THE AUK:

A QUARTERLY JOURNAL OF

ORNITHOLOGY.

VOL. XXV. APRIL, 1908. No. 2.

THE ECOLOGICAL SUCCESSION OF BIRDS.

BY CHARLES C. ADAMS.

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"Of all truths relating to phenomena, the most valuable to us are those which relate to their order of succession. On a knowledge of these is founded every reasonable anticipation of future facts, and whatever power we possess of influencing those facts to our advantage."— JOHN STUART MILL.

"Indeed, some geologists seem to take pride in lack of knowledge of principles and of their failure to explain the facts observed in the terms of

the elementary sciences. I have heard a man say: 'I observe the facts as I find them, unprejudiced by any theory.' I regard this statement as not only condemning the work of the man, but the position as an impossible one. . . . The geologist must select the facts which he regards of sufficient note to record and describe. But such selection implies theories of their importance and significance. In a given case the problem is therefore reduced to selecting the facts for record, with a broad and deep comprehension of the principles involved, a definite understanding of the rules of the game, an appreciation of what is probable and what is not probable; or else making mere random observations. All agree that the latter alternative is worse than useless, and therefore the only training which can make a geologist safe, even in his observations, is to equip him with such a knowledge of the principles concerned as will make his observations of value."— PRESIDENT C. R. VAN HISE.

I. INTRODUCTION.

Almost every observer of animals has noted that certain kinds of birds are usually found associated in certain conditions, as, for example particular species of sandpipers and plovers upon the sandy beach, or the Meadowlark and Dickcissel upon certain prairies; but this is rarely considered a subject worthy of serious scientific study. To discuss the significance and value of such ecological study and suggest phases for investigation is the object of this paper. By the ecological distribution of birds is meant that correlation between environmental conditions and the occurrence and association of certain species of birds. In such study special attention must be devoted to the places of breeding; nevertheless the associations of birds at all seasons of the year are of importance. It is not the isolated occurrence of these species, but their relative abundance, the association of certain species, and their persistent occurrence in such conditions which is significant. In the literature of ornithology there is a vast amount of isolated data bearing on this subject, but very little of it has been organized and systematically studied.

When once the facts and general ecological relations have been determined, so that the representative bird associations or societies of given localities have been correlated with their proper environments, it will then be possible to determine how one society becomes transformed into another, whether this is due primarily to other birds

or to other environmental influences. A knowledge of the succession of bird societies and of the laws of change will not only lead to new ideas as to the influence of the environment, but will also have a marked influence upon the practical field studies of the bird student. It should lead to a more intelligent understanding of the relation of birds to the world about them, or even better, to the world of which they form a part.

Attention should further be directed to the fact that simply the occurrence of the bird in a definite habitat is not by any means the sole aim of such work. The influence of the environment should be studied in its bearing upon all phases of bird life. Not only should the most favorable habitat or optimum be recognized, but also the influence of the less favorable conditions; thus the nesting site, composition of the nest material, food, abundance, feeding grounds, migrating habits and all like relations are needed for an adequate and exhaustive study of the ecological distribution and succession of birds.

It is therefore not surprising that such requirements will be difficult to meet because the facts themselves are difficult to secure. Then there are further difficulties which are due to the limitations of the student himself, and are psychological in their nature. As examples of this class of difficulties two may be cited, because they are of frequent occurrence in all kinds of scientific work and not by any means confined to the study of birds. For, contrary to our youthful ideas, naturalists have the same limitations as humanity in general! We may divide naturalists into two classes, depending upon their primary type of mind. First, those who tend to see only the infinite detail of isolated facts and observations. This type of mind is particularly impressed with the multiplicity and variety in nature, and is one to which a general statement is almost a cause of irritation because there are usually exceptions to any general statement. The constructive imagination seems feebly developed in this type. To this class belong many extremely valuable and useful students, because of the data which they, often with extreme conscientiousness, collect. They are collectors of facts rather than students of relations. To the second class belongs that type of mind whose primary interest is in generalizations, principles, relations, and which tends to neglect isolated facts and

observations. The constructive imagination is liable to be developed in this type. This includes many extremely valuable and useful students on account of their tendency to condense, sift and formulate great masses of isolated facts. They are students of ideas and relations rather than collectors of "facts."

Each class, especially the well-marked types and extremes, often finds it difficult or impossible to understand the point of view of the other class. This frequently leads to misunderstandings and often to mutual contempt. Cope and Marsh clearly illustrate these two types of minds among our American naturalists.

By this time some may wonder why this subject has been introduced. It has been with a definite purpose, because frequently these opposed points of view cause delays in the development of many subjects. Thus a forewarning to students of bird ecology may produce good results if the individual student makes a conscious effort to counterbalance such deficiencies as go with his particular type of mind. In the past, details have tended to produce confusion through the neglect of general ideas. It is rarely that a word of warning on this subject is out of place, because the balanced "golden mean" investigator is never too abundant. The quotations at the head of this article have an immediate bearing upon the subject at this point.

Not only is habitat preference, the association of avian species, their succession, and the laws expressing these relations of much interest, but they are of much importance scientifically as well as in a practical way. It is therefore desirable that naturalists realize the necessity of understanding the "rules of the game" if the true relations of birds are to be studied to the best advantage. No adequate substitute has yet been devised to replace a grasp of general principles.

Throughout this paper emphasis is placed on the *definiteness* of the dominant major environmental influences and complexes because the irregular features have apparently received undue emphasis and have retarded the recognition of certain important definite relations.

II. REPRESENTATIVE LITERATURE ON HABITATS AND SUCCESSION.

1. *Habitat Preference.* The American literature on habitat preference and succession, as a subject of special investigation, is very limited. By succession is meant the change or replacement at a given place of one or several species (an association) by others; as when a swamp is invaded by a dune and the representative swamp birds are replaced by those of the dune; or even again when the dune becomes fixed by vegetation and is inhabited by still another association of bird life. This is a much neglected subject; however, isolated observations on habitats are abundant in the biographies of the various species. The fragmentary character of these biographies tends to make them composite and they lose what peculiarities they may have which are due to a response on the part of the bird to its particular conditions of life. These unfortunate limitations clearly show that here is an extensive field worthy of careful investigation. The work already done will be a useful guide in many cases, but the student who wishes to develop this subject must turn to the fields and forests rather than to the literature, both for his inspiration and his data.

Perhaps a further word should be added concerning the limitations of the *composite* life-history method, as this will aid in making clear the kind of work needed in the future. This composite or generalized method of describing habitats and life histories and the response of birds to them, tends to lay undue emphasis upon the *average* conditions of life and habits, and tends to neglect those *detailed responses* to the environment which reflect the laws of local influence. These results are similar to those produced by systematic students who are "lumpers" and who do not recognize local races or varieties. Thus a nest may be built upon the ground at the base of a shrub or bunch of grass, or in the brush, but what conditions determine such sites? In a dry meadow a Song Sparrow may build directly upon the ground, but in a swamp, in order to have a dry nesting site, it builds in a willow shrub. In many cases the causes of these differences will be difficult to determine, but in others it is a relatively simple question for any one familiar with the species to solve. There are also geographic variations of habits

as well as those of habitats just cited, and for this reason it is necessary not to confuse such variations with those confined to some restricted area. These local and geographic relations are very intimately related, but they are subjects which can only be worked out in detail when local studies give proper attention to local environmental responses.

In the following account of the literature no attempt is made at completeness, but the papers cited are believed to be representative. These papers will help to give some idea of the kind of observations and records already made, and will be suggestive as to future work. Mention will first be made of the literature on habitat preference, and then of that on succession.

By far the best discussion we have found on habitat preference of the birds of a given region is that by Townsend ('05) on Essex County, Massachusetts. The primary avian environments are described, the representative birds listed, and their preferred habitats are briefly discussed. Thus, the ocean and its birds, the sand beach and its birds, the sand dunes and their birds, the salt marshes and their birds, and the fresh marshes and their birds, give a general idea of the subjects treated. Regarding the birds of the sand beaches, he remarks: "Among the Plover, the Black-bellied, Semipalmated, and Piping Plovers are above all birds of the beach, although the first two are occasionally found in the marshes, while the last-named rarely strays from the beach and the adjoining sand dunes. The Golden Plover, although at times found on the wet sands, is much more likely to hunt for food on the dry sands above the highest tides, or still farther inland, while the Killdeer generally avoids the beach altogether, preferring the fields" (p. 21). And regarding the birds of the sand dunes he remarks: "Savanna Sparrows nest in numbers at the foot of clumps of tall beach grass throughout the dunes, and on the edges of the tidal inlets from the marsh. The nests of the Red-winged Blackbirds and the Bronzed Grackles are abundant in the bogs and groves of the birches. The Crow, in the absence of tall trees, builds perforce in the stunted pines and birches, at times only ten or twelve feet from the ground" (p. 34). In the case of the Crow, note that he records the response to the dune environment.

