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COMMENTARIES

Genetic Distance and Hybridization of Black Ducks and Mallards: A Morph of a Different Color?

G. R. HEPP, J. M. NOVAK, K. T. SCRIBNER, AND P. W. STANGEL^{1,2}

Ankney et al. (1986) assayed genetic variation within and among North American populations of Mallards (*Anas platyrhynchos*) and American Black Ducks (*A. rubripes*). They concluded that their "genetic data do not support even subspecific status for the Black Duck." Morgan et al. (1976) also reported that biochemical characteristics of these two species were very similar, but suggested that there were sufficient differences to maintain separate species status for Mallards and Black Ducks. We propose to clarify issues related to the designation of a species and thereby provide an additional perspective on the Black Duck-Mallard issue.

Ankney et al. (1986) used 2 lines of evidence to argue that Mallards and Black Ducks should not be regarded as distinct species: 1) low estimates of genetic distance (D) between the species based on their electrophoretic data, and 2) other data suggesting that reproductive isolating mechanisms are no longer effective. We will focus on these two main issues.

GENETIC DISTANCE

Genetic distance (D) is a measure of the amount of genetic divergence between groups. D of zero implies no genetic difference between groups, and a maximum value indicates fixation for alternate alleles. Genetic distance is based on the mean number of electrophoretically detectable gene substitutions for protein coding (structural gene) loci that have accumulated since the divergence of two groups from a common ancestor (Nei 1972, 1975, 1978). It is computed from allele frequencies at the loci examined.

The low estimate of genetic distance ($D = 0.0006$) provides little, if any, support for combining Black Ducks and Mallards into a single species, for the following reasons: 1) low genetic distances are not uncommon even between undisputed species of birds; 2) variance in genetic distance values is large among bird taxa; and 3) the magnitude of D is not indicative of the propensity for hybridization.

Magnitude of genetic distance values.—Birds exhibit conservative or short genetic distances at equivalent taxonomic levels, relative to non-avian taxa (Barrowclough 1980, Avise and Aquadro 1982, Patton and Avise 1986). Within the genus *Dendroica*, 76% of the species pairs examined had a Nei's D < 0.05, and 23%

had a value ≤ 0.005 (Avise et al. 1980). A distance of zero was recorded between two biologically good species pairs: *D. pensylvanica*-*D. magnolia* and *D. coronata*-*D. discolor*. Thus, although the Nei's D between the Black Duck and Mallard was small, it is within the range of values recorded for other congeneric avian species ($\bar{x} = 0.110$, range = 0.000-0.578, $n = 372$ comparisons, 42 genera, 6 orders). Comparisons among taxa are valid only if homologous proteins are used (Corbin 1983, Houde 1987) and when the rates of evolution within the groups can be assumed to be equivalent (Sarich 1977, Houde 1987).

Variance in genetic distance values.—Mean genetic distance generally increases as taxonomic groups become more inclusive (Gutiérrez et al. 1983, Marten and Johnson 1986). Their usefulness depends both on the rate of protein evolution within groups and the estimated variance of these divergence values (Avise 1975, Sarich 1977). Genetic distance values among local populations and species of birds should be viewed cautiously because these values largely overlap genetic distances between genera and subfamilies (summary in Patton and Avise 1986).

Genetic distance may be more indicative of the partitioning of genetic variation among various levels of geographic structure rather than of absolute taxonomic relationships as currently understood (Patton 1985). This is true because genetic distance measures are related mathematically to F_{ST} values which estimate the amount of genetic variation accounted for by differences between sample localities (Hartl 1980). For current avian taxonomic hierarchies, there is no absolute value of D upon which to base taxonomic decisions (Marten and Johnson 1986).

Genetic distance and hybridization.—Genetic distance does not indicate a species' propensity for hybridization. For example, Black-capped (*Parus atricapillus*) and Carolina chickadees (*P. carolinensis*) have a Nei's D of 0.001 (Braun and Robbins 1986) and regularly hybridize along contact zones (Robbins et al. 1986). Black-capped Chickadees also hybridize with Mountain Chickadees (*P. gambeli*), but the genetic distance (0.072) between these two is an order of magnitude greater (Braun and Robbins 1986). Blue-winged (*Vermivora pinus*) and Golden-winged warblers (*V. chrysoptera*), two species which regularly hybridize and produce fertile offspring, are separated by a Nei's D of 0.001-0.012 (Gill 1987, Avise et al. 1980, respectively) while nonhybridizing species such as *D. pensylvanica*-*D. magnolia* and *D. discolor*-*D. coronata* have a genetic distance of zero (Avise et al. 1980).

