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## TIME AND SPACE AND THE VARIATION OF SPECIES

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### INTRODUCTION

It is not intuitively obvious why a square yard of meadow, say, should not be exactly like the next square yard in species-composition, yet it must have been noted many times, and from the earliest times, that it rarely or never is so. Yet a few square yards may contain a large fraction of all the species of plants that can be found on an acre. This approximate sameness, yet unequivocal and persistent difference, reached "the literature" at least a hundred years ago (Williams 1943b), and became an active subject of discussion in the present century.

If we observe moths as they enter a light trap, we may very likely find that the first half dozen are all of different species. The same thing may happen if we note the singing males on an early morning bird count in May; and it may happen again if we note the species of trees in a tropical forest. At first we have as many species as individuals, but in all cases the ratio of species to individuals falls rapidly as our observations increase, and we soon reach the point of diminishing returns. However, we never seem to reach the point of zero returns, though ultimately the ratio of individuals to species may run into the hundreds of thousands.

When we are dealing with botanical material, the subject centers around the concept of the species-area curve, where the early work goes back to Arrhenius (1921) and Gleason (1922). Here we are dealing with a phenomenon that concerns the space under observation. Williams (1943) made the comment that "Doubling the time of trapping (of moths in a light trap), at any level, except for very small samples, always adds about thirty species to the total." This is a restatement of Gleason's expectations, but refers to time instead of space. Preston (1948) commented that the rule would necessarily hold, to a first approximation, over a fairly long range of

observations, if we were taking increasingly large samples from a fixed lognormal distribution. But since, in practice, the universe being sampled tends to increase as the sample itself increases, complications can occur. None the less, Williams' observation does raise the question as to how far time and space may be essentially equivalent in some ecological problems.

In a companion paper I hope to show that if we have a series of independent, isolated, populations or "universes," then the relation between species and individuals should, on theoretical grounds, follow not the Gleason law but the Arrhenius one to a very close approximation. This law states that

$$N = kA^z$$

where  $N$  is the number of species on an area  $A$ , and  $k$  and  $z$  are constants which Gleason treated as arbitrary and to be found by observation. In the other paper it will be shown that, for the conditions above specified,  $z$  should be 0.27 approximately, and  $k$  can be defined in terms of the density of individuals to the unit area. Thus there are no strictly arbitrary constants.

Most often in dealing with species-area curves we are dealing with a geographical continuum, in which small areas are portions of the larger ones. Under these circumstances, the small areas tend to act as "samples" of larger ones, though we cannot define the size of the larger ones of which a given collection is a sample, except by the internal evidence of the sample itself (Preston 1948). It is a property of such samples that the ratio of species to individuals is much higher than in the complete "universe," and the distribution is a truncated lognormal, not a complete one. When we translate this from species/individuals to species/area, this means that small areas tend to be over-rich in species. They receive an enrich-

ment from contiguous areas, which they could not do if they were complete isolates.

The relation between the size of an area and the number of species it holds has been largely the province of plant ecologists. Thus Vestal (1949) gives tabulations of species-area relationships for about 300 instances of plants but only 3 for animal groups. From the time of Clements onwards and perhaps before, there has been a belief that a stand of vegetation, comprising a number of species, constitutes a "community" (Oosting 1948), though Gleason's (1936) views quoted by Watts (1947) seem contrary: "The final step is (Gleason's: to him the plant association is merely a fortuitous juxtaposition of plant individuals." Underlying the concept that the community may be a genuine organic unity, however, is frequently a second concept, that the rarer species are not essential to it. This is similar to the views of petrographers who consider that to qualify as a true granite a rock must contain quartz, feldspar, and mica, the "essential minerals," while minor ingredients such as sphene and zircon are merely "accessory" minerals. On this view the plant association can be defined by its more plentiful species, the rest being regarded as merely adventitious, and a great deal of the literature is therefore concerned with the problem of what minimal area is sufficient (Cain 1938, Hopkins 1957). From this point of view a minimal area is one that will make sure that the "essential" ingredients are present. From the point of view of the present paper the idea is a faulty one: a sufficient area or quadrat is one which will give the same count, rarities included, as another quadrat of the same size. In practice this does not happen at any size of quadrat, so that no size of quadrat is absolutely satisfactory.

In the present paper we propose to proceed empirically, as was done by earlier writers, and to find out what actually is the appearance of the species-area curve, for one or 2 specific instances, over its complete range. We shall do this for the breeding birds of an area, and the area will extend from an acre or so to continental and global areas. Then, having studied species-area or species-space as being more accessible to us, in a big way, than a species-time curve, because we do not know in much detail what happens over vast stretches of time, we can speculate that time and space may be equivalent variables, and see if the known facts fit that hypothesis.

### *Succession*

The resemblance between time and space, in its simplest form, may be seen by driving a stake

into the open water of a lake and then taking a transect toward the shore. We pass first through planktonic vegetation, then perhaps water lilies, then marsh, then grassland, then a succession of forest stages to climax forest. But we can pass through the same succession in the same order without moving at all. We may just sit by the stake for a few years or centuries and the seral stages will come to us one after the other as the lake fills in or drains.

Since there is so much literature on species-area properties, and on succession, I hope I may be forgiven for not reviewing it all except where it seems especially pertinent to the equivalence of time and space. In the present paper we are concerned with changes brought about by the lapse of time, whether they are regarded as mere fluctuations without any particular direction, or as methodical "succession" as that is usually understood, or as evolution when the time scale is long. Similarly, we are concerned with changes in the ecological set-up as we go from place to place, whatever the cause or causes of that change. The more obvious causes might be variations in the underlying geological formations or the character of the soil, variation in altitude or aspect, and, on a large scale, in climate, rainfall, temperature, or the different geological histories of the various regions of the earth.

As we go to longer and longer times, from a few thousand years to a few million, "succession" passes by degrees into "evolution" as ordinarily understood or is superseded by evolution, and it would be still less possible to review the literature of that subject. It seems sufficient here to concede that there will be changes of species with time and not to attach particular labels to those changes.

### THE SPECIES-AREA CURVE

The precise form that the species-area curve takes will vary according to the place where we begin. We shall get somewhat different curves if we place our first quadrat in the eastern North American deciduous forest or in the lowland neotropical forests of Panama. Having chosen a place to begin, we should double our area by taking in a contiguous or adjacent similar area, or as similar and as nearby as we can. This is the same principle as applies in *time*. If we count moths this year, we should double the collection by trapping next year, and not wait 50 years and then trap for a second year.

Since there is more information about the birds of the eastern deciduous forest, we should first examine them. In the nearctic it is sometimes

estimated that there is about one pair of birds per acre, averaged over the whole region. In the deciduous forest it tends to run higher, perhaps 2 or 3 pairs per acre (see below, on the birds of "Neotoma"). But in this forest there can be found breeding 200 or 300 species, so that if all species were equally common and a 2nd pair of species could not be fitted in until every other species was represented by one pair, the minimum area that would achieve representation of all species would be around 100 acres. But some birds are vastly more common than others, thousands of times commoner, and their distribution is not regularized but more nearly random. It follows that even 100,000 acres will rarely achieve full representation of species, and that another 100,000 acres will not be identical in its count. None the less, much smaller areas give interesting information. In particular, it will be found that areas of equal size tend to give roughly equal numbers of species, if we avoid choosing areas that are, for instance, half forest and half marsh. Thus it becomes possible to construct a species-area curve which does not have excessive "scatter" or dispersion of the observed points from a single curved line.

#### *Methods of plotting*

In much of the work on plant associations and the species-area curves of such associations, the quadrats are increased in size or in number in a geometric progression, but none the less the results are plotted by some writers on an arithmetical scale for both area (as abscissa) and number of species (as ordinate). This seems illogical. It results in the observed points being crowded toward the left hand end, or origin, of the curve, and in their being very sparse toward the right hand end. If the areas are increased in geometric series, the plotting should normally be on a logarithmic base, thus making the spacing of the points uniform.

If however the double-arithmetical plotting is used, it becomes apparent that the curve approximates in many cases to a generalized parabola, with its vertex at the origin and axis horizontal. See, for example, Hopkins (1957). Such a curve would become a straight line on a "log-log" plot, *i.e.* if both ordinate and abscissa are plotted logarithmically. This is, in effect, what Arrhenius (1921) did, though he provided no graphs, only the data for them.

While logic, in the first instance, and experience of the results in the second, seem to call for a logarithmic scale for abscissae, it is only experience that can decide whether the ordinate should

be so plotted. Gleason (1922) seemed to get better results with arithmetical ordinates. In the present paper we use both methods for the same data, the "Gleason plot" for Fig. 1, the "Arrhenius plot" for Fig. 2. Each has its uses, and neither produces a straight line over the whole range of the graphs; and there are sound reasons for not expecting it to.

#### *Statistical Difficulties of Some Earlier Plots*

For the purposes of some of the earlier writers, particularly when they were concerned with the defining of communities in terms of a few of the commonest species, the quadrats had to be small or they got too many species. This is exactly the opposite of the situations generally desired in the present paper. Here the fundamental problem is not how small the quadrat can be made and yet define a community, but how many species we must have in order to obtain statistical utility. In general we should like this to be 100 species or more, though we must sometimes settle for half that number. But in the early quadrat studies the number of species was often less than 10, sometimes only 2 or 3, and rarely much more than 20. Whatever results flow from studies of this, the extreme left end of the complete curve, they are not necessarily, or apparently usually, applicable to studies of the main part of the curve, as will be seen from Fig. 2. This difference between the initial and central parts of the species-area curve may influence our attempts to reconcile the present findings with those of MacArthur (1959) or Kohn (1958) and others, which deal chiefly with small numbers of species (see Hairston 1959).

#### *Log-Log Plottings*

##### *The Arrhenius Equation*

We may derive this empirically as follows. We can expect that in almost all cases increasing the area will tend to increase the total number of species. It cannot decrease it. We can imagine a situation, which some quadrat specialists would consider ideal, where the 2nd and subsequent quadrats were identical with the first. Then if  $S$  is the number of species and  $A$  the area (in acres or any other unit)

$$S = KA^0, \text{ where } K \text{ is a constant} \quad (1)$$

since  $A^0$  is unity.