While Townsend recognizes changes in the environment, as in the

dunes and beach (pp. 21, 30), yet he does not see their relation to the bird life in the definite way in which he sees their habitat preferences, nor does he appear to clearly recognize the fundamental relation of association within the breeding habitat. To him the environment is static. However an excellent feature of his work is the record of seasonal changes in the bird life of the various habitats. In this connection attention should be called to certain papers which will greatly aid in the study of the dynamics or changing environmental factors which influence sea or lake shores bordered by dunes and swamps; conditions represented on the Massachusetts coast. Gilbert ('85) has discussed the general principles and topographic features of lake shores; and Gulliver ('99) the shore line of the sea. But in addition to these physiographic forces, the vegetation also has a dominating influence upon bird life. For general principles relating to this subject Cowles ('01) should be consulted for his discussion of the vegetation of inland shores and dunes, and Ganong ('03 and '06) for his treatment of the Atlantic coastal conditions. These authors discuss the succession of the vegetation, a factor of the utmost importance in the study of avian succession.

While considering Townsend's results, it may be well to outline briefly a general succession of bird life along the shore as indicated by his records. It is evident from the map accompanying his volume that the currents and waves are constantly modifying the coast line and forming spits, bars and islands; and that the barrier beach area is increasing, and thus tending to become continuous at the expense of some of the ocean habitat. As the continuity of the beach develops, the area of swamp land behind it tends to increase and thus to further restrict the open water and increase the swamp habitat. The beach sands, once free from the waves or ground water, are caught up by the winds to form dunes, and may migrate into the swamps and thus transform them. Thus with the extension of the beach the sea birds are replaced in dominance by the shore birds, and a succession is produced.

In a similar manner the dunes encroach upon the swamp, and swamp birds are succeeded by those of the dunes. As the wandering dunes become anchored by vegetation and forests grow upon them, still other birds will invade them. Thus all stages may be expected,

from ocean to beach birds, onward to those characteristic of wandering and fixed forested dunes. These relations are outlined simply to indicate the problem and its causes, which need detailed investigation.

In Michigan a few habitat studies have been made. One in the Porcupine Mountains, on the south shore of Lake Superior, and another on Isle Royale. Both are by McCreary; the paper on the latter area is unpublished. The summer birds of the Porcupine Mountains are listed (McCreary '06) by selected localities and the habitat preferences are discussed as follows: water birds, birds frequenting the shores and banks of streams, birds frequenting grassy meadows and alders, birds frequenting tamarack and cedar swamps, birds frequenting hemlocks and maples, and birds frequenting the cliff and mountain top. In its emphasis upon habitat preference this paper is the only one so far seen which at all approaches Townsend's discussion of this subject. McCreary's work was done without a knowledge of Townsend's.

In southeastern Michigan, Brown ('06) made a locality study and outlines the habitats as follows: birds found in orchards, birds of the open woods, birds of the open fields, birds of the thicket, and birds of the marshes and river. Brown's paper is intermediate in character between the preceding papers and those of an economic nature, to be mentioned later, because the area studied has been so much influenced by man.

There are a few papers which, although primarily faunistic or geographic, contain habitat data. Such, for example, is Ridgway's ('74) discussion of the birds of the Wabash Valley and ('89) the birds of the Illinois prairie (pp. 13–16). An exceptionally good paper of this character on the Louisiana birds is by Beyer, Allison and Kopman ('06), although its aim and method of treatment differs from that of Townsend. The bird life is, however, closely correlated with the vegetation and the physical conditions of the State.

The papers previously mentioned have been written from a regional standpoint. The study however of all the various conditions frequented by a given species or some natural group is also an important and neglected method of ecological study which possesses certain important advantages. As an illustration of this method may be mentioned Palmer's ('00) study of the Maryland

Yellow-throat. He has shown that different varieties have different habitat preferences. Jacobs ('04) has given us an interesting habitat study of a single species in Pennsylvania, the Golden-winged Warbler.

Let us now turn to another class of habitat studies, those which through man's influence throw only a subordinate light upon "natural" habitats and succession, and are primarily of economic importance but contain valuable habitat data.

An interesting and rather unique paper belonging to this class, based on observations in Southeastern Michigan, is by Watkins ('00). It is entitled 'Michigan Birds that Nest in Open Meadows.' A few of his statements explain his point of view: "To make more plain the limit and scope of this treatise, which, of necessity must be longer than I hoped, I will include in my list only such species as I have found nesting upon the ground in the open fields and meadows, excluding those found nesting upon the boundary fences or ground; also those nesting in the open marsh lands which are undrained and boggy to the extent of being unfit for hay or pasture" (p. 67). The paper contains numerous notes on the habitat preference and variations in these traits.

By far the most comprehensive and thorough study of any limited farm area is that by Judd ('02) of a farm in Maryland. In this paper habitat preferences are clearly recognized, and discussed rather fully (pp. 12–20). The birds are associated thus:—birds that nest in open fields, birds that depend on covers, birds of less limited distribution (consists largely of remarks on haunts), and birds of varied distribution. His last two sections are rather miscellaneous in character and show that the principles of classification for habitats were not clearly defined in his own mind.

The only other paper discussing habitat preference in detail is also the latest upon the subject, and is by Forbes ('07). This is a preliminary report on a bird census across the corn belt of Central Illinois in the early autumn; a study of the feeding grounds and preferences as influenced by the dominant crops of the area traversed, corn, pasture, and stubble. By means of this census, the habitat preferences for different crops and the association of species in them is statistically determined. The paper is particularly suggestive for its bearing on the subject of dominance; however,

the suggested method of study has even greater significance when applied during the breeding season. Doubtless opinions will vary as to the validity of the method as applied by Forbes, even by those who would approve of it for the detailed study of a limited area, or a breeding habitat. For large areas some coöperative method may be necessary.

2. *Succession.* Turning now to the literature on succession, it is found to be extremely limited in amount. So far as known to the writer, only two American authors seem to have realized the existence of succession. In his discussion of the biotic succession in the Porcupine Mountains of Michigan, Ruthven ('06) clearly included the birds, although they did not receive separate treatment, and might for this reason be overlooked. His position is clearly stated (p. 43) as follows: "Owing to the dependence of forms of life on their environment, biotic changes are necessarily closely related to environmental changes. These biotic changes may occur in two ways; the forms must either be able to respond to the new conditions, or be supplemented by other forms. That they tend to become adjusted cannot be questioned, but in many cases at least, this adjustment lags behind the changing conditions, and the forms are replaced by others from adjacent habitats which are adjusted to the conditions toward which the particular habitat is changing, thus bringing about a succession of societies." In speaking of the biota of the hard-wood forest he further says: "This region has been reserved for the last, for the conditions are evidently those toward which the other habitats tend to be changed under the present conditions. . . . This society thus represents the climax society of the region. It consists of the forms that are adapted to or associated with the conditions which prevail in this region in the last stages of the mutual adjustment of all the environmental processes. As the processes become adjusted to one another, the habitat of the climax society is increased at the expense of the other habitats, and the associated biota tends to become of general geographic extent in the region."

The only other paper discussing avian succession is that by Frothingham ('06), and this is not a "natural" succession but one influenced primarily by man. He clearly expresses a bird succession correlated with the reforestation of burned lands. The area

studied is the Michigan forest reserve on Higgins Lake. The region was originally covered with White and Norway pine, but repeated fires first kill off the pines, later the oak and maple; and finally the dominant vegetation is sedge, sweet fern, huckleberry and prairie willow. With the fire protection afforded by the reserve, Frothingham anticipates a reversal of the above succession of destruction, and further remarks: "With the types of vegetation which mark the different stages of the plant succession just described there seem to be correlated certain definite bird forms. These forms are for the most part such as frequent observations in northern Michigan have identified as generally characteristic of the respective environments." This is followed by lists of birds characteristic of different kinds of vegetation. While these lists do not correlate perfectly with the implied succession, yet the general statement of the problem is clearly expressed.

The burning of forests has long been known to change the character of the vegetation and fauna of areas, but this is often referred to as the change of a "life zone." Thus Merriam ('99, p. 47) states that a fire in the Canadian zone on Mt. Shasta is followed by the Transition zone and remarks: "But in the meantime a new growth of Shasta firs has started, and in ten or twenty years is likely to overtop and drown out the Transition zone species, enabling the Canadian zone to reclaim the burn. . . . But on the steeper slopes, especially rock slopes, if the vegetable layer is burned off, the (lower) zone which creeps up to replace the (higher) one destroyed becomes permanent or nearly so. . . . Deforestation of an area therefore tends to lower its zone position." Birds are not mentioned in this discussion nor the relation of "zones" to the general problem of succession. Such "zones" are thus only particular phases of succession.

