THE SPECIES—THEN AND NOW[1]

BY DEAN AMADON

CHARLES DARWIN was particularly interested in speciation and taxonomy. This is evident both from the title he chose for his great work on evolution and from the monographs he wrote on the barnacles collected during the voyage of the '*Beagle*.' Although evolution had a prominent place in biology from the time of Darwin on, systematics has had a more checkered career. For many years new collections poured in so rapidly from all quarters of the globe that the harried taxonomist merely found time to publish brief Latin descriptions of new species or to puzzle over the endless questions of nomenclature. Meanwhile, laboratory genetics and related phases of biology advanced very rapidly, so rapidly that their results were not integrated with those of evolution or systematics.

This unfortunate state of affairs began slowly to improve a generation ago, but the rapid development of what is known as the "new systematics" has come in the last 15 or 20 years. Ornithologists played a prominent part in this movement, perhaps because birds are very well known taxonomically. As a result, the student of this group has been free to study such problems as variation within the species. A group of American ornithologists was among the first to call attention to such variation by the use of subspecific names. Long before the close of the last century Elliott Coues in his famous "Key" introduced such innovations as listing the Florida Jay as a race of the western Scrub or California Jay. Half a century was to pass before other ornithologists accepted this and similar proposals.

So long as the taxonomist was concerned primarily with supplying a name for each specimen to come before him, attention centered upon the individual specimen. When he began to study geographical variation, attention shifted from the individual to the population. Description of average or fluctuating differences became the order of the day. This point of view proved very enlightening, since speciation itself was found to be a process of gradual change in geographically isolated populations. Thus, the new systematics came into being when the taxonomist again became a student of speciation, just as Darwin had been. Today, he is aided by many discoveries in genetics, biometrics, and other fields that were not available to Darwin or his contemporaries.

[1] Part of a Symposium Presented at the Buffalo Meeting of the A. O. U., October, 1949.

With the shift in emphasis from individuals to populations, the older morphological definition of the species became unsatisfactory. Some species were found to contain very distinct geographical populations which, nevertheless, interbreed and intergrade completely wherever they come into contact. In other groups, perfectly good species, which rarely or never interbreed, are so similar morphologically that it is difficult to separate them. The small American flycatchers of the genus *Empidonax* are an example, but still more extreme ones are provided by certain species of insects that are completely inter-sterile and yet so similar that they cannot be separated by ordinary taxonomic comparisons.

Although complete or nearly complete sterility is proof that speciation has occurred, the converse is not true. Sterility is often a more or less incidental result of the genetic drifting apart of two populations and is uneven in time and degree of appearance. Many species still capable of producing at least first generation hybrids are distinct enough to be placed in different genera by most taxonomists, and in at least one instance species now placed in separate families produce such hybrids (Guineafowl, *Numida meleagris*, by Domestic Fowl, *Gallus gallus*). When hybrids between two populations are less viable than either of their parents, natural selection may accelerate the appearance of sterility, or it may work to set up other isolating mechanisms to prevent crossing, such as differences in the breeding season or in courtship or mating behavior.

Among birds, differences in courtship are often important in preventing hybridization. The Mallard and Pintail, *Anas platyrhynchos* and *A. acuta*, for example, very rarely hybridize in nature, but under crowded or sexually unbalanced conditions in captivity hybrids are produced and these are fertile.

A somewhat similar situation may occur in nature when an individual of one species occurs as a rare straggler in the range of another. Lodge (1946: 72) has written of the re-introduced Capercaillie, *Tetrao urogallus*, in Scotland: "Sometimes capercaillie make sudden movements into fresh territory, and when this happens it is the females which move first, to be followed by the cock birds the next year. It is quite common to find that in the first breeding season in their new place they will mate with blackcocks [*Lyrurus tetrix*] and produce hybrids." A somewhat similar situation in two American grouse has been found by Baillie (1949: 167–168, and oral communication). Manitoulin Island, Lake Huron, was recently colonized by both Prairie Chickens, *Tympanuchus cupido*, and Sharp-tailed Grouse, *Pedioecetes phasianellus*. The latter occur in much smaller numbers

and, presumably as a result of their failure to find mates of their own species, a high percentage of the Manitoulin grouse thus far examined show evidence of hybridization.

