

THE RELATION OF FIELD CHARACTERS TO THE QUESTION OF SPECIES AND SUBSPECIES.

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IN A recent number of 'The Auk,' Dr. Stone¹ has ably discussed the subspecies question, bringing the various ideas that have been expressed on the subject up to date. For some years I had been entertaining a number of ideas concerning the relationships of species and subspecies. Dr. Stone's paper served to clarify these ideas, and I am presenting them here.

It has been generally considered that the museum ornithologist with large series of skins to study, is the final authority on all questions as to what are species and subspecies. The field ornithologist, that is, the student of living birds in their natural environments, is not supposed to have anything to say about it. But the facts are that the moment a bird is dead it has lost a large number of the characters of the species to which it belongs. Its characteristic habits and actions, its call-notes, alarm-notes, songs, the habitat it selects in which to breed, the type of nest its instinct prompts it to build, and the kind of place in which its nest is located are all just as much characters of the species as are the coloration of its feathers and the length of its wing or tarsus.

When two species in the same genus differ only slightly in coloration, but widely in these field characters, the degree of difference seems, to the field man, much greater than it does to the museum man. Conversely, when species do not differ in these field characters, even though their plumages are quite distinct, there is reason to think that the degree of difference is really less than the museum man is likely to make it.

Many years ago Coues,² discussing the Eastern and Western Wood Pewees, wrote, "We may have to acknowledge, in some cases, that species are better determined in the field than in the closet. If this be true in any case, it holds with the little flycatchers."

I should hesitate to identify the Least and Alder Flycatchers in the field by sight alone. I should have greater certainty in separating two such subspecies as the Prairie and Northern Horned Larks. This agrees with Dr. Stone's statement that "many subspecies . . . are as easy to identify in the field as are many species" (p. 37). But if, in either case, the bird in question produced some sound, the Flycatcher would be immediately identified beyond question, but the Larks could not be separated by that means.

If we find these two Flycatchers nesting on their breeding grounds, the

¹ Some Aspects of the Subspecies Question. *Auk* LII, pp. 31-39.

² *Birds of the Northwest.* p. 248.

habitat alone is sufficient to name them. If we find the nests and compare them as to materials and location, to say nothing of the eggs, we appreciate why these two birds are distinct species much more clearly than we could by examining skins. The degree of difference between them is really great.

In the vicinity of the Allegany School of Natural History, where I am now writing, four species of the genus *Hyllocichla* are to be found in summer. It takes careful observation, under the best light conditions, to distinguish them by sight. But a mere hearing of a single call-note identifies each species unmistakably. The "pit-pit-pit" of the Wood Thrush, the "chuck" of the Hermit, the "whit" of the Olive-back and the "wheooh" of the Veery are field characters that distinguish the species much more certainly than plumage and even more certainly than songs.

There are few subspecies, however, that the field student can distinguish with certainty. Their determination is best inferred from the range, or, when that cannot be done, they should be left undetermined. I record the Grackle on my spring lists in southern Connecticut, but seldom attempt to say which subspecies of Grackle I have seen till the migration is over and I know that the breeding birds are Purple Grackles. Here in Allegany State Park, New York, I do not yet know certainly whether the Song Sparrow is the Mississippi Song Sparrow or the Eastern Song Sparrow. Subspecies do not show differences in the field characters of the living bird.

The Northern and Southern Flickers are subspecies indistinguishable to the field student. The Northern and Red-shafted Flickers are distinguishable, but by color only. If a field student were sufficiently color-blind he would find them indistinguishable. Both species have the same habits and call-notes. Both call "kuleeup" in characteristic fashion. Both alternate their drumming with the long, loud "wick-wick-wick" repeated twenty to eighty or more times. In the mating season both, in company with mate or rivals, sidle around the limbs of trees, or bow to each other, calling "ooweeka, ooweeka." The nests of both are similar, and except that the species of trees are different because of geographical range, the habitats are essentially alike. Settlers in western Montana, who came to that region from various states in the Mississippi Valley, still call the bird "Yellowhammer" and most of them seem never to have noticed the difference in coloration.

It is well known that along the border of the ranges of these Flickers, hybrids are commonly found. Or should I say intergrades? The degree of difference between them is greater than between the Northern and Southern Flickers, so they are considered to be species. To the museum ornithologist they are absolutely distinct. But in the field, where coloration cannot always be seen to advantage, they seem hardly more different than sub-

species. The relationship between them is certainly much closer than between the Flycatchers and Thrushes I have discussed. But there is nothing in our present methods of classification or nomenclature that indicates this difference in relationship.

In the genus *Dendroica* the various eastern species, occupying overlapping breeding ranges, are distinct not only in plumages, but in songs, nesting habits and other field characters. But, if we consider the Myrtle and Audubon's Warblers that are separated geographically, we find a case not unlike the Flickers. The two forms are different in coloration, but they call the same loud "tsick," have the same twittery sleigh-bell song, and breed in habitats that are essentially alike. To an eastern field observer, the first acquaintance with Audubon's Warbler gives him the impression of just a Myrtle Warbler with a yellow throat. Yet the arrangement of species in our 'Check-List' does not indicate the much closer relationship that the Myrtle Warbler has with Audubon's Warbler on one side, than with the Black-throated Blue Warbler on the other.

