

CRITERIA FOR THE DETERMINATION OF SUBSPECIES
IN SYSTEMATIC ORNITHOLOGY.¹

BY FRANK M. CHAPMAN.

I AM fully aware that an adequate presentation of this subject would require far more time than could well be accorded me on this occasion. Nor in any event could I expect to treat it in a manner which would meet with the approval of systematists generally. I feel, however, that it is a subject which demands discussion. The principles governing the procedure of systematists are now so diverse that until they have been harmonized it is useless to expect uniformity in method. This paper, therefore, is offered with a hope that it may lead to a general exchange of views and thereby prepare the way to the establishment of common standards in determining the status of representative forms.

The cytologist reaches definite conclusions concerning the status of a species through a study of its germ-cells; the experimental biologist determines the relationships of allied forms by the results of his attempts to breed them, but the systematic ornithologist defines species in terms of their external characters of size (including relative proportion of parts), color, and pattern of coloration plus their distributional relationships and, in some instances, their habits and voice.

The fundamental test of specific standing is non-intergradation with other forms. The indisputable proof of the specific distinctness of two or more forms is their occurrence together when breeding without intergradation.

The Greater and Lesser Scaup Ducks, the Downy and Hairy Woodpeckers, the Alder and the Acadian Flycatchers, the Common Crow and Fish Crow, the Gray-cheeked and Olive-backed Thrushes are more like each other than are many subspecies; but wholly aside from the absence of intermediates, the fact that they occupy in whole or part the same area when breeding and still maintain

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their distinguishing characteristics is, to the ornithologist, final proof of their specific distinctness. The cytologist may discover the same number of chromosomes in the germ cells of the Crow and the Fish Crow, the experimental biologist may produce fertile offspring from a union of the Greater and Lesser Scaups, but they will still remain species in the eyes of the systematist simply because they are associated in nature when breeding but do not intergrade.

In cases of this kind, therefore, the ornithologist is not at loss for a satisfactory test of specific distinctness without regard to degree of difference. It is when forms which resemble each other more or less closely are not associated while breeding but replace one another in areas which may or may not be connected that, lacking specimens to demonstrate their exact relations, he must decide whether to treat them as species or subspecies.

The easiest way out of this difficulty is to follow one or the other of two general rules in more or less current use.

1. Within certain limits of differentiation to consider all presumable representative forms as subspecies whether or not they are known to intergrade and whether or not their breeding ranges are contiguous or are widely separated.

2. To treat all obviously representative forms as species until their intergradation is proven.

While the adoption of either of these rules has the merit of consistency, their use often leads to such biologically incorrect results that no mere question of expediency can, in my opinion, pardon their acceptance.

Better be inconsistent than deliberately to handicap one's experience and discrimination by blind adhesion to a law which, however convenient it may be in practice, inevitably leads to false and misleading representations. Furthermore, it seems perfectly logical to insist that if a systematist refuses to rank certain forms as subspecies until their intergradation is proven, he should also refuse to treat them as species until the fact of their non-intergradation is established. Certainly in many cases we have no more right to assume that intergradation does not occur, than we have to assume that it does occur. Errors we are bound to make in any event, but there is assuredly no excuse for making them by unreasoning adherence to a purely arbitrary man-made law.

Is it not more scientific to treat each case on its merits, basing our conclusions on due consideration of all the available pertinent evidence? Systematic zoology has a higher end to serve than mere classification, and its nomenclature, should, so far as its limitations permit, express our knowledge of relationships. In the study of both physical and geographic origin of species it is of fundamental importance for us to know whether given forms are species or subspecies. It is evident, therefore, that their value as factors in problems of evolution and zoogeography is measured by the correctness of our classification. To the best of his ability and in the light of his material and experience the systematist should attempt to supply this information. If his labors have brought him into disrepute among biologists is it not because he has so often treated his specimens as dried skins rather than as biologic facts?

Our problem seems deceptively simple. Briefly, it requires us to decide when to treat representative forms as species, and when as subspecies. "Form," it should be explained, is the indefinite term which the systematist employs when he is in doubt whether to write "species" or "subspecies." Representative forms, then, are species or subspecies which so closely resemble one another that one evidently replaces the other. Whether they have descended from a common ancestor by different lines of descent, or whether one has arisen from the other, whether their differentiation is due to environmental or external factors or to mutational and internal causes are all subjects for inquiry, and our findings are, in a measure, expressed by our nomenclature.