In grouse the females come to the display grounds of the males and mating occurs with very little preliminary association between the sexes. Similar mating habits are responsible for the high incidence of hybrids in such families as the hummingbirds (Trochilidae) and birds of paradise (Paradisaeidae). The elaborate plumes and courtship performances of the males of these families, differing from species to species, doubtless have been molded through natural selection and prevent much hybridization, but they are not completely effective under all circumstances.

Hybridization by stragglers within the range of another species may occur even in birds in which mating is usually delayed for some time after pair formation. Nichols (1947: 172) has published information concerning a Cerulean Warbler, *Dendroica cerulea*, which was observed to build a nest and lay eggs near Lyons, New Jersey. "No male was seen and no young were hatched. It is probable that this female wandered far from the usual breeding grounds and, at the proper time, followed the normal nesting pattern but, of course, the eggs were infertile." Here hybridization did not occur, but it is easy to visualize how such an incident might favor it. It is quite probable that hybridization under such conditions produced Sutton's Warbler, *Dendroica potomac*, although one of the supposed parents, *Dendroica dominica* has not yet been found within the range of the other, *Parula americana*, in the relatively small area in West Virginia where Sutton's Warbler is believed to summer.

Making due allowance for such incidental hybridization as that discussed above, Mayr and others have defined the species as a population whose members *freely* interbreed with one another but do not do so with the members of other populations under natural conditions. In other words, a species is a sexually isolated population. There is no difficulty in deciding that the Mallard and Pintail or the Prairie Chicken and Sharp-tailed Grouse hybridize so infrequently in nature as to have no real effect on their deserved status as species. It seems improbable that the few genes of another species that might be acquired by such crossing (assuming fertility of the ensuing generations) would be of much importance. In some plants, however, such "introgressive hybridization," as it is called, is of importance. Sutton's Warbler may just possibly represent Yellow-throated Warblers in which some genes of the Parula Warbler have been acquired by hybridization followed by breeding back with Yellow-throated Warblers.

It is possible that even under natural conditions certain areas, in particular small islands, may rarely act as natural "cages" wherein two species elsewhere reproductively isolated hybridize to form an intermediate population and perhaps eventually a species. Some of the Galapagos finches of the smaller islands have an intermediate appearance and may have originated in this manner, although Lack (1947) is now inclined to doubt it and offers an ecological explanation. Subspecies circles such as those found in the Herring Gull group or the Old World *Parus major* group wherein the terminal links meet without interbreeding offer no particular difficulties. In other cases the reasons for geographical variations in the hybridizing behavior of two populations are more complex. The Eastern and Western Meadowlarks, *Sturnella magna* and *S. neglecta*, are said to interbreed in some areas but rarely, if at all, in others. Since the attainment of sexual isolation, even though it is the crucial step in speciation, is a gradual process, we cannot expect that it will occur simultaneously throughout populations that come in contact over long distances or in several different areas.

Enough has been said to indicate that it is not always easy to determine whether two populations interbreed freely, producing fertile hybrids, and hence belong to the same species. When morphological analysis indicates complete intergradation the burden of proof would seem to be upon those who maintain that two species are involved. The genetic basis of the variable characters will, in such cases, determine just how gradual the intergradation can be. The existence of differences in this respect is reflected in the concept once in vogue that species (may) hybridize but subspecies intergrade. As Miller (1949) has emphasized, there is no basic difference between subspecific and specific characters, either morphologically or in mode of inheritance. This idea was discarded along with the morphological concept of the species. Indeed, conspicuous characters, with a simple alternating mode of inheritance but often without any taxonomic significance at all, are found in color phases and other forms of polymorphism.

In certain populations of *Junco* discussed by Miller (1949) extensive hybridization occurs but is limited to a rather narrow zone not marked by abrupt ecological change. This, Miller considers to be an indication that hybridization is not undertaken freely or that the hybrids have reduced fertility or viability. Regardless of whether we agree with him that it is best to call these populations species, careful study of such cases is needed. This may help us determine whether differentiation in populations which have always been in contact does, with

any regularity, proceed on to speciation or whether a period of complete isolation is required. Certainly many of the species which now meet and hybridize to a limited extent were once completely isolated. They may be brought into contact again either by natural phenomena such as the melting of glaciers (Rand, 1948) or by man-made changes such as deforestation or irrigation.