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There is no a priori reason to expect that there is an absolute value of *D* upon which to base hybridization potential or species status. Birds, like most organisms, are characterized by mosaic evolution, where different character sets evolve at different rates (Mayr 1963, 1970). Differential evolutionary rates are particularly evident for characters involved in sexual selection, given the importance of visual and auditory stimuli in this process. Thus, in some birds morphological evolution may proceed much more rapidly than structural protein divergence (i.e. genetic distance).

HYBRIDIZATION

Hybridization of Mallards and Black Ducks has increased since the early 1900s. Before then, Mallards were uncommon in eastern North America, even as migrants (Heusmann 1974). Ankney et al. (1986) imply that the lack of effective pre-mating isolating mechanisms resulted in hybridization as the result of secondary intergradation. Important to their argument is that hybridization has increased because of the natural expansion of the Mallard's range. As early as the 1920s, however, increases of Mallards in the northeastern United States were attributed to the propagation and release of Mallards by gamekeepers, sportsmen, etc. (see Heusmann 1974). We contend that hybridization of Mallards and Black Ducks increased largely because of game-farm Mallards released in the eastern United States. Hybridization was at least partially man-induced and was not a useful measure of species integrity (Mayr 1963). Our contention is based on three arguments.

1. *Mallard releases.*—Mallards have been propagated and released by several state wildlife agencies to supplement natural duck populations for hunting. The two largest programs, operated by Pennsylvania and Maryland, released approximately 300,000 and 275,000 Mallards, respectively. Maryland continues to do so. These totals exclude the substantial number of birds released by private individuals. For example, three private farms in Maryland have contributed 171,800 Mallards since 1962 (Soutiere 1986). Although annual survival rates of hand-reared Mallards (male = 0.39, female = 0.27–0.55) are usually lower than those of wild Mallards (male = 0.58, female = 0.42; Soutiere in press), a substantial number survive and are available to breed with wild birds.

2. *Behavioral and physiological differences.*—Game-farm and wild-type Mallards differ in both behavior and reproductive physiology. Domestication of Mallards has resulted in longer breeding seasons (Donham 1979), higher levels of plasma testosterone (Paulke and Haase 1978), and changes from a monogamous to a more promiscuous mating system (Desforges and Wood-Gush 1976). In Ontario and Quebec, hybridization of Mallards and Black Ducks has been suggested to occur primarily after the failure of first nests, and not before (Ankney et al. 1987). We agree that

the potential for hybridization is greatest at this time. Longer breeding seasons, higher testosterone levels, and a more promiscuous mating system would make male, game-farm Mallards more available and competitive for mates during reneating attempts.

3. *Isolating mechanisms.*—Habitat separation, plumage characteristics, and courtship displays are pre-mating isolating mechanisms that reduce the frequency of interspecific matings in many vertebrates, including birds (White 1978). Mallards and Black Ducks traditionally have been separated during the primary time of pairing, which reduced hybridization. Pair formation of Mallards and Black Ducks occurs in autumn and winter, and females arrive at breeding areas paired. In North Carolina more than 95% of female Black Ducks were paired in November (Hepp and Hair 1983). Current winter distributions of these two species overlap considerably, but are separated to some extent at the regional and local level. Band-recovery data show that Black Ducks are distributed more north and east of Mallards, and Black Ducks exhibit greater fidelity to wintering areas (Diefenbach et al. in press). In the early 1970s, Black Ducks wintering in Massachusetts were associated with maritime habitats, and Mallards were distributed mostly inland (Heusmann 1974). The situation has changed in Massachusetts and the ranges overlap, but changes have occurred to a greater extent when winter habitats of Black Ducks are close to park habitats where game-farm Mallards are abundant (Heusmann pers. comm.). In many areas Mallards and Black Ducks are still separated by habitat, but contact has increased during autumn and winter due to habitat modification and human disruption of historic distribution patterns.