The systematist knows that many proved subspecies differ far more from one another than do many species. It is not necessary therefore for us to distinguish between them when we list the characters on which species and subspecies are usually based. These are:

1. Size, including relative proportion of parts.
2. Color, including variations in intensity of color and actual differences in color.
3. Pattern of coloration, including variations in area, due primarily to increased or decreased pigmentation; variations in marking of individual feathers and the presence or absence of such "unit

markings" as wing-bars, pectoral crescents, superciliary lines, etc.

4. Shape, as it may be affected by increase or decrease in size or be expressed in the form of certain feathers.

In spite of the fact that these characters are present in both species and subspecies, we inquire which of them are most commonly considered of specific, which of subspecific value?

VARIATIONS IN SIZE.

Wide-ranging species so frequently differ in size geographically that laws have been formulated to express the normal trend of this type of variation. Thus J. A. Allen in 1870, writing on 'Geographical Variation among North American Mammals, Especially in Respect to Size,' advanced the following generalization¹.

"The maximum development of the individual is attained where conditions of environment are most favorable to the life of the species." Generally speaking it is the individuals of a species from the highest latitudes and altitudes which are the largest. Wide-ranging species, therefore, are sure to encounter conditions which usually produce variation in size and if their range be continuous the change in these conditions—and hence the change in size—is as gradual as the change in latitude or altitude itself. Variation in size, therefore, is the most common type of geographic differentiation. It is exhibited by great numbers of species which in other respects are essentially alike throughout their range. Moreover, as an expression of environment it keeps pace with range, and when a species is more or less continuously distributed we expect a complete intergradation in size between its largest and smallest members.

The assumption therefore seems warranted that when representative forms differ from each other only in size they will intergrade if their ranges are connected. The question, however, arises if the ranges of such forms are not connected and when their differences in size are not bridged by individual variation, shall we treat them as different species or shall we assume that they are organic units which would fuse were their ranges to be joined?

¹ Bull. Geol. and Geogr. Surv., II, No. 2, p. 310.

Our action here may be governed by either one or the other of the procedures above mentioned or it may be determined by the light of our experience. On the one hand we know that many representative forms differing only in size intergrade and are therefore properly classed as subspecies. On the other, we know that size alone is in some cases a specific character and that species differing only in size nest in the same area without intergrading. From Bolivia to eastern Colombia two Toucans (*Ramphastos curvieri* and *R. culminatus*), which are minutely alike in color and differ only in size,¹ occur together without intergrading. The difference between them is not extremely pronounced, but it is obviously sufficient to keep the two apart as distinct species. Now it happens that two other Toucans (*Ramphastos ambiguus* and *R. abbreviatus*) are found which also differ from each other only in size. In this case, however, their ranges do not coincide, the larger bird occurring in the Subtropical Zone of eastern Colombia, the smaller in the Tropical Zone of western Colombia. Whether or not their ranges are connected I do not know. Meanwhile shall we treat them as species or assume that if their ranges were connected they would intergrade and hence rank them as subspecies?

If the two Toucans first mentioned had not shown us that to them mere size may make a species, I confess I should treat these two representative Colombian Toucans as races on the assumption that they did or would intergrade, but reasoning by analogy I accord them specific rank.

In Central America two species of Flycatchers of the genus *Myiarchus* are found associated which differ only in size, and that so little that Ridgway,² after naming one of them as distinct from the other expressed doubt of its validity. Bangs,³ however, has shown that they are distinct, and in this belief he is supported by Miller and Griscom who have met both birds in life. Possibly both Toucans and Flycatchers may possess notes and habits which distinguish them.

A more familiar illustration of representative species which differ only in size, plus the presence in one of a slight whitish

¹ *R. culminatus* averages, wing, 199; tail, 146; culmen, 123 mm.

² *R. curvieri* averages, wing, 242; tail, 155; culmen, 172 mm.

³ *Myiarchus nultingi brachyurus* Ridgw., Bull. 50, IV, U. S. N. M., 1907, p. 630.

⁴ Proc. Biol. Soc. Wash., 1909, p. 34.

margin on the wing-coverts which is absent in the other, is afforded by our Black-capped and Carolina Chickadees. In spite of the fact that these two birds more closely resemble each other than do hundreds of subspecies, and that their ranges are not separated, they do not intergrade. Here we know that there are differences in voice markedly apparent to our ears and doubtless more so to Chickadees'.

Other well-known cases of species which are distinguished wholly or almost wholly by size are supplied by the Greater and Lesser Yellow-legs,¹ Hairy and Downy Woodpeckers, Common Crow and Fish Crow, and here also we know that there are recognizable differences in voice.