That however is not the kind of world we live in.

We can next imagine a situation where nothing on the 2nd quadrat resembles anything on the first. Perhaps there are exactly as many indi-

viduals and exactly as many species, but there are *no* species common to the 2 quadrats. Such a situation approximately exists if we take as our quadrats Australia and the continental United States, which are of equal size but well isolated from each other for geological lengths of time. In that case we should have

$$S = KA \quad (2)$$

where  $A$  is to the first, not the zeroth, power.

Strictly speaking this is not a *limiting* case, if we can choose to take our areas or quadrats in the order  $a - b$ , and refuse  $b - a$ , for the 2nd area might be much richer in species than the first. This would be the case if we added South America to the nearctic for instance. But by stipulating that we must strike an average of the  $a - b$ , and  $b - a$  arrangements, equation (2) becomes essentially a limit.

It will now be obvious that the simplest assumption we can make is that in real life

$$S = KA^z \quad (3)$$

where  $z$  is an exponent somewhere between zero and unity.

We have derived this equation in an empirical fashion, partly because it does, under some circumstances, approximate the theoretical relationship for complete lognormal ensembles, and partly because our Fig. 2 is an "Arrhenius" plotting, in the sense that a log-log plotting should give a straight line if the Arrhenius equation is observed. Since, however, our purpose is not to check the Arrhenius equation but to ascertain the degree of resemblance between time and space, we are not here justified in pursuing the matter further.

#### *Ideal Method of Obtaining Increasingly Large Areas*

What we should like to do is to take as a "core" an area in the form of a circle with a radius of a quarter of a mile. It would have an area of about 125 acres. Then from the same center we would describe circles of greater radius, in the ratio of  $\sqrt{2}$ , 2,  $2\sqrt{2}$ , 4,  $4\sqrt{2}$ , and so on, thus doubling the area every time and expanding equally in all directions. The areas would become 250, 500, 1000, 2000, etc., and the radii would include, at every second step,  $\frac{1}{2}$  mile, 1 mile, 2 miles, etc.

If we could do this, starting from a dozen or twenty "cores" in the deciduous forest area<sup>2</sup>, we

<sup>2</sup> The term "Eastern Deciduous Forest" as used in this paper frequently means the region in which the deciduous forest is the typical natural cover, and does not specifically mean the woodland facies of this region. It will be obvious, I think, from the context just what is

could get an average picture that would be very useful. But we have no such information and must depend on less ideal selections.

#### *The Nearctic Avifauna, beginning in Western Pennsylvania*

In Table I are listed some dozens of counts and estimates of the number of species of birds breeding on areas of different sizes in the nearctic. It was not possible to begin at a single point and extend the count by doubling and redoubling by the use of strictly contiguous areas. We did the best we could in that respect, beginning with small areas in western Pennsylvania, but taking other samples in Ohio and other nearby states. These areas are treated as independent samples and are not combined. They merely serve to confirm that areas of a particular size in this general area tend to have about the *same number* of species though they may not be the *same* species. We then consider the counts of counties and similar areas, and by degrees we progress to the whole of western Pennsylvania as defined by Todd (1940) and to other statewide estimates of breeding species. Where two counties are contiguous we have sometimes combined their areas and their counts, thus getting an additional point on our curve; and we have used the same tactics with the states, first combining western Pennsylvania and West Virginia, then combining these with Ohio, then adding in turn New York State, Maryland, Indiana, and Illinois. In each case the addition has a substantial boundary in common with the preceding area, so that we are dealing with a geographical continuum. We next take the eastern United States up to the 100<sup>th</sup> meridian (but not the eastern part of Canada) and then the nearctic exclusive of Greenland. Our next step takes in the whole world.

I am indebted to many collaborators for the estimates recorded in Table I: most of it is unpublished information and has been obtained by correspondence. Their names are given in Table

meant. Even under natural conditions the region includes, in the west, areas of prairie, and in the east, areas of salt marshes and seashores. Several states have frontages on Lakes Erie and Ontario, and most have smaller lakes, large rivers, and fresh-water marshes; along the high ridges of the Alleghenies are "balds" and spruce forests, and under the disturbed conditions of the present day are unnatural grasslands and cultivated areas. Except for quite small areas, it is impractical to segregate out the woodland areas from the rest, still less to make distinction of the several sorts and seres of forest, very little of which is climax of any sort. The text will usually make clear with what we are dealing when we speak of the "forest." "Eastern" refers to eastern North America.

TABLE I. Species-area information, beginning in the eastern North American deciduous forest country. Reference numbers B begin in neotropical

| Ref. No. | Area (acres)            | Locality                              | Species breeding in one year | Authority                            |
|----------|-------------------------|---------------------------------------|------------------------------|--------------------------------------|
| 1        | 0.5                     | Butler, Pa.                           | 4                            | Preston                              |
| 2        | 6                       | Butler County, Pa.                    | 18                           | Earl Schriver                        |
| 3        | 23                      | Eastern U.S.A. <sup>1</sup>           | 23                           | Audubon Breeding Bird Counts         |
| 4        | 62                      | Eastern U.S.A. <sup>2</sup>           | 32                           | Audubon Breeding Bird Counts         |
| 5        | 69                      | Hocking Co., Ohio <sup>3</sup>        | 43                           | Ed S. Thomas                         |
| 6        | 90                      | Butler County, Pa. <sup>4</sup>       | 42                           | Norris (1947)                        |
| 7        | 130                     | Temple Hollow, Beaver County, Pa.     | 38+                          | R. Edeburn                           |
| 7a       | 150                     | "Sapsucker Woods", Ithaca, New York   | 65                           | A. A. Allen                          |
| 8        | 482                     | Near Chicago, Illinois                | 72                           | Beecher (1942)                       |
| 9        | 1.7 x 10 <sup>4</sup>   | Western New York State                | 87                           | Saunders (1936)                      |
| 10       | 2.04 x 10 <sup>5</sup>  | Caroline County, Indiana <sup>5</sup> | 79                           | Chandler Robbins                     |
| 11       | 2.19 x 10 <sup>5</sup>  | Lucas County, Ohio                    | 105                          | Louis W. Campbell                    |
| 12       | 2.36 x 10 <sup>5</sup>  | Monongalia Co., W. Va.                | 107                          | Maurice Brooks                       |
| 13       | 2.85 x 10 <sup>5</sup>  | Beaver County, Pa.                    | 88                           | W. E. Clyde Todd                     |
| 14       | 2.87 x 10 <sup>5</sup>  | Pymatuning, Pa.                       | 113                          | Grimm (1952)                         |
| 15       | 2.1 x 10 <sup>5</sup>   | Prince Georges Co., Maryland          | 105                          | Chandler Robbins                     |
| 16       | 3.9 x 10 <sup>5</sup>   | Jackson County, Illinois              | 88                           | Richard Brewer & Chas. Kendeigh      |
| 17       | 4.19 x 10 <sup>5</sup>  | Freston Co., W. Va.                   | 125                          | Maurice Brooks                       |
| 18       | 4.55 x 10 <sup>5</sup>  | State College, Pa. <sup>5</sup>       | 80                           | Merrill Wood                         |
| 19       | 6.33 x 10 <sup>5</sup>  | Cayuga County, New York <sup>6</sup>  | 122                          | Allen H. Benton                      |
| 20       | 6.5 x 10 <sup>5</sup>   | Champaign County, Illinois            | 82                           | Richard Brewer & Chas. Kendeigh      |
| 21       | 6.55 x 10 <sup>5</sup>  | Monongalia & Freston Cos., West Va.   | 123                          | Maurice Brooks                       |
| 22       | 6.6 x 10 <sup>6</sup>   | Maryland (State)                      | 177                          | Robert E. Stewart & Chandler Robbins |
| 23       | 1.54 x 10 <sup>7</sup>  | West Virginia (State)                 | 162                          | Maurice Brooks                       |
| 24       | 1.57 x 10 <sup>7</sup>  | Western Pennsylvania                  | 168                          | W. E. Clyde Todd                     |
| 25       | 2.3 x 10 <sup>7</sup>   | Indiana State <sup>7</sup>            | 141                          | Val Nolan, Jr.                       |
| 26       | 2.65 x 10 <sup>7</sup>  | Ohio State                            | 177                          | Ed S. Thomas                         |
| 27       | 3.11 x 10 <sup>7</sup>  | W. Pa. and W. Va.                     | 180                          | W. E. Clyde Todd & Maurice Brooks    |
| 28       | 3.19 x 10 <sup>7</sup>  | New York State                        | 191                          | E. M. Reilley & Kenneth C. Parkes    |
| 29       | 3.47 x 10 <sup>7</sup>  | Illinois State                        | 156                          | Melvin Traylor                       |
| 30       | 5.76 x 10 <sup>7</sup>  | W. Pa., W. Va., Ohio                  | 191                          |                                      |
| 31       | 8.94 x 10 <sup>7</sup>  | W. Pa., W. Va., Ohio, N. Y.           | 222                          |                                      |
| 32       | 9.6 x 10 <sup>7</sup>   | W. Pa., W. Va., Ohio, N. Y.           | 234                          |                                      |
| 33       | 1.19 x 10 <sup>8</sup>  | All above plus Indiana                | 237                          |                                      |
| 34       | 1.54 x 10 <sup>8</sup>  | Add Illinois                          | 240                          |                                      |
| 35       | 9.3 x 10 <sup>8</sup>   | Eastern U.S.A.                        | 317                          | Peterson (1947)                      |
| 36       | 4.6 x 10 <sup>9</sup>   | Neartic, excluding Greenland          | 625                          | Kenneth Parkes                       |
| 37       | 1.25 x 10 <sup>11</sup> | Whole Earth                           | 8600                         |                                      |
| B 1      | 3.75                    | San Isidro del General, Costa Rica    | c30                          | Alexander Skutch                     |
| B 2      | 15                      | Vera Cruz State, Mexico               | 84                           | Davis (1952)                         |
| B 3      | 15                      | Vera Cruz State, Mexico               | 102                          | Davis and Morony (1953)              |
| B 4      | 15                      | Vera Cruz State, Mexico               | 106                          | Davis (1955)                         |
| B 5      | 600                     | Barro Colorado Island                 | c150                         | Eisenmann (1952)                     |
| B 6      | 6 x 10 <sup>5</sup>     | Panama Canal Zone and adjoining       | c343                         | Sturgis (1928)                       |

(TABLE I. Continued)

| Ref. No. | Area (acres)           | Locality                                     | Species breeding in one year | Authority        |
|----------|------------------------|--|------------------------------|------------------|
| B 7      | 1.8 x 10 <sup>7</sup>  | Republic of Panama                           | 680                          | Eisenmann (1955) |
| B 8      | 6.4 x 10 <sup>8</sup>  | Middle America (Panama to Mexico, inclusive) | 1181                         | Eisenmann (1955) |
| B 9      | 5.13 x 10 <sup>9</sup> | Middle America plus Neartic                  | 1503                         |                  |

<sup>1</sup> 1951, Average of 26. Audubon Field Notes Vol. 5. pp. 316 *et seqq.*<sup>2</sup> 1951, Average of 4.<sup>3</sup> Average of 10 years at Neotoma.<sup>4</sup> Average of 2 years. Preston Laboratory grounds.<sup>5</sup> A minimum.<sup>6</sup> 1949—Breeding Birds of Cayuga Co. (Unpublished).<sup>7</sup> Regular breeders only: estimate may be conservative.