It is thus seen from the above outline of literature that habitat preferences have been outlined for a few widely separated localities and for some agricultural conditions, but there has been no comprehensive discussion of the problems of habitats and succession, even in a preliminary manner, either from a scientific or economic standpoint. This fact seems rather remarkable in view of the great utility of a knowledge of the general principles underlying economic practice. There are, however, certain phases of biotic

succession which have been discussed by a few authors. These subjects have either been discussed in a very general manner or are detailed discussions of special regions or groups of plants and animals. For this reason, perhaps, their bearing upon other groups than those specifically mentioned are very likely to be overlooked by those who take little interest in any subject or discussion which does not specifically mention their specialty or locality. This phase is mentioned in order to show that while avian successions have been considerably neglected, advances have been made elsewhere, by means of which some general principles appear to have been fairly well established. This is particularly true of plant succession, as shown by the writings of Cowles ('01), and in considerable detail by Clements ('05). The discussion by Clements will be particularly valuable to the student of avian succession.

III. THE MAJOR AVIAN ENVIRONMENTS.

As has been seen in the preceding review of the literature on haunts, no comprehensive discussion has been given of the environmental influences or ecological distribution of (extra-tropical) North American birds. Various authors have discussed their geographic distribution, and certain geographic variations have been referred to certain environmental influences, but a general ecologic treatment, as contrasted with a primarily faunistic one, has not been made. This is remarkable when we recall the fact that the collections of North American birds are, considering the large area concerned, the best in the world both as to quality and as to quantity (Stejneger, '03). This means that there have been many trained collectors; but what has become of the notes and observations on the environments and conditions of life of these birds, which must necessarily have been known to successful collectors? Part of these observations have been published, and perhaps no one is to blame because more have not; but the point of significance is that we have, in fact, hardly made a beginning in the careful detailed study of the bird environment and its development as a distinct field of study. In common with the remainder of the North American biota, several general principles are known, but they do not appear to be current among ornithologists.

The following discussion and suggestions on the larger environmental units attempt only an outline of certain phases of the problem, in order to call attention to certain principles which seem useful as a background for the intelligent study of bird habitats and succession. From such a standpoint as this, the *dominant* influences of given areas and environments are of particular interest and of fundamental value. By focussing attention upon the importance of recognizing these dominant environmental influences, we may hope to escape some of the confusion which appals those who are keenly impressed with the chaos and complexity of the problem. These dominant factors are usually not single isolated forces, but resultants of several or many influences. Thus, as in the case of the vegetation, it is not one factor, but a complex, which influences different birds in different ways. Nevertheless there is what may be called a mass or dominant effect.

A major habitat unit may be considered as a combination of conditions which are dominant in a certain area. *The very dominance means that a relatively limited number of forces or complexes are operative.* With departure from such a center of influence the dominance changes, as other influences are encountered and other dominants are established.

When we consider that certain ecological groups of birds are world-wide in their environmental relations, it becomes evident that such characters are of fundamental importance. Thus water birds may occur in any part of the world where water is a dominant environmental factor. This is not a simple ecological group of birds, but one of the greater units of association which may be subdivided into many minor classes; as those which frequent the sea, and others the inland bodies of water. The shore birds form another natural ecological group, and also the inland birds a third. There may thus be considered to be three primary ecological groups of birds which are closely correlated with definite and dominant environmental influences; thus:—

1. Water birds.
   Those frequenting the sea and the adjacent rocks on which they nest, and inland waters.
2. Shore and Marsh birds.
   Those frequenting shores of all kinds, seas, lakes, swamps and rivers.

3. Inland birds.
   Those frequenting deserts, grass lands and forests.

Of course these ecological classes are not sharply defined, and yet they are so distinct that they can be easily recognized. It should be noted that the above groups are closely correlated with certain dominant physical features of the earth — the sea, the shore and the inland environments.

The relative abundance and dominance of these classes of birds will be determined largely by the dominance of such physical conditions as most distinctly favor a particular ecological group. Thus at sea the water birds are dominant; on shore, the shore birds; and inland, still other kinds. The linear character of the shore habitat and the adjacent breeding grounds gives it a rather unique character, as the two other habitats occupy large expanses. However, the swampy, somewhat shore-like conditions of the far north most nearly approach, for the shore birds, the expansive character so usual for water bodies and inland areas.

In the present discussion the emphasis placed upon the inland vegetation does not mean that the dominance of other influences is not recognized, but simply that it makes a convenient and fairly reliable *index to many other environmental influences,* as, for example, the climate and topography. A further important advantage of the plant index is that the science of plant ecology and many of its general principles and methods are applicable to birds. A general knowledge of plant ecology is therefore becoming one of the most valuable tools in the hands of the field ornithologist. Every field naturalist has observed the general correlation of certain birds with certain kinds of vegetation. This relation is clearly expressed by Ridgway ('89, p. 8) as follows: "There is probably no better index or key to the distribution of birds in any country than that afforded by the character of the vegetation; should this vary essentially within a given area, a corresponding difference in the bird-life is a certainty." This phase of the subject clearly illustrates the oft-repeated experience of naturalists that in order to thoroughly understand one subject — perhaps the favorite one — it becomes necessary to study another, or even several. Thus in order to know the bird life of a region it has become necessary to study the ecological relations of its vegetation.

The study of ecological plant geography is an extensive one, but many of the details, so important to the botanist, are of much less concern to the ornithologist, who needs primarily to know the major plant associations or formations and their successional relations. This implies ability to recognize dominance among plant species and the general method of transformation from the dominance of one to that of another.

By a plant formation is meant that association of species (or plant society) which is correlated with those conditions which tend to prevail over a large geographic area in the last stages of mutual adjustment of all environmental and biotic processes. Such an association or formation tends to occupy such an area to the exclusion of all others, and is thus a climax society.

But absolute dominance of a formation does not occur, because local conditions break the monotony where streams, water basins, bare rock, and similar influences may interrupt the desert, grassland or forest, and produce minor habitats and associations of both plants and animals.

It is not my purpose to discuss in detail the various plant formations of (extra-tropical) North America, but to outline those which are of evident ornithological utility. The following may be recognized provisionally:—

1. The Arid Deserts of Southwestern U. S. and the Mexican Plateau.
2. The Grasslands of the Great Plains.
3. The Deciduous Hardwood Forest of Southeastern U. S.
4. The Coniferous Forests of Eastern Canada.
5. The Giant Conifer Forest of the Pacific Coast and the Rocky Mountains.
6. The Barren Grounds or Cold Desert.
7. The Alpine Deserts.

A mere inspection of this list of avian and vegetational formations shows that the recognition of these large environments is relatively simple. It is also seen that they represent fairly definite physical or environmental complexes of such fundamental importance that there can be no doubt as to their general validity. As to the relative value, influence, boundaries, and the dynamic relations of these formations, much is already known, but not as an organized body of facts and principles. It will also be noted that these regions do

not closely correspond with current faunal areas, although there is a very close correlation in some cases. An avian formation may, in general terms, be considered the analogue of a vegetational formation, although this does not imply that they necessarily have the same boundaries.

As the literature treating of the vegetation of these areas is extensive and scattered, a few papers will be cited as an index to others:—

1. Arid Deserts; Bray, '06; Coville and MacDougal, '03.
2. Grasslands or Plains; Clements, '05; Pound and Clements, '00.
3. Southeastern Hardwoods; Cowles, '01; Harper, '06; Transeau, '05.
4. Eastern Canadian Conifers; Whitford, '01; Transeau, '03, '05–'06; Ganong, '03, '06; Harvey, '03.
5. Rocky Mountain and Pacific Conifers; Whitford, '05; Gray and Hooker, '81; Piper, '06; Young, '07.
6. Alpine; Merriam, '90, '99; Coville, '93; Fernald, '07.

These environmental unit areas as found to-day, are the result of many successions which, in some cases at least, reach rather far back into the past. This is because some occupy ancient land areas, such as much of the Southeastern Hardwood area. On the other hand, some occupy relatively new regions, that is, at least with regard to the dominant factors now in control, as in the glaciated part of North America and on the Coastal Plain. So far as the present is concerned such relations clearly show that these areas are only the end results of extensive past changes or successions which represent the terminal branches and cross sections of development. It is to the study of such regions and associations that we must turn for the fundamental organization or associational relations of the various elements which compose not only the environments but also the associations of animals.

In order to make as definite as possible the *structural and ecological characteristics* of these formations, certain general relations are here formulated. Throughout this paper it should be remembered that the individual birds and associations of given areas form the units of comparison. Such a distinction is necessary because many species show considerable geographic variation in habits and in the habitats frequented. The writer clearly recognizes the risks and difficulties of such an attempt. They are deliberately put in their present form to *invite criticism and qualification* from

field workers. It is desirable to know the validity of these formations, their internal ecological relations and dynamic tendencies, their relation to dominant environmental influences, etc. A complete list is not attempted, and some of the statements may be only fragments of larger generalizations; but it is just such relations as these which will develop if the entire subject is considered critically and synthetically. Some of the leading characteristics of these larger environmental units and their avian *formations* may be briefly outlined as follows:—

1. The dominance of a limited number of physical conditions or complexes, as climate, topography, vegetation, animals, etc., in a given area produces the primary environmental units and formations.