Notwithstanding these and similar instances it is certainly customary for representative forms differing only in size to intergrade if their ranges are connected, and when intergrades are lacking, we are, I think, more warranted in ranking them as subspecies than as species. A distinction, however, should be made between difference in size and difference in proportion. In the first, all the parts commonly used in comparison, bill, wing, tail, tarsus, etc., may show the same relative variation in size. In the latter, their variations may be disproportionate, or one member may be larger, another smaller, than those of the allied form, and such instances are more complex, less explicable than those in which the variations are all in the same ratio.

VARIATIONS IN COLOR.

The color characters which distinguish representative forms from one another may be roughly classified as differences of degree and differences of kind. The first includes those variations in intensity of color which we have learned to associate with climatic environment and which are so strikingly illustrated by the classic cases of the Song Sparrows and the Horned Larks.

A very large proportion of our subspecies are based on these differences in degree of color. Increase in the color of plastic, responsive species so commonly accompanies increase in rainfall,

¹ In this connection, however, reference should be made to J. T. Nichols' description of the skeletal differences between these two species and particularly to his suggestive comment that they are not so closely related as their "similarity in plumage would lead one to suppose" (Auk, Oct. 1923, p. 594).

and the reverse so frequently accompanies decrease in rainfall, that we have come to consider the relation between humidity and dark colors, and aridity and pale colors, as one of cause and effect. Thus the systematist can tell with some approximation to truth the annual precipitation in a given region from an examination of its breeding Song Sparrow. The characters separating representative forms of this kind are apparently the expression of an existing environment. When, therefore, the environments, so to speak, intergrade, we may be reasonably sure that the forms to which they have given rise will also merge; and under such conditions it is customary to rank them as subspecies without the confirmation of intergrading specimens. But again, I ask, when the ranges of such forms are separated, prohibiting fusion by contact, and when the birds are too unlike each other to intergrade by individual variation, how shall we classify them?

The systematist to whom the fact of non-intergradation is a sufficient test replies "as species;" but I am convinced that it is often biologically incorrect and misleading to follow this course.

Is the Towhee of Guadalupe Island any less a race of *Pipilo maculatus* because its range is insular and hence isolated? Is the Horned Lark of the Bogotá, Colombia, Savanna any less a race of *Otocoris alpestris* because its range is separated from its nearest relative by all Central America?

To rank these birds as species is, to my mind, not only biologically false but it results in the adoption of a nomenclature which to an extent conceals their origin and relationships.

In assuming that representative forms of this kind would intergrade if their ranges adjoined, we are on safer ground than with forms differing only in size. Birds which resemble each other in everything but size we have seen may live together as distinct species, but I do not recall an instance of two birds differing only in degree of color being associated as species. It appears, therefore, that this type of differentiation is racial or subspecific rather than specific in character and representative forms distinguished by it may be expected to intergrade.

It is sometimes difficult to distinguish between the cumulative effect of differences of degree and differences of kind in color, as well as in pattern. Increased pigmentation may result in such

excessive deepening of tone as to give an apparently new color, and in such change of area as to produce an essentially different pattern. Examples of these types of differentiation are shown by the Song Sparrow (*Melospiza*), Horned Lark (*Otocoris*), Seaside Sparrow (*Passerherbulus*), and many other species.

Such characters, though far more pronounced than many which separate unquestionably distinct species, are still subspecific in their origin and nature, and their possessors may be expected to intergrade if directly or indirectly their ranges are connected.

When the characters distinguishing representative forms become so pronounced as to be actually different colors they are usually accompanied by change in pattern as well. It is therefore difficult to draw a line between these two types of differentiation. However, among North American birds, the Magpie and Yellow-billed Magpie, the Myrtle and Audubon's Warblers, the Maryland and Belding's Yellow-throats, are examples of representative species which differ in color, but agree essentially in pattern of coloration.

VARIATIONS IN PATTERN AND FORM.

Familiar illustrations of representative forms among North American birds, which differ from each other chiefly in pattern of marking, are the eastern and the western Towhees (*Pipilo erythrophthalmus* and *P. maculatus*), the Mourning and Macgillivray's Warblers (*Oporornis philadelphia* and *O. tolmiei*), the Canada Jay and Oregon Jay (*Perisoreus canadensis* and *P. obscurus*). Although each of these birds more nearly resembles its representative than do many undoubted subspecies, the character of their distinguishing differences has won for them recognition as species.

