

ANALYSIS OF SOME HYBRID POPULATIONS OF JUNCOS

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Our progress toward understanding the mode of origin of races and species of animals depends on the success of bringing together the sciences of genetics and natural history. The geneticist must come to appreciate the factors governing distribution, survival, and isolation in wild populations. The naturalist and student of geographic variation must clearly see the genetic picture. We are not without examples of distinctly successful attempts at this synthesis of fields. I think of F. B. Sumner's analysis of a concrete case of intergradation of geographic races of *Peromyscus* and of Dobzhansky's comprehensive treatment of the problem of "Genetics and the origin of species." The latter work is most illuminating, for it is made clear that the wealth of knowledge about inheritance in the fruit fly, *Drosophila*, can be applied to geographic races and wild populations of fruit flies in order to get at the very heart of the method of race origin.

Ornithology has been at the forefront in advancing our knowledge of geographic variation. Can it go farther than it has already by utilizing the genetic approach? Not many wild birds that are geographically variable lend themselves to experimental breeding on a scale that will permit adequate genetic treatment. The outlook is not hopeless, but it is not good. I am of the belief, however, that we can contribute significantly by adopting the geneticist's viewpoints in analyzing intergrades and naturally occurring hybrids, even when we are limited in the extent to which this analysis may be supported by experimental breeding.

In working upon the genus *Junco*, it became apparent to me that some rather favorable conditions existed for studying natural hybrid populations. The very hybrid complexes which Dwight (Bull. Am. Mus. Nat. Hist., vol. 38, 1918, pp. 269-309) earlier thrust into the background as without significance taxonomically prove to be the most important groups from the standpoint of biologic theory. We may consider some of the general aspects of the work on these hybrids without presenting much of the technical detail at this time.

The Gray-headed Junco, *Junco caniceps caniceps*, of the central Rocky Mountain area, through a combination of factors has proved to be the best subject for special study within the genus. Its breeding range is isolated almost completely by unfavorable desert or plains regions, but on small separated mountain areas around the periphery of its general range are small breeding populations that clearly result from hybridization of *caniceps* with other kinds of juncos. These surrounding kinds happen to be either moderately or very well differentiated from *caniceps*, and the hybrid populations are as a result interesting assortments of individuals. On the north, *caniceps* meets the Pink-sided Junco (*mearnsi*) in the northern, somewhat isolated section of the Wasatch Mountains, and in scattered ranges in southern Wyoming. On the west are hybrids with Oregon Juncos (*J. o. thurberi*) in well isolated mountain tops in southern Nevada and southeastern California. In the south are hybrid groups between *caniceps* and the Red-backed Junco (*J. o. dorsalis*), best known from the Kaibab region north of the Grand Canyon in Arizona, but also from certain mountains in northern New Mexico.

These Gray-headed Juncos apparently have no inhibitions in accepting a member of another race or "species" as a mate. While in the field in northern Utah, I became impressed with the random mating of *caniceps* and *mearnsi*. Mixed pairs were taken with young. There seems to be nothing to prevent the complete interpenetration of *caniceps* and *mearnsi* except partial geographic barriers consisting of ecologically un-

suiting regions. It is difficult to imagine a special survival value in the pink sides of *mearnsi* or in the red back of *caniceps* related to the particular environments. There may be physiological features of the two forms that differ, however. Striking also, is the fact that the distinct types, *J. c. dorsalis* and *J. o. pinosus* have been hybridized in captivity.

From an analysis of hybrid groups we may learn something about the association of characters in the organism. Take, for example, wing and tail length. These two dimensions are correlated within all populations of juncos. It might be claimed that their variation is not genetic and that their correlation is due to the immediate impress of the environment on the growth of all the major flight feathers. However, when two strikingly different forms hybridize, whose differences even in dimensions most certainly must in part be genetic, there is shown the same correlation of wing and tail. We must conclude that there are some common genetic factors that control these parts. In view of this evidence, it is understandable why wing and tail have more or less kept pace in the evolution within the genus. They are likely to continue to do so, for if selection pressure favors long wing, it will favor the continuance of factors in the germ line that determine long tail as well.

In hybrid juncos we find that most dimensions and also the intensity of blackish pigment of the hood blend from one extreme to the other. We may be permitted to assume from the extensive experimental analyses of this sort of phenomenon in other organisms, that there are many genetic factors responsible for these characters. The hybrid populations of southern Nevada and northern Arizona average somewhere between the averages for the parental types concerned in each case. They do not show increased variability, but that is exactly the situation we now know to expect in the F_2 generation in multiple factor inheritance where the number of factors is quite large. The samples of twenty to forty birds are not large enough to reveal F_2 segregation.

We may use these blending characters to determine the proportion to which the two parental types contributed to a given population in a small isolated intervening region. For example, on the Charleston Mountains of southern Nevada this evidence suggests that *caniceps* parentage was somewhat greater than *thurberi* parentage. But on the Kaibab plateau *caniceps* and *dorsalis* seem to have contributed equally to the ancestry of the local group. Probably each is still contributing in some measure through the movement of typical individuals into this area.