2. Secondary environmental dominance is shown by a secondary avian association. Thus in the Northeastern biotic center there is a secondary dominance due to water basins in the forest area.

3. A formation or climax society is composed of a relatively (and usually absolutely) limited number of species which are dominant in a given environment of geographic extent. Such dominance, in general, implies extensive range, relative abundance, and ability to indefinitely succeed or perpetuate itself under given conditions.

4. Where dominance obtains, avian variety is limited so that the greatest diversity occurs where local influences prevail, and at the margins of the formation.

5. Correlated environmental and biotic dominance produces what may be considered a *biotic base*, stratum, or optimum, from which departures may be considered less favorable. This is a relative equilibrium, resulting from complete environmental and biotic adjustment, under given conditions.

6. In each formation there is a normal inter-adjustment of the avian species and individuals, in addition to the adjustment with the dominant physical environment. The former is dominated by their structure, habits, and instincts or behavior; hence the colonial breeding or spacing, migration, etc.

7. Each large environmental area or formation tends to have a full complement or set of species, of diverse but supplementary ecological character, such as water, shore or inland birds. One set is likely to be dominant.

8. Relative stability in an association is correlated with the climax dominance, and generally with extreme and slowly changing local influences. Fluctuation is correlated with intermediate conditions.

9. Diversified associations and isolation are greatest with imperfect dominance, but dominance itself produces isolation of the climax association. This diversification produces associations surrounded by others and hence their isolation.

10. The taxonomic elements in different formations vary much, but there are close analogies in the kinds of taxonomic and ecological groups in different formations,— as the Mniotiltidæ of the New are represented by the Sylviidæ of the Old World. *Cf.* Osborn, '02. Le Conte, '50, p. 239*. *Cf.* No. 7.

11. The roughly zonal arrangement of societies about the climax society (= formation) or the environmental optimum, is primarily due either to local reversals, the lagging influence of local or neutral conditions, or to the influence of adjacent formations. This is a result of the retardation of the complete cycle of successions.

12. The primary environmental conditions tend to encroach upon all others. The local conditions thus tend to become transformed in the direction of the dominant environment and to be appropriated by it. The corresponding avian associations are thus given a definite dynamic trend.

13. The mobility of birds during the breeding season is very generally overestimated. The presence of the nest and young renders them for a time relatively sedentary. There are many causes influencing this, such as other individuals, proximity of food for young, homing, instinct etc.

IV. MINOR AVIAN ENVIRONMENTS AND THEIR ASSOCIATIONS.

We have seen that the larger geographic environments or formations are characterized by definite conditions and associations, and at the same time that even throughout these favorable regions the climax association is not distributed with absolute uniformity

because of local variations in the physical features, such as vegetation, water basins, streams, mountains, etc. For the student of local bird life the real work begins when one attempts to examine into the causes and influences exerted by these conditions which break the monotony of the formation and make possible a diversified avifauna. But birds do not always respond as closely to slight local influences as does the vegetation, and for this reason one must learn by experience just what size of units must be used. Thus in the forest a few wind-falls will attract but little attention, but a burn of a few acres will have a noticeable influence in harboring those species of birds which frequent openings; while swifts and swallows ignore many local influences which dominate other species.

It should also be noted that whenever possible it is of distinct advantage to examine all habitats in their original state, uninfluenced by man.

Instead of discussing the leading features of local conditions and their societies or associations in detail, only an outline of them will be given, and that in a form to facilitate use and revision.

1. Minor environments are primarily dependent upon local conditions, and are thus in a sense correspondingly independent of the dominant forces of the region. This is, of course, a relative condition.

2. Minor environments are, as a rule, relatively limited in area. In general their limited area favors their short duration, but age is primarily a result of the rate of change.

3. Marked isolation, even when of extensive linear extent,— as a shore line, along a stream, or an elongate rocky ridge,— is also characteristic of minor environments.

4. Minor environments tend to become encroached upon by the dominant regional influences and ultimately to become extinct. The succession of societies in local habitats is a declining one, while that of the geographic or climax habitat is an increasing and ascending one.

5. Local habitats produce most of the variety within the dominant area, and make possible a diversified avifauna. The structural differentiation within a formation (zones, etc.) is thus largely, in addition to variations in the formation itself, of local origin.

6. Local associations or societies, in general, furnish the essen-

tial clues as to the earlier successions which have attended the evolution or development of regional dominance. The variations in these are due both to the kind of life and to the influence of adjacent associations and centers of dominance.

7. Marginal societies are particularly liable to variation in composition, due to the combined influences of adjacent formations or centers of dominance as well as to local conditions.

8. Comparative studies of local habitats will form the most general and practical guide in the determination of the successions in the formation.

9. Local habitats and societies, in common with the larger environmental complexes, are characterized by the dominance of few physical and biotic factors, and by a limited number of species.

V. AVIAN SUCCESSION.

1. *General Remarks.* Since the breeding grounds are of fundamental importance in the ecology of birds, the study of them in such situations furnishes the greatest source of insight into their life relations. By an avian association, formation or society is meant different combinations of species which *regularly occur together in the same breeding habitat* or area. These breeding grounds must be considered broadly, and include not only the nesting site but also the feeding grounds, even when they are physically very different, because ecologically these conditions form a unit during the breeding season.

It is well known that when a given set of physical conditions are dominant, as in a dense conifer forest, a swamp or an extensive orchard, relatively few individuals and kinds of breeding birds are characteristic of such conditions, except in the case of those nesting in colonies. The field relations of these colonial and isolated breeders are quite different. It is also of importance to recall that abundance is a relative term, with a very different meaning in the case of seed-eating and predaceous species.

Bearing in mind these conditions, bird succession means a change from the dominance of certain species or associations to that of others. Thus in the beginning a slight change in abundance of a

species may be noted, with a corresponding decrease in another; and this proportion may continue to change until the intruder becomes dominant and the rival form may disappear entirely. This process of change, as a rule, is not limited to a single species, but usually involves several or all of the members of the association, as when a dune invades a swamp and the swamp birds are completely replaced by those frequenting the sand dunes.

2. *Succession on Isle Royale.* With these preliminary considerations in mind, we will turn to the ecological succession of bird life upon Isle Royale, Lake Superior. The field work upon the island was carried on by a party from the University Museum of the University of Michigan, under the direction of the writer. Aside from succession, the general ecological relations of the birds were studied by Otto McCreary and Max M. Peet, and elsewhere detailed descriptions of the region and detailed notes will be published. The writer has based his main records of habitat preference upon their work. For this outline of succession only the primary features of the location need be given.

In the present treatment an attempt will be made to follow the genetic succession; at least in its broader outlines. Various qualifications and reservations have been made, and others will follow, so it is hoped that no confusion will be produced by this method of treatment.

Geographically, Isle Royale, Michigan, is an island in Lake Superior, near the North Shore, not far from Port Arthur, Ontario. The *topography* forms a part of an ancient peneplain of moderate relief, glaciated and with an abundance of elongated low ridges and valleys with numerous water basins. The *soil,* which is locally absent, is generally humic or mixed in character, bordering and in the depressions; but is mineral, stony and residual elsewhere. The combined shore and beaches are extensive, largely stony and gravelly, and contain but little sand; much of the shore line is rocky and precipitous; many outlying islands. *Vegetation,* herbaceous in shallow inland waters and as a ground cover except where the shade is too dense, and upon rocks; shrubs on protected beaches, in more open places in the forest and in burns; the forest consists of Tamarack, Black Spruce and Arbor Vitæ in bogs; and elsewhere in mesophytic conditions of Balsam Fir, Arbor Vitæ,

White and Yellow Birch, and rarely Sugar Maple. Upon the dry ridges, Jack Pine; and in burned areas, Aspen and Paper Birch. *Climate,* seasonal changes very pronounced; winters very long and cold, and summers short and cool; a relative humidity of about 80% in December and of about 70% in July (*cf.* Johnson, '07); a mean temperature for January of 7.97° F.; and for July, 62.24° F. (Port Arthur data). Early, deep snows. *Predaceous animals,* as the Lynx, Marten, weasels, Red Squirrel and bats are directly in competition with the birds for food, or prey upon the birds.