The Yellow and Red-shafted Flickers, *Colaptes auratus* and *C. cafer*, interbreed freely over a wide zone wherever their ranges come into contact, and it is easy to visualize circumstances under which their differences could be entirely swamped out. It has been suggested to me that they are species whose courtship patterns happened to remain identical, permitting free hybridization. This, in itself, would conflict with the biological concept of the species.

This concept is sometimes interpreted to mean that "biological" (non-morphological) differences between populations, such as those in voice, habits, etc., assume added significance. This is true only to the extent that such differences act as isolating mechanisms and keep populations from interbreeding. Biological differences are often found in populations not even subspecifically distinct. The real criterion is that a species must be effectively isolated reproductively, not that it must possess any particular level of differentiation in either morphological or non-morphological characters. If one considers the birds of a single region, this reproductive isolation of species is one of their most obvious characteristics and gives them an objective reality not possessed by any other taxonomic category. It is only when we consider species in the process of segmenting geographically into new races and species that difficulty is sometimes encountered in deciding whether speciation has been completed.

The above remarks are not meant to minimize the importance of differences in voice or behavior to the taxonomist, particularly in difficult genera such as the American flycatchers. If interpreted with discretion, behavior data are perhaps even more helpful at the level of genus or above, as shown by such contributions as that of Delacour and Mayr (1945) on the classification of the waterfowl.

Thus far we have considered forms whose ranges come into contact at least marginally. Mayr (1948) is of the opinion that subspeciation and speciation in sexually reproducing animals always requires geographical isolation, and in the vast majority of cases isolation must be complete or almost complete to permit differentiation to proceed beyond the subspecific level. We thus have the near paradox that although breeding behavior in nature is usually the only test of specific status, a great many forms whose status is doubtful do not

occur together. We can then only study the amount of variation in the group in question and decide arbitrarily whether a particular isolated form is best considered a species or a race. There is no way of *proving* whether the Ipswich Sparrow, *Passerculus princeps*, of Sable Island is a race of the mainland Savannah Sparrow, *P. sandwichensis*. Although as a rule relationships are perhaps best expressed by listing geographical representatives as subspecies whenever possible, great caution must be used in difficult genera containing many similar species. On such grounds one may seriously question Hellmayr's decision that the Northwestern Crow, *C. caurinus*, is a race of the Fish Crow, *C. ossifragus*, or that the American Crow, *C. brachyrhynchos*, is a race of the European Carrion Crow, *C. corone*.

Exceptions to the above statements are provided by related forms proved to be sterile or nearly so by breeding experiments. So far as birds are concerned, this has rarely been demonstrated except for forms so distinct their specific status is scarcely open to question. This is true of the Wood Duck, *Aix sponsa*, and the Chinese Mandarin *A. galericulata*, but their failure to produce fertile eggs from matings in captivity was a surprise, in view of the many hybrid waterfowl known from less closely related parents. Yamashina's cytological studies have now shown that this sterility in the genus *Aix* is due to incompatibility of the chromosome sets of the two species, a condition that arose, perhaps more or less by accident, during their long period of complete isolation.

This discussion has sought to emphasize the important part played by ornithologists in the development of the modern species concept and the present status of this concept. The contribution to the new systematics of those not primarily ornithologists has been mentioned only casually. Needless to say, the taxonomist working with birds will be greatly aided both in the planning and interpretation of his work by maintaining a measure of familiarity with the systematic aspects of genetics, cytology, embryology, serology, and other fields of biology. The non-taxonomist will probably find comfort in the emphasis in recent studies of speciation upon aspects of behavior and ecology that can only be answered by field studies of living birds and on the tendency to de-emphasize the subspecies which has followed the realization that almost every population or segment thereof can be shown by careful analysis, statistical or otherwise, to possess some "subspecific" characters.

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