With this as a background, other characters may be studied which seem to rest on smaller numbers of genetic factors. Between both *thurberi* and *caniceps*, and *mearnsi* and *caniceps* there are distinct differences in the color of the back area. *Caniceps* has a single pigment, a reddish phaeomelanin, that gives the rich mahogany red back. In *thurberi* there is a yellowish phaeomelanin in the bases of the barbules and a dusky eumelanin on the tips of the barbules in a proportion that produces a tan-colored back. *Mearnsi* is similar to *thurberi*, but the yellow phaeomelanin is of slight amount and the tips of eumelanin are extensive. The result is a drab brown back.

In crosses of these forms it is clear that the eumelanin and phaeomelanin pigments are inherited more or less independently. The phaeomelanins, the red and yellow pigments, do not show intermediacy in the crosses; the pigment clearly is one or the other. In the *thurberi-caniceps* hybrids the red apparently is dominant to yellow. In the Charleston Mountain group, the preponderance of red over yellow is far out of proportion to that expected on the basis of evidence of parentage derived from the blending characters. The one experimental hybrid in which the same characters are involved is red-backed (F_1 generation).

The eumelanin in hybrids either is present in full amount, absent on the outer vanes of many of the feathers, or absent entirely. There results from the independent assortment of these pigments some types of back coloration unlike either parent. Most striking is one that is a clear light yellow, owing to yellow phaeomelanin (*thurberi*) and complete absence of eumelanin (*caniceps*).

In some of the mountains in California that lie east of the Sierra Nevada are *thurberi*-like populations, that have had some mixture with *caniceps*. Perhaps some of the Charleston Mountain hybrids have crossed with typical *thurberi* here. On one small mountain top in the Panamint range, the yellow-backed birds are so prominent in the population as to suggest a "new form" of junco. Were it not for our knowledge of the inheritance of the characters concerned, these yellow-backed birds would be very puzzling. Actually we have here a situation that might lead to a new race. All that is needed is a little better isolation and greater homogeneity. Suppose that through fluctuation in population the colony on this small isolated range was rebuilt from homozygous yellow-backed types, or that through inbreeding the other variants were eliminated, a striking insular form would be established. The Panamint hybrid group is one that missed by a narrow margin being a well-characterized natural race. It still has a chance.

In the *caniceps-mearnsi* hybrids, the *mearnsi* yellow pigment is dominant over the red of *caniceps*, the reverse of the situation in *caniceps* and *thurberi*. The eumelanin behaves in the same way.

The sides of *caniceps* are pale gray in contrast to the yellowish and cinnamon pink of *thurberi* and *mearnsi*, respectively. The gray is a eumelanin, the yellow and pinks, phaeomelanin, all rather dilute. In crosses, these pigments do not mix. There is no intermediate pigment and rarely are the two pigments in the same part of a feather. But, some feathers may be gray on part of the web and pink elsewhere, and in the side area totally gray feathers may be mixed with pink feathers. In the *thurberi-caniceps* hybrids the *thurberi* character is more apparent in females than in males. It appears that there is some interaction with sex factors. In most species of the genus females are more given to developing phaeomelanins than are males. The *mearnsi* type of side seems to be dominant over that of *caniceps* in both sexes.

Interesting evidence of interaction of factors is seen in a hybrid from the White Mountains of east-central California. This bird lacks all phaeomelanin of the sides and hence is gray. The head is quite dark, approaching average *thurberi*. The gray sides, which are produced by eumelanin, as is the head, are darker gray than in any *caniceps*. Apparently there are factors present that determine eumelanin as the side pigment. But the intensification factors for the head, that cause it to be black, also intensify the side area. The bird is a curious-appearing individual. Its dark gray head and sides make it appear like a Slate-colored Junco, but it has a sharply defined yellowish back patch.

One character in the *caniceps-dorsalis* hybrids is worth noting especially. The two forms differ most importantly in the color of the upper mandible, one (*dorsalis*) being black, the other white. Undoubtedly a number of genetic factors is involved, if we may judge from the several intermediate stages that appear among the Kaibab hybrids. It is clear also that the parent races are not entirely homozygous. No completely black bill has ever been found in *caniceps*, nor completely white bill in *dorsalis*. But at least some of the factors occur in the populations of both races and are widely diffused through them. The races differ in the average occurrence of certain genes for bill color and in the presence or absence of others that would lead to extreme manifestations. This is indeed the concept of races to which the genetic approach seems to lead us.

Hidden in the total germ plasm of every race are factors which either because of scarcity, recessiveness or lethal phenomena seldom result in outward expression. Some of these may be residual from ancestral forms or result from intermixture of diverse forms. Others may have come about as new mutations, perhaps repeatedly in different areas, and may have spread to some degree in the populations. Such characters would seem to be the white-wing bars which appear sporadically in a number of kinds of juncos and the mahogany red pileum that is present in 6 per cent of all *caniceps* populations. A feature like red pileum might sometime come to predominate and to characterize a race, as indeed the white-wing bars do characterize, imperfectly, the species *aikeni*.

In conclusion, it is felt that the analysis of hybrid populations has emphasized the possibility of independent evolution of most color characters in the genus *Junco*. It has pointed strongly to the heritability of many racial differences. The necessity of spatial or ecologic isolation in preventing swamping of races has been emphasized. Through such a study we gain a picture of the genetic make-up of races to which we must continually refer in formulating our concepts of the operation of selection and of the mode of segregation of new race units.

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