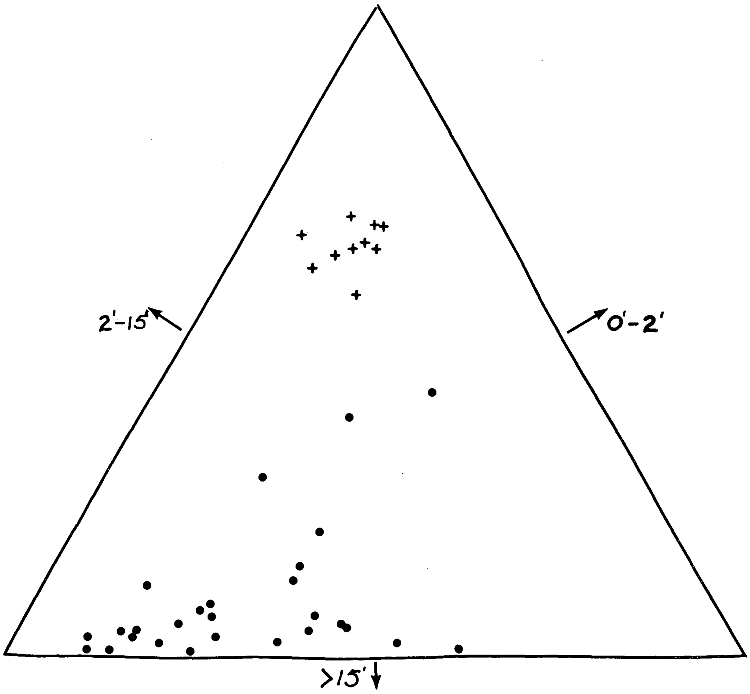

FIGURE 2. The proportions of foliage in three horizontal layers from 100 ft squares of two Pennsylvania habitats. The plus signs are patches of a dense second growth forest, and the dots are a brushy field.

placed in the figures from what they should be, although the cluster size is probably about right.

Clearly there is variability within habitats in the foliage profiles of different 100 ft squares. That is, there are patches in the habitats. And the slash plots and brushy field show much greater variation from patch to patch than do the field or second growth forest. This means that a wider variety of profiles (and hence, perhaps, a wider variety of bird species) are found in the slash and brushy field plots. As a general rule, plots located near the vertices of the triangular graph have little variability; those near the center have great variability. This is no accident; in large part it is due to the greater uncertainty of three approximately equi-probable foliage layers as compared with three layers of which one is overwhelmingly dominant. This is discussed in MacArthur and MacArthur (1961).

Notice that no plots were measured which lay along the middle of the left side of the triangle. That is, no plots had very little foliage in the 2–15 ft layer and yet much in both the 0–2 ft and > 15 ft layers.

BIRD HABITAT SELECTION

During the spring of 1961, breeding bird censuses of a large variety of habitats were made by plotting the territories of singing male birds. Within

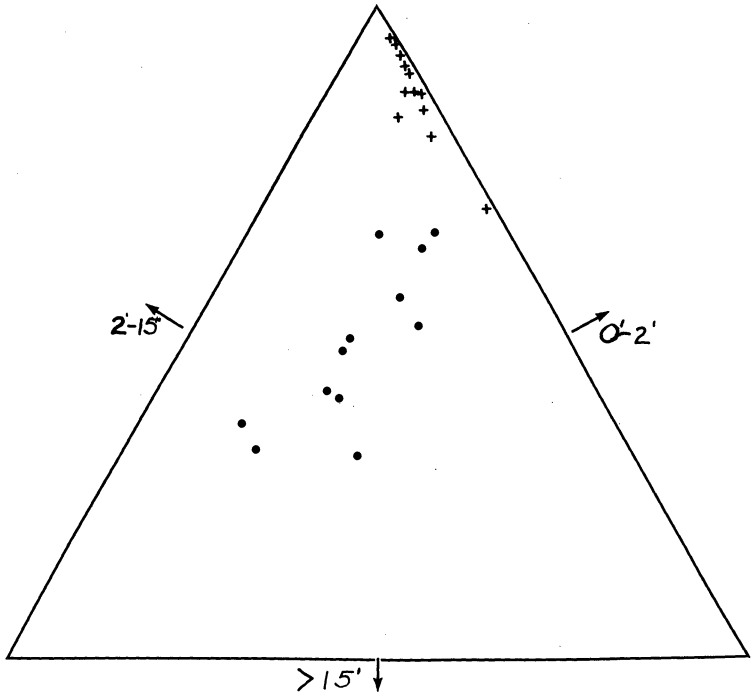

FIGURE 3. The proportions of foliage in three horizontal layers from 100 ft squares of two Vermont habitats. The plus signs are a very dense second growth forest and the dots are a "slash" plot.

each territory, the 100 ft square most used by the bird was selected, measured for foliage profile, and plotted as a point for the bird species which occupied that territory. Figure 4 shows the results of these measurements. (None of the points came from a habitat of which we wished to predict the census.) Notice particularly that the cluster of points for each species is fairly tight; that is, the graph *does* seem to reflect a large part of what the species choose in their habitat selection and each species has a characteristic range of acceptable profiles. (To show that the graph reflects all the bird requires, we must show that every 100 ft square patch whose profile lies in the birds cluster actually has a pair of that species. This is discussed later.) Some locally common species — notably towhee and indigo bunting — are not included. Such species, setting up their territories on an "edge," seem to require two kinds of patch. Pairs of points would be required for each such territory. No such measurements were made. Many species are not included simply because few or none of their territories were measured.