The above environmental factors are dominant features and give us a general picture of the conditions, largely in terms of common experience. In the life of the birds, however, a complete reassortment and change of intensity in these factors occurs when they are combined as habitats. The surrounding lake, the numerous bays, small lakes and ponds compose the aquatic habitat and make it a characteristic feature. The very irregular and extensive shore line and limited beach area characterize the coastal border, while inland, excepting the main bodies of the few larger lakes, the encroachment of the bog vegetation upon the shores is such as to prevent an extensive development of sandy open beaches. The above mentioned habitats are open unforested areas; the remainder of the island, with the exceptions of the bare rocky ridges, the clearings and burned over areas, are forested. Very extensive swamp forests abound in the elongate valleys and the borders of the water bodies, and are composed of Tamarack, Black Spruce and Arbor Vitæ. The mesophytic forest occurs on drained areas and is characterized by Balsam Fir, White Spruce and Paper Birch; the burned areas by second growths of aspens and Paper Birch. Then there are also influences which are exerted upon the bird life in general, as for example, migration. In this case, undoubtedly both external conditions and the habits and the behavior must be correlated. Another general and dominant influence should be reiterated here, and that is that all open areas tend to become invaded with vegetation and finally forested, whether they are lakes, ponds, bogs, rock openings on the ridges, burns or clearings. The mesophytic Balsam-spruce forest tends to monopolize *all* habitats, and gives a definiteness to all succession upon the island.

From a genetic standpoint the past and present dominance of the

surrounding Lake must be recognized. This formerly stood at a level much above that of the highest ridges upon the island, as is clearly evidenced by the abandoned beaches on the north shore of Lake Superior. Such relations prove that Isle Royale was once a rocky reef in the lake, which, as the Lake level was lowered (it is quite unlikely that the island has been materially elevated) became exposed as a wave-washed beach. These conditions are approximated to-day by the low outlying islands. The beach or shore is thus the *original* habitat upon Isle Royale, and in general, all others have been derived or developed from it. To discuss these as a truly genetic series would require that these be described *simultaneously,* as the differentiation took place. These habitats did not develop as isolated phenomena, but several developed at the same time, or abreast. Thus as soon as enough of the land surface had become exposed so that its inequalities began to have an influence, the ridges would be the parts best drained, and certain depressions would tend to accumulate the drainage. This process would lead to a simultaneous development or differentiation of the well, moderately, and poorly drained habitats. Almost all of the residual soil formed as the region was baseleveled was probably cleared away by the glaciers; or later, as the waves fell from the island, by the pounding of the waves. Thus the relative absence of a soil must characterize all habitats. At what period life first reached the island in post-Glacial time is not definitely known; but it is likely that the pioneer vegetation of lichens, mosses and low herbaceous vegetation reached it soon after its *exposure.* If the biota reached the island about the time of the formation of the Algonquin beach, which, roughly speaking, may have been at about the present elevation of 475 feet above the Lake surface, it has since spread upward and downward from that level. The composition of the initial societies is not liable to as much variation as the later ones. Thus if the Herring Gulls returned to the region at this early period of the exposure, they were probably the pioneer birds; but if only at a much later date, still other species might have accompanied them. While such variations as this may be expected, and due allowance must be made for them, yet there can be little reasonable doubt but that *water birds* and those frequenting *open places* tended to become the pioneers, and that later, with the development of a soil and forests, other associations of birds became established.

There are at least five important factors which enter into the composition of the past and present conditions which have moulded and are even now moulding the formation of the habitats upon Isle Royale. These five are:— *first,* past climatic changes; *second,* the local topography; *third,* the falling lake surface; *fourth,* dynamic tendency of the vegetation; and *fifth,* the habits and structure of the birds. With these guiding principles, let us now turn to certain details of the resultant succession.

a. The Aquatic Association and Habitat.

The expanse of Lake Superior, the irregular shore line producing coves, the inland water bodies and streams, together furnish an extensive and expansive area of habitat. The cutting of the Lake waves encroaches upon the land habitat, and the deposition by them elsewhere causes minor extensions of the land habitat (as at Rock Harbor where a sand spit furnishes a nesting site for a Kingfisher). Inland the encroachment of the vegetation tends to restrict the water areas, as the falling Lake level has, in the past, tended to increase the land habitat. These processes must be recognized in order to grasp the dynamic tendencies of the habitat.

The *characteristic* aquatic society is composed of the Herring Gull, Loon, American and Hooded Mergansers, and the Pied-billed Grebe; mainly fish eaters and scavengers. Other species, of greater inland tendencies, are attracted by the fish food, as the Eagle, Osprey and the Kingfisher. The Gulls show a decided preference for the great Lake, and the Loon for the inland waters. The presence of the Kingfisher was influenced by the harbor with its attendant sand banks and bars. As all these water bodies near Isle Royale freeze over in winter, the strictly aquatic birds must normally migrate to secure food. Of course none of these birds nest in the open waters, but on the island beaches (Gulls), near the mouths of streams, and inland in marshy places; but all, as a rule, nest near the water. The very young soon attend their parents, and are thus in the water at an age when many land birds are yet helpless in the nest, thus confirming their aquatic habits and habitat. During migrations many other species frequent this habitat.

Where Isle Royale now is, once rolled the open Lake; and it is

not improbable that as the island appeared the Herring Gull was one of the first species to discover it. Such a bird might even reach the island under climatic conditions of the Ice Age, for the species now ranges far north along the shore of the Arctic Sea. A species of such extensive chronological and geographical range will tend to give much stability to succession. The present breeding range of the Mergansers and the Loon is not so far north, and for this reason they may have arrived under milder climatic conditions. But if the island became exposed under mild post-Glacial conditions, all of these species may have arrived at much the same time. But even with the chances for such variations the general succession seems to have been initiated with the aquatic association as the pioneer society.

In following the genesis of the habitats and associations from this point onward, divergence and differentiation becomes so marked that it is impossible to develop all lines abreast. A linear treatment becomes necessary, and therefore certain general relations are liable to become obscured unless specifically mentioned in advance.

The aquatic and beach habitats possess a marked tendency toward a zonal arrangement. From the Superior beach the transition is through open or shrub zones into the climax forest. The topography of the island with its longitudinal ridges and valleys form a dominant factor in impressing this zonal structure upon the biotic associations. This series,— from the water, through the beach, open and shrub marginal zone, into the climax forest,— may be considered as the genetic vegetative succession. They change simultaneously and are due to the same general cause,— the falling Lake surface, which transforms the water area into beach, the beach into forest margin, and forest margin into the climax association. But as mentioned, it is manifestly impossible to discuss all these transitions at once, and each ecological unit must therefore receive separate genetic treatment.

This tension line or marginal zone between the Lake and the forest shows such a wonderful diversity and complexity in its conditions, that several plant and animal associations are formed within

this zone. With its onward march there are simultaneous changes in several associations which, while they will vary in their changes, yet all tend to converge in harmony with the dominant factors. These conditions migrate or radiate from the highest land. On the other hand, the inland marginal zones, which border the smaller water bodies, migrate inwardly; and being closed areas, tend to become extinct. This marginal zone, particularly beyond the upper beach, forms one of the most interesting and complex conditions found upon the island. It is not an ecological unit, but is composed of several of them. This is where most of the confusion arises in actual field work of habitat studies.

b. The Shore and Marsh Association and Habitat.

As the area of the islands expanded and the shore line was lengthened, the habitat for shore birds increased; but the steep and rocky shores were unfavorable for the development of beaches because loose rock, as tools for the waves, was limited in amount. The local character of the shingle and gravel to-day found in the various coves clearly indicates their local origin; and much the same conditions have obtained in the past. On account of these conditions, the sandy beaches are very conspicuously absent. The dynamic tendencies of the beach are those which cause the extension or restriction of the aquatic and beach habitats, supplemented by the drift which is tossed upon the shore. Where there is shallow water, and mud accumulates, favorable conditions are furnished for invertebrate food for birds. Inland, the numerous lakes, ponds and marshes furnish shore conditions which tend to become extinct through drainage or overgrowth of the vegetation, except in those parts of the larger lakes where wave action tends to scatter such accumulations as rapidly as formed, or to prevent its formation altogether.

Although observations on this subject are quite limited, yet it seems fairly safe to consider the Spotted and Solitary Sandpipers as characteristic birds of this association. Upon such a rocky coast, sandy and gravelly beaches are quite exceptional and are confined to protected coves. Additional diversity is produced where small streams enter these coves and produce deltas.

Little is gained by sharply segregating the marsh and shore birds, although the marsh birds show a preference for conditions better represented or correlated with topographically older coasts, protected and inland conditions. Attention should be directed, however, to the significant fact that successions initiated with such diversity will produce a variation in the composition of the associations. Also that so far as possible these variations should be considered comparatively and synthetically in reconstructing and anticipating successions.

The American Bittern, Lesser Yellow-legs, Swamp Sparrow and Marsh Hawk belong to this society of marsh birds. As in the case of the aquatic association, these birds generally nest in close proximity or entirely within these shore or marsh conditions. Still other species frequent this belt to feed, as it is an open area; but their presence is mainly conditioned by the adjacent shrubs or forest. The very limited number of species in the aquatic and shore associations is worthy of particular mention.