I, and where no date follows the name, it should be assumed that it is information by correspondence in the years 1956-1958. We attempted to obtain uniformity of treatment by specifying, in the case of counties and larger areas, that only *regular* breeders would appear on the lists used for Table I, and "regular" breeders were defined as those that certainly nested within the area in 9 years out of 10. For most species this presents

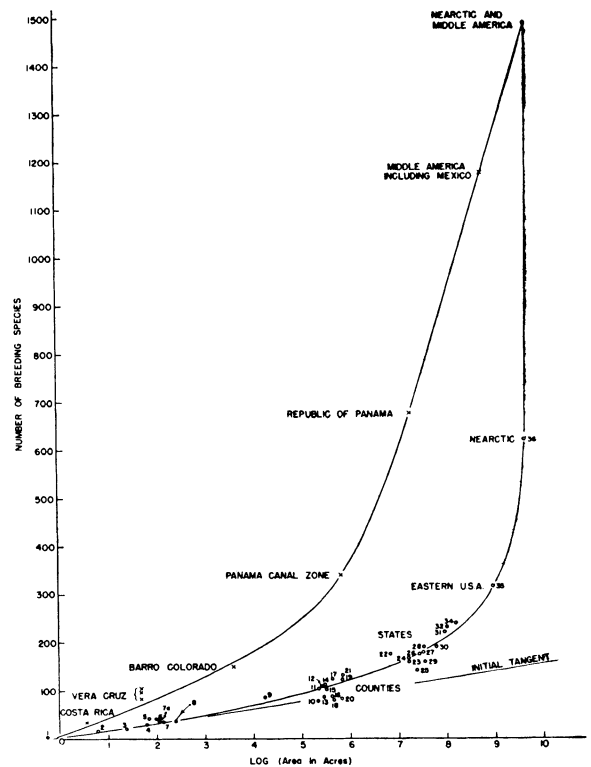


FIG. 1. Birds of the nearctic and neotropical Regions. Number of breeding species for various sizes of area = abscissa logarithm. The lower, or nearctic, curve starts in the deciduous forest of eastern North America. The Costa Rica point on the upper curve is believed by Dr. Skutch to be higher than typical. (This is a "Gleason plot").

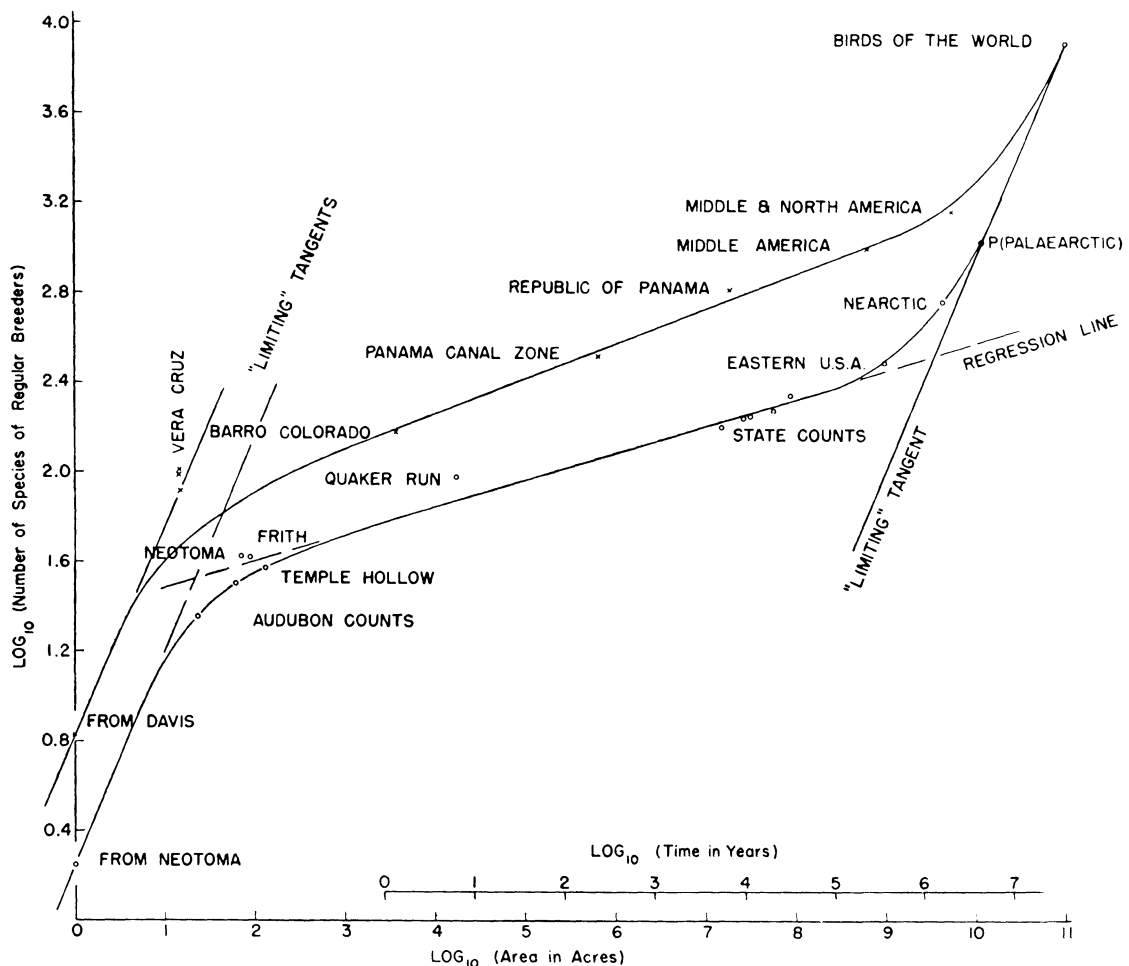


FIG. 2. "Log-log" plotting of the same data as in Fig. 1. A time-scale has been added as an alternative to the space-scale. Since a single year or breeding season ( $\log \text{ time} = 0$ ) is the shortest time with any meaning, the graph suggests that a couple of thousand acres in the smallest area of eastern deciduous forest that is meaningful in species-area studies of birds. This assumes that space and time are "equivalent," and that the two scales are correctly adjusted sideways. This is an "Arrhenius plot."

no difficulty; they nest there unequivocally every year. But there is a shadowy margin of irregular breeders which usually nest there, but it is difficult to assert that they nest there 9 years out of 10. The best of authorities collaborated, but some may have been slightly more conservative than others. Some scatter from these causes must be expected. Other divergencies are "real," *i.e.* due to ecological conditions.

For the smaller areas we generally used actual counts, either the count in a particular year, or the average of several counts made over a period of years. In the case of "Neotoma," for instance, it was the average of 10 years of counting.

The nearctic material of Table I is graphed in Figure 1 on a semi-logarithmic basis, that is to say, areas are plotted logarithmically as abscissae,

while the species-count is plotted arithmetically as ordinate.

The same material is graphed in Figure 2 on a logarithmic scale for both abscissa and ordinate. If the law of equation (3) applied, this plotting would produce a straight line and the exponent "z" could be ascertained from it.

In Fig. 3 we have plotted the first differential of the nearctic curve of Fig. 1. That is to say, plotting as abscissa the logarithm of the areas, we have plotted as ordinate, on an "arithmetical" scale, the number of species that are added at each doubling of area.

In Figures 1 and 2 we have also plotted our findings for the neotropical, which are tabulated in Table Ib and are discussed a little later.

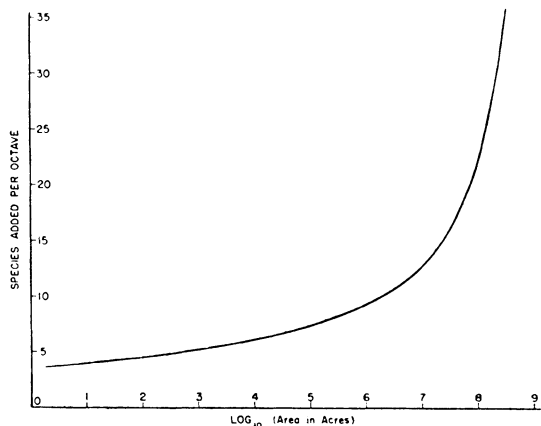


FIG. 3. First differential of Fig. 1, for the nearctic. This shows that the effect of doubling the area under study is likely to add a number of species which increases steadily as the size of area to be doubled increases.