PREDICTION OF BIRD CENSUS

Armed with knowledge of birds' habitat choices and the variety of habitats present in a given area, it is now simple to predict the census of breeding birds, at least roughly. In fact, all we have to do is superimpose the graph of the birds' habitat requirements on the graph of the patch variability of the habitat whose census is to be predicted. And if the habitat contains many 100 ft square patches which are suitable for a bird species (as indicated by figure 4), then we predict that species should be common, and so on. If this prediction fails — if a bird is absent whose preferred vegetation profile is present — then we can conclude that there is some other requirement (other than the vegetation profile) which must be described before we can predict that species accurately. If, on the other hand, the prediction is fairly accurate — if a bird is present whenever patches of vegetation with the appropriate profile are present — then we can conclude that a proper profile alone is sufficient to make that patch occupied by that species.

It is actually possible to make a numerical prediction by counting the number of vegetation patches which lie in the species' zone, but this is unrealistic because it assumes that all species have the same territory size and will settle one pair to a 100 ft square patch, throughout the habitat. For this reason we will be content, at this stage, with a qualitative prediction and will only guess which species should be common, which uncommon and which absent.

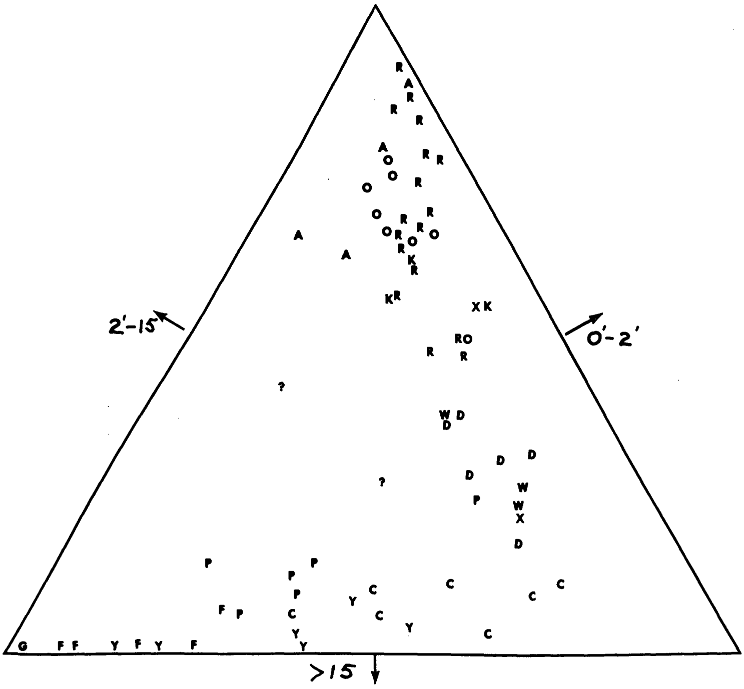

FIGURE 4. Each letter indicates the foliage proportions for a 100 ft square in the territory of a given pair of birds. A = Acadian flycatcher, C = yellow breasted chat, D = catbird, F = field sparrow, G = grasshopper sparrow, K = Kentucky warbler, O = ovenbird, P = prairie warbler, R = red-eyed vireo, W = white-eyed vireo, X = cardinal, Y = Maryland yellowthroat.

Let us now turn to the actual habitats to be predicted, remembering that the bird habitat preferences were measured on other plots. Accurate censuses of the recently abandoned Pennsylvania field (bar graph in figure 1) and the Pennsylvania brushy field (dots in figure 2) were made to compare with the predictions. The recently abandoned field has vegetation patches lying in the preference zones of grasshopper sparrow, field sparrow and yellow throat. And, these are the three species which bred in the field—field sparrow commonly, one pair each of the others. Meadowlark may possibly have bred too, but in any case no data on its habitat profile was obtained.

Superimposing the bird species preferred profile zones of figure 4 onto figure 2 which shows the brushy field, we predict a more diverse census: Field sparrow, yellowthroat, prairie warbler and yellow breasted chat should all be common, and perhaps a pair of catbird, cardinal or white eyed vireo should be present. The actual census was: three prairie warbler, three yellow throat, two yellow breasted chat, two field sparrow, one cardinal, one catbird, one towhee, one blue-winged warbler, one robin, one yellow-billed cuckoo. Bearing in mind that the last four species were not plotted in figure 4 and so could not be predicted, this is remarkably close to the predicted census.

