

SOME CONCEPTS OF HYBRIDIZATION AND  
INTERGRADATION IN WILD POPULATIONS OF BIRDS

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A PERSISTENT conception among a considerable group of taxonomists holds that intergradation and hybridization are contrasting phenomena and that the terms should be used as antonyms. They regard an intergrading situation as denoting involvement of two races and hybridization as involving two species. Accordingly, all one needs to do is to find out which phenomenon is displayed where two forms come in contact, and the troublesome borderline cases between race status and species status are thereby correctly indicated and classified.

This chain of reasoning I regard as fallacious, for it is an oversimplification of the factors and it does not clearly emphasize the best criteria for species. This incorrect reasoning seems to be an outgrowth of a view now abandoned by nearly all geneticists and students of evolution that species possess one sort of character and races another, or in other words, that species display qualitative differences and races quantitative differences which blend or intergrade. The truth of the matter is that both types of characters may differentiate races from races and species from species and that there is no sharp distinction between these kinds of characters anyway.

Intergradation in its typical manifestation in continental areas indicates two things: (1) blending inheritance of the characters involved, and (2) frequent, if not free, interbreeding of individuals. Hybridization indicates: (1) non-blending or alternate type of character manifestation, usually with few genetic determiners involved in any one character, and (2) free, or partial, or at least a little, interbreeding. Since the kind of inheritance and the kind of character expression, whether blending or of discontinuous-alternate type, are not decisive criteria of species, what do these situations tell us about the important matter of freedom of interbreeding and subsequent fertility? One implies freedom or something close to it, the other may involve a state of freedom but also a state of rare, sporadic interbreeding. The two situations are thus not clearly contrasted in this important matter.

It is well to look into the exact meaning of the words "hybridize" and "intergrade." To hybridize is to cross or interbreed organisms that are different, whether of varieties, races, species, or genera. How different must they be? The difference may be a matter of eye color, or only of bristle size or number in *Drosophila*. It may involve black or white rats of the same species, or short and tall corn plants. When, in wild populations, we can see that hybridization must have taken

place, we use the term. Hybridization is easy to detect when unit or alternate characters are involved and when parents of very diverse type interbreed. But, in the wild, the fact of hybridization is not easily detected from inspection of the offspring if a bird with a wing length of 80 millimeters crosses with one of 82 millimeters. The phenotypes do not segregate clearly and we can not, from the partial evidence, see that hybridization occurred even though it has. Hybridization takes place in an area of junction (primary or secondary) of weakly differentiated, blending races between slightly different parents just as truly as it does between strongly contrasting parents or between those whose characters segregate well.

To intergrade means to merge or grade through a series of intermediate types. This demands characters that will blend in areas of interbreeding. The emphasis is placed on the type of character. One of our terms then refers chiefly to the mode of inheritance or character expression (intergrade), the other chiefly to the fact of interbreeding (hybridize) which may be of high or low frequency. Hence my view that the two are not antonyms, that one process is often, indeed usually, involved with the other.

Some illustrations may serve to show the interplay of these phenomena. The white-crowned sparrows, *Zonotrichia leucophrys*, of the southern Canadian Rockies recently called to attention by Rand (Auk, 65: 426, 1948) are differentiated by means of the presence (*oriantha*) or absence (*gambeli*) of a black loreal area. The change in proportion of black-lore types increases from the Jasper Park area south to Waterton Lakes in a freely interbreeding series of populations. The characters show no real blending and the population at any one point appears mixed or hybrid. Adults of one type are hybridizing with the other. Yet, the frequency of occurrence shifts gradually along a north-south line; there is gradation in this sense. Because of the evidence of free interbreeding and evident fertility, these forms are correctly regarded as races, even though they show evidence of hybridization.

Comparably, the salt marsh song sparrows, *Melospiza melodia*, of the San Francisco Bay region possess a character of yellow-colored underparts which is lacking in adjoining upland races. There is no gradation in this character, according to Marshall (Condor, 50: 238-239, 1948); it is either present or absent, although when present it fluctuates in intensity. In a short-range geographic gradient, this character becomes less and less frequent as upland areas are approached. Free interbreeding has been fully proved along this gradient; mixed pairs have often been observed. Yellow and white birds thus hybridize, and hybrid populations are produced. At the same

time, these birds display some differentiating features of dorsal coloration which are not of the alternate or discontinuous type. These intergrade in the same populations from one extreme to the other and, as usual in the extremes, there is "normal," but blending, individual variation. There is no doubt here of racial status even though we have hybridization.