Contrary to Ankney et al.'s (1986) statement, mate selection in Mallards has been studied experimentally by a number of workers (see Williams 1983). Cheng et al. (1979) used wild-type and game-farm Mallards to show that males raised in pure-strain groups displayed more intensely toward and paired with females of their own strain. Males reared in mixed-strain groups displayed and paired with females of either strain. Bossema and Kruijt (1982) reported similar results using wild and domesticated white Mallards. In contrast, early experience did not influence selection of mates by female Mallards. Instead, females paired with males that displayed most intensely to them regardless of the male's strain (Cheng et al. 1979). Kruijt et al. (1982), however, reported that mate preferences of female Mallards were influenced to a certain degree by early experience. These studies indicate that barriers to introgression exist between Mallards (game-farm and wild-type) and Black Ducks during the normal courtship and pairing process. Brodsky and Weatherhead (1984) observed that co-occurring males of both species exclusively courted and paired intraspecifically. After all female Mallards paired, male Mallards courted female Black Ducks.

We contend that the small genetic distance between Black Ducks and Mallards does not provide convincing evidence for considering these two taxa as conspecific. Geographic isolation, species-specific courtship displays, and mate selection were probably the most important factors in developing reproductive isolation between these groups. Pre-mating isolating mechanisms are very susceptible to environmental perturbation.

Mallard-Black Duck hybridization has been largely man-induced through the propagation and release of Mallards in the eastern U.S. by state and private organizations. Survival rates of these game-farm ducks are significant and differences in their reproductive behavior and physiology probably make them more competitive than male Black Ducks for mates during certain periods of the breeding cycle. There also is evidence that pre-mating isolating mechanisms of Mallards and Black Ducks still operate during the main period of courtship and pair-bond formation. Current information on the genetics and hybridization of Mallards and Black Ducks, therefore, does not provide good evidence for considering them a single species.

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Response to Hepp et al.

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Perhaps several thousand more years of geographical isolation would have resulted in the "Black Mallard" becoming a good biological species. However, the arguments presented by Hepp et al. will not make that happen. We respond to their arguments as follows:

1. *Genetic distance*.—We have no quarrel with their literature review. It is simply an expanded version of our statements (Ankney et al. 1986: 706, 708): "We agree with the arguments of Barrowclough (1980), Gutiérrez et al. (1983), and Johnson and Zink (1983) that the genetic distance between two taxa does not, per se, indicate their taxonomic status," and "Thus, our data showing a very low level of genetic distance between Mallards and Black Ducks are consistent with the species' incomplete reproductive isolation."

2. *Game-farm Mallards*.—Their argument is irrelevant for two reasons. First, game-farm Mallards are, of course, still Mallards. More important, hybridization of Mallards and Black Ducks occurred long before captive release programs: "There are however, other interesting variations in *A. tristes* [= *rubripes*], such as the irregular occurrence of characters that are essentially Mallard. I mean here variations that occur outside of the rather common hybrids with the Mallard" (Phillips 1912).

Hepp et al. apparently think that the mating system

of the million or more Mallards that now breed in Ontario and Quebec is like that of Aylesbury ducks (i.e. white barn-yard ducks), because their argument about promiscuity was based on a study of such ducks. To us, Ontario/Quebec Mallards look and behave like wild Mallards, e.g. those breeding on the prairies. We cannot, however, comment on the behavior or appearance of Mallards in the southeastern U.S.

3. *Isolating mechanisms*.—Hepp et al. state that the two taxa have "species-specific courtship displays." They must be unaware of Johnsgard's (1960) classic paper which showed otherwise.

Fortunately, or perhaps not for the "Black Mallard," the answer to this debate, unlike many in evolutionary ecology, lies in the present and future, not in the past. The two taxa provide an excellent example of what happens when geographical barriers to mating break down before pre-mating isolating mechanisms have evolved.

We predicted (Ankney et al. 1986, 1987) that the outcome of this will be genetic swamping of the "Black Mallard" through introgressive hybridization. It is irrelevant to this prediction whether or not the two taxa retain their specific status. Furthermore, nothing in the comments by Hepp et al. moves us to change this prediction. We stand by everything that we said in Ankney et al. (1986).

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