

CONCERNING CERTAIN ECOLOGICAL METHODS OF THE ILLINOIS NATURAL HISTORY SURVEY.

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It gives me great pleasure to appear on a biological program at this place and at this time, especially because it was here that I made my debut in biology 56 years ago—that I began my career as a scientific investigator; and it was here that I devised and began to use in research the methods of inquiry and inference which are the principal subject of my present paper—methods that are now so generally understood and utilized that they may seem to you merely common-place and well-known standards in ecological investigation. Still some of the objects to which they have been applied, some of the forms of use which I shall describe and some of the illustrations which I shall present, are of rather recent origin, and may be suggestive to you of other kinds of problems which they may help to solution.

From the beginning of organized biological survey work in Illinois, back in the seventies of the last century, it has been a part of our program to record our data of observation, so far as possible, in definite numerical terms, substituting ratios and percentages of quantities, numbers, and frequencies for the vague estimates and variable forms of expression then in general use among field biologists. Besides thus giving to our records and averages an unmistakable meaning, such that they might be brought into accurate comparison with others made at other times and places, a compact body of knowledge being thus built up by a uniform process of gradual accumulation, we presently found that by an analysis of our product, it was possible to establish generalizations and frame hypotheses whose validity could be tested by additional data similarly organized, and to disclose relations which would otherwise remain imperceptible. It is the purpose of this brief paper to give examples of the way in which a few of these things have been done.

In our studies of the local or ecological distribution of species, we have made frequent use of frequency ratios, by which is meant the relative frequency of the occurrence of a species in collections made from any given ecological situation as com-

pared with its average frequency in all the collections made over the whole area of its distribution; or this frequency ratio may be defined as the actual frequency of the local occurrence of a species compared with its hypothetical frequency if the same numbers of it were equally distributed everywhere, regardless of ecological situations, in which latter case its frequency ratio would have been invariably one in every situation. Thus when I say that a minnow known as the stone-roller (*Campostoma anomalum*) had in our 105 collections of it a frequency ratio of 3.26 in water with clean bottom, and one of only .31 in water with a bottom of mud, this means that it occurred about three and a fourth times as often in the first situation, and less than one-third as often in the second, as would have been the case if it had been uniformly and equally distributed everywhere.

By the use of this terminology we are able not only to place on record ecological preferences and avoidances of a species as shown by our collections of it, and the comparative strengths of such tendencies of preference and avoidance, but we can readily compare one species with another in these respects, and can make up lists of those agreeing in their ecological preferences and brought together thus in definite societies; and can further learn whether such ecological associations are permanent and continuous, or whether they are subject to temporary dissolution with a change of seasonal conditions, as in the migration period, for example, or in the winter or spring as compared with the summer or fall. This form of record has also the inestimable advantage that it gives, in each case, the numerical basis of the computation, to which additions may be made at any time by any one anywhere, the conclusions indicated being thus tested and revised, or perhaps disproved and discarded as the evidence accumulates.

It is by the use of such data of observation so recorded that evidence has begun to accumulate of the existence of what we may call ecological barriers to the intermingling of closely allied species where there is no other apparent obstacle to their distribution in every direction—barriers which may be as effective for the isolation and establishment of nascent species as are the geographical barriers now generally regarded as indispensable to the permanent differentiation of species arising from a common stock.

An example may be found in the Illinois distribution of three little fishes of the cat-fish family generally known as the

stone-cats. Two of these, the common and the brindle stone-cats, *differ* in their Illinois distribution, the former inhabiting the northern half of the state only, and the latter only its southeastern Wabash drainage, but they *agree* in their absence from ponds and lakes and in their preference for running water with rapid current and clean bottom; while the third species, the tadpole-cat, whose *distribution* covers in Illinois the areas of both the other species, is in strong contrast with them ecologically, occurring in still water with a muddy bottom more frequently than in clean, running streams. In other words, two of these little fishes, which are separate from each other by a difference in distribution, agree in ecological affinities; while the third, which coincides with the others in distribution, avoids them nevertheless by its different ecological preferences. We have other similar cases among the 151 species of Illinois fishes, but this must answer as an illustration.

Of course any number of such cases of complete and permanent separation of allied species by differences of ecological relation would not of themselves prove that this segregation was a true cause or a condition *sine qua non* of their specific differentiation; it would appear only to be a possible part of the cause which must be taken into account in any complete theory of the origin of the species.

Our use of statistical data in a study of the distribution and numbers of the several species of the birds of Illinois has enabled us to analyze the migration movements in a way to measure their development, climax, and decline, to determine their composition in their different stages and to disclose internal features otherwise not distinguishable.

These results are arrived at by a determination of the number of each bird species per square mile in any given district at the beginning, climax, and decline of the migration movement, and these numbers for each species show the changing proportional make-up of the migration wave as it progresses, all expressed numerically and hence proportionally. By this means the migration may be followed in detail from south to north in spring and from north to south in fall.

The culmination and subsequent decline of a migration wave is thus shown to be due in part to the fact that the bird population of an extended area does not merely move northward or southward in a mass at an equal rate, but that the movement begins first at the farther edge of the area of distribution, the most

northerly robins, for example, starting south sooner than the more southerly ones and a temporary congestion of the robin population resulting. By this method of investigation and record, it is also shown that there is often—perhaps always—a concealed internal movement of a seasonal migration in each species classed as a permanent resident in its area, its numbers becoming less dense at the north in winter, and at the south in summer, although the whole area is occupied by it continuously throughout the year. As an example of such a wave of migrants, we may take our data of all birds per square mile in the late winter and spring of northern and central Illinois at four intervals between March 2d and May 29th, 1907. In the *first half* of March in *northern* Illinois, winter still reigned, but there was already a forecast of the change to spring in the fact that while 96.7 per cent of the birds seen were either winter residents or belonged to permanent resident species, 3.3 per cent were summer residents and one-half of one per cent were migrants lately arrived from the south. The number of all birds in northern Illinois in early March was 394 to the square mile; while in central Illinois, March 20, it was 543 to the square mile, in early April it rose to 790, and in late April to May it fell again to 549. The migration wave had thus culminated in central Illinois in early April, when the square mile number was 45 per cent greater than the week before and 44 per cent greater than some three weeks afterwards. This could only mean that the more southerly birds had felt the migration impulse first—that birds were coming in more rapidly from the south than winter residents were leaving for the north, and the crest of the wave was followed by a downward slope in its rear, as the winter residents hastened their departure and dwindling numbers of the latest migrants and summer residents came in.

