THE SPECIES CONCEPT IN ORNITHOLOGY

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PART I

The choice of this topic was dictated by selfish motives. For some time questions about species have bothered me. Occasionally, too, others have posed such questions which I have been unable to answer — and in some unfortunate cases have answered anyway. It has been gratifying to me that my rather restricted research on this topic has given me the answers I have sought. It has in fact destroyed some of the illusions I had about species and species formation in the past, ideas which I thought I was taking from my less formal reading on this topic.

At the outset it is appropriate that I point out that I accept the basic ideas of evolution as fact, not hypothesis. Until recently I thought that this was something virtually every person with a smattering of experience or training in biology accepted. That I have now encountered even biology teachers who either dispute this or are unwilling to accept it as more than hazy theory leads me to make this statement so that my comments will be taken in the light of this acceptance.

The central question here is, of course, what constitutes a species? Interestingly enough the answer to this question would have called for not a paper but a debate before 1940. Since then, however, ornithologists have been drawn together under the leadership of Ernst Mayr and have reached fair agreement on a basic species definition. Because this definition has evolved from differing original concepts, we will best consider it in its appropriate historical perspective.

The basic difficulties in the species concept arise in the virtually opposite approaches to the problem of two of the greatest biologists of all time, Linnaeus and Darwin. Linnaeus systematized the study of natural history with his classification of the plant and animal kingdoms. Inherent in his classification is his own belief, later modified, in the "reality, objectivity, and constancy of species." Contrast this with Darwin's idea of the fluidity of evolution. On the one extreme we have separate discontinuous groups called species, each created at Genesis. Morphological (size, shape, color) differences mean delegation to a different species category. On the other extreme we have the Darwinian view of continuous integradation from one species to the next. This view, carried to its logical conclusion, would throw out the entire species classification. This idea of intergrading populations was expanded by students of Mendelian heredity right down to about 1910, the species falling into almost complete disrepute in the biology laboratory.

That their theories have been modified should not detract from our respect for the stature of these two great scientists. Careful examination of their writings shows them to be much more modern in their views — and usually more moderate also — than their followers. Linnean classification spelled the end to the older biological concept of one species giving direct rise to another species, and to the philosophical idea that only individuals exist. It also provided a framework for experimentation and recording of

local data for comparison with data from other regions. Without this wonderful tool we would have very few modern advances in biological science, perhaps even fewer bird watchers. Darwin, fine field naturalist that he was, noticed the discontinuities that appear in nature — the lack of intermediates between species — and gave serious consideration to this problem. In this respect he is the first of a long line of natural historians who saved the important species concept and who in modern times have made it central to biological studies.

During the first three or four decades of the present century every scientific discipline had its own definition of the species, several being in direct contradiction. Species definitions were as varied as the description by the three blind men of the elephant: one describing it as a massive column, the second as a rope, and the third as a giant snake, the men having approached the beast from different directions. That a single rather well accepted definition should evolve from this situation is at once a severe criticism of the many definitions offered by paleontologist, biologist, cytologist, geneticist and others,, and at the same time a commendation of the unifying leadership much of which came from the field of ornithology.

Let us examine now Mayr's 1940 definition of species: "groups of *actually or potentially interbreeding natural* populations which are *reproductively isolated* from other groups." Within this fifteen word definition are most of the answers — and most of the problems too. The concept is virtually completed by Charles Sibley's statement that "species are gradually formed from pre-existing species by the accumulation of differences *in isolated populations* through the fixation of micromutations."

REPRODUCTIVELY ISOLATED. The basic test of a species unit is a biological test. It is not a matter of comparison of plumage in birds or skin color in humans. Within this test is the difference between what is called the "old systematics" and the "new systematics." It is certainly true that morphological differences, external and internal, usually go hand in hand with reproductive isolation. And thank goodness! As a matter of fact it is necessary that the first classification be concerned with external characters, that only after the original delineation is established can the biological test be applied. Most families are not at the stage of the ornithological families. For example, of the forty-four species of fruit flies known in Texas in 1942, only seven were known in 1921. More species are discovered every day. Birds on the other hand are virtually finished by the standards of the old systematics and are almost uniquely ready for the more mature approach of the new.

This modern concept of the species has meant that the number of bird species has been cut from about 20,000 to about 8,500. Mayr estimates that less tran two per cent (170) are still to be found. Thus it is changes from the old morphological classification to the new biological classification which is the basis for most of the revisions in nomenclature as in the A. O. U. check list.

ACTUALLY OR POTENTIALLY INTERBREEDING NATURALLY. Here we have two cases: sympatric (occurring together in nature) and allopatric (ranges not overlapping) species. Few problems arise in the case of sympatric species. In the case of the warbler genus *Vermivora,*

nine species with thirty-six (n(n-1)/2) species gaps, only two (Blue-winged and Golden-winged Warblers) are open to question on the basis of reproductive isolation. This is six per cent. In the *Dendroica* genus, twenty-three species and 253 gaps, again only two (0.5%) are questionable so there is little difficulty.