### Comments on the Nearctic Tabulations

#1 This is a suburban count, averaging about 4 species (and 4 pairs of birds) on a half acre. The count is too high to be typical of the eastern deciduous forest, though it may be typical of some suburbs, where the avifauna is impoverished in species by the elimination of those that nest at ground level, but nonetheless a high density of the remaining species is achieved. A better point could be located by a consideration of the count at Neotoma, #5 of this list. Here on an area of 69 acres the average number of pairs was 115.3 or 0.84 pairs per half acre. Since 0.84 pairs will not include more than one species, we may estimate that half an acre of eastern forest will average something like one species.

#2 This area of 6 acres is remote from even a village, in southern Butler County, Pennsylvania, but it contains Schriver's cottage and once more the count comes high, due perhaps in part to quasi-commensal species. In 1956 Schriver had 22 species on the 6 acres but over a period of years he estimates that about 18 would be the average number of species. This, like #1 above, is a very rich fauna, but again it is probably somewhat artificial.

#3 & #4 Audubon Field Notes publishes once a year a number of breeding bird counts. We have here used the reports of 1951, confining them to counts within the eastern deciduous forest area. Thirty counts were used, from Vol. 5, pp. 316 *et seqq.* We divided them into 2 groups, according to acreage. The first 26 counts relate to areas from 9 to 37 acres; the other group of 4 counts involves areas of 50 to 75 acres. Unlike counts 1 and 2, these counts, 3 and 4, appear to be on the low side, but they are, as mentioned above, an average of 30 individual counts at different places.

#5 In the Hocking Hills of south central Ohio, Dr. E. S. Thomas of Ohio State Museum has owned for many years a 69 acre tract of second-growth forest, and in 10 of those years has made a rather careful census of the breeding birds, both as regards the species present and the number of pairs of each species. The data are recorded in Table II, and, together with the information in several of the other counts

where individuals as well as species were tallied, will be used below in an attempt to discriminate "sampling errors" from changes in ecology, and to estimate whether time and space act alike on the species-count.

#6 We return from Ohio and other points in the eastern forest to the Preston Laboratory grounds. This is the area reported on by Preston and Norris (1947). Since observations were fairly complete for 2 consecutive years, this count also helps with the problem of "sampling errors."

#7 Beaver County, Pennsylvania, adjoins Butler County on the east, and the State of Ohio on the west. Edeburn observed the birds on a 130 acre tract called Temple Hollow for 2 years. His figures are corrected to give a fair estimate of the number breeding in a single year. See also Edeburn (1946).

#7a Sapsucker Woods presents problems, as does #8 below, due to diversity of habitat. Dr. Allen reports an average annual count of 55 species, which puts the point well above our line, but when corrected (as nearly as we can correct it) for this diversity, the point comes quite close to the line.

#8 Beecher was not interested specifically in the species-area question, and chose a place where 2 distinct ecological assemblages adjoined. His species count is therefore high. It is possible by a reasonable argument to estimate what would be the species-count on a more homogeneous area, either the upland or the marsh, and so to obtain a point for a smaller area and a smaller species-count. This has been done on the graph and the displacement of the point indicated by an arrow.

#9 We now pass to much larger areas, and with Aretas Saunders' Birds of Quaker Run Valley we reach the last of the areas where we have a count of individuals as well as of species. Quaker Run Valley is not entirely homogeneous in its ecology, but this count is particularly useful because it is big enough to establish with fair accuracy the lognormal character of the distribution of commonness among the various species, and therefore permits a good estimate of how many species ought to be added by doubling the area, since this is essentially a case of moving the "veil-line" one octave to the left. (Preston 1948). In combination with the observed trend of the species-area curve this gives us an idea of how much change is due to the fact that we are dealing with a lognormal universe, and how much is due to an expanding universe, i.e. a change of ecology.

#10 to #21 These 12 are county lists, covering areas in the range from about 300 to about 1000 square miles. They are tabulations of species only. Necessarily they are subject to some uncertainties, as my authorities tend to point out. But the errors are probably not too serious and the statistical effect permits us to draw our species-area curve with some confidence among the plotted points.

#22 to #34 These involve states, or substantial portions of states, and combinations of adjoining states. We are now dealing with areas of the order of hundreds of thousands of square miles.

#35 We take the breeding-species count for the eastern U.S.A., an area of about 1½ million square miles.

#36 The nearctic is taken as including Alaska, Canada, and the United States, but excluding Greenland. We have, to a first approximation, included only the

land area of the nearctic, and there is not much question that we ought to have included a considerable area of sea. For though the pelagic birds nest on land, they would **not** do so in the absence of sea. On the other hand it is not clear that the Greenland ice-cap or other completely ice-covered regions in the arctic have any influence on enriching the avifauna of the region. Superficially they merely have the effect of reducing the total area of the globe that is habitable by birds.

#37 In dealing with the whole earth I have used its total area, land, sea, and ice. For the scattered islands of the ocean are the breeding places of many pelagic species, and the home of many endemic species.

### *The Species-Area Curve for the Nearctic Birds*

In Fig. 1 we plot the data of Table I, on a semi-logarithmic basis, as far as the figures for the nearctic. To plot the figure for the whole world would require the graph to be 12 times as high. In the same figure we plot also data for part of the neotropical area, *viz.*, the area around Panama. The latter may be extended smoothly to include Middle America and Mexico, at a point far above the top of the graph here given, and still further to a point representing Middle America plus the nearctic, to which point above the lower curve, nearctic plus Middle America, also smoothly converges.

The curve drawn among the points seems to represent them fairly. There is some scatter but the reason seems fairly clear. The point takes account of the effects both of sampling a log-normal distribution and of sampling areas of varying diversity of habitat. Thus Indiana and Illinois lie below the line, presumably because they are states of rather uniform habitat, while Maryland and New York lie above it, because they include high mountains, lowlands, and sea coast. Similarly Sapsucker Woods as reported by Allen and the area outside Chicago reported by Beecher lie, in their uncorrected condition, well above the line, but yield points near the line if they are supposed to have at least 2 entirely different habitats inhabited by quite different groups of species. We discuss this later under the heading of "Edge Effect."

In Fig. 1 we have drawn the tangent to the very early part of the curve, which indicates that in these areas doubling an area adds about 4.7 species. This, however, is better examined in Fig. 3. As the area gets bigger, the slope steepens, and the number of species added for each doubling of area increases.

It will be seen that the Gleason or Williams law is not obeyed by the curve in its entirety. This would call for the curve of Fig. 1 to be a straight, sloping, line. Yet it is also clear that

over the range from say 10 acres to 100,000 or perhaps even 1,000,000 acres, the curve is a sufficiently close approximation to a straight line that, in the absence of information on larger areas, we should undoubtedly "graduate" it as a straight line and believe we had proved the point, that the law was true in space as well as in time, and that it held over a range of at least 4 or 5 orders of magnitude.

Now an order of magnitude, or decupling, is 3.3 octaves or doublings, so that the law is at least approximately true over a range of some 15 octaves, at least in terms of space. (Whether it is true in *time* we do not yet know). This means that the explanation which I gave of it in 1948 is inadequate. For in that paper (p. 257) the coefficient "a" of the exponent in the equation

$$n = n_0 e^{-(aR)^2} \quad (5)$$

tends to come out consistently with a value around 0.2 and with such an exponent the substantially straight part of the integral curve (p. 274, Fig. 11) is certainly not going to extend over 15 octaves. This means that ecological assemblages are always in a state of flux with the passage of time. In the present paper, by examining the species-area curve, we see how the universe we are sampling expands in space.

Fig. 3 gives the "first derivative" of Fig. 1. Using the same scale for abscissa it plots as ordinate the number of "new species" brought in by doubling the area. When the area is about 10 to 100 acres, doubling it adds about 4 species. At 1000 acres, doubling produces about 5 new species, and at 10,000 acres it produces 6 or a little more. At 100,000 acres it produces  $7\frac{1}{2}$ , and at a million,  $9\frac{1}{2}$ . Beyond this the curve steepens at an astronomical rate.

In Fig. 2 we plot the same information as in Fig. 1 with logarithmic ordinates as well as logarithmic abscissae. This permits us to extend the curve to the avifauna of the whole world. The curve seems to rise very steeply from its origin at the left hand end of the graph, then to flatten for a long distance, from about 100 acres to  $10^8$  acres or more, and then once more to rise steeply at a slope similar to its initial one. This is to be expected, for reasons discussed later. The curve is, in a sense, sigmoid, but the tangents at the 2 ends, though parallel to each other, are not vertical lines.

### THE EQUIVALENCE OF SPACE AND TIME

If time and space really are equivalent, we should be able to draw our Fig. 3 on a log-time



basis instead of a log-area basis and find for various times, instead of areas, the number of new species that are introduced by doubling the time.

### *Causes of Change*

It may be advisable to consider first the causes that produce, in a given locality, changes of fauna with the passage of time. In detail they are many, but in broad outline they seem to be 2, or perhaps 3:

(a) There is what I have called "sampling error." This may not be the best possible term, but it comes close to expressing my meaning. As the spring migration passes over western Pennsylvania a substantial proportion of the birds are newcomers that will breed for the first time. They are not returning to a place where they nested last year, but are looking for a place to settle down. Their selection is, from one point of view, a matter of chance; the early arrivals have a choice of several or many locations, and select one for reasons unknown to us, or "for no particular reason." Later arrivals, of the same or other species, may be excluded from the locations chosen by the earlier ones, since the whole locality is full, apparently, when a certain number of individuals occupy it. From our point of view the result is much the same as if we took at random a given number of individuals (or pairs of birds) from a "universe" of birds, and if we try the same experiment the next year, even if the "universe" is identical, the sample will be different. These differences I have called the "sampling error."

(b) As the years go by the habitat changes for a great variety of reasons. The forest may be buried in volcanic ash, burnt by lightning or man-made fires, or cut down for lumber or pit props. Thereafter it may regenerate through a long cycle of "ecological succession," or it may be turned into pasture, ploughed land, or suburban development. A succession of wet or dry years may change the ecological picture substantially. So may the arrival, or departure, of new predators like domestic cats or competitors like the European starling, or of new sources of food, either insects or plants. All of these and many many more factors can be grouped under the heading of ecological changes.

(c) The slow course of evolutionary change of species with time.