It seems evident that the evolutionary influences which produce these qualitative differences of color and form are not the same as those to which we may attribute quantitative variations in the same color. The former are mutational in character and appear to be the external expression of internal or germinal processes stimulated by unknown factors, past or present; the latter seem to be the obvious product of an existing climatic environment.

The differences in color or pattern separating two species may be less in quantity than those which distinguish two subspecies, but they are obviously unlike in quality and the birds exhibiting

them give proof of the truth of this belief by living together, or in adjoining ranges without intergrading.

This fact, therefore, must be taken into consideration when in the absence of specimens and detailed information in regard to range, we attempt to determine the probable relationships of two representative forms.

OTHER FACTORS IN THE PROBLEM.

Aside from the extent and nature of the characters separating representative forms there are other factors to be considered in forming an opinion of their relationships.

Differentiation in but one sex.—The differentiating characters of both species and subspecies may be shown by only one sex, either the male or the female, without affecting the status of the form. Thus the males of representative forms may be exactly alike but if the females show those differences in color and pattern which we commonly consider of specific value, then, notwithstanding the similarity of the males, the two birds should rank as species. The same rule applies when the males are unlike and the females alike.

Intergradation through a common ancestor.—It sometimes happens that two forms which have departed from a still existing common ancestor by different geographic routes, and have developed different characters subsequently meet without intergrading. Let us assume, for the sake of illustration, that a still existing Meadowlark of the Rio Grande region is the common ancestor of both the eastern *Sturnella magna* and the western *Sturnella neglecta*. These two forms we know meet in the Mississippi Valley without intergrading.¹ Intermediates are occasionally found, perhaps the result of crossing, but there is no fusion, both forms retaining their distinctive markings and uttering their quite unlike calls and songs even when their breeding ranges overlap.

In such cases birds may be subspecifically related through a third form in one part of their range, and specifically distinct in another. Our system of nomenclature is not sufficiently comprehensive and adaptable adequately to express this kind of relationship.

¹ The relationships of these birds is treated at length in Bull. Am. Mus. Nat. Hist., XXII, 1900, pp. 297-320.

In the case I have mentioned the circumstances are pronounced because the two forms actually meet in nature. There are, however, many others in which the biological problem involved is essentially the same, but in which the extremes of a connected series of intergrading races are geographically remote from each other. Under this circumstance we are less apt to ask whether they would meet as subspecies or species.

Assuming, again for the sake of illustration, that our twenty-odd races of Song Sparrows form a connected series of subspecies, it seems improbable that the comparatively small, pale *Melospiza melodia fallax* of southeastern California would intergrade, for example, with the large, dark *Melospiza melodia insignis* of Alaska.

It is not, of course, to be expected that every subspecies in a large, widely differentiated group is subspecifically related to every other race in the group. Nevertheless, even when through the exigencies of distribution they meet without intergrading and thus conform to our chief requirement for specific standing, it seems proper that we should recognize the continued existence of a common ancestor by treating them trinomially.

Intergradation by hybridization.—Intergradation by hybridization unlike intergradation by geographic variation is accomplished regardless of climatic conditions along the line of contact of the ranges of the hybridizing forms. In racial intergradation occasioned by the action of environment, it is customary to find only intergrades in the area of intergradation.

When intergradation is due to hybridization it is customary to find typical specimens of each of the parent forms as well as hybrids between them in the intergrading area. The Bronzed Grackle, for example, breeds from Texas north to Great Slave Lake and Newfoundland without exhibiting any appreciable variation but in a comparatively narrow strip from southern New England southwest along the Alleghanies, where its range meets that of the Purple Grackle, it evidently intergrades with that species by hybridization.¹

Again, the Yellow-shafted and Red-shafted Flickers hybridize where their ranges meet throughout an area extending from Texas

¹ For the data on which this statement rests see Bull. Amer. Mus. Nat. Hist. IV, 1892, pp. 1-20.

along the western border of the Plains to Canada and northward to British Columbia.¹ In at least a portion of this area (Wyoming and Montana) hybrids are the prevailing type. Here, although complete intergradation occurs, the fusion of the two forms has not yet produced a uniform intergrade.

On a lesser scale hybridization also occurs with more or less regularity between the Blue-winged and Golden-winged Warblers chiefly at the junction of their ranges from northern New Jersey to the Connecticut Valley, and casually to eastern Massachusetts. The Black-capped and Carolina Chickadees also hybridize, Mr. W. De W. Miller tells me, where their breeding ranges meet in central New Jersey.