The gray-headed juncos, *Junco caniceps*, of the Kaibab Plateau of northern Arizona consist of a population of mixed black- and white-billed birds, the black-billed birds derived from *J. c. dorsalis* to the south of the canyon, the white-billed birds from *J. c. caniceps* in the mountains to the northward in Utah (Miller, Univ. Calif. Publ. Zool., 44: 186-189, 1941). Some intermediate bill types occur, but in general the bill coloration sorts out into a small number of discrete types. In any event, complete freedom of interbreeding occurs in the Kaibab population, and the group presents the appearance of a hybrid swarm. At the same time the gray of the head blends between two extremes in these birds; the group as a whole shows a wide range of variability, but the variations are gradient, with an intermediate average. There are no available breeding grounds immediately north or south in which, as in the preceding examples, the frequency of the alternating characters of bill could gradually shift. Hence we have a single hybrid swarm, not a geographic gradient either of blending or of alternating characters or both. Yet we see complete freedom of interbreeding of the diverse types (no mate preference) that have taken up residence on this isolated plateau; moreover, the group of characters separating the extremes is neither great nor especially complicated. Racial status seems wholly proper.

Other examples may serve to show intergradation where interbreeding is impeded or not free. Theoretically, such situations might arise in areas of continuous distribution owing to differentiating fertility factors or reproductive divergences which would reduce gene flow between organisms that overlap or intergrade in all observable features. Some examples have been noted in groups other than birds, but it is perhaps significant that in birds examples are not evident that do not entail the aiding circumstance of geographic isolation—a most important factor of course in race and species formation.

Loggerhead shrikes, *Lanius ludovicianus*, on the mainland of southern California close to the shore line are intermediate between the coastal population generally and the race on the offshore islands (Miller, Univ. Calif. Publ. Zool., 38: 82, 1931). No passage of shrikes to and from the islands is certainly known or is likely. The similarity of some mainland birds to the island race is probably due to the in-

fluence of a set of environmental conditions along the shore, which are similar to conditions on the islands and which operate on island and mainland birds alike. Here then, we assume, is intergradation caused by grading selective forces of the environment but certainly not involving free interbreeding of the extreme types.

Another instance may be found in the isolated groups of pygmy nuthatches, *Sitta pygmaea*, along the detached mountain tops of southern California (Grinnell and Miller, *Pac. Coast Avif.* No. 27: 320-321, 1944). These discrete populations intergrade very completely in characteristics, yet interbreeding must be very rare between groups as a result of occasional dispersal across the several intervening barriers.

It is rather widely agreed that species usually differ from one another by many more characters than do races. Heritable characters in general are probably most often manifest as blending features, less often as distinct alternate features. Therefore, species which differ by many characters are more likely than races to show some features which will be of the non-blending type and which will yield the obvious picture of hybridization where they interbreed. This general truth is perhaps partly responsible for overstressing the hybrid complex as a sign of species status.

In seeking criteria for classifying the borderline cases between species and race status we obviously should not use the mode of inheritance of the characters involved, but the degree of freedom of interbreeding and the degree of fertility—barriers to free interchange of genic material other than simple geographic isolation. Commonly we are forced to guess whether such barriers exist. Fertility may be lacking even though hybrids occur. Island forms may be widely separated yet, could they be tested naturally, might interbreed freely. A typical picture of contiguous or continuous populations showing intergradation rather well assures that there is no significant bar to gene flow. If there is also transgressive intergradation, overlap through individual variation of every character in insular groups, it is a rather safe assumption that there is potential freedom of exchange. But in instances of hybrid junction we must look with care for the true biological criteria for species, namely for some degree of actual reproductive isolation. Such isolation may be present in the form of lowered viability or fertility, even when hybridization is freely undertaken. I suspect it occurs sometimes where a zone of hybrids between two forms persists as a narrow belt in the face of full geographic continuity and in the seeming absence of ecologic differentiation of the ranges of the parental forms. This possibly is the situation where *Junco caniceps* and *Junco oreganus* meet in southern Wyoming and where *Junco oreganus* and

*Junco aikeni* meet in southern Montana; in the last instance there may also be a partial ethological barrier contributing to the reproductive isolation.

In brief, a group of hybrids linking two forms can neither be assumed to indicate species status because of "hybrid appearance" nor can they safely be supposed, regardless of their number, to indicate full or even partial breakdown of reproductive isolation and hence racial status.

The situation must be completely explored to determine the manner and degree of reproductive isolation, and we should not always expect therefrom a simple positive or negative answer.

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