I think we can regard (a) and (b) as "causes" of change, but (c) is rather to be regarded as an "effect." We shall attempt to separate (a) and (b) from one another later in this paper.

Let us now return to the computation of a few examples.

TABLE II. Breeding bird censuses, Neotoma (69 acres). Compiled by Charles F. Walker and Edward S. Thomas

| Species                      | YEARS |     |     |     |    |     |    |    |     |     |
|------------------------------|-------|-----|-----|-----|----|-----|----|----|-----|-----|
|                              | 23    | 24  | 26  | 27  | 30 | 31  | 36 | 37 | 38  | 40  |
| Turkey Vulture.....          | 1     | 1   | 0   | 0   | 0  | 1   | 0  | 0  | 0   | 0   |
| Black Vulture.....           | 1     | 1   | 1   | 1   | 1  | 1   | 1  | 1  | 0   | 0   |
| Sharp-shinned Hawk.....      | 1     | 1   | 0   | 0   | 0  | 0   | 0  | 0  | 0   | 0   |
| Ruffed Grouse.....           | 0     | 0   | 0   | 0   | 0  | 1   | 0  | 0  | 1   | 0   |
| Mourning Dove.....           | 1     | 2   | 1   | 4   | 2  | 2   | 2  | 2  | 4   | 2   |
| Yellow-billed Cuckoo.....    | 0     | 0   | 2   | 1   | 1  | 1   | 1  | 0  | 1   | 1   |
| Black-billed Cuckoo.....     | 0     | 1   | 0   | 2   | 1  | 2   | 1  | 1  | 1   | 1   |
| Screech Owl.....             | 0     | 0   | 0   | 0   | 0  | 0   | 1  | 0  | 1   | 0   |
| Horned Owl.....              | 0     | 0   | 1   | 0   | 0  | 0   | 0  | 0  | 1   | 1   |
| Whip-poor-will.....          | 8     | 8   | 8   | 7   | 5  | 5   | 3  | 3  | 4   | 2   |
| Hummingbird.....             | 1     | 5   | 1   | 2   | 2  | 1   | 3  | 1  | 2   | 2   |
| Flicker.....                 | 2     | 1   | 0   | 1   | 0  | 1   | 0  | 0  | 1   | 0   |
| Pileated Woodpecker.....     | 0     | 0   | 0   | 0   | 0  | 0   | 1  | 0  | 1   | 0   |
| Red-bellied Woodpecker.....  | 1     | 0   | 0   | 0   | 0  | 0   | 0  | 0  | 0   | 0   |
| Hairy Woodpecker.....        | 0     | 1   | 1   | 0   | 0  | 0   | 2  | 0  | 1   | 1   |
| Downy Woodpecker.....        | 1     | 1   | 0   | 1   | 1  | 1   | 1  | 2  | 1   | 1   |
| Crested Flycatcher.....      | 3     | 2   | 1   | 1   | 2  | 1   | 2  | 1  | 2   | 2   |
| Phoebe.....                  | 7     | 4   | 3   | 5   | 4  | 4   | 5  | 6  | 4   | 3   |
| Acadian Flycatcher.....      | 3     | 6   | 5   | 5   | 5  | 3   | 5  | 8  | 8   | 10  |
| Wood Pewee.....              | 2     | 4   | 2   | 2   | 2  | 2   | 0  | 0  | 1   | 1   |
| Blue Jay.....                | 1     | 0   | 0   | 0   | 0  | 0   | 1  | 0  | 0   | 0   |
| Crow.....                    | 0     | 0   | 1   | 0   | 1  | 1   | 1  | 1  | 0   | 1   |
| Carolina Chickadee.....      | 1     | 2   | 3   | 2   | 1  | 4   | 1  | 1  | 3   | 3   |
| Tufted Titmouse.....         | 2     | 2   | 2   | 2   | 1  | 1   | 2  | 1  | 4   | 2   |
| White-breasted Nuthatch..... | 1     | 1   | 2   | 1   | 1  | 1   | 1  | 1  | 2   | 1   |
| Bewick's Wren.....           | 1     | 0   | 1   | 0   | 0  | 0   | 1  | 1  | 0   | 0   |
| Carolina Wren.....           | 4     | 7   | 0   | 1   | 1  | 2   | 0  | 0  | 0   | 0   |
| Catbird.....                 | 1     | 1   | 1   | 0   | 0  | 0   | 0  | 0  | 0   | 0   |
| Robin.....                   | 1     | 1   | 0   | 3   | 1  | 0   | 1  | 1  | 1   | 1   |
| Wood Thrush.....             | 7     | 5   | 4   | 2   | 2  | 2   | 4  | 2  | 3   | 3   |
| Bluebird.....                | 1     | 2   | 2   | 2   | 1  | 0   | 0  | 0  | 1   | 1   |
| Gnatcatcher.....             | 1     | 2   | 2   | 1   | 3  | 3   | 2  | 1  | 2   | 2   |
| White-eyed Vireo.....        | 4     | 3   | 4   | 2   | 3  | 2   | 1  | 1  | 0   | 0   |
| Yellow-throated Vireo.....   | 1     | 1   | 0   | 1   | 0  | 1   | 0  | 0  | 1   | 1   |
| Red-eyed Vireo.....          | 8     | 10  | 9   | 7   | 7  | 11  | 14 | 16 | 13  | 18  |
| Black & White Warbler.....   | 2     | 2   | 4   | 1   | 3  | 2   | 3  | 1  | 5   | 4   |
| Worm-eating Warbler.....     | 4     | 3   | 6   | 3   | 4  | 6   | 7  | 7  | 7   | 7   |
| Blue-winged Warbler.....     | 3     | 4   | 2   | 2   | 2  | 1   | 2  | 2  | 1   | 1   |
| Yellow Warbler.....          | 0     | 1   | 0   | 0   | 0  | 0   | 0  | 0  | 0   | 0   |
| Cerulean Warbler.....        | 4     | 3   | 3   | 2   | 1  | 2   | 2  | 2  | 2   | 4   |
| Prairie Warbler.....         | 5     | 4   | 2   | 2   | 1  | 1   | 1  | 1  | 1   | 1   |
| Ovenbird.....                | 3     | 7   | 3   | 2   | 2  | 9   | 5  | 5  | 11  | 6   |
| Louisiana Water-thrush.....  | 4     | 3   | 3   | 1   | 1  | 1   | 1  | 1  | 1   | 2   |
| Kentucky Warbler.....        | 1     | 3   | 2   | 0   | 2  | 0   | 1  | 2  | 2   | 2   |
| Northern Yellowthroat.....   | 1     | 1   | 1   | 1   | 0  | 0   | 1  | 1  | 1   | 0   |
| Chat.....                    | 12    | 7   | 6   | 6   | 6  | 4   | 2  | 2  | 1   | 2   |
| Hooded Warbler.....          | 4     | 4   | 6   | 1   | 2  | 2   | 1  | 1  | 1   | 0   |
| English Sparrow.....         | 0     | 0   | 0   | 0   | 0  | 0   | 0  | 0  | 1   | 0   |
| Cowbird.....                 | P     | P   | P   | P   | P  | P   | P  | P  | P   | P   |
| Scarlet Tanager.....         | 4     | 4   | 4   | 2   | 2  | 3   | 2  | 2  | 3   | 4   |
| Summer Tanager.....          | 3     | 3   | 3   | 3   | 1  | 1   | 1  | 2  | 3   | 1   |
| Cardinal.....                | 5     | 3   | 7   | 5   | 2  | 3   | 3  | 3  | 5   | 5   |
| Indigo Bunting.....          | 6     | 5   | 3   | 4   | 4  | 2   | 2  | 5  | 2   | 4   |
| Towhee.....                  | 3     | 4   | 8   | 6   | 5  | 5   | 2  | 3  | 4   | 2   |
| Chipping Sparrow.....        | 2     | 2   | 1   | 2   | 2  | 2   | 1  | 2  | 2   | 3   |
| Field Sparrow.....           | 8     | 6   | 9   | 7   | 7  | 5   | 2  | 2  | 2   | 3   |
| Song Sparrow.....            | 2     | 1   | 3   | 1   | 1  | 1   | 0  | 0  | 1   | 0   |
| TOTAL SPECIES.....           | 47    | 47  | 42  | 42  | 41 | 42  | 44 | 38 | 46  | 39  |
| TOTAL PAIRS.....             | 143   | 146 | 133 | 107 | 97 | 104 | 97 | 95 | 120 | 111 |

### *Neotoma*

In Table II we give Dr. Thomas' tabulation of the species and individuals (pairs) breeding at Neotoma over a period of 18 years. Unfortunately, in only 10 years out of the 18 was a complete accounting made, and this complicates our

figuring. We can however make an approximate estimate of what was going on.

Restricting ourselves to the 5 pairs of consecutive years, 1923-24, 1926-27, 1930-31, 1936-37, and 1937-38, we find that the species present in the 2nd year of the pair, but absent in the first, number 3, 6, 4, 0, and 12 respectively, while the species present in the first year and missing in the 2nd amount to 3, 6, 3, 6, and 4. The average of these 10 changes is 4.7. If we take the 10 years observed as being equivalent to consecutive years, and observe that in the 10 years 57 species were seen, while the average was only 42.8, for an increase of 14.2, then since  $10 = 2^{3.3}$ , the effect of doubling the period of observation is to increase the count of species by  $14.2/3.3 = 4.3$ . This estimate is probably a little higher than if the years had been strictly consecutive. Still another way of looking at it is this: In the 10 years that were actually sampled, there were 3 species that appeared only once, and in each case they were represented by a single pair. It is reasonable to assume that if we had the counts for the missing 8 years, we should have found about 3 more species that appeared only once. This would make a total count of species of 60 in 18 years, up 17.2 from the average number of 42.8. Now 18 is  $2^{4.17}$ , and so 4.17 is the number of doublings available to us. Then  $17.2/4.17 = 4.12$ , which is the number of "new" species added by doubling the *time* of observation. By these 3 methods then we have estimates of 4.7, 4.3, and 4.12, as the number of species added by doubling *time*, on an area of 69 acres. The average of these 3 figures is **4.47**.

