# NON-GENETIC MATING PREFERENCE AS A FACTOR IN EVOLUTION

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The purpose of this paper is to consider some of the aspects of sexual isolation in birds as a possible step toward the "thorough understanding of the nature and functioning of isolating mechanisms" that Dobzhansky (1937*a*:419) emphasizes is essential before a "trustworthy picture of the mechanism of evolution can be drawn." By sexual isolation is meant the lack of sexual attraction between members of different populations, which lack inhibits to various degrees the amount of cross-mating between the groups involved. This type of isolation is but one of several listed by Dobzhansky (1937*b*) as physiological isolating mechanisms, all of which act as barriers to the free exchange of hereditary materials between populations. Various instances among birds where sexual isolation may well be involved have been reviewed by Huxley (1938*a*:7, 8, 10), Goldschmidt (1940:155), Mayr (1940:249-278) and others, and the existence of the phenomenon is known in other animals, for example in the mice of the genus *Peromyscus* (Dice, 1940:289-311) and among the species of flies in the genus *Drosophila* (Dobzhansky and Koller, 1938; Patterson, 1940; Spencer, 1940). However, in spite of the well established fact that such isolation exists, present knowledge of the details of its physiology is small.

Among birds and other higher animals, preferential mating rests on a complex basis involving the interaction of many factors. However, certain facts can be extracted from this complexity that prove useful in its analysis. Among these is the well known one that in some cases it is possible arbitrarily to classify the factors conditioning mating preferences into two groups, one consisting of those resting upon an hereditary basis, the other upon a non-hereditary one. The interaction of these two groups results in the establishment of a mating preference and hence may effect sexual isolation.

With relation to the above classification, one can expect two extreme types of mating preference. The first includes those cases in which preferential mating is based chiefly upon genetically controlled factors, capable of environmental modification only with difficulty if at all. The second includes those instances in which preferential mating is based largely upon non-genetically controlled factors, preferences being formed anew with each generation. Of course, between these extremes various intermediate relationships are possible; however, for the purpose of clarity and also because of lack of analysis of such intermediate cases, we will confine further discussion to the extremes.

The cowbirds represent a good example of the genetic extreme in birds, for in the parasitic species of this group it is apparent that young birds, separated from their parents before birth, probably inherit the ability and desire to mate with their own kind. One should note though that Friedmann (1929:70) observed three instances where males of *Molothrus bonariensis* displayed to birds of other species, which suggests that even in the cowbird the genetical group of factors may be capable of some modification. As far as our knowledge goes, however, there seems to be no reason to believe that non-hereditary factors are of importance in the establishment of the mating preferences in cowbirds, for, if they were, the species could not enjoy their peculiar habits and survive. Because sexual isolation at the genetic extreme just noted for cowbirds also occurs in *Drosophila* and has been discussed by Dobzhansky in several publications (1937*b* and 1940), the remainder of this paper will be concerned with the non-genetic extreme.

Dobzhansky (1937*a*:237) writes that Serebrovsky and co-workers have obtained large deviations from the normal behavior in domestic animals through experimentation. One of the examples quoted is that "male turkeys were induced to attempt copulation with fowls," and in general, it is stated, that many otherwise unobtainable hybrids can be obtained by such experiments. Further evidence of a non-genetic extreme has been furnished by Whitman (1919), who has shown that the social environment of pigeons conditions their mating preferences almost entirely. These observations have been summarized (p. 98) as follows: "Pigeons normally pair with members of their own species and this preference has generally been regarded as instinctive in character. But the data of this volume show rather conclusively that the species preferences exhibited by birds [pigeons] at maturity are to a large extent acquired and are functions of the social environment in which the birds are reared. We are told that young birds raised under foster parents of a different species are very apt to prefer a mating not with their own kind, but with a member of the species among which they have been reared." It is pointed out that knowledge of this property of pigeons had much to do with success in obtaining a great variety of interspecific hybrids. The words "very apt" in the above quotation suggest that the method is not infallible; however, one can see that pigeons are apparently quite close to the non-genetic extreme and form a sharp contrast with the cowbirds.