Allopatric species (species geographically separated) are a matter of judgment. Whether these birds would pair and product non-sterile offspring if brought together is a matter of question. It is not enough to place the birds in a cage. Even intergeneric matings have been produced in this way. Such an approach does not answer the question, and we can go back to what Darwin said in 1859: "In determining whether a form should be ranked as a species or a variety, the opinion of naturalists having sound judgment and wide experience seems the only guide to follow." The competent naturalist must decide if the two groups are potential breeders. Mistakes can be and are made.

DIFFERENCES ACCUMULATED IN ISOLATED POPULATIONS. Here is the really interesting and indeed unsuspected aspect of the species. At some time in the history of the group it must have been separated from other birds of the same lineage. We can see this process as it takes place by means of a series of diagrams:

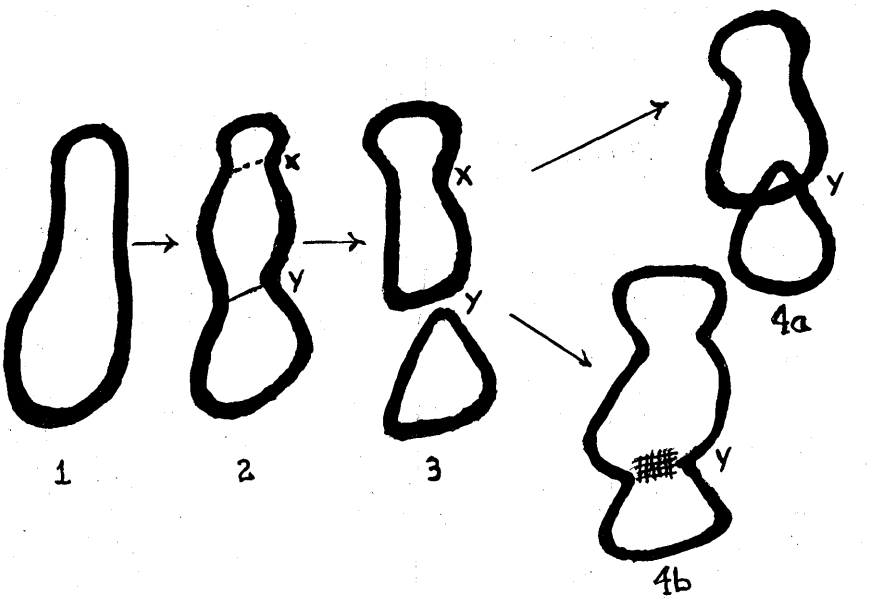

Figure 1

Here is the history of species formation. At 1 (in time) a species is uniformly distributed. By 2 some factors have tended to separate the original population into three groups, the division at x brief or incomplete leading only to the possible development of a racial difference, the division at y leading in 3 to complete separation. 3 is the case of allopatric popula-

tions. The secondary contact in 4a and 4b at y produces sympatric (species geographically overlapping) populations. In 4a the case is clear-cut. The separation has been long enough to make the process of speciation complete. In 4b there is hybridization at y, showing that the process is incomplete.

In this last case no hard and fast rule can be made. It is entirely a matter of the degree of hybridization whether the two populations are considered subspecies or species. An example of how complex this problem can become is the case of Mexican towhees studied by Charles Sibley. His speculative history of the situation as it evolved is that a southern part of the original species became isolated and tended to distribute itself in relict populations at higher altitudes. After some time the northern population invaded the southern area making three zones of contact with the southern populations. In the southernmost zone of contact, Oaxaca, there is no hybridization. At Mount Orizaba there is a slight hybridization and at Cerra Viejo, the northernmost point of contact, there is complete hybridization. In the last two areas the separation was not long enough to complete the speciation process. (In time here is included mutation rate and degree of selection pressure.) Here is a tough decision.

In summary then the species is based on biological distinctiveness rather than morphological differences so it is a biological rather than a morphological problem. The species is made up of populations rather than individuals, but it is defined by isolation from other populations rather than by relations among its own populations.

THE REGINA, CANADA MEETING

LILLIAN C. STONER

The Regina, Canada, meeting of The American Ornithologists' Union August 25-30, 1959 at Saskatchewan Natural History Museum was well attended by people coming from widely scattered localities. In fact the registration of 389 was the next to the largest attendance in the history of this organization.

The distinction of coming the greatest distance goes to M. A. Badshah, of the Madras Forest Service, South India, and to J. B. Alvarez of the Philippines. Other ornithologists came from California, Louisiana, Texas, Florida, Eastern and intervening states as well as many provinces in Canada. Included in this were 12 members of our Federation of New York State Bird Clubs, Inc.; namely six from Buffalo, two each from Albany and Ithaca, and one each from New York City and Pittsburgh, Pennsylvania.

Papers were presented by the following four Federation members during the three day paper sessions.

Harold D. Mitchell of Buffalo Ornithological Society, Buffalo, used motion pictures and slides to illustrate his paper entitled "A Nesting Involving Prothonotary and Yellow Warblers".

Ralph S. Palmer, New York State Museum, Albany, spoke on "Reproductive Pattern of the Loons".

Kenneth C. Parkes, Carnegie Museum, Pittsburgh, Pennsylvania pre-