Referring now to Fig. 1 or, better, to Fig. 3, and noting that  $\log 10^{69}$  is 1.84, we find that the effect of doubling the *area* is to add 4.3 species. The agreement seems to be almost exact.

Note that at Neotoma the ecological set-up was not static; the forest was growing up over those 18 years. The change therefore includes both "sampling error" and change of habitat. Some species definitely tended to become more common or regular and others to become less so. In including both effects, the change with time is similar to the change with area.

#### *The Preston Frith*

The Preston Laboratory Grounds, or Frith, have an area of about 90 acres. Preston and Norris (1947) give the breeding species of 1944 as 42, including the Cowbird. From 1944 to 1958 inclusive the count has risen to 61, an increase of 19 over a period of 15 years, which is 3.9 doub-

lings. This is an increment of 4.87 species per doubling in *time*. From Fig. 3 we should expect about 4.7 for a doubling in *space*. Again the agreement is good.

The matter may be tested more directly and without reference to Fig. 3. The Pennsylvania Manual gives the area of Butler County as 794 square miles or 510,000 acres, which is 5,700 times the area of the Preston Laboratory Grounds (c. 90 acres "inside the fence"). Now  $5,700 = 2^{12.5}$ , or 12.5 doublings. The man who today probably knows the avifauna of Butler County better than anyone else is Mr. Hal H. Harrison, who lives just beyond its margin and travels about it a great deal. His estimate is that there are **99 regular** breeders in the County, while Norris found 42 or 43 annually on the Laboratory Grounds. Now  $99-42 = 57$  and  $57/12.5 = 4.6$  species per doubling of area. Though Harrison's list is longer than mine (he knows the outlying parts of the County better than I do), I know of one or 2 regular species about which he is doubtful, and this would bring the tally to 4.7 per doubling. In any one year we can expect at least a few irregular species to breed, so the tally will run a little higher, agreeing in space almost exactly with the calculation for time. It may be noted that if Butler County were average, *i.e.* if it fell exactly on our line, it should have about 113 regular breeders, but to the best of our knowledge it falls well below this level, as does the neighboring Beaver County as estimated by Todd.

#### *Sapsucker Woods*

Sapsucker Woods, near Ithaca, New York, affords another opportunity to check space against time, for records have been conscientiously kept and observations go back for 50 years. The situation is a little complicated because the 150 acres of the woods consist of 120 acres of woodland, 10 of water, and about 20 of bushy fields. This variety tends to make the species count high. On 120 acres of woodland we should, from our graph, expect about 34 species: Dr. Allen reports that over a period of 50 years some 59 species have nested in the wooded area, though only 36 are true woodland species.

Let us begin however by lumping the whole area together. On the 150 acres, in the years 1957, 1958, and 1959, there nested 57, 51, and 58 species, for an average of 55. In the course of 50 years, 84 species have been recorded as nesting on the area or 29 more than the average for a single year. Now  $50 \text{ years} = 2^{5.6}$  or 5.6 doublings, and  $29/5.6 = 5.2$  for each doubling of

time at Sapsucker Woods, which is not far from the figures we find elsewhere, though a little higher, probably because of the 10 acres of water.

Dr. Allen notes that in the Cayuga Lake basin, of which Sapsucker Woods is a part, 156 species have been known to nest. The area of the basin is about 1600 square miles or  $1.02 \times 10^6$  acres. On such an acreage, our curve (Fig. 1) predicts about 123 regularly breeding species. (The number in a single year may be slightly higher since some irregular ones may be present each year). Therefore  $156 - 123 = 33$  species, and if we assume that something like a hundred years accumulated this excess, then since  $100 = 2^{6.6}$  or 6.6 doublings, we have  $33/6.6 = 5.0$  species for each doubling of time on the Cayuga Lake basin.

We may now test also for the effect of area, as well as time:

The area of Cayuga Lake Basin is  $2^{12.7}$  times the 150 acres of Sapsucker Woods. The number of species nesting in the basin was 156, and I assumed this was for 100 years. In 50 years it should be about 151. The number nesting in Sapsucker Woods over a period of 50 years is 84, as mentioned above, and  $151 - 84 = 67$  species. Then  $67/12.7$  gives 5.3 species for each doubling of area in this locality. This is quite similar to the figure for doubling of time, as in the previous paragraph.

We thus have 3 figures as follows:

On doubling time at Sapsucker Woods, we add about 5.2 species.

On doubling time over Cayuga Lake Basin, we add about 5.0 species.

On doubling area in this locality, we add about 5.3 species.

Note that in the absence of an actual count for the Basin in a single year, we had to use our curve to get the figure of 123 "regular" species. This, however, is probably not far out, for Dr. Benton (our point 19) gives the count for Cayuga County as 122, and the area of this county is 0.63 times the area of the Basin, so the Basin would be expected to have about 127 or 128, and this is close enough.

### *The Avifauna of States*

When we get to larger areas, such as states, the number of species that are irregular, sporadic, or doubtful, is probably not nearly so well known. In correspondence, Val Nolan, Jr. gives the number for Indiana as 18, Traylor gives about a dozen for Illinois, Todd gives 14 for western Pennsylvania. Yet quite a number of species might once

in a while be represented by a single pair in any state and escape notice. Thus I think it possible that in the course of 50 or 100 years, 30 species might nest once or more but be missing in at least 5 or 10 years. This would produce about the same figure, 4 or 5 per doubling, we find for the smaller areas of Neotoma and the Frith. This means that if we converted our abscissae in Fig. 3 from an area to a time basis, a year would fall at some point not very far from the lefthand end of the curve. We cannot locate the point with any real accuracy because the curve here is too flat. The right-hand end would be more useful, and this takes us far outside the records of history and we must have recourse to the fossil record.

### *The Fossil Record*

In correspondence, Dr. Wetmore informs me that few of our modern species of birds appear to go back beyond the Pliocene. He writes, "It is my personal conclusion that the existing species of birds had their period of evolution into their present form in the latter part of the Tertiary, presumably during the Pliocene, so that they were definitely established as distinct entities at the beginning of the Pleistocene or Ice Age. Some, the song sparrows for example, have apparently had continued evolutionary change as marked by the numerous subspecies now evident. Others were already stabilized and did not show such changes." (See also Wetmore 1959).

Brodkorb (1958) concurs: "As far as identifiable, all *genera* in this (Middle Pliocene) avifauna occur in the present avifauna of Oregon, but the *species* are extinct, whereas the Upper Pliocene avifauna contains a large proportion of living species. This affords additional evidence that living species of birds have a time span extending no further back than the Upper Pliocene." (Brodkorb 1955). (The italics are mine and I have rephrased the statement slightly). In other words, if we sample our birds now, and had sampled them some 4 or 5 million years ago, we should have practically no species common to the 2 samples. This is what happens with the passage of time. When does the same thing happen with increase in space? By referring to Fig. 2 we see that it really happens at the total area of the whole world, where the curve from both the nearctic and neotropical origins become tangential to the limiting tangent. We might say the curves are substantially parallel to this tangent at  $10^{9.5}$  or  $10^{10.5}$  acres.

Thus 4 or 5 million years, or  $10^{6.5}$  to  $10^{6.7}$  years, are equivalent to some  $10^{9.5}$  or  $10^{10.5}$  acres,

and so a year is equivalent to something like 1000 acres or 10,000 acres, or say one to ten square miles.

On this basis the area that we can compare from year to year, that is, on a basis of 1, 2, 4, 8 years, etc. is 1000 acres or a little more, and here doubling the area should produce about 5 or 6 "new" species. Similarly, counting for 2 seasons instead of one should produce about 5 or 6 new species. This seems likely to be nearly enough correct.

The evidence suggests that time and space are in fact essentially equivalent or at least that there is a strong resemblance.

#### SEPARATING THE EFFECTS OF "SAMPLING ERROR" FROM THE EFFECTS OF CHANGING ECOLOGY

Confining our attention to the nearctic, for which our information is more complete, we can obtain from Fig. 1 the number of species of breeding birds to be expected on an area of given size,

and from Fig. 3 we can obtain the number of species we may expect to add by doubling the area. Then dividing the second figure by the first and multiplying by 100, we can obtain the percentage increase in species. This percentage for a number of different sized areas is plotted on Figure 4 (upper curve).

From about a thousand acres to a hundred million acres this percentage increase is around 8 or 10%. This percentage figure is similar for nearctic and neotropical regions.

However, it consists of 2 components. There is first the "sampling error," which is the big element with very small samples, and, second, there is the inevitable change of ecological set-up and diversity of habitat when we come to large areas.