Whitman's work on pigeons illustrates another point important to this paper, namely, that the mating preference, while acquired, apparently becomes fixed at an early stage in the life of the bird, long before sexual maturity. A limited period of plasticity seems to exist, during which a particular preference can be established and after which it can only be altered by special experimental techniques. The ease with which such a preference can be broken down after it is once fixed may, of course, vary. That it may be broken with difficulty is seen in the specific case of the male passenger pigeon (*Ectopistes migratorius*) reared by ring doves (*Streptopelia* sp.) which would make no advances to females of its own species even after being removed from the company of female ring doves for a whole season (Whitman, 1919:28). This same kind of fixation has been observed by Barrington and others in those birds that acquire their songs (Wallace, 1895:104). Such birds learn the song of their parents, foster or normal, early in life and these songs rapidly become "fixed" and unmutable shortly after this.

The work of Lorenz (summary, 1937) furnishes much additional evidence on the non-genetic nature of the specificity of mating, of the following-reactions and other activities of birds other than pigeons, and also on the phenomenon of early fixation and subsequent rigidity of such acquired behavior. The widespread occurrence of such conditioning is indicated by the species referred to by Lorenz, which are: great horned owl, South American bittern, raven, greylag goose, muscovy duck, mallard duck, partridge, jackdaw, and shell parakeet.

In summary, we see that in many species of birds there exists a mechanism for the establishment of mating preferences, the specificity of which appears to be largely non-heritable and needs to be re-established and fixed early in each generation.

The existence of such a mechanism opens the way to some speculation, for, given a species with its breeding population broken into sub-units, all that seems necessary in order to reduce the number of successful matings of migrant exchanges between sub-units is that the factors conditioning sexual preferences come to vary among these sub-units. Such variation should elicit different mating responses, which, if more or less permanently established before the young leave their parental influences, should result in an isolation. Such an isolation would be as strong as the conditioning factors are different within the populations involved. The greater the differences, the less apt the conditioned young would be to recognize and react to stimuli in a group other than their own. The extent to which differences in conditioning factors between populations can accumulate and thus increase the strength of the sexual isolation involved is unknown.

The nature of these conditioning factors and the causes of their variance undoubtedly differs from species to species and any detailed treatment is beyond the scope of this paper. Such characters as color, voice, size, and particular mannerisms are probably concerned. The variance of these among sub-populations can be the result of mutation, with or without selection (the latter when the conditioning genes become fixed in a sub-population through random fluctuations in the manner discussed by Wright, 1931:201-208), or possibly even the result of environmental influences without the aid of genetic change. This last possibility is suggested by the refusal of some birds to breed in captivity unless the proper background or nest materials are provided, by the fact that others breed better or sooner depending upon population size (*Huxley*, 1938*b*:18-19), and by the possibility that some birds acquire their songs from their parents (Wallace, 1895).

As it is evident that the existence of the sexual isolation under discussion is made possible by the presence and change of conditioning factors, some persons may prefer to consider them as the true isolating mechanism. However, the fact remains that at the preference level itself, some kinds of birds appear to inherit their mating preferences while others acquire them. This difference should not be disregarded as a possible influence in their evolutions, for the re-enforcing by sexual isolation of any geographical or ecological isolation arising within a population would seem to be more readily attainable by species with non-genetic mating preferences than by those with genetic ones. In this connection a further point should be made. As there is evidence to suggest that the conditioning factors themselves may sometimes depend for their specificity upon an environmental basis, it is conceivable that an initial sexual isolation may arise entirely as the result of environmental influences without the occurrence of genetic change. Although such isolation would seem to be of a relatively weak and temporary nature, it could nevertheless be of potential advantage, at least in the earlier stages of speciation, by helping to provide a proper degree of semi-isolation between sub-populations, for Wright (1931:208) conceives of a population broken "into small, incompletely isolated groups" as one best deployed "not merely for branching of the species, but also for its evolution as a single group."

One phenomenon in need of investigation from the point of view suggested by Whitman's and Lorenz's work is that of "double invasions" of oceanic islands as described by Mayr (1940:271). In such invasions, the same species is known to have successfully immigrated to an island at two different times, the two populations, however, behaving as distinct species and not interbreeding. Of special interest here is the double invasion of the western Canary Islands by a pigeon which now exists there as the forms *Columba lavirovra* and *C. bolli.* Study of such cases may result in a more modern interpretation of the old general idea (see for example, Baldwin, 1902; and Gulick, 1905) that acquired non-heritable behavior may have some influence upon the evolution of the forms possessing it. This of course does not mean that such behavior comes to be inherited in time, but rather that it is a factor that can affect the population mechanics with respect to heritable characters.

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