Finally, this work should not be interpreted as suggesting that all species use only the foliage profile in choosing their habitat, but merely that there is a large collection of species whose presence can be predicted from foliage profile measurements. A few species (for example, acorn woodpecker, crossbills) may require specific tree species in their habitats; certainly water birds must use very different criteria. And there is no proof that the birds themselves use the profile in their choice; all we can say is that the profile is closely associated with what they use for their choice. P. Klopfer is investigating this last point in his aviaries.

DISCUSSION AND RELATION TO TROPICAL DIVERSITY

As mentioned earlier, perhaps some species in choosing their habitat require profiles of two types. For instance, perhaps a cardinal requires both woods and open areas, rather than some mean profile. For such species, to be strictly accurate, we would have to plot not just a cluster of points, but a cluster of joined pairs of points, the two joined points being the two types of profile which must be present before the territory is acceptable. For predicting these species the habitats would also have to be plotted as clusters of joined pairs of points. This would be nice but clearly requires a more detailed set of measurements than we possess. There is little doubt, however, that this situation is important enough to be a real source of error in the crude predictions of this paper.

Another source of error lies in the way the clusters of points for habitats were constructed. Here the habitat was laid out in 100 ft squares with no reference to what might be "natural patches." But the bird territories were plotted as they were; although a 100 ft square was chosen within each one, this square had no reference to an arbitrary preassigned grid. This is altogether proper but causes a few species to be missed in the predictions, since by hunting for an appropriate patch a species may find one which lies across the grid so that it is not reflected in the cluster of points.

In the previous paper we showed that bird species diversity could be predicted from the *mean* foliage profile of the habitat; in fact it was proportional to foliage height diversity. In this paper we are predicting not only the bird species diversity, but also the census, and this is done in terms of the variety of patches within the habitat. In this light, why was the bird species diversity proportional to the foliage height diversity? The bird species diversity actually was best estimated by .46 + 2.01 (foliage height diversity). Now bird species diversity and foliage height diversity were logarithmic measures. For our present purposes we can restate these conclusions in terms of the *number* of equally common species which would give the observed diversity and the number of equally dense layers of foliage which would give the observed diversity. In these terms, the result becomes (using 2 instead of 2.01):

"Number of equally common bird species is proportional to the square of the number of equally dense layers." And in the former paper we guessed that it increased with the square of the number of layers because the number of combinations of layers which a bird could require increases about with the square of the number of layers available (for 1, 2, 3 layers, the number of combinations possible is 1, 3, 7 respectively). How does this result accord with the present paper? It means that the number of bird species whose habitat requirements (for example, figure 4) include the habitat under consideration — that number of bird species increases about with the square of the number of equally dense layers of vegetation. And, since the number of bird species which will breed in a given habitat whose patches of vegetation are plotted as in the clusters of figures 1, 2, 3 is the number of bird species whose habitat preferences (as in figure 4) overlap the habitat cluster, we can conclude that the number of bird species should increase as the area of the habitat cluster increases. More accurately the number of bird species might be proportional to the area of the cluster plus a margin around it of width 1/2 the diameter of the bird species habitat clusters. These areas, imagined roughly from figures 1, 2, 3, do correspond roughly to the number of bird species. Thus a large part of the cause of bird species diversity is the amount of patchiness within the habitat. Another part is caused by many-layered forests being able to support ground species (for example, ovenbird), shrub species (for example, Kentucky warbler) and canopy species (for example, scarlet tanager), but this obvious cause seems much less important than the within-plot variability — the patchiness.

Let us turn, now, to the factors involved in tropical diversity. Three factors could be associated with the increased bird species diversity in the tropics: (1) Tropical habitats could have more internal variability (that is, larger clusters of points). (2) Tropical birds could have more refined habitat selection (that is, smaller clusters of points on that graph). (3) More species could share the same profile (that is, more of the species clusters should overlap). Some evidence for (2) or (3) is gathered in Klopfer and MacArthur (1960, 1961), but this type of graphical analysis should permit better disentangling of the factors associated with tropical diversity. The central question of tropical diversity (given enough time, will the temperate regions support as diverse a fauna as the tropics now have, or has speciation reached a limit?) remains to be answered. The approach of Southwood bears more directly on this problem.

CONCLUSION

(1) A fairly accurate census of breeding birds can be predicted from measurements of the amounts of foliage in three horizontal layers. The abundance of each species is roughly determined by the number of patches of vegetation whose foliage profile is acceptable to that species. This suggests that many species are rare only because their chosen foliage profile is rare.

(2) The main reason one habitat supports more bird species than another is that the first has a greater internal variation in vegetation profile (that is, a greater variety of different kinds of patches). A second reason is of course that a forest with vegetation at many heights above the ground will simultaneously support ground dwellers, shrub dwellers and canopy dwellers. With a few exceptions, the variety of plant species has no direct effect on the diversity of bird species.

(3) Comparable plotting of tropical bird requirements should disentangle three of the possible factors associated with the tropical increase in diversity.

ACKNOWLEDGMENTS

This work was supported by grant G-11575 of the National Science Foundation. Drs. Peter Klopfer, Monte Lloyd and Ernst Mayr have made very useful criticisms.

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