A closer analysis of these data, showing the square mile numbers of each species at each of the above periods, enables us to follow the shifting composition of each residence class—that is, permanent resident, winter resident, summer resident, and migrant—as the season advances, due to the quicker response of some species of each class to the migration stimulus and the slower response of others.

To illustrate the way in which a partial or concealed seasonal migration movement of a permanent resident species is disclosed and the importance of it is measured numerically, we may take our data for the well-known northern flicker (*Colaptes*

auratus), called also the yellow-hammer or high-hole. Although this is a species classed as a permanent resident throughout the state, being found from our northern to our southern boundaries at all times of the year, our seasonal and sectional averages per square mile nevertheless show a strong *fall* migration movement to southern Illinois and beyond, and a return movement, of course, in *spring*. Thus our winter square mile average of flickers was 14.4 for southern Illinois, 1.7 for central, and 10.28 for northern; but when the spring readjustment began, the southern Illinois number rose from 14.4 to 24 to the square mile and then fell to 9.5 in summer after the migration had passed, bringing the central Illinois summer average up from 1.7 to 22 and the northern Illinois average from 10.28 to 21.

The common crow, also a permanent resident of Illinois, gives another striking example of a similar seasonal movement within our borders. Its numbers to the square mile for the state as a whole averaged, according to our data, 54 in fall, 96 in winter, 19 in spring, and 12 in summer, differences which can only mean that as winter approaches it is driven into Illinois from the north in much greater numbers than those which leave the state for a warmer latitude. An escape from Illinois southward in winter is shown, however, by the fact that we found in 1907 southern Illinois numbers to be 138 to the square mile in fall, and in winter only 16.

In our record for the successive seasons of the square mile numbers of another permanent resident, the prairie horned lark, we have similar evidence of an ebb and flow, a movement to and fro, not only within the state, but in the larger area of the general distribution of the species. The number here is largest in winter—48 to the square mile—due no doubt to the fact that the colder weather northward has driven even this hardy bird to shift, in part, to the warmer latitude of Illinois; but when spring comes on, it begins to flit northward again, our square mile number for the state now dropping to 41. This movement is slow, however, and the lowest stage of its ebb is not reached until summer, when the number falls to 21, rising again in fall through 36 to the 48 for the winter season.

These are very simple applications of the statistical record; but I have found a more complex one in attempting to use the data of our collections to *distinguish ecological associations*, to *determine their limits*, and to *evaluate the strengths* of the ties which hold an assemblage of species together as a more or less

permanent natural community. This I have done by taking note of the frequencies with which the several species inhabiting an area actually occur together in the same collections, then subtracting from these numbers the frequencies of what may be called merely chance joint occurrences—those which we should have had if each species had been scattered at random over its area—and determining the ratio of the *actual* to the *chance* number of joint occurrences, which ratio I have called the coefficient of association. If I have, for example, a thousand collections of fishes made from all kinds of waters in all parts of the state and at all times of the year, and I find on examining and comparing the contents of these collections that one of two species of fishes occurring in them has been taken 150 times and another of the two 100 times, but that both of them have been taken together 50 times in the same collection, the question at once arises, "Is this collocation merely accidental, or does it signify, in part, that the two species are being brought and held together by like preferences for certain features of the environment in which they are living?" The calculus of probabilities gives a ready means of answering this query, and by its use we find that 15 of these 50 joint occurrences may be ascribed to what we commonly call chance and that the remaining 35 must have an ecological explanation. As the 50 actual joint occurrences are $3\frac{1}{3}$ times those attributable to chance, this number is the coefficient of association for these two species. By repeating such comparisons on each pair of species of any area or of any group and tabulating the results, we get the data for a selection of the species most closely allied ecologically, and a measure also of the closeness of the ecological alliance.

I have applied this method also to our ornithological observations, using the species and numbers of birds seen on a strip 150 feet wide in crossing a single field or other unit of area as the equivalent of a collection, and in this way distinguishing and measuring the ecological affinities of the bird population of any given area or situation in any part of the state for a recognition of definite associations among them and the relative strengths of the bonds by which all such associations are held together. But many species are members of several ecological communities and we need to know with which of these communities they are most closely identified and what are the comparative degrees of such identification; and furthermore species endowed, like fishes and birds, with powers of rapid and long-con-

tinued locomotion, may change their social relations with changes of season, food supply, and other features of their environment, and a means is needed of following them statistically in these changes. Finally, as I have said elsewhere, "A knowledge of definitely circumscribed, or merely distinct, local association does not by any means exhaust the subject of associate relations, for the animals of a region can not be wholly divided up into such definite societies, and such society groups as can be clearly recognized rarely have any precise boundaries. For a full knowledge of the intricate web of the relations to their physical environment, and through that to each other, of the animals of any composite area, it is necessary that the entire assemblage of the inhabitants of that area should be studied as a compound unit," and it is in part with a view to their use in such an inquiry that the foregoing methods have been developed, and they are now being so used by our state natural history survey.