This same condition is also illustrated in the Juncos. I have no field acquaintance with the southwestern forms, but those that I do know, constituting seven forms and four species as recognized at present, *hyemalis*, *aikeni*, *mearnsi*, and *oreganus*, differ from each other in coloration only. Their calls, songs and nesting habits, so far as I have observed them, are all alike. I believe that their breeding ranges are all actually distinct geographically, though it might be difficult to realize this from reading the ranges given in the 'Check-List.'

Considering these facts it seems to me that we have been applying the term species to forms whose relationships within the genus are of two different sorts. First there are those forms that are distinct not only in coloration, but in field characters. They may or may not occupy overlapping breeding ranges, but they are so distinct that we need not use our judgment as to degree of difference. They rarely hybridize. Second there are those forms that differ only in coloration or measurements, and not in field characters. Their breeding ranges are always separated geographically, and wherever these ranges meet we find, or should expect to find, hybrids or intergrades, whichever we choose to call them. Among these forms are some we call species and some we call subspecies and nothing but our judgment as to degree of difference determines which word we should use for a given form. Our judgment is bound to differ individually. So long as we continue to use the same term (species) for some of these forms that we do for forms that are clearly distinct the matter will never be conclusively settled. In other words nature has established two distinct kinds of forms, geographical forms and fully established¹ forms. Our terms

¹ I do not mean to imply here that these forms are fixed and unchangeable.

“species” and “subspecies” do not comply with the natural condition but with an artificial, indefinite distinction based on our judgment of degree of difference with no uniform basis for such judgment. This has been brought about because we have made our studies of distinctions chiefly from dead birds and have neglected to consider the characters of living ones. It would be more logical to call all geographical forms subspecies and established forms species.

Such an action is probably too radical, at least for the present, but I believe the future will bring about some sort of recognition of these differences in what we call species, and some sort of treatment in our nomenclature or classification that will show the difference. The chief trouble lies in the fact that bird skins cannot preserve the field characters. In cases where we are not sure which group a particular form belongs to, we must rely on accurate, scientific field studies of songs, call-notes, habits, breeding habitats, etc., of two or more forms that are related. In this connection, if there still remains, in the minds of a few, the old-fashioned notion that the study of dead birds and skins is somehow higher and more scientific ornithology than study of the living bird, the way is being paved to eradicate it.

There is one point that may help to explain why we do not always find hybrids or intergrades when the geographical range would lead us to expect them. That is the fact that the breeding range of a species is not merely geographical, but also ecological. The White-winged Junco, for example, breeds in mountain ranges and hills that lie east of the main chain of the Rocky Mountains. It breeds only in forested areas. These mountains and hills are surrounded by open, grass-covered treeless plains, and are like islands in a prairie sea. The bird's breeding range is therefore separated from that of other Juncos by miles of open grass where no form of Junco breeds, and it is as much isolated as if it were a true island form.

The well known case of hybridizing in the genus *Vermivora* is of interest when we consider field characters. The Blue-winged and Golden-winged Warblers are distinct in plumage and in territory songs. They seem to be identical in call-notes, breeding habitat and nesting habits. The second song, used more commonly late in the breeding season, is also identical so far as my experience goes, but that experience is rather limited in the case of the Golden-winged Warbler. The two forms are therefore closer in relationship to each other than are any two eastern species of *Dendroica* for example. Perhaps they should be considered northern and southern geographical forms.

In considering these Warblers it is evident that differences in breeding habitat and nesting habits are more important in keeping related species apart than differences in plumage and song. If the territory theory is right, it is evidently the instinct of the male to select the breeding habitat, and of

the female to choose the nest site. These instincts are important characters in each species. There would seem to be no physical reason why a Chestnut-sided Warbler should not build its nest in a hemlock tree or a Blackburnian Warbler put its nest in a blackberry bush. That they do not is a matter of inherited habit, which, to my mind, is the best definition of what we call instinct.

The instinct to choose a habitat probably has more to do with the abundance of a particular species than any other factor. If a bird breeds in a variety of habitats, like the Robin, it is common. If its habitat covers a large area, like the Red-eyed Vireo, it is also common, but if the habitat is a restricted one, as in the case of the Worm-eating Warbler, it is comparatively rare or local in breeding distribution. If activities of man increase the area of its habitat, the species increases, as evidently has happened with the Chestnut-sided Warbler. If man changes or destroys large areas of its habitat it decreases or becomes more and more local, a fate that is gradually coming upon the Seaside and Sharp-tailed Sparrows, at least in Connecticut.

In considering the problem of the origin of species I believe this matter of habitat selection to be of importance. Much has been said in the past about the importance of isolation. Subspecies are generally considered to be the result of geographical isolation. Writers have also suggested physiological isolation due to differences in sex development. Neither of these seems very logical as an explanation of the existence of the species of such genera as *Dendroica*, *Hylocichla*, *Empidonax* and others. It seems likely that the ancestral species, that gave rise to such genera, ranged over a variety of breeding habitats, much as the Robin does today. Gradually, however, the descendants developed the habit of returning to the habitat where they first originated, and the instinct to select that particular kind of habitat developed. Groups of individuals became isolated from other groups of their kind by this difference in instinct, what we might call psychological isolation. Thus the condition, which it has been argued, is necessary for the beginning of a new species, the isolation of groups of individuals, would be brought about.

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