In these and similar instances both parents and their hybrid offspring are found in the area of intergradation, and they thus conform to the conditions which distinguish intergradation by hybridization from intergradation by geographic or environmental variation where only the connecting intermediates are found in the area of intergradation.

Of the cases mentioned no ornithologist would question the specific distinctness of the two Flickers and two Warblers. But it is obvious that their marked differences in color and in pattern are accorded greater significance by the systematist than by the birds themselves. Certainly they are not sufficient to prevent these species from freely mating and producing fertile offspring. It is clear therefore that they are organically more closely related than their superficial unlikeness indicates. In notes and habits the Flickers are alike, the Warblers much alike, facts which no doubt have an important bearing on their mating.

The whole subject is far too wide to be adequately treated in this connection and it is introduced chiefly to illustrate the difficulties which the systematist encounters in attempting to employ nomenclature consistently. If we are to be governed by our own definition of a subspecies as an intergrading form, the Red-shafted Flicker would be known as *Colaptes auratus cafer*, the Golden-winged Warbler as *Vermivora pinus chrysoptera*. But whatever the birds may think, it would be difficult to convince the systematist that both Flickers and Warblers are not distinct species.

¹ See Allen, Bull. A. M. N. H. IV, 1892, pp. 21-44.

Accepting therefore our artificial standards we may treat these comparatively rare cases as exceptions to the rule and continue to rank the hybridizing parents as specifically distinct. But there will always be cases of intergradation which some ornithologists will attribute to hybridization, others to the action of environment, and their nomenclatural treatment will vary accordingly.

SUMMARY.

Following this superficial review of the more important evidence to be considered in the case of species *vs.* subspecies, I append a summarized statement of the criteria which, in default of specimens, may aid us in reaching a conclusion regarding the status of representative forms.

First, the nature of their differentiations; whether they are positive or comparative in character.

Second, the degree of difference attained.

Third, the relations in space and time of their ranges; whether they are connected or separated, and if separated the extent and nature of such separation.

Fourth, the relations in their respective ranges of the environmental factors which appear to be responsible for the differentiations exhibited whether or not they merge.

Fifth, the relative plasticity of the species and of the group to which it belongs.

Sixth, relative adaptability in habit permitting continuity of range under a widely varying environment, as with the Song Sparrows, for example.

Seventh, information to be derived from the study of other birds and other organisms in the areas concerned.

Eighth, probable lines of descent with relation to the existence or non-existence of a common ancestor.

Ninth, similarity or divergence in habit and in voice.

Finally, while admitting that the relationships of representative forms can be learned conclusively only by the study of adequate collections from throughout their ranges, I nevertheless maintain that the experienced systematist employing the criteria here mentioned can, in most cases, more correctly predicate their status than if he were to act in conformance with certain rules.

And I am convinced that the systematist who will thus treat his specimens as exponents of their environment will make a far more valuable contribution to biology than he who regards them merely as objects to be classified and named.

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DIVING OF GREBES AND LOONS.

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MR. EDWARD H. FORBUSH in a preliminary paper in the 1921 Bulletin of the Essex County Ornithological Club, and in an extensive one,—Bulletin No. 8, 1922, of the Massachusetts Department of Agriculture,—has presented a great mass of evidence on the subject of the under-water use of the wings and feet in Grebes and Loons and some other birds as a result, mainly, of a questionnaire sent by him to “accredited observers of the Division of Ornithology, and Fellows, Members and Associates of the American Ornithologists’ Union.” One must conclude, if all this evidence is equally reliable, that it is a matter of indifference or of individual variation whether the feet alone or the feet and wings are used by Grebes and Loons, but that the majority use their wings under water. As I have studied this matter for some years and have published a paper on it in 1909,¹ I have been interested to analyze these reports of Mr. Forbush, for their perusal leaves one, I believe, in a confused and false state of mind, and I am sure that he would be glad to have this confusion cleared away, if possible. I am inclined to think I am anticipating him in this analysis for he calls even his Department Bulletin “a preliminary report.”

Before attempting this analysis, which I have limited to Grebes and Loons, one should bear in mind several general considerations. A good observer should of course have no preconceived bias towards either side in a controversy, but, in observations of diving birds, which must be made in brief and often unexpected instants, he must hold clearly in mind the possibilities, else he may see only

¹ The Use of the Wings and Feet in Diving Birds. ‘Auk’ XXVI, 1909, pp. 234-248.