Now it appears that the sampling error is always about 3 or 4 species per doubling. At Quaker Run the lognormal curve shows that doubling the sample would theoretically increase the species by about  $4\frac{1}{2}$ . In the very much smaller

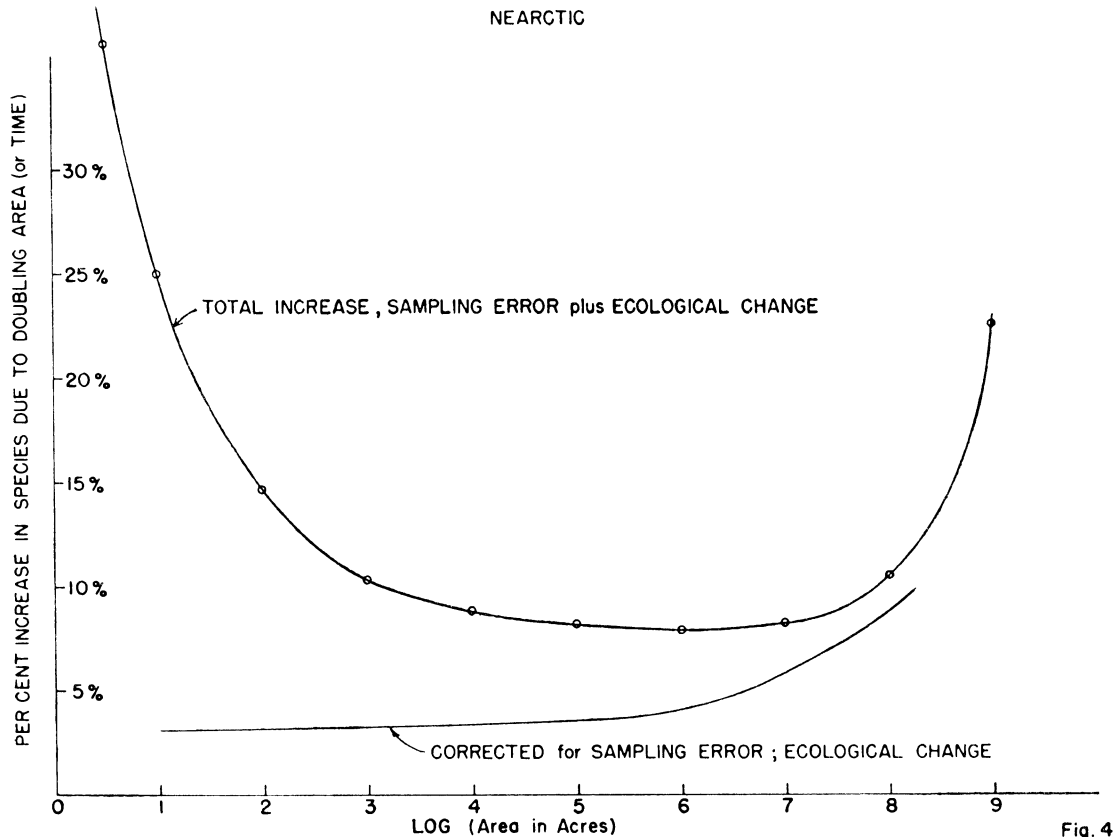


FIG. 4. Increase in species of breeding birds due to doubling area or time, expressed as a percentage of the species before doubling. The upper curve is the percentage increase actually observed, and is compounded of the "sampling error," due to the fact that 2 equal, random, samples of a lognormal population are likely to differ substantially in the species they produce, especially with small areas and hence small samples, and of the effect of ecological change, which becomes increasingly important with large areas. The lower curve subtracts the sampling error and gives an estimate of the increase in species due solely to ecological change, or diversity, as we increase the area (or elapsed time).

areas of Neotoma and Preston Frith, where doubling takes the form of doubling time and not space, the evidence is that the figure is again close to 4. The state counts indicate that it is still no greater than 4, and may be a little less, our judgment once more being based on doubling time; that is, we take account of sporadic or occasional or intermittent breeders. Finally, when we come to the bird population of the whole world, and note that most species try to breed at least once every year, we can agree that we are not likely to add more than 4 species by using a 2 year count instead of one.

Thus to a first approximation we can probably agree that over an immense range of area and of time, doubling our sample is likely to produce an increment of species due to what we have called the sampling error, as distinct from the variation arising from changing ecology, not far from 3 or 4 species, no matter what the size of the area.

But 3 or 4 species is a much larger percentage of the total species in small areas than in large.

If we deduct this percentage from the upper curve of Fig. 4, we are left with the lower curve thereof as representing the increment due to changing ecology. This curve is virtually flat at about  $3\frac{1}{2}\%$  over a very wide range.

#### *Some Special Problems*

Before we leave the nearctic and its avifauna, a few comments by way of explanation may be useful on two or three points.

##### *The Initial Steep Rise of Fig. 2*

It can be shown that if the complete population of an area such as an isolated island or a quasi-isolate such as the eastern deciduous forest conforms to a complete lognormal distribution, then a small sample will be abnormally rich in species in proportion to the number of individuals. This would be true if it were a strictly random sample, and thus when we collect a small sample or study a small area, we find our collection growing "richer" in species, at an abnormal rate. In the case of territorial birds, the "enrichment" is even faster, and both these factors tend to make the early part of the curve too steep. An opposite effect can be expected with flocking birds in winter, or colonially-nesting birds, or with most plant quadrats, since most plants are more or less clumped or "contagiously distributed."

##### *The "Edge Effect"*

It is commonly stated that birds are more plentiful at an ecotone, or the margin of a habitat, where it adjoins another habitat, than they are in

the middle of a habitat; for instance, they are more plentiful at the edge of a wood than in its interior. The same thing has been urged for mammals, especially big game. It has been argued that they may depend on the one habitat for shelter and the other for food, or that their requirements are better met by the resources of 2 habitats than of one. This is called the "Edge Effect" but whether it is a genuine effect, causing individuals to concentrate at the ecotone, or whether it is merely an appearance, due to an enrichment of species to be seen at the margin, I am not completely sure. The problem does concern us a little, however, in the present paper, because the points that fall appreciably above our curve do so mainly because of an enrichment in species due to the presence of more than one kind of habitat, *i.e.* to the presence of an important "ecotone."

Suppose we take a wooden frame in the form of a square, intended to delimit a quadrat of 150 acres, and drop it at random upon an area of uniform climax forest in our deciduous eastern forest country. Then by reference to our species-area curve, Fig. 1, we should expect it to enclose about 37 species of breeding birds. If we now drop it somewhere else, not far away, on a similar area, we should again expect about 37 species, though several of these species might be ones that we did not net at the first drop. This is the inevitable consequence of sampling a lognormal population, with some species sufficiently uncommon that we cannot expect to net even a single pair in a 150 acre quadrat.

Now let us suppose that adjoining this climax forest we have a large area of open marsh. This might be just as thickly populated with birds as the forest, and if we dropped our frame on it we might again net 37 species, and quite conceivably not one of them would be a species that breeds in the forest.

But if the ecotone between marsh and forest is sharp, and sometimes it is, we might drop our frame so that it included 75 acres of forest and 75 of marsh. Then, referring once more to our species-area-curve, we should expect to net 32 species of forest birds and 32 of the marsh, for a total of 64 species. This is 72% more than if we drop the net on a single habitat clear of the ecotone.

Sapsucker Woods is an area of 150 acres where Dr. A. A. Allen has long kept track of the breeding species, and he has provided me with a list of them. Those found in a single year averaged 55 species, which seemed excessively high. In our

discussion of the subject, it soon became clear that it was the presence of two distinct habitats, forest and open marsh, that was producing the result. The computation made above, therefore, is not entirely hypothetical; it is a rough approximation to the Sapsucker Woods situation.

When the corrections are made, Sapsucker Woods falls nearer to the curve (Fig. 1) than do Neotoma or Preston Frith, though they are not nearly so far off as Sapsucker Woods was in the uncorrected form. The reason they are not exactly on the line may be that they are not strictly homogeneous habitat, a point on which Norris (1947) comments in the case of the Frith. Similarly, Saunders comments that Quaker Run Valley is not homogeneous, and probably for this reason his point also lies above the curve, though at no great distance from it.

Beecher's 482 acre area near Fox Lake, Illinois, is also highly heterogeneous. He recognizes 4 distinct habitats, but it is probable the birds recognize fewer, perhaps only 2. If these 2 were equal in size and equally well populated, then, instead of reporting 72 species on 482 acres, he would report 36 species on 241. If we assume this is as good a correction as we can make in so complicated a situation, the new point, 36 on 241 acres, falls almost exactly on the line, though the original point falls far above it.

When our quadrat reaches the size of a county, several hundred square miles instead of a hundred or a few hundred acres, or the size of a state, some scores of thousands of square miles, we must expect that the random dropping of the net will include a variety of habitats, and so we must necessarily get composite samples representing 2, or several, populations of birds. Thus the curve will tend to climb above the initial tangent. The points will be scattered somewhat, some climbing higher than others, according to the diversity of habitats in the various counties or states. We no longer attempt to correct for this, but obtain as best we can a representative sample of counties and states, plot the points, and draw the curve through the middle of them.

The properties of the palaearctic avifauna may be expected to be similar to those of the nearctic, but the palaearctic is much larger in area and has many more species of breeding birds. De Beaufort (1951) credits it with 1110 species; I estimate the area to be about  $1.22 \times 10^{10}$  acres. This area is plotted at P in Fig. 2, on the nearctic curve, where it corresponds to an avifauna of 1090 species, very close to de Beaufort's figure. In other words, if the nearctic were as big in

area as the palaearctic, it would most likely have as many species as the palaearctic now has. The inference seems to be that if we had a complete species-area curve for the palaearctic, beginning in a region as similar as possible to the eastern deciduous forest, the curve could be superimposed on the nearctic curve and would fit it exactly.

The situation with the neotropical avifauna is different, and merits a slightly larger discussion.

#### THE NEOTROPICAL AVIFAUNA

It will be interesting to see if we should reach somewhat similar conclusions by starting our investigations in a totally different environment, and so I have attempted to outline what happens in the neotropical forest. Here we are naturally even worse off for authentic information. I have had to rely heavily on just 2 or 3 authorities, Sturgis (1928), Eisenmann (1952 and 1955) and Irby Davis (1952, 1953, and 1955). The information is tabulated in Table 1, and graphed in Figs. 1 and 2.

#### *Comments on the Tabulation*

I could find no information on the number of pairs or of species in strictly small areas in Panama, whence most of the other figures came. I used some of Davis' results of tropical lowland and rain forest in Vera Cruz State, Mexico. The points seem to lie above the expected level, ranging from 84 to 106 species when we might expect 55 or 60. The reason is not clear. We have also some information from Dr. Skutch in southeastern Costa Rica. In a letter dated December 1, 1958 he says of his home area at Quizzara, southeastern (Pacific coast of) Costa Rica, 2500 ft above sea level, in the 12 months September 1, 1943 to August 31, 1944, on 3.75 acres:

"Species counted as resident, 33; individuals counted as resident, 110; density, 29.3 breeding birds per acre; nests found with eggs, 83. Many of the resident birds foraged beyond this area in the neighboring woods and thickets. I believe I had a rather unusual concentration of breeding birds about my house at that time."

#B5 Barro Colorado Island, in the Panama Canal. Eisenmann (1952, p. 3) says that though we have positive evidence of the breeding of only about 100 species, it is probable that about 200 breed *more or less* regularly on the Island. (Italics mine). Since we are concerned with those that breed *quite* regularly, I thought 150 to 160 might be a fair estimate.