The Yellow-legs, Spotted Sandpiper, Bittern and Marsh Hawk range far to the north, even to the Barren Grounds, and thus suggest chances, as in the case of the aquatic association, of an early arrival and succession upon the island.

With the growth of the island, there has been a corresponding extension of the outer and inner shore habitats, although the encroaching vegetation has had a marked tendency to restrict the area of the inland habitat. The dominant environmental influences in this habitat appear to be, 1, the physical character of the shore and beaches; 2, the dynamic forces of the water bodies and streams; 3, the encroachment of the vegetation; 4, the downward migration of the shore; and 5, the habits and structure of the birds.

As a general rule, we may say that the beach of the outer lake tends to be succeeded by either the bog or upland associations, and those inland by the bog association.

c. Bog-forest Association and Habitat.

As just stated the outer coast or an inland one may develop into a marsh or bog habitat or association. In the bog, the Tamarack, Black Spruce and Arbor Vitæ are the pioneer trees in transforming

the open marsh into a forested one; while upon the outer shore the alders and aspens tend to precede the conifers as a general rule. From the bog forest the transition to the Balsam-White Spruce forest may be perfectly continuous, and thus there will be a series characterized by the dominant conifers. In places Arbor Vitæ may form the dominant swamp forest, but this is only a variation in the conifer dominance. With improved drainage or the accumulation of vegetable debris, these habitats become converted into the Balsam-spruce climax forest and hence the environmental dynamic tendency.

As the forest encroaches upon the open bogs the Tamarack, Black Spruce, Arbor Vitæ, Cassandra, Labrador Tea and alders are accompanied by birds characteristic of this early stage; such as the Red-breasted Nuthatch, Yellow-bellied Flycatcher, Golden-crowned Kinglet, Cedar Waxwing, Chickadee, Canada Jay, White-winged Crossbill. Where alders abound the conditions are favorable for the Redstart and the White-throated Sparrow. But later, as the bog conifer forest becomes continuous and dominant, the Waxwing, Redstart and White-throated Sparrows diminish in numbers and finally disappear. Still later, as the swamp becomes eliminated with the development of the climax forest, the Yellow-bellied Flycatcher will also become excluded.

This is perhaps the simplest succession from the water to the climax forest, via the bog forest. This series is very perfectly preserved in all stages and has an extensive range. The number of species in the association is rather large when compared with the preceding associations.

d. Aspen-birch Association and Habitat.

This series develops from the beach as the waves fall from the ridges or low rock surfaces and leave the bare expanses. As the rock disintegrates, decomposes, and humus accumulates, a soil is formed, mainly in depressions or at the bases of the ridges, and from these it tends to encroach upon the open places with a zone of Jack Pine, aspens, or White Birches. These areas are largely strips along the crests of ridges or small park-like openings on rather level rock. In no case are these single areas large, so that the

habitat is only extensive in the aggregate. With the presence of the open aspen and birch woods, the following society is likely to be characteristic:— Junco, Oven Bird, Red-eyed Vireo, Chipping Sparrow, White-throated Sparrow, Flicker, Cedar Waxwing, Wilson's Thrush and the Chickadee. As the deciduous trees are replaced by the open encroaching conifer forest, the Song Sparrow, the Nashville, Myrtle and Black-throated Green Warblers and Wilson's and Olive-backed Thrushes, which frequent the forest margins, increase in abundance. The Oven Bird has an extensive northern range from Labrador into the Yukon Valley and may well have been a very early pioneer upon the island as the aspens and birches were probably the first broad-leaved tree arrivals. From the above it is seen that this means an extensive variety, but as the dominance of the climax forest encroaches this number again becomes reduced.

The composition of the society varies somewhat, depending upon the surroundings, as proximity of the present shore or distance from it. Many of these openings are continuous with the present beach. It is not improbable that this was a prominent society whenever the waters fell rapidly from the island between rather stationary levels. This has been a society decidedly on the decline with the encroachment of the forest.

Probably this association varies considerably in its composition, and has done so in the past; but its main features are fairly constant. These variations seem likely, through the influence of openings produced by fires which, when extensive, may have caused a new equilibrium among those species frequenting openings.

The Burned Area Association.

This phase should perhaps be considered as supplementary to the aspen-birch association just considered. A fire brings about a reversal of conditions through the destruction of the forest, and in some cases, a part of the soil as well. As there are all degrees of extent and completeness in this process, there is a corresponding variation in the details of the resulting succession, at least in its early stages. It is only when there is a very complete destruction of the vegetation that the continuity with former occupancy is wholly broken.

The easily inflammable character of these conifers, even when in a green condition, makes it likely that natural causes, such as lightning or marsh gas (*cf.* Penhallow, '07), may have been influential. The proximity of the gas supply and the conifers is of interest as this may influence their liability to fire and thus to this sort of reversal of conditions. Thus liability to fires is rather characteristic of the region, and man's influence has tended merely to reinforce rather than to introduce this feature. Thus it seems probable that fires have been a factor in supplementing the natural park-like openings. In addition to the burned areas found upon Isle Royale, other limited open areas are due to cultivation and are kept open.

The birds characteristic of the more open situations are the Sharp-tailed Grouse, Song and Chipping Sparrows, Flicker, and the Purple Finch. The Grouse is a Plains form, is near its eastern limit, and is perhaps a late arrival upon the island. The other species are wide ranging in the Canadian coniferous forests but are not of such northern range as the aquatic and shore associations. There is nothing in their range to suggest their arrival earlier than the forest association. Taking all the birds of the openings together, it is not improbable that they arrived at about the same time as those of the forests, but frequented different situations,— the forest kinds occupying the slopes and drier valleys, and the others the openings.

e. The Climax Association or Formation and Habitat.

The climax association should not be considered in such a way as to lead one to think that it is *distinct* from the other associations. It belongs to *all* of them as the end of their series under existing biotic and environmental conditions. Thus the aquatic association, through the bog conifers, is transformed into the Balsam-spruce association; and from the beach through the aspen-birch association again to the balsams and spruces. The climax association is the condition of adjustment toward which all societies move under the present conditions. For this reason the earlier stages, conditions and associations of the climax have been outlined in the preceding discussion.

In the dominant forest the dense shade prevents an extensive

ground cover of herbaceous plants; and although Ground Hemlock is abundant locally, yet in places the forest floor is quite open and free from lower shrub growth. The remarkable preservation of trails or roads through such tracts shows clearly how slowly changes take place. Such a habitat must be relatively equable in its temperature and moisture relations.

Geographically speaking, the primary characteristic of the climax is its *relative stability*, due to a dominance or relative equilibrium produced by the severe environmental and biotic selection and adjustment throughout the process of succession.

At this point attention should be called to the fact that dominance is a resultant of an equilibrium produced by neutralizing or overcoming other forces and influences. We may think of the process of succession as a stream of forces whose development may be compared with the transformation of a drainage line,— such as, for example, that of a rivulet into a creek, and then into a river. The stream and the character of the ground mutually influence each other and the course followed is a resultant of the mutual adjustments. The stream is deflected by one condition and then another, just as succession varies with local conditions; yet the water continues to run down grade and seeks an equilibrium, and similarly, biotic succession continues on its course deflected here and there by local influences, yet forever tending toward a state of biotic equilibrium. The dominance of the climax society or formation, considered as a process rather than a product, has much in it that is analogous to the dominance produced by the process of baseleveling.

The characteristic birds of the climax forest are:— the Chickadee, Golden-crowned Kinglet, Red-breasted Nuthatch, Canada Jay, Downy, Hairy, Arctic Three-toed and Pileated Woodpeckers, and the White-winged Crossbill. Here again the association becomes small in variety of species and comparable with the small society which must have been associated with the complete dominance of the Lake waters. Thus there has been a development of diversity from simplicity, with later a return to simplicity. To these birds of the forest should also be added those species of general distribution, as the Eagle, Swift, Swallows, etc., a class of birds whose predaceous, insect-feeding and wide ranging habits make them particularly difficult to properly associate. A careful study of

this class of birds will be necessary before they can be satisfactorily correlated with their proper avian associations.

But let us not overlook the fact that even this dominance is only *relative*, for since the Ice Age even this *entire formation* has migrated northward, and a true succession has been produced with its attendant changes in the conditions and in the composition of the associations. Just as upon Isle Royale a definite dynamic trend was given to the complete environment by the falling Lake surface, so in the post-Glacial northward migration there was a northward migrating climate. These conditions determined that on the *north side* of this immense succession or migration habitats and associations were developed which are comparable to those attending the downward march of the Isle Royale beach; and even to-day, by passing from Isle Royale to the tree limit with its zone of aspens and birches, one may find representatives of the various kinds of associations which in all probability moved north, just as to-day in passing from the forest to the rocky beach balsams and spruce are encountered before the aspens and birch. If however, this is only another case of convergence and not at bottom the same or a comparable process, we are then certainly far from an understanding of even the general nature of the problem.