#B6 The Panama Canal Zone itself has an area of about 500 square miles. Sturgis (1928, pp. XII and XIII) estimates that if we include a modest amount of contiguous territory that is not politically in the Zone,

we should meet about 434 species of birds of which 21% do not breed there, so that 343 species do. The area of the contiguous territory she does not specify. I have assumed that it may be as large as the "political" part of the Zone, giving a total area of about 1000 square miles or 600,000 acres. Clearly we are making a lot of assumptions and must end with only a rough approximation.

#B7 Take next the Republic of Panama whose area is about 28,575 square miles or  $1.83 \times 10^7$  acres. Using Eisenmann's (1955) list of Central American birds, it appears that about 680 species breed within the Republic of Panama. An indirect estimate from Sturgis (1928) gave roughly 700. The agreement is good.

#B8 Passing outside Panama to the west and north, we can check the species in Eisenmann (1955) that breed in Middle America from Panama to Mexico inclusive: these apparently total about 1180 species, while the area of the countries, from other sources, appears to be about 985,000 square miles or  $6.3 \times 10^8$  acres. There is a good deal of sea coast to Middle America, and once more we face the problem of how much sea we ought to include. Since this problem is insoluble, we have used simply the land area. This might justify us in reducing the total species count by the number of pelagic species. But these are only a small fraction of the total of 1180.

#B9 We have now brought the nearctic and neotropical into contact at the Mexico-U.S.A. border and may add either A to B or B to A. In either case we finish with an area of  $4.13 \times 10^9$  acres. From Eisenmann's 1955 list it appears that species that breed in both nearctic and Middle America number about 303, so that the total breeding species of the 2 combined areas is  $625 + 1181 - 303 = 1503$ .

When this point is plotted on an extension of Fig. 1, it lies very neatly on both curves, each of which is virtually straight, with this sort of plotting, above the level of 600 species. When it is plotted by the log-log method of Fig. 2, it lies neatly on the neotropical curve as this proceeds on its way to the final point, the birds of the world. It does not fit so well on the nearctic curve, since the relatively small area added by Middle America produces such an enormous increase of species. The nearctic curve does however head reasonably well for the ultimate point, birds of the world.

From Davis' figures it appears probable that on a single acre of neotropical lowland forest we may get as many as 7 species of birds nesting. But whether the figure is 1, 7, or 14, it will make little difference to the general shape of the species-area curve in Fig. 1. A smooth curve can be drawn readily through all the points of Fig. 1, except those for the 15 acre counts, and it continues smoothly through two other points on the extension upwards of Fig. 1, e.g. the points corresponding to B8 and B9.

When we plot by the log-log method, as in Fig. 2, we find once more that there is a long stretch of the curve that is virtually straight, from an area of 1000 acres or less to an area that takes in all Middle America, almost to  $10^9$  acres. The equation of this straight line is approximately

$$S = 40 \sqrt[6]{A} \quad (8)$$

More observational information might modify it somewhat. It is subject to greater uncertainties than the equation for the Eastern deciduous forest.

#### *Comparative Density of Species and Individuals in Neotropical and Nearctic*

In Fig. 1 the curves for the neotropical forest and the eastern deciduous forest have an interesting property. From their origin at about one acre to areas of  $10^5$  acres the neotropical curve lies at just about 2.55 times the height of the other. In other words the neotropical forest contains  $2\frac{1}{2}$  times as many species as an equal area of eastern deciduous forest. For areas greater than  $10^5$  acres the factor is somewhat higher than  $2\frac{1}{2}$ , rising in fact to a little over 4. The reason for this increase is not clear, though it is probably real. One possibility is the presence of larger numbers of endemics, species of relatively local distribution, in the neotropical, but I am not sure that this is sufficient to account for the whole of the increase.

Apart from the increase to  $4\frac{1}{3}$ , the general level in smaller areas of  $2\frac{1}{2}$  times the eastern deciduous forest population carries some interesting implications. I have heard it said that in the neotropical forest, though the avifauna is much richer in species, it is not richer in individuals. If our curves are both correctly drawn, this does not seem possible. For the upper curve looks as though it maintains its relative altitude down to the smallest areas, and this seems to be confirmed by Irby Davis' figures. Even down to a one acre quadrat we seem to have  $2\frac{1}{2}$  times as many species, and we must therefore have  $2\frac{1}{2}$  times as many individuals. (Davis' figures would set the ratio as 4.1 rather than 2.5).

The discrepancy in richness of species appears more spectacular if we express it, not as the number of species on equal areas of neotropical and nearctic terrain, but as the areas of the 2 terrains that contain equal numbers of species. If our curves are correct, we can find 100 species breeding on 200 acres of neotropical landscape, while it takes 200,000 acres of eastern deciduous forest to run up the same total. Two hundred species can be found on 300 square miles of neotropical land, but it takes 70,000 square miles to provide that number in the nearctic.

The discrepancy in number of individuals is also a matter of interest. The boundary between nearctic and neotropical is drawn somewhat differently by different authorities, but according to one delineation the neotropical area in its entirety is some 30% bigger in area than the near-

tic, though some of it is not tropical. However, the great bulk of it lies in warm zones, contrary to the state of affairs in the nearctic. Thus it seems likely that the neotropical may contain  $1.3 \times 2.5 = 3\frac{1}{4}$  times as many individual birds as the nearctic.

At a recent symposium of the A.O.U. at Cape May, New Jersey, the question was raised as to whether the tremendous influx of northern birds into South America, during the northern winter, might not depress the population of neotropical species. But if *all* the birds of the nearctic went south of the Rio Grande for the winter, it would raise the density of birds there by only 30%. In practice a large proportion remain north of the Rio Grande, so the increase in density in the neotropical is probably no more than 10%. Even if it is 20%, it is still much less of a population pressure than results from the fledging of the young of the neotropical species themselves.

On the high plateau of Mexico in Jalisco near Guadalajara, I estimated that probably more than 75% of the (individual) birds were wintering northerners, but at San Blas in Nayarit, at sea level, it seemed likely that less than 25% were from the north. Sr. Miguel del Toro tells me, that in Chiapas, southern Mexico, in the central part of the State, where the cover is deciduous forest, about 50% of the birds in midwinter are from the north, but in the humid regions it falls to 25% or less. Dr. Alexander Skutch writes that in the tropic forest in Costa Rica, at San Isidro del General, there is only one wintering northerner near ground level, the Kentucky Warbler, and this is a quite negligible proportion of the whole; in more open country, where there is some cultivation, the proportion may rise to as much as 20%. He adds that in Honduras and Guatemala the proportion would be considerably higher than this. In Panama it seemed to me that in the forest the proportion of northerners was negligible, but in the swamps and by the sea it might be appreciable, though perhaps not high.

Dr. Alden H. Miller reports on his experience in Columbia:

"particularly in the subtropical forests at the 6,000 foot level, there were three species of North American birds that were quite common right through the winter, namely, the Blackburnian Warbler, Canada Warbler, and the Swainson Thrush. We did have occasional individuals of other species, and at times in the first part of the fall migration rather considerable numbers of Wood Pewees. Through the winter also were a few Acadian Flycatchers.

"I have tried to recall how often I encountered these species, particularly the two abundant warblers. I would say that in the aggregate they do not represent

more than ten per cent of the individuals seen as one works through the subtropical forests. This, as you will recognize, is truly a rough estimate."

Thus in the forest regions of South America proper, the pressure exerted by wintering northerners would seem likely to be trifling.

### *The Probable Lognormal Distribution of Neotropical Birds*

The number of species of birds breeding in the nearctic is about 625. The number in the neotropical is 2500 (de Beaufort 1951). The ratio is 4 to 1. We have estimated that perhaps the number of individuals is in the ratio of  $3\frac{1}{4}$  to 1. It seems to follow that on the average a neotropical species is represented by about as many individuals as is a nearctic one. We have reason to believe that the nearctic population is distributed lognormally among its species, according to the formula

$$N = N_0 e^{-(aR)^2}$$

where  $N_0 = 65$  and  $a = 0.19$  (Preston 1948, p. 281)

It would seem that a first approximation to the distribution of neotropical birds might be given by

$$N = (pN_0)e^{-(aR)^2} \text{ or } N = 4 N_0 e^{-(0.19R)^2}$$

At least it seems likely that the constant "a" is not far from 0.2, a thing we have found to be true for a great many biological populations. This, however, I hope to discuss from another point of view in a later paper.

### *Relative Rates of Evolution in the Neotropical and Eastern Deciduous Forest*

The slope of our curves (Fig. 1) is  $dN/d(\log A) = A \, dN/dA$  and we have seen that for a given value of A this slope is some  $2\frac{1}{2}$  to 4 times as steep in the neotropical forest as it is in the eastern United States. If we can safely draw the analogy between time and space, we should have  $t \, dN/dt$  some  $2\frac{1}{2}$  to 4 times as steep for a given interval of time (t). In other words it suggests that evolution (of birds) proceeds several times as fast in the tropics as in the temperate zone.

This has been suspected by others, not simply for birds but for forest trees and other groups. Indeed it has been suggested that the tropical rainforest is a sort of nursery where species are raised and from which they are sent out to populate the temperate regions. Our argument in this paper does not prove the point, but it suggests it and would be consistent with such a supposition.



## CAUSE AND EFFECT

It is not difficult to concede that the organisms of two continents differ because they have not shared too closely their evolutionary history. This was Darwin's conclusion during the voyage of the Beagle. It is also a point made by Williams. This allocates the cause to time and the effect is found in space. Since space and time are co-existent, it seems philosophically unlikely that cause is limited to one and effect to the other. Indeed we are all aware that the effect, the change of species, is seen in time as well as in space. We might also argue that the driving force of evolution, as of history, arises from the fact that at any one time things are different in one place and in another. Sooner or later, and usually continuously, this produces an interaction which is visible both as an effect in time and as an effect in space. In the absence of variations from place to place, it seems likely, or at least possible, that the tempo of evolution in time would decline to zero.

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