3. *Internal Factors.* With the idea of succession, as exemplified by Isle Royale, let us turn to other factors which influence the internal relations of the birds within an association or society, because such relations are also necessary to an intelligent understanding of succession. Some of these general relations have been outlined, but certain others are needed which have been well expressed by Brewster ('06, p. 62–63): "Many if not most birds show a marked preference for breeding in certain regions, throughout which they are more or less evenly and generally distributed, but within which their numbers do not seem to increase beyond fixed maximum limits no matter how carefully the birds may be protected or how successful they may be in rearing their young.... I have observed — as, indeed, who has not! — that few birds — excepting those which, like Swallows, Terns, Herons, and Gulls, are accustomed to nest in colonies — tolerate very near neighbors of their own species during the season of reproduction. At its beginning each pair takes possession of a definite tract of wood-

land, orchard, swamp or meadow, which the male is ever on the alert to defend against trespassers of his own kind and sex, although he often seems quite willing to share his domain with birds of other and perhaps closely related species. The extent of the area thus monopolized varies exceedingly with birds of different species. An apple orchard which affords sufficient room for — let us say — two pairs of Yellow Warblers, two pairs of Orioles, three or four pairs of Chippies and four or five pairs of Robins, seldom or never harbors more than a single pair of Kingbirds or Crested Flycatchers .... As a rule, the species which roam over the most ground in the course of their daily wanderings claim and maintain the broadest preserves, while those of sedentary habits often content themselves with very modest freeholds. Whatever the extent of the domain, the birds who occupy it as a summer home evidently regard it as exclusively their own. The readiness and celerity with which trespassing birds are accustomed to retire when attacked or even merely threatened by the established tenants, has seemed to me to indicate that the claims of temporary ownership are respected by all right-minded birds.... In my opinion the desire for exclusive possession so conspicuously shown by the male, and often by him alone, is usually the direct result of *sexual jealousy*. This, as is natural, makes him intolerant, during the breeding season, of the near presence of rival males. If his concern were chiefly in respect to the food supply, it would be equally manifested at every season and towards all birds who subsist on the same food that he and his mate require — which is certainly not the case."

The tendency or pairs and species to *space themselves* and to become *relatively sedentary* is thus a characteristic condition in an association, and is an important element in an understanding of succession because it shows the internal organization and habit with which an invader or pioneer from another association has to contend. As Dixon ('97, p. 91) has pointed out, this spacing tendency is an important factor in the extension of range of species and is intimately related to the location of nesting sites. These facts clearly show that both these internal influences and the environmental ones must be distinguished if we wish to determine the relative influence of each and their bearing on succession. The above quotation from Brewster clearly shows that in general not only a

greater number of birds can live in a given area, but also that they can live closer together, if they vary in kind. Then again, within the association there are marked differences in habitat preference. Thus in the forest there are those birds which nest in the trunks or among the topmost branches of the trees, or even upon the ground; and these are differences largely distinct from the spacing of the pairs of the same species. These influences must be recognized among the dominant influences within the association, and upon which much emphasis must be placed.

4. *Environmental Factors.* Then in addition to these internal factors, there are the dominant physical factors. In the following discussion primary emphasis will be placed upon succession as found in the Northeastern Biotic or Conifer Center, because successions at other centers with different biotic components and other dominant physical conditions must possess a certain amount of individuality, in addition to those features common to succession in general. The dominant biotic tendency or dynamic trend of this center, as a *resultant of all internal and environmental influences,* is for the conifer biotic association to *encroach upon all other societies and habitats and to become the dominant or universally distributed association.* Thus, in general, all habitats produced by local influences tend to become transformed into the dominant biotic association or formation. In general also, small bodies of water are rapidly encroached upon by inwash, vegetation or drainage, and tend to become extinct and forested. All other openings, as the rocky ledges and ridges or burns, are encroached upon as soil accumulates or fires are prevented, and the forest biotic association spreads over the entire area.

From such relations it will be seen that our knowledge of the causes and conditions of succession must largely result from the study of these *local environments or habitats and their biotic succession,* because, where dominance is established the succession is almost completely obliterated. *Each minor habitat and society is to be looked upon as simply a stage, more or less temporary, in the onward wave toward the dominant or climax association.* Thus in the marshes, birch or aspen woods, rock openings and ponds may be "orginal" conditions which are becoming cumulatively transformed in the direction of the final dominance of the climax biotic type.

The relatively slow rate of change in many environmental processes and the relative stability of the climax biota,[1] is doubtless the basis for the current view that such conditions are relatively constant or fixed; but that change and not constancy is the normal and usual condition in nature is quite evident upon a moment's reflection. Almost every one notices these changes after an absence of a few years from a region. Thus intimacy tends to blind us to changes unless a *habit* of giving attention to them is deliberately cultivated. For this reason some find it almost impossible to recognize environmental changes or to comprehend their significance. It is therefore of practical value to clearly recognize under what conditions changes may be most readily perceived. Therefore the importance of the study of *local influences* is emphasized, and the necessity recognized of distinguishing the dominance of geographic and relatively stable conditions or formations as contrasted with those due to local and often relatively changeable conditions. Then among these changes we must distinguish those which are mere fluctuations and those which are indicative of the true progressive succession. This is mainly accomplished by attention to general relations and the subordination of minor details.

5. *Environmental and Associational Convergence.* At the present imperfect stage of ecological development, comparison must furnish us the most important and general clues to the processes of succession; and undoubtedly this method must long remain as our main guide on account of its comprehensive application and the magnitude of the problem to be solved. It is therefore desirable that the limitations of the method should be clearly borne in mind. It is often assumed that the implied successions of a given place are the same as those which have developed at that place in the evolution of the present climax. But as we positively know that *many different causes are able to produce the same or very similar results,* such conclusions must be received with due caution. That the dominant geographic conditions tend to override local influences seems very fairly established because *diverse local or original conditions are transformed into the climax or dominant type.* This clearly shows that in time diverse local influences have flowed into the general environmental trend or current and have become a part of it.

[1] For the migrations of climax societies, *cf.* Adams, '05.

There is thus a very strong *convergent* tendency. By convergence is meant the independent production of the same kind of association from diverse starting points or habitats and associations. Quite minor ecological units may show similar but temporary convergent tendencies in their succession. It is therefore not surprising that any marked environmental dominance will tend to produce similar or convergent results, even in local areas. Under such circumstances similar associations or societies may be independently and repeatedly formed by the selecting environmental influences, such as, for example, are found in the numerous small lakes scattered throughout the coniferous forests. This convergent phenomenon is certainly a fertile source of confusion throughout all phases of science. Perhaps the best guide through such a labyrinth will be to clearly bear in mind the relative value of general and local influences, and watch with an "eternal vigilance" for convergent results due to diverse causes. This convergent phenomenon is particularly liable to occur in the case of environments produced by reversible physical conditions. It should further be stated that a study of these problems from a genetic and dynamic point of view will aid in recognizing such results. Under such circumstances attention is primarily directed toward the dominant causes and conditions of change rather than to the stages, products, and results produced by them. Convergence thus viewed is the result of several causes and should be considered a product rather than a process. This same distinction may be made for all societies, associations and formations. *Convergent phenomena are thus particularly liable to confuse wherever products rather than genetic processes receive primary emphasis.*

6. *Succession and Environmental Evolution.* The relation of succession to general biological problems is very intimate. This opens up a very extensive field which is only mentioned to indicate its general relation to succession. The facts of succession and evolution must ever remain far in advance of our knowledge of their causes. If, however, one turns to the standard evolutionary treatises and searches for a discussion of the evolution of the environment, as correlated with animal evolution, only the most general, or the elementary and superficial phases, are as a rule discussed. To be sure, certain papers and treatises take up special phases of

the problem, and the broadest phases are treated by the geologists; but none of them seem adequate as a comprehensive treatment of so important a subject. Succession, broadly and genetically considered (dynamic rather than static), is a phase of environmental evolution.

7. *The Relation of Succession to Organic Evolution.* Mention has been made of the relation of succession to environmental evolution, but its relation to the organic evolution of birds should also be indicated. The mutual relations of organic and environmental evolution have been and will continue to be the battleground of biological thought for an indefinite length of time. Here lies the tension line between the two main schools of biological interpretation.

One school maintains that all *causes* of evolution are *internal*, and that the environment is only a *condition*, not a cause. From this point of view the fundamental causes are internal and therefore environmental conditions can only indirectly influence evolution through the weeding out of those forms not in harmony with the conditions; and hence it has a *selective* rather than an *originative* influence. From this point of view succession and environmental evolution can contribute nothing to the elucidation of the *causes* of organic evolution, though they may to an understanding of the selection produced by the succession of conditions in which organic evolution has taken and is taking place. In harmony with this point of view, succession, broadly treated, should furnish a fundamental method of treatment for the process of selection, and the detailed principles of its working. This would certainly be an important advance because natural selection has frequently been reproached for its indefinite methods and lack of definite treatment. Succession from this point of view is primarily related to the Darwinian factors of evolution. No doubt this is one reason why Darwin himself put such high value upon the study of ecological relations of animals, *i. e.*, their relation to their complete environment, or their struggle for existence.

If, however, all causes are internal and not directly subject to external influences, they must be beyond experimentation to a corresponding degree. Under such conditions evolution becomes a *descriptive* rather than a *causal* science, and all that investigation

can do is to describe the succession of forms produced by these internal causes.

On the other hand the rival school maintains that both internal and external conditions may be real *causes* of organic evolution. This is thought to be brought about by the direct or indirect influence of the environment upon the germ cells, by environmental selection, or even by both combined. From such a point of view the environment may thus be either a *cause* or a *condition* of organic evolution, or both. From such a standpoint the evolution of the environment receives increased importance, as under such conditions organic and environmental evolution are causally related, and thus intimately correlated. Viewed thus, environmental evolution is more than the description of the succession of conditions, but may be explanatory as well.

The particularly significant feature is that environmental evolution and biotic succession are of great value and can contribute either to the causes or conditions, or to both, of evolutionary advancement.

VI. SOME ADVANTAGES OF A KNOWLEDGE OF THE LAWS OF SUCCESSION.

The study of succession implies a detailed knowledge of the field relations of birds, and as this has received so little attention as a subject of special study, it is perhaps worth while to briefly mention some of the practical and scientific advantages which we may reasonably expect will result from the development of this phase of investigation.

The current discussions of environments are generally very fragmentary and chaotic, and the careful study of bird habitats and succession will greatly improve this phase of ecology. Here is a field of study in need of distinct recognition as a subject worthy of detailed investigation, in addition to those lines already current. When once this field is developed, then and only then will it be possible to intelligently discuss the evolution of avian environments and to correlate them with the evolution of birds themselves. It is quite probable that one of the main conditions which prevents a

more rapid advance along evolutionary lines is in a large measure due to the almost utter failure to analyze dynamically environmental complexes. Succession, studied in its broader aspects, should greatly aid in the formulation of the laws governing the "struggle for existence," which is frequently condemned for its indefinite character.

From another point of view there are very important reasons for urging extensive studies of this character at a relatively early date, because the encroachments of civilization, which by the destruction of the forests, the drainage of the land, irrigation, farming and grazing of the grasslands, are rapidly destroying original environmental conditions before they are studied ecologically. Much of Europe has already gone through this stage of demolition, and it is only to new and relatively unmodified countries that we can look for an adequate statement of these problems and their relations in their original and primarily evolutionary and developmental form. It is not improbable that the next generation may wonder why some subjects, the investigation of which might have been delayed, have received detailed attention, while others equally or perhaps even more important have been almost ignored and must forever remain unknown because of this neglect to secure the "vanishing data." (*Cf.* Haddon, '03.)

Such ecological studies may be expected to have a valuable reflex influence upon the naturalist himself. We may hope that the future revisor of a group of birds will consider a knowledge of the field relations of his specimens as an essential qualification, just as at the present time a large series of specimens is held necessary. Fifty years ago a limited series was considered no disqualification, just as to-day the lack of a knowledge of their ecological relations is not so considered. Perhaps our ideas of relative values must change. In this connection a statement from Tristram ('94, p. 472) is to the point:— "The closet systematist is very apt to overlook or take no count of habits, voice, modification and other features of life which have an important bearing on the modification of species. To take one instance, the short-toed lark (*Calandrella brachydactyla*) is spread over the countries bordering on the Mediterranean; but along with it, in Andulusia alone is found another species, *Cal. baetida*, of a rather darker color, and with the second-

aries generally somewhat shorter. Without further knowledge than that obtained from a comparison of skins, it might be put down as an accidental variety. But the field naturalist soon recognizes it as a most distinct species. It has a different voice, a differently shaped nest; and, while the common species breeds in the plains, this one always resorts to the hills. The Spanish shepherds on the spot recognize their distinctness, and have a name for each species."

Many examples of similar character might be cited to show the scientific value of a knowledge of the environmental relations of birds, and a moment's reflection will show that the problem of succession is only a small part of the general problem of environmental relations of plants and animals. Attention has already been directed to the relation which this general subject bears to evolutionary problems.

It is not at all unlikely that succession is very closely related to some of the causes of bird migration, and that with advance in this subject much light would be thrown upon migration. Migration is doubtless another illustration of convergent phenomena. In all probability, migration has originated not only independently in very diverse kinds of birds, but perhaps repeatedly, from different causes, even in the same group. The causes of migration must be numerous, varying with different ecological groups, which appear to be the true natural units for study and comparison. Thus the comparative study of migrations of different kinds of associations, as formations and societies, should lead not only to a better understanding of the various associations, but should also contribute to the general subject of migration which seems to have shown a tendency toward stability in the current methods of study. It scarcely seems probable that with the diverse formations inhabited by birds, and with their ecological diversities there should be only a few causes of the phenomena.

To keep pace with successions animals must either adjust themselves, change their habitat, or migrate. From such relations it is evident that various supposed environmental responses must be *tested primarily within the association and environment to which the animal normally belongs.* To this class belongs protective coloration and allied phenomena. To be of fundamental value, the

influence must have some permanence and this may be sought in the *dynamic* trend and dominant influences of different associations. It is difficult to conceive of other more reliable methods of approach to such problems.

In addition to the scientific value of this line of investigation, there are important economic applications of the laws of avian environment. This is particularly true of forestry and agriculture. The forestry problem is continually becoming more important, but the relation of bird life to forests and forest succession has received little attention. As agents for scattering seeds of trees and shrubs, birds are very important. Here is where the interests of the avian ecologist and forest ecologist overlap. The student of bird life will wish to know how a region is to be reforested, and what succession of bird life will attend the succession of the forest as reforestation progresses. On the other hand, the forester will wish to know how birds will aid or retard him in the process of reforestation. Then, in guarding or protecting the forest, what help can be secured from birds with regard to insect pests? These are only samples to show that here is a field which, as time advances, will become of more and more importance, and that these problems will eventually call for specially trained men to handle them.

In connection with forestry and agriculture we have quite exceptional conditions for extended experimental studies in bird succession as related to forest succession, crop rotation, etc. The relation of birds to agriculture appeals to a much larger number of people than does their relation to forestry. There are several reasons for this; first, because more persons are interested in farm and horticultural crops than in forests; and second, because birds are soon attracted in such large numbers by the food supply of grains and fruits which these crops so greatly increase, that the extensive destruction by birds readily attracts attention. And while we hear much of the great reduction of certain species of birds in parts of the country, it is not at all improbable that with the destruction of the forests (which were dense and dominant and tended to *limit* the abundance of many species frequenting the open), and the increase of food in cultivated fields, there has been an increase in the total number of birds, even in spite of the great numbers killed by man.

But to the phase of succession with which we are primarily

concerned, almost no attention has been given, in spite of its fundamental relation to crop rotation and the corresponding avian succession attending this. Indeed there seems to be a very decided need of a thorough investigation and discussion of the general principles underlying all these economic problems, that they may be brought into harmony with the advances made in some other phases of ecology.

Hull Zoological Laboratory, University of Chicago.
October 21, 1907.

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THE BIRD COLONIES OF THE OLYMPIADES.

BY WILLIAM LEON DAWSON.

THE recent creation by executive order of three reserves among the islands which lie off the west coast of Washington has served to call attention for the first time, in an ornithological way at least, to this hitherto little-known coast. The reasons for previous neglect are not far to seek. No really safe harbors offer, for even the smallest craft, between the mouth of Gray's Harbor, Lat. 46° 56′ N., and the Straits of Juan de Fuca, Lat. 48° 24′ N. The prevailing winds are westerly, and the aspect of the coast so menacing, as viewed from the seaward side, that mariners have always given it a wide berth, save when seized by some hapless mischance of reckoning or tackle.

No commercial exploitation of the tributary country has been attempted, beyond the preëmpting of timber lands some twenty years ago, and the occupation by hardy settlers of a few small prairies and rich alluvial bottoms. Only recently a spur of the Northern Pacific Railway has been built from Hoquiam, on Gray's Harbor, to Moclips, on the coast; and this latter point marks nearly the northern extension of a splendid sea-beach, hard as macadam, which stretches south, practically to the Columbia River. To the north of Moclips the beginning of the rough way is marked by Point Grenville, and the ocean drive becomes a tradition.